AN ABSTRACT OF THE THESIS OF

Klaus J. Puettmann for the degree of Doctor of Philosophy in Forest Science presented on February 27, 1990.

Title: The Size-Density Relationship of Pure and Mixed Red Alder/Douglas-fir Stands and its Use in the Development of a Growth Model.

Signature redacted for privacy.

Abstract approved: David E. Hibbs

The increased interest in red alder (*Alnus rubra* Bong.) management instigated research in growth and yield and stand development of red alder in pure and mixed red alder/Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands.

This study had the goals of evaluating the accuracy of the currently existing growth and yield tools for red alder and investigating the size-density relationship for pure red alder and Douglas-fir stands and mixed red alder/Douglas-fir stands. The database consisted of long-term remeasured plots in western Oregon and Washington and southwestern British Columbia.

The comparison of the data with the red alder yield tables suggested lower accuracy for the Normal Yield Table for Red Alder than the Empirical Yield Table for Predominantly Alder Stands in Western Washington for prediction of both pure and mixed stand yield. Growth projections of the Stand Projection System for pure and mixed red alder/Douglas-fir stands were not accurately enough to ensure a reliable estimate of future stands conditions.

The intercept and shape of the size-density trajectory and the relative density at which mortality starts (0.44) for red alder was independent of initial density. The Douglas-fir self-thinning line was above the red alder line but had a shallower slope (-0.525 for red alder vs. -0.638 for Douglas-fir).

The size-density surface for pure and mixed stands exhibited a near-linear region for stands with a high proportion of red alder and a curvilinear portion for stands with a higher proportion of Douglas-fir. Stand density, relative dominance and species proportion were found to be the major determinate of stand development. The information on the size-density relationships and stand development were incorporated into a growth model.

The Size-Density Relationship in Pure and Mixed Red Alder/Douglas-fir Stands and its Use in the Development of a Growth Model

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed February 27, 1990

Commencement June 1990

APPROVED:

Associate Professor of Forest Science in charge of major

Head of Department of Forest Science

Dean of Graduate School

Date thesis is presented February 27, 1990

Typed by Klaus J. Puettmann

Acknowledgements

My major professor David Hibbs and co-major Bill Emmingham deserve my sincerest gratitude for all their encouragement, support, and, most of all, for their friendship during the years. You guys kept me running!

I would also like to thank my minor professor David Hann, whose contribution to this thesis was not minor. Thanks for all the good ideas in our many afternoon sessions.

Financial support for my work was provided by the Hardwood Silviculture Research Cooperative. I would like to thank all its members for this and for the fruitful discussions during the Coop meetings.

A countless number of faculty and fellow students brightened my life over the years. Those of you who left town showed me that there is a way out. Others are still here, thanks for hanging in with me. I consider the discussions, group sessions, conversations, and chats a valuable part of my education. They made me aware that I was not the only one with problems. To my "late working" friend, who helped me keep my priorities straight, remember: Russ's is open almost till midnight. Hang on to that spirit, we're not even yet.

A special thanks to my family and friends "back home" for all your postcards, letters, care packages, visits,

phone calls, and thoughts. Knowing I can count on you gave me the strength to leave the old world.

Thanks to all the hospitable friends, who opened their hearts and houses. You made Oregon more than a residence for me. Home is, where the heart is.

Maureen and Chester, we did it.

Meinen Eltern gewidmet

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Chapter I

General Introduction

This thesis was initiated in response to increased interest in red alder (Alnus rubra Bong.) management in the Pacific Northwest. Even though red alder is widely distributed and covers 13% of the commercial forest land in the Douglas-fir sub-region of Oregon and Washington (Resch 1988), it has been neglected as a subject of forest management. Instead, the major research focus has been the competitive effect of red alder in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) plantations (Newton 1978, Cole 1984, Walstad and Kuch 1987). However, the perception of red alder as a weed species is changing for several reasons. First, the value of red alder wood has increased substantially over the last ten years. Second, the loss of herbicides as a weed control tool on public land has increased the costs of removing red alder from conifer plantations. Third, the extent of laminated root rot (Phellinus weirii Murr. Murr.) infected land has also increased the interest in red alder, as an immune species

(Nelson et al. 1978). Fourth, higher prices for fertilizers and increased concerns about long- term productivity raised interest in management of nitrogen fixing species, either in alternate rotations or in mixed species stands (Tarrant et al. 1983). Lastly, highly successful efforts to ensure conifer regeneration in the last two decades have lead to concern about future red alder fiber supply (Gedney 1982, Gedney et al. 1986a, b).

The focus on red alder as a competitor in Douglas-fir plantations is also reflected in research activities. Research on silvicultural practices, especially effects of density management on growth and yield, is limited (e.g. Hebner and Bergener 1982).

The increased interest in red alder management and the need for red alder research led to the foundation of the Hardwood Silviculture Cooperative (HSC) at Oregon State University in 1987. When the HSC discussed research options, the lack of published reports and data on growth and yield of red alder in pure and mixed stands was identified (Puettmann et al. 1988). Therefore the HSC focused its efforts in two directions: utilization of the available data and installation of new growth and yield plots to fill the data needs.

This thesis is a summary of the project initiated to use the existing data sets. The project was a preliminary exploration of stand growth and development of red alder in pure stands and mixed with Douglas-fir. After collection of the available data sets, a two phase study was initiated. The first step was to find and use the data to evaluate the accuracy of the currently existing growth and yield prediction tools: 1) Normal Yield Table of Red Alder (Worthington et al. 1960), 2) Empirical Yield Table for Predominantly Alder Stands in Western Washington (Chambers 1974), and 3) the Stand Projection System (Arney 1985a, b).

The objective of phase one was to examine the strengths and weaknesses of these tools and indicate areas needing improvement. This step also allowed managers a more informed choice of the tools to meet management objectives. The examination of tools is presented as Chapter II.

The data base was not sufficient to allow construction of a growth and yield simulator. However, it was useful to analysis certain aspects of stand development, particularly the size-density relationships and stand mortality rates. Thus, the investigation of the size-density trajectories for pure red alder stands and the development of a size-density surface for mixed red alder/Douglas-fir stands were chosen as phase two.

Because the species mixture of red alder and Douglas-fir stands must be viewed as a continuum from pure red alder to pure Douglas-fir, additional data from installations in pure Douglas-fir stands were collected and included in the analysis. Since the size-density relations of monospecific stands are less complex than those of mixed stands and since the data base for pure stands was stronger, pure stands were analyzed separately. Chapter III describes the investigation of the size-density relationship of both species in monospecific stands. A special focus was on red alder and evaluation of its size-density trajectory, onset of initial mortality, and effect of regeneration method.

Knowledge gained in the analysis of pure stands was then used to investigate the size-density surface of mixed stands. Chapter IV explains the expansion of the size-density concept to include both pure and mixed stands.

Chapter V explores the complexity of the size-density surface by investigating underlying stand dynamics. The dynamics were analyzed through models of mortality patterns and shifts in species proportion. In addition, the size-density, mortality and proportion relationships were combined into a growth model. The model had two foci: 1) an understanding of the underlying dynamics of the size-density relationship for pure and mixed red alder/Douglas-fir stand, and 2) its use as a research tool. However, this growth model must be viewed only as a first approximation.

Future research is needed to fill the gaps and expand it to accurately reflect the full range of existing stand conditions.

Chapter II

Comparison of Stand Characteristics from Long-Term Remeasured Plots of Red Alder with Yield Table and Growth Model Predictions

Introduction

Decisions on management strategies for forest stands depend on knowledge about tree and stand growth and yield. Accurate prediction of growth and yield is crucial for prescription of appropriate management activities. Growth and yield information for red alder (Alnus rubra Bong.) is available in a variety of forms (Hann and Riitters 1982). It can be separated in two distinct groups (Clutter et al. 1983). The first are yield tables, which provide detailed information about average stand characteristics for a given stand age. However, yield tables do not provide information about growth and development of a stand. Second, growth projection tools predict development of the stand. They project the current stand into the future and thus provide information about growth.

The yield prediction tools most widely used in Oregon and Washington are the Normal Yield Table for Red Alder (Worthington et al. 1960) and the Empirical Yield Table for predominantly Alder Stands in western Washington (Chambers

1974). The Stand Projection System (SPS) (Arney 1985a, b) is a growth projection model for red alder in pure and mixed stands. So far, no comparison of these tools with independent data sets has been performed to evaluate their quality. Comparison of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) growth models and yield tables with independent data sets (Curtis 1987) and with each other (Mitchell 1986, O'Hara and Oliver 1988) have shown the usefulness of this kind of evaluation.

This paper is a comparison of predicted values with stand data from remeasured permanent plots. The comparison was limited to the range of stand conditions represented in the permanent plot data set. Differences between predicted and observed values can be due both to problems within the permanent plot data set and/or inaccuracy of the prediction. The results, therefore, can not be conclusive but they can help a user estimate the accuracy of the tools. The objectives was to evaluate the ability of the yield tables to reflect the current stand conditions of pure red alder stands and the red alder component in mixed stands. SPS was evaluated for its ability to predict red alder growth and mortality in pure and mixed stands and Douglas-fir growth and mortality in mixed Douglas-fir/red alder stands. The specific objective was to give a user information about the strong and weak points of the three most common tools used for red alder prediction.

The use of remeasured permanent plots allowed the investigation of "normality" for red alder stands. The concept of "normality" was initially developed by German foresters in the eighteenth century (Hundeshagen 1826). It was improved upon over time and became one of the most important concepts in forestry. Even though "normal" stands are rarely found in nature, the concept was the basis for development of the normal yield tables (Daniel et al. 1979). A normal stand is defined as a natural, fully stocked stand that has developed with no significant disturbances (Curtis 1972).

The objective for this section was to investigate what stand characteristics can be used for evaluation of normality and whether red alder stands develop towards normal stands as defined by Worthington et al. (1960) in the Normal Yield Table for Red Alder.

Methods

Growth and Yield Tools

Normal Yield Table for Red Alder

The data base used for establishment of the Normal Yield Table for Red Alder (Worthington et al. 1960) consisted of fixed area plots located in northern Oregon, western Washington and southern British Columbia. Multiple regression equations were fit to the data and in turn applied to produce the tables. The information was divided into three separate tables for trees with a minimum diameter at breast height (DBH) of 0.6, 5.6 and 9.6 inches.

The input variables for use of the tables are the total stand age and the 50-year (total age) site index. The following stand characteristics are presented in the tables: trees per acre, basal area per acre, quadratic mean diameter (diameter of tree with average basal area), and cubic feet per acre. In addition, a table of board feet per acre (Scribner rule) is presented for trees with a DBH of greater than 9.5 inches.

Empirical Yield Table for predominantly Alder stands in Western Washington

Empirical yield tables are based on stands with average rather than normal stocking (Burkhart et al. 1984). Chambers (1974) produced yield, stand and stocking tables for red alder stands. To allow application to a variety of stand conditions, basal area per acre was used as an additional input variable. Actual basal area was set in relation to normal basal area to give a density measure for the particular stand. The yield table can therefore be labeled a variable density yield tables (Burkhart et al.

1984). Normal basal area was based on the equations from the Normal Yield Table for Red Alder and interpolated for the minimum diameter at breast height of 7 inches.

The data base consisted of prism plots located in western Washington. To reflect different stand conditions the yield table presents separate tables for different relative densities, expressed as percentage of a normal basal area. The yield table was developed through yield equations in the same manner as Worthington et al. (1960). Because the yield table focuses on merchantable wood, the minimum diameter at breast height is 7 inches. This reduces their usefulness as a silvicultural tool, because the yield table does not provide information about stand dynamics at younger stages of development.

The required input variables are total age, 50-year (total age) site index, and basal area per acre. The first two characteristics are used to calculate normal basal area per acre. The relationship of stand basal area over normal basal area is expressed as Percent Normal Basal Area (PNBA). PNBA is then used as an input variable. Information about trees per acre, quadratic mean diameter, total cubic volume and Scribner board foot volume (6-inch top) is presented in the yield tables.

Stand Projection System

The Stand Projection System is a commercially available growth and yield model described as an diameter class, distance-independent stand-projection model, as defined by Munro (1974). It was originally developed for coastal Douglas-fir (Arney 1985a, b). Through the use of modified Douglas-fir equations, it has since been expanded to include red alder and other species both in pure and mixed stands. This modification (Version 2.1) is limited to parameters in the top height increment equation, a relative site index, the number of years to reach breast height, bark ratio at 80% DBH and height to 80% DBH. Red alder top height increment was based on the site index equations developed by Harrington and Curtis (1986). Diameter growth and height growth were determined by prediction of a diameter growth/top height increment and height growth/top height increment ratio, respectively. The equation predicting these ratios and the mortality equations were identical to the ones used for prediction of Douglas-fir. SPS can use either average stand conditions, a stand summary table, or a tree diameter list as input. It projects the stand forward in steps of height increments of 12 to 15 feet.

The output values are quadratic mean diameter, basal area per acre, trees per acre, top height, crown ratio, total cubic foot volume, gross cubic foot volume, gross board foot volume, number of logs per million board foot, log diameter inside bark, relative density, and crown competition factor.

Data Sets

Forty-six plots were used for this comparison. All of these plots are permanent, fixed area plots with at least two measurements. The minimal proportion of basal area for both red alder and Douglas-fir combined was 80%. The number of measurements of individual plots ranges from 2 to 8 measurements with an average of 4 measurements. This resulted in a total number of 212 measurements. The average time between the first and last measurement of individual plots is 13 years.

The plots were located in south-western British Columbia, western Washington, and north-western Oregon. The coverage within this geographical range was not sufficient to allow investigation of a north-south effect.

Although some of the early measurements (before 1959) were included in the data set used to construct the Normal Yield Table (Scott 1987), these data were only a minor part of the full data set used. The data sets were therefore considered "almost independent". Both the Empirical Yield

Table and the Stand Projection System were developed from data independent of the ones used in the comparison.

The data covered a wide range of site indices, ages, basal area per acre, and species proportions as presented in Figure II.1. The lack of data with proportions of red alder less than 20% is due to a requirement for the plots to contain a substantial amount (greater than 20%) of the total basal area in red alder.

Since the yield tables do not predict future development but only the current stand condition at a given point in time, each measurement was used independently and categorized by its proportion of basal area in red alder in pure (80% and more) and mixed (less than 80%) stands. SPS projects a stand or plot forward and predicts future development. The mixture at time of the initial measurement was used to categorize all subsequent measurements of the plots. Thirty plots were categorized as pure red alder and sixteen as mixed red alder/Douglas-fir stands.

Worthington et al. (1960) indicated the site index and age range of the data used for yield table establishment. Only plot measurements which fell within this range were used for comparison with the Normal Yield Table. Chambers (1974) did not give any information about the data range used. Only plot measurements which showed trees greater than 7 inches DBH were used for this evaluation. All measurement were used for the evaluation of SPS. The initial plot measurement determined the input into the model and all subsequent measurements were used in calculation of the growth comparison. The number of measurements in pure and mixed stands used for evaluation of each prediction tool are presented in Table II.1.

Assumptions used in Comparisons

The definition of variables differs among the three prediction tools. A different plot size or measurement method implies a different definition of a variable, e.g., a basal area determined from a 1/5-th acre square plot is not equivalent to a basal area determined on a variable radius plot. The effects of different measurement techniques cannot be separated from inaccuracies of the prediction. However, foresters apply the prediction tools with different plot designs or plot sizes. Therefore, ignoring the difference in variable definition led to a comparison more realistic to the user.

For stands where total stand age was not available, it was calculated as mean breast height age of red alder plus two years, as proposed by Worthington et al. (1960). SPS uses breast height age for the stand table input. The original conversion values supplied by Arney (1989) were used. The conversions from total age to breast height age varies with site index. Red alder site index was not available for some plots. In these cases, the red alder site indices were calculated after Hoyer (1978).

Quadratic mean diameter (QMD), trees per acre (TPA) and basal area were selected as the most meaningful variables in terms of the comparison objectives. Because of the reliance on the accuracy of volume equations and their use of the above mentioned variables, additional comparisons using volume would not yield new information.

Statistical tests were not performed in these comparison, because individual user needs vary and there are no general criteria for sufficient accuracy of predictions.

Normal Yield Table for Red Alder

Worthington et al. (1960) presented yield tables for trees larger than 0.5, 5.5, and 9.5 inches (DBH). Since the minimum diameter of plot measurements was 1.5 inches, the comparison had to be restricted to the tables for trees greater than 5.5 and 9.5 inches DBH. However, to define proportion in a similar manner as Worthington et al. (1960) all trees in the stand (greater 1.5 inches) were used for determination of the species proportions. The exclusion of trees with a DBH between 0.5 and 1.5 inches in determining species proportion was not seen as a major factor influencing the analysis since they contribute very little to the total basal area.

Worthington et al. (1960) provide the equations used for the establishment of the tables. These equations were used in this comparison to avoid interpolation of ages not presented in their table section. The plot values of trees per acre, quadratic mean diameter (inches), and basal area (square foot) per acre were calculated from each plot measurement and compared with the predicted values. The differences were calculated as absolute difference using the following formula:

Difference = predicted value - actual plot value.

These differences for pure red alder and the red alder proportion in the mixed red alder/Douglas-fir stands were plotted over age, site index and proportion of basal area in red alder and examined for trends. In addition, a correction factor of (1/proportion) was evaluated for its usefulness to adjust for species mixture.

Empirical Yield Table for Predominantly Alder Stands

As with the Normal Yield Table, the equations presented by Chambers (1974) were used for calculation of the predicted values to avoid interpolations. The 50-year (total age) site index and total stand age were used to predict Normal Basal Area. To accommodate for the mixture, only the proportion of basal area in red alder was used in the calculation of PNBA for mixed stands. PNBA was calculated using the formula:

$$\text{PNBA} = \frac{\text{actual basal area}}{\text{normal basal area.}}$$

PNBA was then used with stand age and site index to obtain predicted values for quadratic mean diameter and trees per acre. As with the normal yield table, a correction factor of (1/proportion) was evaluated for its usefulness to accommodate for species proportion. The differences between table values and plot values were calculated and examined for trends the same way as for the Normal Yield Table.

Stand Projection System

Since SPS is a growth simulator, net growth variables were used for comparison. Stand tables containing number of trees per acre and heights were used as input for projection with SPS together with information about age and site index. The tables were projected forward and stand summary outputs were printed for each plot at all ages when a subsequent measurement was taken. The differences between the initial input values and the observed and predicted values were used as net growth (for QMD and basal area) or mortality. The projected growth and mortality values for quadratic mean diameter, basal area per acre, and trees per acre were compared to the actual plot values as described above for the yield tables.

Concept of Normality

To investigate the concept of normality for pure red alder stands, the mean differences between the observed and predicted values were also plotted over measurement number of the individual plots (first plot measurement equals 1, second equals 2 and so forth). The plots were examined for trends towards "normal" values as defined in the Normal Yield Table for Red Alder and the Empirical Yield Table in Predominantly Red Alder Stands in Western Washington. This permitted an investigation of the development of each stand through time without the confounding factor of age.

Results and Discussion

Normal Yield Table for Red Alder

Pure red alder stands

The mean values observed in the plot measurements and predicted by the Normal Yield Table are presented in Table

II.2. In addition the mean difference (predicted - observed), its standard deviation (Std. Dev.) are shown in the tables. The QMD for trees greater than 5.5 inches DBH was very close to the observed mean, and the variation is low. The QMD for trees greater 9.5 inches DBH did not show this close agreement.

Basal area per acre and TPA showed greater differences between observed and predicted values and also exhibited higher standard deviations. The values of both of these variables were underestimated for trees greater than 5.5 inches DBH and overestimated for trees greater than 9.5 inches DBH. This indicated a difference in diameter distributions between the data sets used in this comparison. The data set used for yield table establishment had a diameter distribution which was more positively skewed compared with the permanent plot data base used in this project.

For both yield tables with trees greater than 5.5 and 9.5 inches DBH the QMD showed a slight underestimation for young stands and an overestimation for older stands (Figures II.2A and II.2B). The trend for TPA was reversed, with overestimation for young stands and underestimation for older stands (Figures II.2C and II.2D). These two effects cancel each other so that basal area per acre did not indicate any trend over age.

Mixed stands

Table II.3 presents the results of the comparison of predicted and observed values for mixed red alder/Douglas-fir stands. The differences were larger and the same trends as stated for pure stands for quadratic mean diameter and TPA existed for mixed stands (Figure II.3). Since the yield tables did not account for the mixture it was expected that both basal area per acre and TPA were overestimated at lower proportions of red alder (Figure II.4).

To adjust for the mixture, the proportion of basal area in red alder (calculated from all trees) was used as a correction factor. Basal area per acre and TPA values were divided by this correction factor, and the corrected basal area and TPA were compared with the predicted values. This simulated a pure red alder stand, but used only the existing red alder for comparison.

Because basal area was the basis for the correction factor, its values showed more improvement than the values for TPA (Table II.4). The trend of basal area over red alder proportion was eliminated through the correction. The correction also eliminated the trend of TPA over red alder proportion for the table for trees greater 5.5 inches DBH. However, TPA were still overestimated at low proportions of red alder for trees greater 9.5 inch DBH. The correction could not eliminate overestimation of TPA in stand with low site indices and of young ages for both tables.

Empirical Yield Table for Predominantly Alder Stands

Pure red alder stands

The data sets used for establishment of the Empirical Yield Table (Chambers 1974) showed an average density (PNBA=1.2) higher than the permanent plot data set used for this project. The average PNBA for the permanent plot data set was 0.85.

Table II.5 presents the differences of QMD and TPA for the comparison of the plot values with the yield table of Chambers (1974). The accuracy of QMD and TPA was very good compared the yield table of Worthington et al. (1960). This was expected because of the additional information (basal area per acre) used in the calculation of these values.

Qmd showed a trend of underestimation in stands which had a lower PNBA and overestimation in stands with higher PNBA (Figures II.5A). Tpa showed a reversed trend over PNBA (Figure II.5B). Qmd showed a trend of overestimation in plots with lower site index and underestimation in plots with higher site index (Figure II.5C).

Mixed stands

For mixed stands the basal area per acre used for determination of PNBA was calculated using the red alder proportion only. Using this method, the accuracy for both QMD and TPA was good (Table II.5). The trends for QMD as stated for pure red alder stands also existed in mixed stands (Figure II.5D). No trends were detectable for TPA.

Stand Projection System

Since SPS (Arney 1985a, b) projects both red alder and Douglas-fir in pure and mixed stands, the stand characteristics for the red alder and the Douglas-fir components were evaluated separately.

Red alder component

Pure red alder stands

The average predicted diameter growth was within 25% of the observed diameter growth but basal area growth was overestimated substantially (Table II.6). This was confounded with the underestimation of mortality, which resulted in prediction of a higher number of trees left in the stands.

Diameter growth showed a trend of overestimation for young stands and underestimation for older stands (Figure II.6A). Overestimation of basal area growth and underestimation of mortality increased with age and the length of the prediction period (Figures II.6B and II.6C).

Mixed stands

The values for mixed stands are also presented in Table II.6. Qmd was slightly underestimated on plots with a lower proportion of red alder and its variance increased with length of the prediction period. The same trends as stated for pure stand also held for the prediction of mortality in mixed stand (Figure II.6D) indicating that these problems were inherent in SPS and not to peculiarities of the permanent plot data set.

Douglas-fir component of mixed stands

The average QMD of the Douglas-fir component in mixed Douglas-fir/red alder stands was underestimated at younger stands and overestimated at older stands and at longer projection periods (Table II.7) (Figure II.7A, II.7B). Mortality showed a trend of underestimation and increasing variance with increasing age and projection length (Figures II.7C and II.7D). The underestimation of Douglas-fir mortality in combination with overestimation of red alder mortality (Figure II.6D) indicated that stand dynamics of mixed stands are not modeled with sufficient accuracy.

The Concept of Normality

The plots of differences between observed and Normal Yield Table values in basal area per acre and QMD over measurement number indicated no trends. Also, PNBA did not indicate a trend towards the "normal" value of 1. Only for trees greater than 9.5 inches DBH did the number of TPA show a clear trend toward the Normal Yield Table value. Tpa with a DBH greater than 7 inches, showed a trend towards the density corrected values from the Empirical Yield Table as shown in Figure II.8 was found (see also Figure II.2C). The different results for the stands with a lower diameter limit of 5.5 and 9.5 inches coincided with the findings of McArdle et al. (1961) for Douglas-fir that only at a high diameter limit TPA was a useful indicator of normality. However, the argument of McArdle et al. that basal area was also a good indicator of normality could not be supported for red alder stands. Based on the history of some permanent Douglas-fir plots, Meyer (1933) and later Brigleb (1942) also argued that stands tend toward normality, i.e. their density trends toward "normal" yield table values. This seemed to be the case also for red alder stands, when

TPA with a minimum diameter of 7 or 9.6 inches DBH is used as a measure.

Summary

This comparison disclosed strength and weaknesses of the most commonly used growth and yield prediction tools. It indicated the necessity for development of an improved growth simulator. Even though the permanent plots probably were located in parts of stands without major disturbances, the average plot of the permanent plot data set was not normal, as defined in the Normal Yield Table for Red Alder (Worthington et al. 1960). Therefore differences between plot values and Normal Yield Table values were expected and at least partially can be attributed to that factor. Consequently, a user has to be very careful when relying on Normal Yield Table predictions for individual stands. In particular, the estimation of TPA and QMD has to be viewed with caution.

The estimation of the red alder component in mixed red alder/Douglas-fir required a correction to accommodate for the proportion in red alder. The use of 1/proportion as a correction factor resulted in the same accuracy for mixed stands as found for pure red alder stands.

The Empirical Yield Table for Predominantly Red Alder Stands in Western Washington (Chambers 1974) showed the advantage of a Variable Density Yield Table over a Normal Yield Table. The additional input of basal area yielded a much greater precision when predicting QMD and TPA. Some trends over PNBA and site index did occur, but the prediction accuracy was so high that for practical purposes they could be neglected. The use of the red alder basal area component for calculation of PNBA provided a simple and adequate method to predict the yield of the red alder component in mixed red alder/Douglas-fir stands.

SPS showed severe weaknesses in predicting red alder growth and mortality. Inaccuracies existed especially with prediction of QMD growth. The problems with basal area growth were confounded with the problems in prediction of mortality. The accuracy of prediction decreased rapidly as projection length increases. These problems also existed for prediction of the Douglas-fir component in mixed stands. Whether these were problems inherent to the Douglas-fir prediction or are due to the mixture could not be addressed due to limitations of the data.

The average projection length in this comparison was only 13 years and the results suggested caution in the use of SPS for projection of red alder plantations over a full rotation length. The modification of individual parameters from the Douglas-fir equations might not be sufficient to produce accurate prediction of red alder stand dynamics. The inaccuracies displayed the need for caution in the use of SPS for prediction of Douglas-fir growth and yield and indicated the necessity for evaluation of SPS with an independent Douglas-fir data set.

This comparison showed that the concept of normality also applies to red alder stands. A minimum DBH of 7 or 9.5 inches TPA could be used as an indicator of normality. When followed over time, stands tended to develop towards normal values, i.e. values in the Normal Yield Table.

Conclusions

The following recommendations about the use of growth and yield prediction tools for red alder could be drawn from this study:

The accuracy of the Normal Yield Table for Red Alder (Worthington et al. 1960) when compared with actual stands was not sufficient for most uses. A forester concerned about yield prediction should measure basal area per acre and then use the Empirical Yield Table for Predominantly Alder Stands in Western Washington by Chambers (1974). The Empirical Yield Table accurately predicted red alder yield in pure and mixed red alder/Douglas-fir stands.

The growth predictions using the Stand Projection System (Arney 1985a, b) were not satisfactorily. SPS cannot be recommended for longer-term projection of red alder in pure and mixed stands. The poor performance of Douglas-fir in mixed stands raised questions about the use of this model for uses other than pure Douglas-fir stands.

Figure II.1: Range of site index, stand age, basal area and proportion of red alder represented in the permanent plot data set.

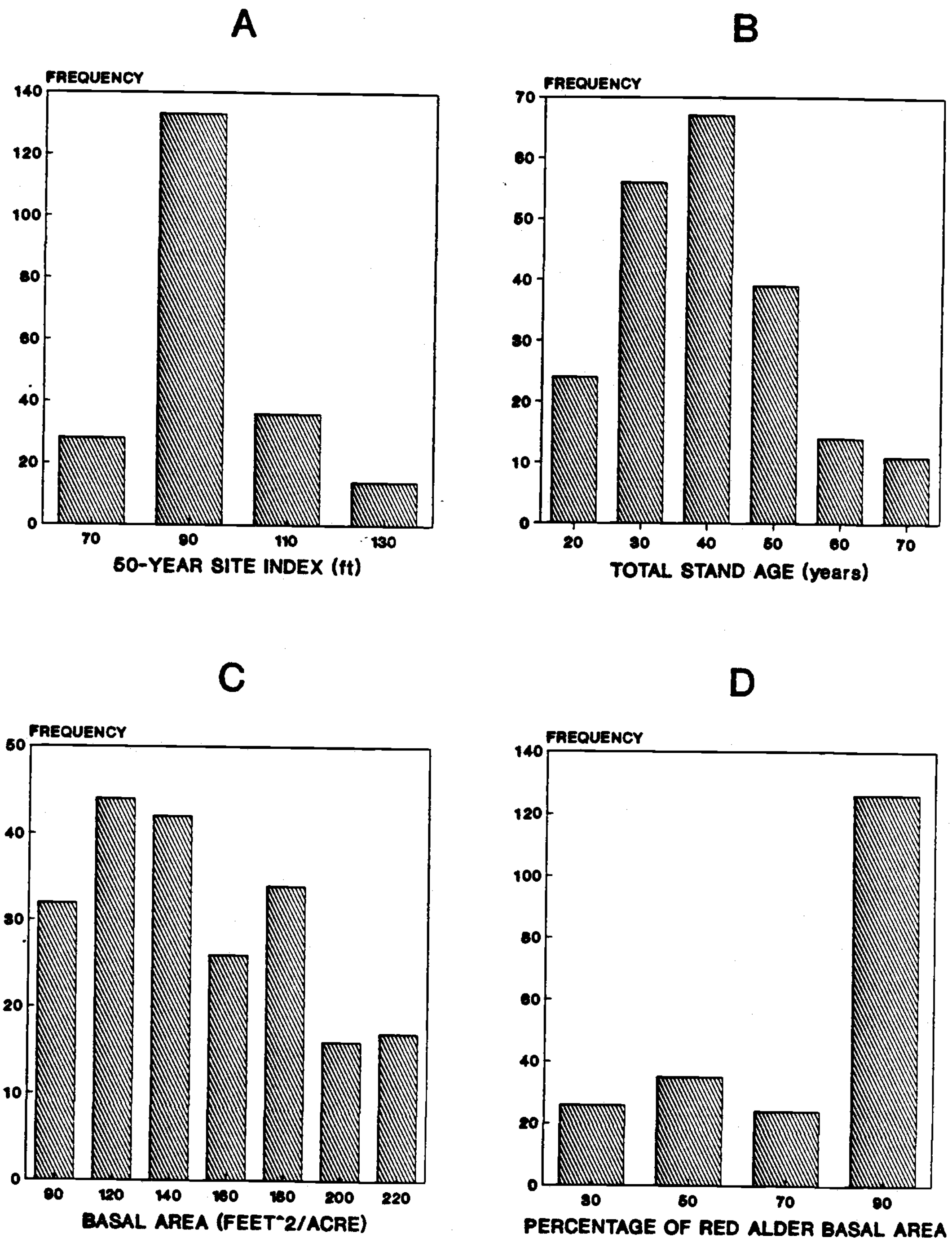

Figure II.1 (continued)

Figure II.2: Predicted minus observed quadratic mean diameter (A, B) and trees per acre (C, D) over total stand age for pure red alder stands. Predictions are from the Normal Yield Table for Red Alder (Worthington et al. 1960).

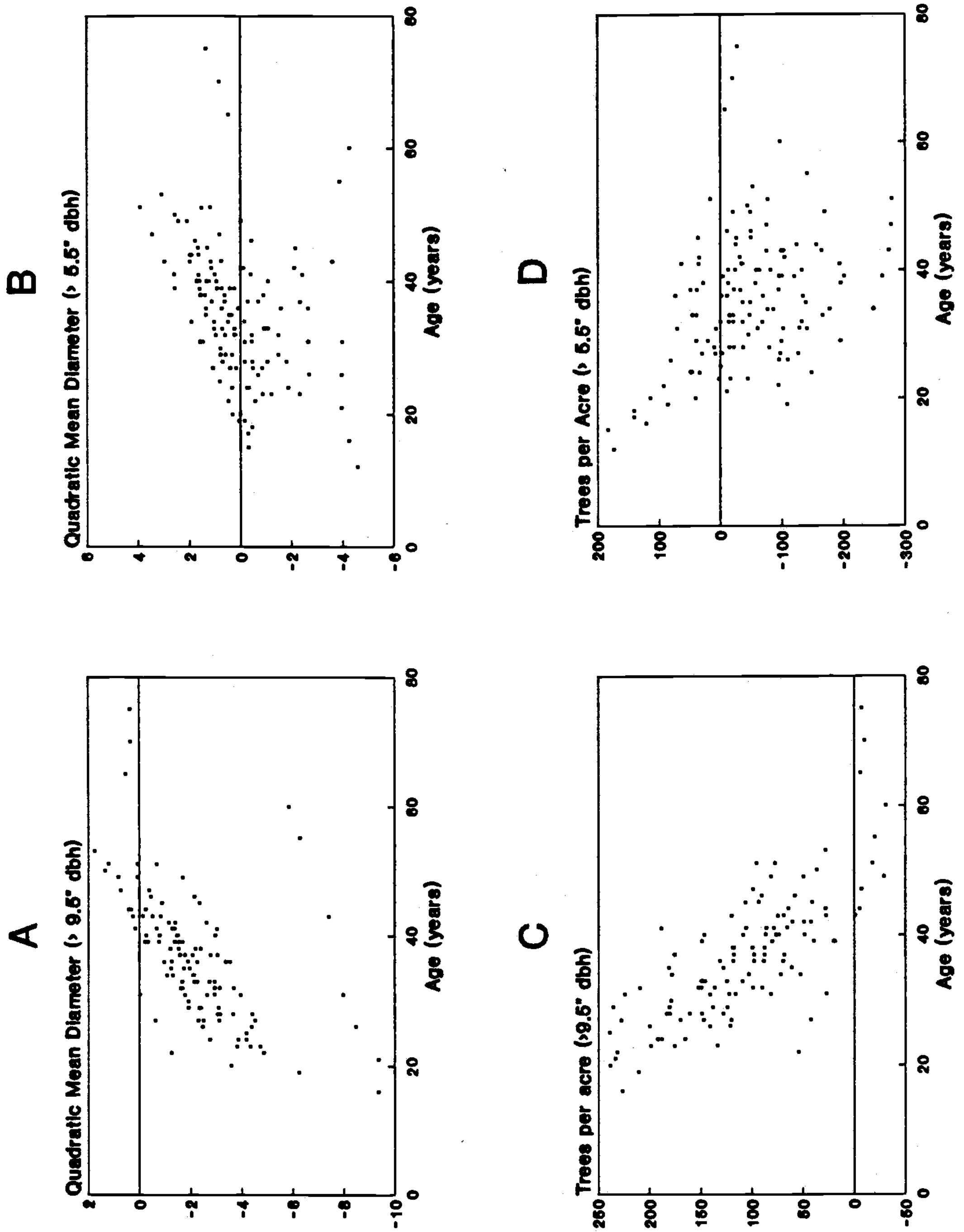

Figure II.2 (continued)

Figure II.3: Predicted minus observed quadratic mean diameter (A, B) and trees per acre (C, D) over total stand age for red alder in mixed red alder/Douglas-fir stands. Predictions are from the Normal Yield Table for Red Alder (Worthington et al. 1960).

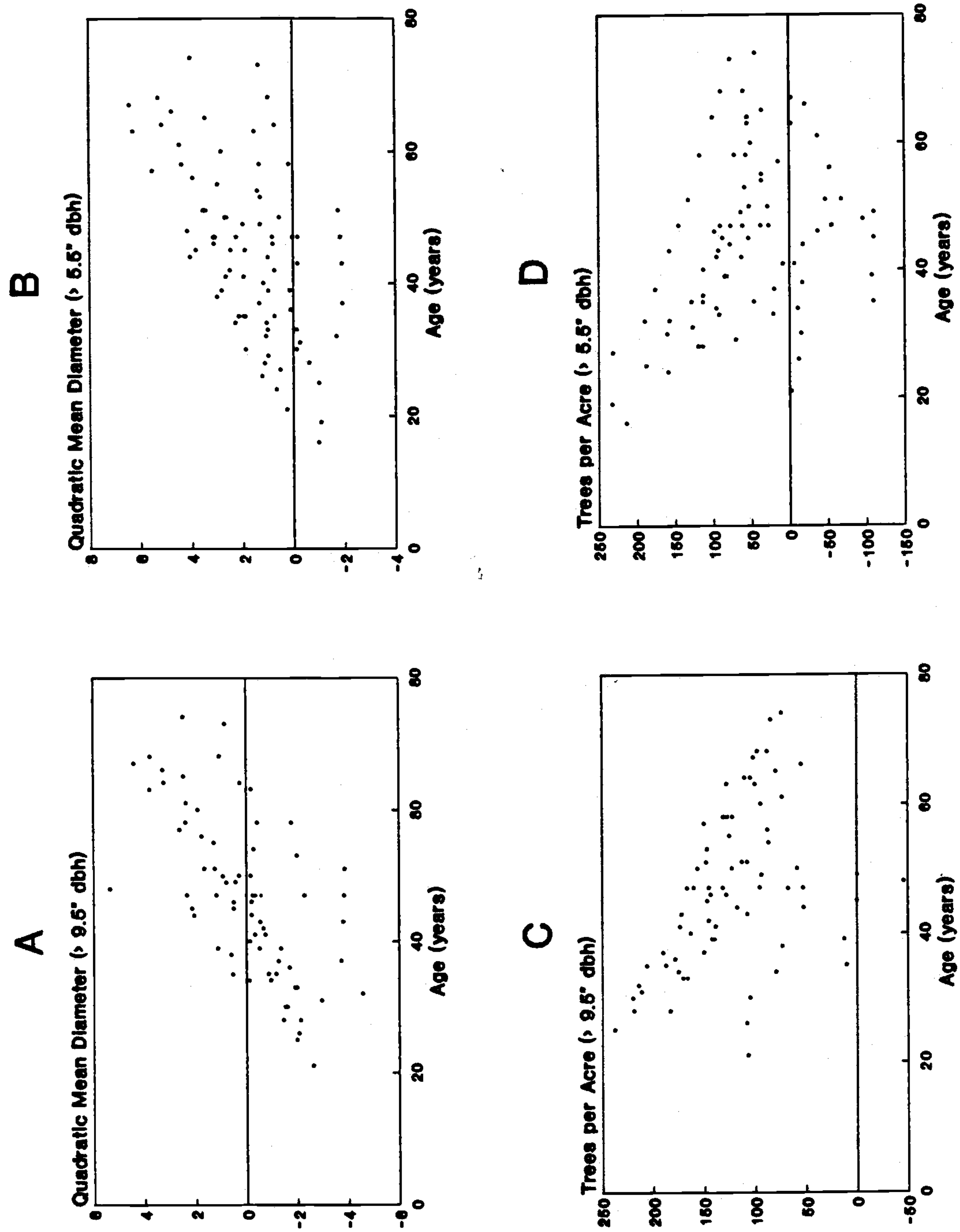

Figure II.3 (continued)

Figure II.4: Predicted minus observed basal area per acre (A, B) and trees per acre (C, D) over red alder proportion for red alder in mixed red alder/Douglas-fir stands. Predictions are from the Normal Yield Table for Red Alder (Worthington et al. 1960).

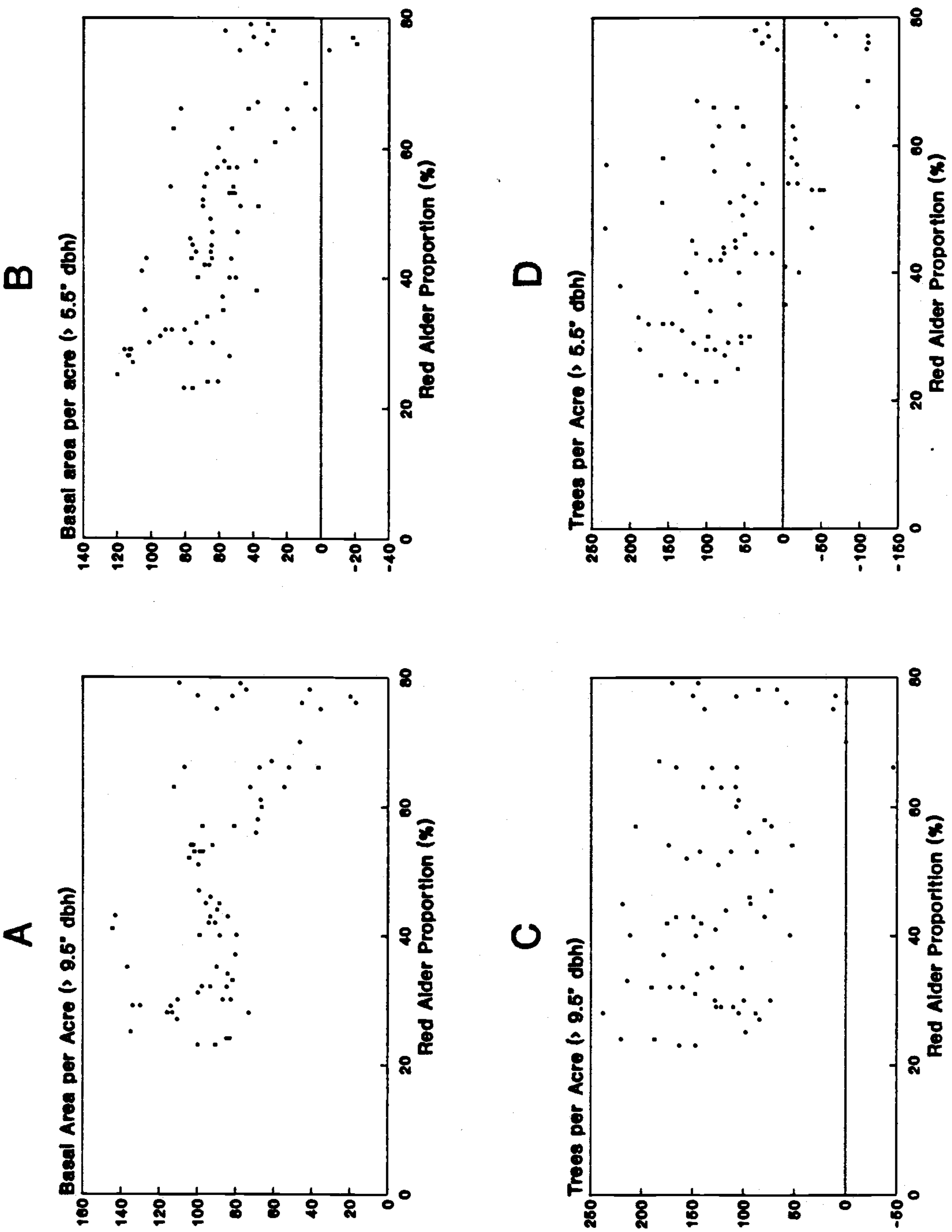

Figure II.4 (continued)

Figure II.5: Predicted minus observed trees per acre (A) and quadratic mean diameter (B) over Percent Normal Basal Area for pure red alder stands. Quadratic Mean Diameter over site index for pure red alder stands (C) and over Percent Normal Basal Area for red alder in mixed red alder/Douglas-fir stands (D). Predictions are from the Empirical Yield Table for Predominantly Alder stands in Western Washington.

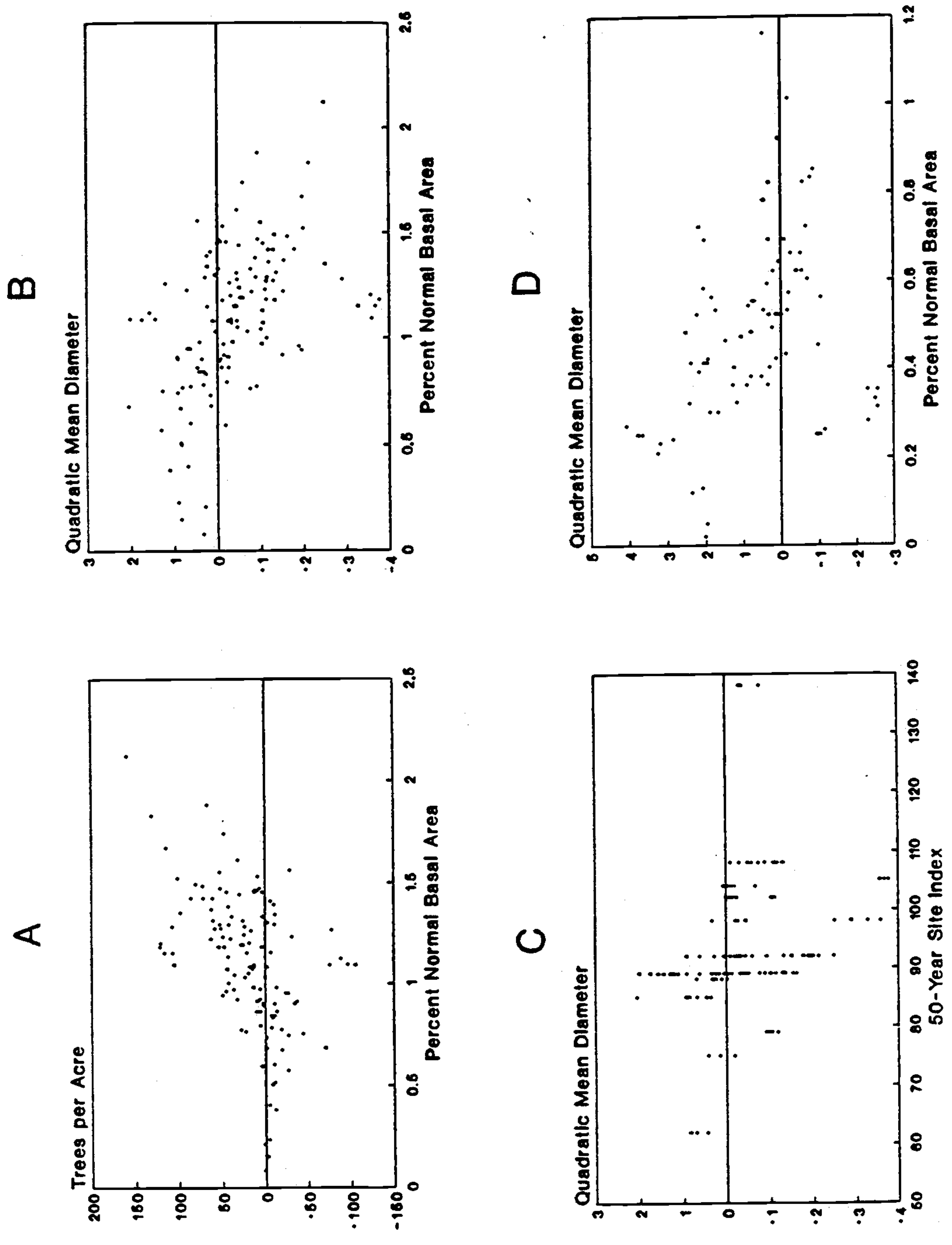

Figure II.5 (continued)

Figure II.6: Predicted minus observed quadratic mean diameter growth over total stand age (A), basal area per acre growth (B) and mortality (C) over length of projection period for pure red alder stands. Predicted minus observed mortality over length of projection period for red alder in mixed red alder/Douglas-fir stands. Predictions are from the Stand Projection System (Arney 1985b).

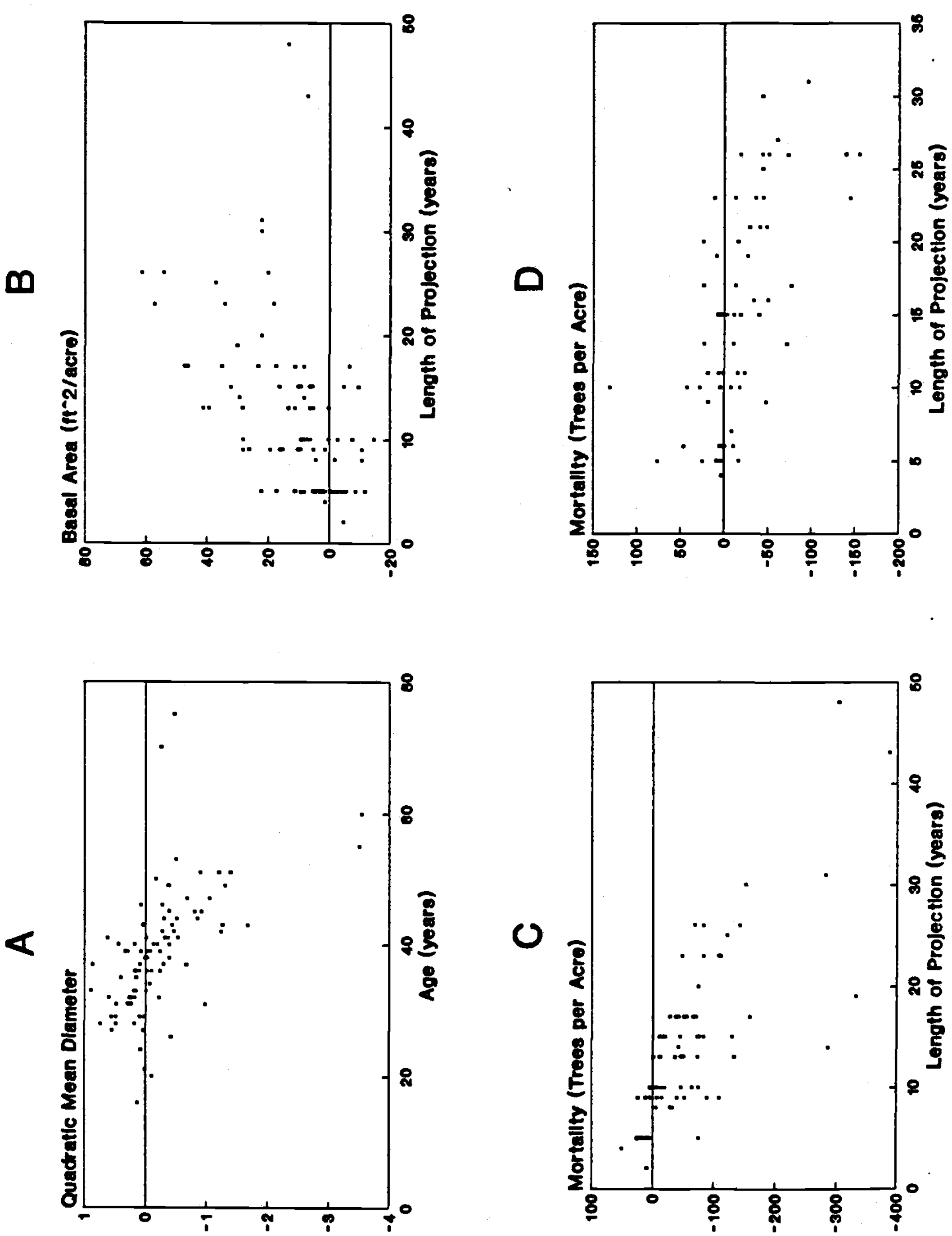

Figure II.6 (continued)

Figure II.7: Predicted minus observed quadratic mean diameter and mortality over total stand age (A, C) and length of projection period (B, D) for Douglas-fir in mixed red alder/Douglas-fir stands. Projections are from the Stand Projection System (Arney 1985b).

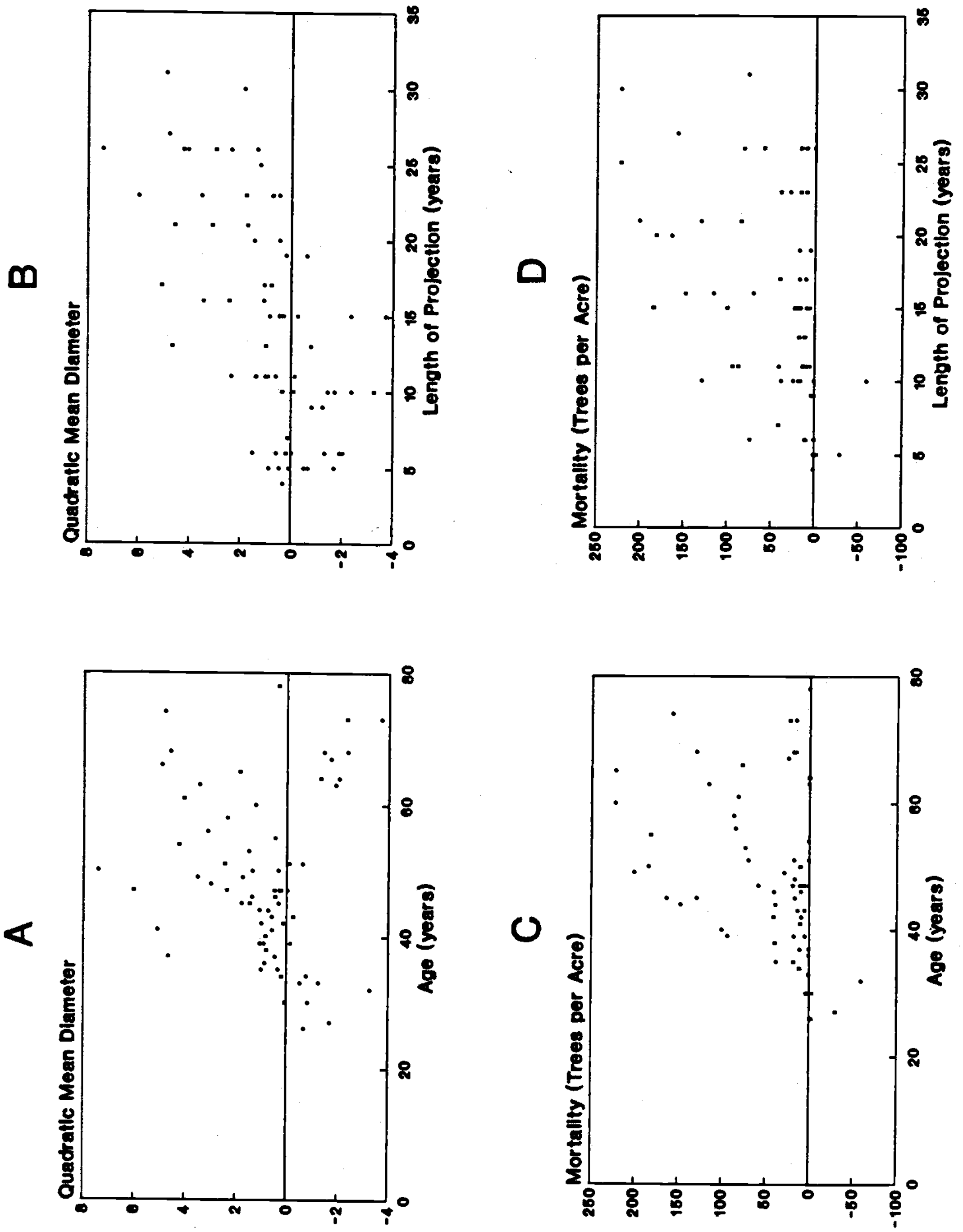

Figure II.7 (continued)

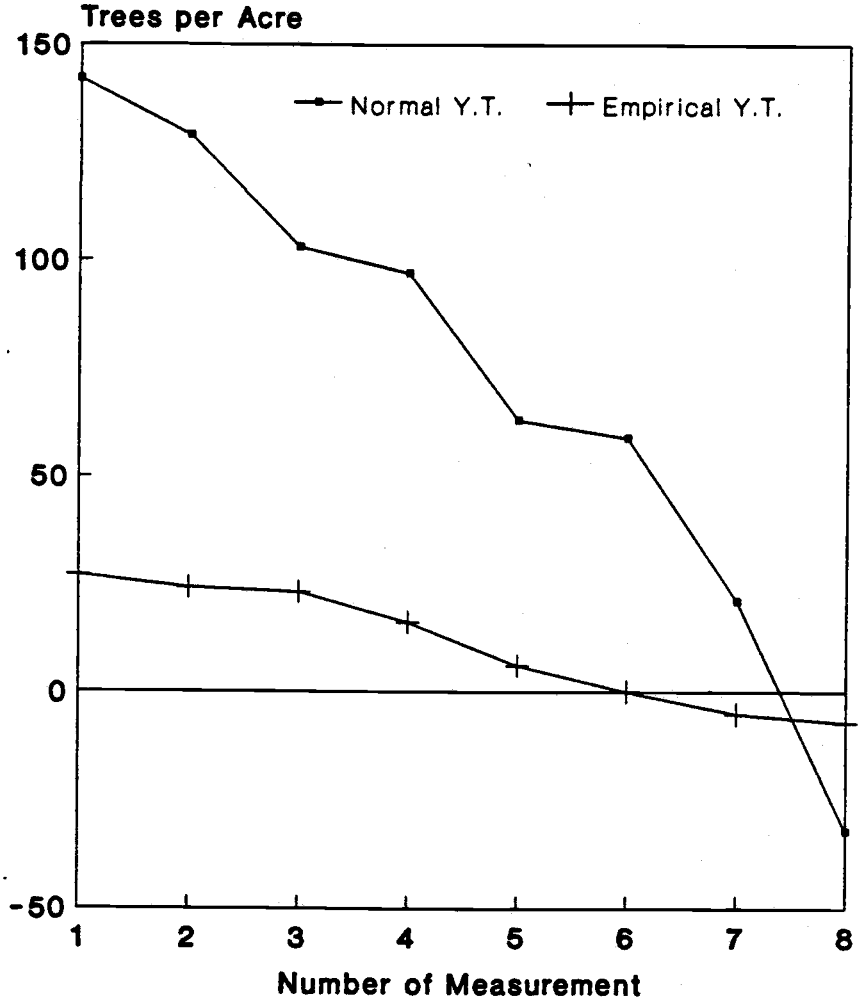

Figure II.8: Mean values of predicted minus observed trees per acre for the Normal Yield Table (Worthington et al. 1960) (> 9.5" DBH) and the Empirical Yield Table (Chambers 1974) over the number of measurement (First measurement equals 1, second equals two, and so forth).

Table II.1: Number of comparisons for the prediction tools

	pure stands	mixed stands
Normal Yield table		
trees >5.5"	126	81
trees >9.5"	119	72
Empirical Yield Table		
trees >7"	128	81
Stand Projection System	96	80

Table II.2: Differences between plot values and predictions of Worthington et al.'s (1960) yield table for pure red alder stands (predicted - actual).

Trees with a DBH greater than 5.5"

Variable	predicted	observed	pred.-obs.	Std.Dev.
Basal area per acre	113.82	129.56	-15.74	27.52
Quadratic mean diameter	9.99	9.92	0.08	1.69
Trees per acre	211	258	-47	90

Trees with a DBH greater than 9.5"

Variable	predicted	observed	pred.-obs.	Std.Dev.
Basal area per acre	117.56	85.30	32.25	29.27
Quadratic mean diameter	10.20	12.43	-2.22	2.06
Trees per acre	210	104	106	66

Table II.3: Differences between plot values and predictions in Worthington et al.'s 1960) yield table for mixed red alder/Douglas-fir stands; uncorrected (predicted - actual).

Trees with a DBH greater than 5.5"

Variable	predicted	observed	pred.-obs.	Std.Dev.
Basal area per acre	127.77	66.34	61.43	29.70
Quadratic mean diameter	11.44	9.76	1.68	1.90
Trees per acre	185	129	56	79

Trees with a DBH greater than 9.5"

Variable	predicted	observed	pred.-obs.	Std.Dev.
Basal area per acre	134.27	46.61	87.66	26.13
Quadratic mean diameter	11.92	11.94	-0.02	2.08
Trees per acre	179	59	120	56

Table II.4: Differences between plot values and predictions in Worthington et al.'s (1960) yield table for mixed red alder/Douglas-fir stands, corrected for basal area proportion of red alder (predicted - actual).

Trees with a DBH greater than 5.5"

Variable	predicted	observed	pred.-obs.	Std.Dev.
Basal area per acre	127.77	71.74	-56.03	33.84
Trees per acre	185	129	55	79

Trees with a DBH greater than 9.5"

Variable	predicted	observed	pred.-obs.	Std.Dev.
Basal area per acre	134.27	95.54	38.73	36.65
Trees per acre	179	120	59	72

Table II.5: Differences between plot values and prediction of Chambers (1974) yield table (predicted - actual).

Pure red alder stands:

Variable	predicted	observed	pred.-obs.	Std. Dev.
Quadratic mean diameter	9.81	10.24	-0.43	1.13
Trees per acre	216	197	19	45

Red alder component in mixed red alder/Douglas-fir stands:

Variable	predicted	observed	pred.-obs.	Std. Dev.
Quadratic mean diameter	10.40	11.04	0.63	1.48
Trees per acre	94	105	-11	23

Table II.6: Differences between plot values and prediction of SPS (Arney 1985a, b) for the red alder component (predicted - actual).

Pure red alder stands:

Variable	predicted	observed	pred.-obs.	Std. Dev.
Basal area per acre	37.13	25.83	11.30	16.94
Quadratic mean diameter	1.39	1.62	-0.23	0.71
Mortality (trees per acre)	68	116	-47	80

Mixed red alder/Douglas-fir stands:

Basal area per acre	23.59	11.52	12.07	26.00
Quadratic mean diameter	2.34	1.88	0.45	2.48
Mortality (trees per acre)	29	46	-17	44.23

Table II.7: Differences between plot values and prediction of SPS (Arney 1985a, b) for the Douglas-fir component of mixed red alder/Douglas-fir stands (predicted - actual).

Variable	predicted	observed	pred.-obs.	Std. Dev.
Basal area per acre	36.52	27.21	9.31	24.00
Quadratic mean diameter	3.27	4.20	-0.93	2.01
Mortality (trees per acre)	56	45	11	63

Chapter III

Development and Comparison of Size-Density Trajectories for Red Alder and Douglas-fir Stands

Introduction

Red alder (<u>Alnus</u> <u>rubra</u> Bong.) is the most common hardwood species in the Pacific Northwest (Fowells 1965). Because it is invasive, exhibits fast juvenile growth, and had low market value, it has been treated as a weed species in Douglas-fir plantations (Walstad and Kuch 1987). Consequently most research in red alder has focussed on its competitive effect on Douglas-fir seedlings (Newton 1978, Cole 1984, Cole and Newton 1987, DeBell and Turpin 1989). Recently, its growth capacity and increased use in the pulp and lumber industry (Resch 1980, 1988) aroused interest in red alder management for biomass production (DeBell et al. 1978) and as a timber species (Tarrant et al. 1983), especially with a background of declining supply of softwood timber. Red alder's ability to fix atmospheric nitrogen makes it a candidate for improvement of nitrogen-deficient soils (Tarrant 1961, Atkinson and Hamilton 1978, Borman and DeBell 1981, Binkley 1983, Helgerson et al. 1984). Another factor contributing to the increased attention to red alder is its immunity to laminated root rot (Phellinus weirii (Murr.) Murr), a fungal disease in conifers (Hansen and Nelson 1975, Nelson et al. 1978).

However, despite all this interest, knowledge about management and silviculture of red alder is limited. The lack of data has so far limited the development of growth simulation tools, with the exception of the Stand Projection System (SPS) which uses modified Douglas-fir equations to model red alder (Arney 1985b). The shortcomings of the Stand Projection System (SPS) (Arney 1985a, b), the Normal Yield Table for Red Alder (Worthington et al. 1960) and the Empirical Yield Table for Predominantly Red Alder Stands in western Washington (Chambers 1974) are presented by Puettmann (1990, Chapter II).

For species like red alder, for which growth and yield information is not sufficient to develop a growth simulator, a stand density diagram is an especially useful tool. One of the most crucial pieces of information needed to develop a stand-density diagram is the self-thinning line. The self-thinning line is the line connecting the maximum average plant size for a range of given densities (Westoby 1984). The self-thinning concept states that even-aged plant populations develop through a stage in which the average plant size and stocking density can be characterized by the following expression:

$$\log(w) = k - a * \log(N) \qquad (1)$$

(Yoda et al. 1963) where w is the average plant size, N is the stocking density, and K and a are constants. This line is the maximum possible plant size for given density and describes the development an average stand follows (Yoda et al. 1963, Hutchings and Budd 1981, White 1981, Long and Smith 1983). In other words, once a plant population is undergoing self-thinning, an increase in plant size has to be accompanied by a decrease in stocking density. This relationship has been shown to have two remarkable properties. First, the intercepts and slopes of the self-thinning lines vary only slightly among species. White (1980) reviewed studies on 36 species, ranging from trees to annuals and found the slope (a) to vary between -1.30 and -1.8 and the intercept (k) to vary between 3.06 and 4.41, when size is expressed in weight per area (grams/m^2) and number of plants per square meter is used as density variable. Second, within species, this relationship seems to be independent of age and site (Long 1985) with the exceptions of sites which have low stocking potential (Petersen and Hibbs 1989).

Because the slope of the self-thinning line was found to be close to -3/2 when biomass was used as a size variable, the self-thinning concept has also been called the -3/2 power rule of self-thinning. Ford (1975) and Mohler et al. (1978) point out that two assumptions have to be fulfilled for the slope to be -3/2. First, the relationship of diameter to height has to be linear. Second, the relationship of decrease in density to efficiency of space occupation by surviving plants also has to be linear.

The self-thinning rule is an empirical relationship, and no general underlying theory has yet been established. Even though the self-thinning rule has been derived by Yoda et al. (1963) using dimensional analysis, other hypothesis about the self-thinning theory have been suggested. Hozumi (1980) and Aikman and Watkinson (1980) linked basic logistic growth equations with algorithms of competition to explain the phenomena. Pickard (1983) incorporated simple assumptions about photosynthesis and respiration costs into three different models of self-thinning. Perry (1984) linked explicit physiological parameters and plant allometry with plant competition.

Because of its simplicity and empirically consistent results, the self-thinning rule has been adapted to a variety of plant species (for review, see White and Harper 1970, Gorham 1979, White 1980). Its assumed independence of both plant age and site index (Long 1985) makes the self-thinning rule a basis for the understanding of plant interactions between individuals in a population (Hutchings and Budd 1981, Long and Smith 1983).

In the forest literature, applications of the self-thinning concepts frequently use quadratic mean diameter

(diameter of the tree with mean basal area) as the size variable (Long 1985). Quadratic mean diameter is related to total biomass and plant weight through allometric relationships (White 1981). Reineke (1933) was the first to use the self-thinning rule for forest management through establishment of the Stand Density Index (SDI). After Yoda's publication in 1963, the self-thinning concept gained renewed interest. Since then, the self-thinning concept has been applied in forest management for a variety of species (Tadaki 1963 and 1964, Ando 1968, Aiba 1975, Drew and Flewelling 1979, McCarter 1984, Smith and Hann 1984, Hibbs 1987, Long et al. 1988, Hibbs and Carlton 1989, Smith 1989). It is the basis for a number of density indices (Reineke 1933, Drew and Flewelling 1979, Curtis 1982a) and has been utilized in growth and yield projection models (Curtis et al. 1981, Lloyd and Harms 1986, Smith and Hann 1986, Hyink et al. 1988, Hester et al. 1989).

Recently this concept was critiqued by Weller et al. (1985), Weller (1987a, b) and Zeide (1987) with special focus on the methods used for establishment of the self-thinning line. Weller (1987a) suggests the use of principal component analysis (PCA) and major axis regression to analyze the data rather than least squares analysis. However, both methods assume linearity in the variables and parameters. Only the line connecting the maximum size for different densities is shown to be linear; during the initial period of self-thinning, a stand is approaching the maximum line in a nonlinear fashion (Stiell and Berry 1973, White 1981, Smith 1984). Fitting a straight line through the data therefore requires the separation of linear and nonlinear stages (Osawa and Sugita 1989). Before knowing the results of the analysis, this separation can only be done subjectively, as pointed out by Weller et al. (1985). The trajectory tracking the approach of a stand toward the self-thinning line and the movement along the line has been named the size-density trajectory (Hara 1984, Smith (1984). Modeling the size-density trajectory avoids the subjectivity of choosing the data points. In addition, this approach allows the utilization of both stands which approach the self-thinning line as well as stands following along the self-thinning line (Smith 1984).

In a theoretical paper, McFadden and Oliver (1988) suggest two different patterns of the self-thinning trajectory. These are presented in a modified from in Figure III.1. The trajectories have been modified to show a gradual rather than pointed approach of stands to the self-thinning line. Figure III.1A shows a common trajectory which all stands follow, i.e. a trajectory which is independent of a stand's initial density. Figure III.1B depicts trajectories the intercepts of which are negatively correlated with initial density). The idea for the second type of trajectory is based on data from Pete and

Christensen (1987) and the concept of the "zone of competition mortality" by Drew and Flewelling (1979). A thinning study by Pienaar (1965) indicated that stands follow trajectories like those in Figure III.1B, but no other data have been used to test the different trajectories in self-thinning stands. Since initial density is known for part of the data set, the opportunity to test which trajectory form better fits red alder data is available.

Objectives

The goal of this study is to investigate the size-density relationship and develop an analytical model of the size-density trajectory for stands of red alder and Douglas-fir. Within this goal, the following specific objectives will be addressed:

1. Determine whether the size-density trajectories of red alder stands of different initial densities exhibit the same shape.
2. Determine whether the line connecting the points at which density dependent mortality starts is parallel to the maximum size-density line.
3. Determine whether the intercept of the size-density trajectory for pure red alder stands varies with initial density.

4. Develop a size-density trajectory for planted and naturally regenerated red alder and Douglas-fir stands.
5. Determine whether naturally regenerated red alder stands follow a size-density trajectory with the same shape as red alder plantations.
6. Determine whether a single size-density trajectory is sufficient to represent the development of both red alder and Douglas-fir stands.

Methods

Data Sets

This project was made feasible through the data compilation of several agencies and landholding organizations. Only a combined data set had the size needed to sufficiently address the problem. The drawback in using a data set compiled in this fashion is that the individual data collections were focused on the specific purpose. This leads to differences in plot layout and size, measurement accuracies and techniques. Any compilation of data sets is therefore a tradeoff between the size of the data set and compatibility of plots within the data set.

The long-term observations (greater than 25 years) included in the combined data set were limited in number, and their values were frequently reduced due to the small plot size. The data were not collected with an overall plan in mind to cover a wide geographical range, or a range of site indices, stand ages or stand conditions. This limited the potential for investigating the influence of such factors on the size-density trajectory. Also, it precluded the development of a unbiased model for application to the range of conditions present in the Pacific Northwest. Thus the project has the character of a preliminary investigation. The Stand Management Cooperative (SMC) of the University of Washington and the Hardwood Silviculture Cooperative (HSC) of Oregon State University will improve overall planing and coordination in data collection in the future.

All data were from remeasured fixed-area plots, which had at least information about diameter at breast height (dbh), 50-year site index (either Douglas-fir or red alder), and number of living trees per hectare. The number of height measurements or measurements of other variables varied considerably between plots.

Some plots had no mortality or increased density during the measurement periods. Since the equation (see Model Development section) can not model a vertical line and can not accommodate ingrowth, these measurement periods were excluded from the analysis.

Red alder

Pure red alder stands were defined as having a minimum of 80% of its basal area in red alder. A total number of 24 plots (N) with 161 individual measurements (n) came from two kinds of data sets: 1. A red alder plantation spacing study in the Coast Range of northwest Oregon (N=9, n=81). 2. Natural stands growing in western Oregon and Washington and southwestern British Columbia (N=15, n=80).

The spacing study was initiated by the Pacific Northwest Forest and Range Experimental station (DeBell and Wilcox in preparation). The study site is located near St. Helens, Oregon on a high site II Douglas-fir (King 1966) and has a red alder 50-year site index (Worthington et al. 1960) of 35 meters. Eight plots were planted in 1974 in four different densities covering the range of 1,200 to 12,000 trees per hectare. One plot was lost due to low temperatures in a low-lying frost pocket. Two plots from an adjacent study on the effect of red alder on laminated root rot (Nelson et al. 1975) were included in the analysis of the spacing study. The plot size varied from 0.016 hectare to 0.081 hectare. Mortality measurements were taken yearly except at age 3, while diameter measurements were taken yearly starting at age 4. No measurements were taken at age 13. This results in ten diameter-density measurements for each plot, with the exception of one plot, which was harvested at age 13.

The natural stand data were collected from various landowners. To ensure compatibility of the data sets, the selection criteria for all sets included a fixed area permanent plot with multiple remeasurements and the minimum diameter of 4-centimeters diameter at breast height. Because the effect of thinning on individual trees and stand growth is not yet known (Clutter et al. 1983, Smith 1986), only plots in unthinned stands were used in the analysis. The plot size varied from 0.0405 hectare to 0.2015 hectare plots. The mean age for the stands at initial measurements was 25 years with the range of 15 to 44 years. The 50-year site index (Worthington et al. 1960) varied from 19 to 33 meters with a mean value of 27.6 meters. The mean quadratic mean diameter (QMD) of the overall data set ranged from 8 centimeters to 32 centimeters with a mean QMD of 22 centimeters. The number of live trees per hectare varied from 420 to 3370 with a mean density of 1017 trees per hectare. The distribution of age, site index, basal area, QMD and stocking density are presented in Figure III.2.

In cases were the age from seed was not known, the age from breast height was converted to the age from seed using two years as the conversion factor (Worthington et al. 1960).

One plot had ingrowth of sitka spruce (*Picea sitchensis* Bong.) after the stand had reached 30 years. This created a problem because the size-density relationship was developed for even-aged plant populations (Yoda et al. 1963). Even though these trees might have the same age as the stand, they are not considered even-aged in the silvicultural definition (Smith 1986). For this reason, the ingrowth of trees after the stand had reached age 30 were omitted from this analysis.

To check for disturbance-related mortality in the plots, yearly mortality was determined for each measurement period. None of the plots had an overly-high annual mortality rate (greater 6 %), which suggested that these plots did not experience disturbance related mortality during the measurement periods.

The plantation spacing study was treated separately for several reasons. In contrast to the natural stands, the effective planting density (excluding planting mortality) was known. Also, all trees in the plots were measured without a diameter limit. Finally, the measurement period covered the stages of no intraspecific competition, the onset of growth reduction due to competition and the approach of the self-thinning line.

Douglas-fir

The data for Douglas-fir stands come from three sources: 1) The control plots of the installation of the Regional Fertilizer and Nutritional Research Program (RFNRP) of the University of Washington (Opalach 1989) (N=27, n=145). 2) The control plots of the Level-of-Growing-Stock study (LOGS) (Curtis and Marshall 1986) (N=354, n=21) and 3) A data set assembled by J. E. King (1973) (N=90, n=591). All plots are located in western Oregon, western Washington or southern British Columbia.

The first data screening indicated a great variation in annual mortality. Some plots showed an annual mortality rate greater than 20% for a four to five year period. The average annual mortality rate for the data set was 3.19%. Disturbance-related mortality induced by agents like storm, insects or root rot were assumed to be responsible for the extreme high mortality rates. Including these data would bias the analysis of the self-thinning line. Since historic information about individual plots was not available, a limit for density-dependent mortality was set. To do this,the mean and standard deviation of average annual mortality was calculated. All plots which showed annual mortality for a growth period higher then 6.16% (2 standard deviations above the mean) were assumed to have experienced some disturbance-related mortally. This left 59 plots and

282 measurements for analysis of the size-density trajectory. The mean 50-year site index (King 1966) value was 37 meters, and the mean age of all measurements was 37 years. The mean QMD was 23.2 centimeters, the mean density was 1554 trees per hectare and the mean basal area per hectare was 49 square meters. The frequency distribution of age, site index, QMD, basal area, and density are presented in Figure III.3.

Model Derivation

The QMD was selected as the variable representing tree size for several reasons: it is easily measured and it has a close relationship to crown size (Brigleb 1952, Smith 1968) and tree biomass (Hughes 1971).

As proposed by Smith (1984), the size-density trajectory was developed from log-log transformed data and was assumed to consist of two parts: a linear portion, which is the self-thinning line, and a nonlinear portion in which the trajectory approaches the self-thinning line asymptotically. The size-density trajectory was modeled as the difference of the two functions.

Equation 2 expresses the linear portion, the asymptote of the size-density trajectory which is defined as the self-thinning line.

$$Y_{mij} = a_1 + a_2 * X_{ij} \tag{2}$$

where, Y_{mij} = logarithm of the maximum quadratic mean diameter

X_{ij} = logarithm of the actual stocking density

a_1 = intercept

a_2 = slope

i = stand age

j = plot identifier, $j=1,2...N$

The trajectory was assumed to approach the linear portion as developed in Equation 2 as a monotonically decreasing function. A negative exponential function was used to model the actual change in density.

$$Y_{ij} = \exp(-a_3*(X_{1j} - X_{ij})) \tag{3}$$

where the parameters are as in Equation 2, and

Y_{ij} = logarithm of the QMD

X_{i0} = logarithm of the initial stocking density

a_3 = intercept of the exponential function

Using the method of Smith (1984) and Smith and Hann (1984), the size density trajectory was put together by subtracting equation 3 from equation 2, resulting in equation (4).

$$Y_{ij} = a_1 + a_2*X_i - a_1*a_4*\exp(-a_3*(X_{1j} - X_{ij})) \tag{4}$$

where the parameters are as in equations 2 and 3, and

a_4 = adjustment for relative density when mortality starts.

Equation 4 represents a trajectory Type II as defined by McFadden and Oliver (1988). To represent a Type III trajectory form and calibrate the intercept term change for changing initial density, equation (5) was modified.

$$Y_{ij} = a_1 - b_1*X_0 + a_2*X_i - a_1*a_4*\exp(-a_3*(X_{1j} - X_{ij})) \qquad (5)$$

where the parameters are as in equation 2, 3 and 4 and

b_1 = intercept adjustment for initial density.

The initial density of the natural stands was not known. Two methods can be used to accommodate for the missing information: 1. A mortality equation is fit to the stand data and extrapolated to yield initial density. The estimates for initial density can then be used in equation 4, i.e., the system can be solved recursively. 2. The model as in equation 4 can be restructured to not require initial density as an independent variable. Both methods are formulated for evaluation on the data sets.

For assessment of the first option, a mortality equation as presented by Smith (1989) was used.

$$N_i = a_1 * (1 - (1 - \exp(-a_2*k_3))) \qquad (6)$$

where N_i = logarithm of actual stocking density,

k = age from seed,

and a_1 and a_2 are parameters to be estimated. The a_1 was assumed to be the best estimate of the logarithm of initial density (Smith 1989).

To accommodate for the second option, equation 4 was modified in the following fashion. First, the stocking density at the time of first measurement was expressed as a fraction of the initial stocking density.

$$N_0 = k * N_1 \tag{7}$$

where N_1 = trees per hectare at first measurement

N_0 = density before onset of density induced mortality,

f = adjustment factor

Rewriting equation 4 and substituting equation 7 into it yields

$$Y_i = a_1 + a_2*X_i - a_1*a_4*(N_1/k*N_i)\hat{}a_3 \tag{8}$$

where N_i = number of trees per hectare at age i

N_1 = number of trees per hectare at initial measurement

Equation 8 can be rewritten as:

$$Y_j = a_1 + a_2*X_i*(a_1*a_4*f\hat{}-a_3) * (N_1/N_i)\hat{}a_3 \tag{9}$$

Setting

$$a_5 = f\hat{}-a_3 \tag{10}$$

results in following equation

$$Y_i = a_1 + a_2*X_i * a_1 * (a_4+IO*a_5) * (N_1/N_i)\hat{}a_3 \tag{11}$$

with parameters as in Equations 7 and 8, and

a_5 = adjustment factor

IO = indicator variable. IO = 1 if initial density is unknown, 0 otherwise.

The adjustment factor (a_5) includes the adjustment for the onset of mortality (a_4) and adjustment for the difference between initial density and density at the time of first measurement (f). Thus equation 11 can be used to determine the size-density trajectory for stands for which the initial density was unknown.

The combined model for red alder and Douglas-fir stands used the red alder model as a base model. An adjustment for Douglas-fir (b1 to b5) was added to every parameter in the base model (a_1 to a_5) using indicator variables. The a_4 parameter is only applicable in cases where initial density is known and since this was not the case for Douglas-fir stands an adjustment for a_4 cannot be calculated separately but is included in b_5. The combined model is

$$\begin{aligned} Y_i &= a_1 + (I*b_1) + (a_2 + (I*b_2))*X_i \\ &\qquad - (a_4 + (IO*a_5 + I*b_5))*\ a_1 * (N_i/N_1)\hat{}a_3 \qquad (12) \end{aligned}$$

with parameters as in equation 11 and

b_i = adjustment on the red alder parameters (a_1 through a_5), i=1, 2, 3, 5

I = indicator variable, I=0 if species = red alder, I=1 if species = Douglas-fir.

Fitting Method

The nonlinear package of the SAS statistical package (SAS Institute 1987) was used for analysis. The Marquardt-algorithm (Marquardt 1963) was used for model fitting. In instances when the Marquardt-algorithm did not lead to convergence, the derivative free secant-DUD algorithm (Ralston and Jennrich 1978) was used to solve for the parameters. The convergence criterion was

$$(SSE_{i-1} - SSE_1)/(SSE_1 + 10^{-6}) < 10^{-8}$$

where SSE_i = sums of squares for the i^{th} iteration. The goal was to use a biologically sensible model from and solve for statistically significant parameters ($p<=0.05$).

The strategy was to start with a complex model of common asymptote but allow each stand to approach the self-thinning line in an individual fashion. Combining parameters was tested to simplify the model. The sums of squares of the full (individual parameters) and the reduced models (combined parameters) were tested for significant differences (Cunia 1973) with $p<=0.01$.

Information about natural stands did not include information about the initial density before the onset of competition induced mortality. Before the analytical model was applied, a method to estimate initial density was tested on the spacing study to evaluate the best model for use in natural stands.

To reduce the effect of non-density related mortality, the QMD was weighted by the number of trees in each plot. Giving bigger plots more weight de-emphasized random background mortality and favored density- dependent mortality. Ideally, the initial number of trees in each plot should be used as a weighing factor because it assigns weights by initial density and plot size simultaneously. However, initial number of trees in a plot was only known for the plots in the St. Helens spacing study but not for the natural stands of red alder or for any Douglas-fir stands. Since compatibility of the models was very important, plot size was used as weighing factor.

Some assumptions about nonlinear regression have to be considered in the evaluation of the model fitting procedures. Parameter estimates are not normally distributed. Also the estimated mean square error is not an unbiased estimator of the population variance. The confidence intervals are therefore only approximate, or asymptotic if the sample size is large (Radkowski 1978).

Analytical Steps

The model development was composed out of several steps as outlined in the list of objectives.

Objective 1-3. To accomplish the first 3 objectives, information about initial planting density was required. The plantation spacing study had this information. Since the planting densities covered a wide range, the spacing study was used to determine the effect of density on the shape of the size-density trajectory. The next step was to determine the location of the line connecting the densities at the onset of density dependent mortality. The trajectory could then be compared to a trajectory with a shape suggested by McFadden and Oliver (1988).

Two alternative methods (Equations 6 and 11) were suggested to model the size-density trajectory of stands for which initial density is unknown. Since using mortality to predict initial density is an extrapolation beyond the data range, its accuracy cannot be evaluated directly. For this reason, the spacing study, for which initial density was known, was used to determine the accuracy of this approach.

Objective 4. The result of the above mentioned test determined the expression to be used for modeling the size-density trajectory of the natural stands. The next step was to test whether a single model is sufficient to characterize the size-density trajectory for both naturally regenerated and planted red alder stands.

Objective 5. Since no data sets containing information about initial density were available for Douglas-fir, the model form used to model natural red alder stands was fitted to the Douglas-fir data set.

Objective 6. The final step in this analysis was the test whether the size-density trajectory for both species differ.

The size-density trajectories can then be used to develop a relative density index. Relative density was calculated in a fashion similar to Drew and Flewelling

(1979) by dividing the actual stand density by the maximum stand density for the stand QMD.

Model Development and Results

Red alder

The analysis for objective 1 and 2 required the assumption that the size-density trajectory of all plots approaches a common self-thinning line. To allow for an individual approach to this maximum line for the St. Helens spacing study, an indicator variable (I) was used for the individual plots and equation 4 was fitted to the data in following form:

$$Y_{ij} = a_1 + a_2*X_i - a_1*I_{i1}*a_{i4}*\exp(-a_{i3}*(X_{1j} - X_{ij})) \qquad (13)$$

where, Y_{ij} = logarithm of the QMD

X_{1j} = logarithm of the initial trees per hectare

X_{ij} = logarithm of trees per hectare at age i

a_1 = intercept of the asymptote

a_2 = slope of the asymptote

a_{i3} = intercept of the exponential function

a_{i4} = adjustment for the relative density at the onset of mortality

i = stand age

j = plot subscript, j=1,2,..N

The initial estimates for the a_1 and a_2 parameters were calculated from the underlying self-thinning relationship of the Normal Yield Table for Red Alder (Worthington et al. 1960) (a_1=7.3, a_2=-0.623). The results of this fitting process are presented in Table III.1.

To investigate objective 1, whether the approach of stands to the maximum line is independent of initial density, the plot indicator for a_{i4} was changed to a common parameter for all plots (a_4). Otherwise the model was fitted as presented in equation 13. The resulting parameters of this fitting process are presented in Table III.2. The sums of squares of the reduced model (common a_4) were not significantly different from the full model (individual a_{i4}). This indicated that a common parameter representing the approach to the asymptote was sufficient to represent the size-density trajectory for the data set of the spacing study.

The next step (Objective 2) was to test the hypothesis that the line connecting the points at which density dependent mortality starts is parallel to the maximum line. For this test, in addition to the a_4 parameter, the a_{i3} parameter was combined for the data from the spacing study in a_3. Other parameters were as in equation 13.

$$\begin{array}{l} Y_i = 7.84 - 0.69*X_i*(7.84*0.07*exp(-3.92 * (X_1-X_i) \\ \qquad\quad (0.19)\ \ (0.03)\qquad\quad (0.008)\qquad (1.03) \end{array} \qquad (14)$$

MSE=0.00042. Standard errors in parentheses.

The F-Test indicated no significant difference between the sums of squares of the full and the reduced model. The implication is that, for the spacing study, the line at which initial mortality starts is parallel to the maximum density line.

To test the different trajectory forms suggested by McFadden and Oliver (1988) (Objective 3), equation 5 was fitted to the data. The initial parameter estimates are set as a_2 =-0.5 and b_1=-0.123. These values represent constant final basal area (a_2) and Reineke's slope of -0.623 (a_2+a_3). The solution for equation 5 was

$$\begin{array}{l} Y_i = 7.99 -0.07*X_0 - 0.63*X_i - 0.68*exp(-4.95 * (X_1-X_i)) \\ \qquad\qquad (0.49)(0.26)\qquad (0.25)\qquad (0.35)\qquad (1.70) \end{array} \qquad (15)$$

MSE=0.00045. Standard errors in parentheses.

The parameter for the adjustment of the intercept term (0.07) was not significant. The fit statistics (asymptotic adjusted R-square= 0.93) of this model (equation 15) was less compared with the fit (asymptotic adjusted R-square = 0.96) for the model with a common asymptote for all densities (Equation 14). Both the insignificance of the adjustment parameter on the intercept and the difference in fit indicated that the spacing study data did not follow trajectory type III as defined by McFadden and Oliver (1988). Instead the data suggested a model assuming a common asymptote (Equation 4). Further analysis was therefore based on trajectory type II.

Before analyzing the natural stands (Objective 4), a mortality equation (Equation 6) was tested for its ability to predict initial density, by fitting the equation to the data from the spacing study. I used the logarithm of the actual initial density as an initial estimate for the a_1 parameter. The a_1 parameter for the equation using 10 and 7 years of data (age 4 to 14 and age 7 to 14) and the logarithm of the actual density after planting mortality are presented in Table III.3. In the first case (age 4 to 14) the a_1 parameter predicted the logarithm of initial density well. For all plots, the asymptotic 95% confidence interval contained the logarithm of the true initial density. When the morality equation utilized only data from age 7 to age 14, the a_1 parameter did not show the same accuracy. The longer extrapolation resulted in greatly inflated confidence intervals and, for 2 out of 9 plots, the asymptotic 95% confidence interval did not contain the logarithm of the actual trees per hectare. Since in the spacing study, trees grew in a more homogeneous environment than in natural regenerated stands and the mortality equation used a relatively high number of plot measurements, this test can be viewed as very conservative.

Therefore, the failure to predict initial density accurately in a relative short-term prediction (7 years) infers the use of an alternative approach is preferable, especially since the size-density trajectory as analyzed in this project depends on good estimates of the initial density. Consequently, analysis of the size-density trajectory of natural stands was based on the approach as developed in equation 11 which does not require initial density as an independent variable.

For parameter fitting equation 11 was rewritten as

$$Y_i = a_1 + a_2 * X_i - a_1 * I_{i1} * a_{i5} * \exp(-a_{i3} * (X_1 - X_i)) \qquad (16)$$

with parameters as in equation 12 and

a_5 = adjustment for onset of mortality and stage of current mortality

The initial parameter estimates for the asymptote were calculated from the Normal Yield Table for Red Alder (Worthington et al. 1960) (a_1=7.3, a_2=-0.623). The parameter estimates determined by the algorithm are presented in Table III.4. Using the same starting values a reduced model with common a_3 and a_4 parameters for all plots was calculated and resulted in

$$Y_{ij} = \underset{(0.09)}{7.11} - \underset{(0.01)}{0.58} * X_i - 7.11 * I_{i1} * \underset{(0.003)}{.014}$$

$$* \exp(-\underset{(1.63)}{4.23} * (X_1 - X_i)) \qquad (17)$$

MSE=0.0005. Standard errors in parentheses.

The F-test did not show any significant differences between the sums of squares from the full and the reduced model. This indicated that a simplified model with common parameters was sufficient for all plots in natural stands.

To test whether plantations and natural stands follow the same trajectory (Objective 5), the data from the spacing study with natural regenerated stand data were combined and used in solved the following equation:

$$\begin{aligned} Y_{ij} &= I_p{*}a_{n1} + I_p{*}a_{n2}{*}X_i - I_p{*}a_{n1}{*}a_4{*}\exp(-a_{n3}{*}(X_1 - X_i)) \\ &\quad + I_n{*}a_{p1} + I_n{*}a_{2p}{*}X_i - I_n{*}a_{p1}{*}a_5{*}\exp(-a_{p3}{*}(X_1 - X_i)) \end{aligned} \tag{18}$$

where, parameters are as in equation 12, and

I_n = indicator variable, I_n=1 if natural stands, 0 else

I_p = indicator variable, I_p=1 if plantation, 0 else

The resulting parameter estimates are presented in Table III.5.

The reduced model as developed in equation 12 assumes a common size-density trajectory for both natural and planted red alder stands. It used the combined data set in

$$\begin{aligned} Y_{ij} &= a_1 + a_2{*}X_i - I_p{*}a_1{*}a_4{*}\exp(-a_3{*}(X_1 - X_i)) \\ &\quad I_n{*}a_{p1}{*}a_5{*}\exp(-a_{p3}{*}(X_1 - X_i)) \end{aligned} \tag{19}$$

where variables are as in equation 12 and 18.

The best fit regression (19) gave

$$Y_{ij} = \underset{(0.05)}{7.46} - \underset{(0.007)}{0.638}*X_i - I_p*7.46*\underset{(0.002)}{0.07}*\exp(-\underset{(0.35)}{3.84}*(X_1-X_i))$$

$$I_n*7.46*\underset{(0.02)}{0.14}*\exp(-3.84*(X_1 - X_i)) \tag{20}$$

MSE=0.000496. Standard errors in parentheses.

The reduced model was not significantly different from the full model (Equation 18), indicating that a common size-density trajectory is sufficient to represent development of planted and naturally regenerated red alder stands. The model has an adjusted asymptotic R-square of 0.96 indicating a very good fit to the data and suggesting that plantations follow the same size-density trajectory patterns as natural stands. The slope of -0.638 does not include the slope (-0.623) suggested by Reineke (1933) in the 95% confidence interval. The Stand Density Index (SDI) (Reineke 1933) of the asymptote for a stand with a QMD of 25.4 centimeter is 751. The steeper slope of the asymptote compared with the one determined by Reineke (1933) results in a slowly increasing SDI with decreasing density. The data used in analysis and the asymptote of the size-density trajectory are shown in Figure III.4.

Douglas-fir

The method of origin was not known all stands of the Douglas-fir data set, the majority of the plots were located in naturally regenerated stands, and the initial density is not known for any of the Douglas-fir plots. Therefore the same model form as used for natural red alder stands (equation 13) was also applied in the analysis of all Douglas-fir stands. Initial parameter estimates were selected on the assumption that the size-density trajectory of Douglas-fir has the same intercept as red alder (a_1=7.46) and the self-thinning line has the slope determined by Reineke (1933) (a_2=-0.623). The least square fit yielded

$$Y_{ij} = \underset{(0.07)}{6.92} - \underset{(0.001)}{0.52}*X_i - 6.92*\underset{(0.002)}{0.3}*\exp(-\underset{(4.18)}{22.68}*(X_1 - X_i)) \tag{21}$$

MSE=0.000859. Standard errors in parentheses.

The data used in this analysis and the asymptote of the size-density trajectory are presented in figure III.5. The slope the asymptote (-0.52) does not include the slope determined for red alder (-0.638) or the slope suggested by Reineke (1933) (-0.623) in the 95% confidence interval. It also does not include -0.5, the slope which is equivalent to constant basal area in the confidence interval, i.e. a slope of -0.52 represents stands which have a slowly increasing basal area. At a QMD of 25.4 cm the asymptote results in a SDI of 1196 (metric units). Due to the difference in slope, the SDI of the asymptote decreases with decreasing density.

Both species

The combined model for both species used initial parameter estimates as developed in equations 19 and 21. The initial parameter estimates for the b-parameters were calculated as the difference between the appropriate parameters in the two equations. The least square fit yielded

$$
\begin{aligned}
Y_{ij} = {} & \underset{(0.09)}{7.33} - (I_s * \underset{(0.11)}{0.40}) - (\underset{(0.13)}{0.619} + (I_s * \underset{(0.02)}{0.09})) * X_i \\
& -(7.33 - (I_s * 0.40) * (\underset{(0.004)}{0.08} + I_p * \underset{(0.005)}{0.07} + I_s * \underset{(0.005)}{0.015})) \\
& * \exp((\underset{(0.49)}{-3.12} - I_s * \underset{(3.52)}{13.58}) * (X_1 - X_i))
\end{aligned}
\tag{22}
$$

MSE=0.000729. Standard errors in parentheses.

All parameters in the combined model for both species are significant ($p<=0.05$). To test whether the full model can be simplified, a reduced model was calculated by dropping the adjustment parameter indicating species difference. The model parameters were determined to be

$$
\begin{aligned}
Y_{ij} = {} & \underset{(0.06)}{7.14} - \underset{(0.007)}{0.55} * X_i - (7.14 * (\underset{(0.006)}{0.12} - I_p * \underset{(0.05)}{0.09})) \\
& * \exp(\underset{(0.22)}{-1.31} * (X_1 \_ X_i))
\end{aligned}
\tag{23}
$$

MSE=0.001414. Standard errors in parentheses.

The F-test comparing the sums of squares of the full and the reduced model and the significance of all parameters in the full model showed the two to be different ($p <= 0.01$). Thus the two species model could not be simplified and required species indicators at all parameters as presented in equation 22. The size-density trajectories for stands of different densities of both species are presented in Figure III.6.

Discussion

The size-density trajectories for red alder and Douglas-fir were established using a mathematically unbiased method. The data sets used in establishing the trajectories were compiled from a large number of different research projects. Even though the data cover a wide range of densities, the coverage of site index or geographic region is not sufficient to allow a detailed exploration of these factors. Ultimately, long-term spacing studies set up to cover the range of conditions present in the region are needed to explore the problem area to its full extent.

Because of the knowledge of effective planting density, the analysis of the red alder spacing study allowed the examination of some characteristics of the size-density trajectory for this species. First, the pattern at which the size-density trajectory curves towards the self-thinning line is independent of initial density. This has also been found by Smith (1984) for red alder seedlings, and by Smith and Hann (1986) for red pine (Pinus retinosa Ait.) stands. This leads to the implication that the size-density relationship is implicit in stand development and a characteristic which varies with species.

In addition, the analysis of the spacing study 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. Smith and Hann (1986) found red alder seedlings started density related mortality at a constant relative density of 0.31, but mortality in red pine started at a lower relative density in low density stands. On the other hand, DeBell et al. (1989), when analyzing size-density relationship for loblolly pine (Pinus taeda L.) suggested that mortality in low density stands starts at a higher relative density than in denser stands. However, their mortality threshold line (more than 3% of the initial number of trees died) is determined by analyzing data which were collected at measurement intervals of 5 to 7 years. A more frequent measurement interval, as in the St. Helens spacing study, might have led to a different conclusion concerning the mortality threshold of loblolly pine.

To address the question about the onset of density dependent mortality in a more thorough fashion requires spacing studies which contain replicated plots covering a wide range of initial densities. Single spacing studies, however, cannot access the influence of site quality on mortality pattern. A number of spacing studies which cover the range of site quality are therefore needed. Important factors in the spacing studies include measurement of the effective planting density (density after planting mortality) and frequent remeasurements of the plots.

The spacing study data allowed the comparison of two different forms a size-density trajectory can take. Recently, McFadden and Oliver (1988) suggested the theoretical possibility of an inverse relationship between the intercept and initial density, which is equivalent to a size-density trajectory as shown in Figure III.1B. This concept can be compared with the traditional form with a common asymptote to all stands (Figure III.1A) as used by Smith (1984) and Smith and Hann (1984, 1986). In this study, both types were fit to the spacing study data and the fit statistics were compared. The model representing a single asymptote for all stands showed a better fit than the model which allowed for different intercepts for stands with different initial density. In addition, the parameter adjusting for the different intercepts as a function of initial density (b_1) was not significant. This indicated that a trajectory with a common asymptote for all stands regardless of initial density was more suitable than a trajectory type with varying intercepts. The same results were found for Douglas-fir in an analysis of a French spacing study (Hann 1989). However, both the red alder spacing study and the French Douglas-fir spacing study are still fairly young (14 and 23 years, respectively) and do not cover later stages in stand development when stands move along the trajectory at lower densities. A more thorough comparison of these two trajectory types requires data sets which cover the full range of stand development from the stages when a stand approaches the asymptote to substantial movement along it.

Before modeling the size-density trajectory for natural stands, adjustments were made to accommodate for the fact that the natural stand data did not contain information about the initial density of the stands. The approach was tested (Smith 1989) by fitting a mortality equation to the spacing study data and comparing the predicted with actual initial density. Extrapolating initial density from densities of four to fourteen years showed reasonable accuracy. Utilizing only data of seven to fourteen years of age resulted in a predicted initial density which was judged not sufficient, considering that the model for the size-density trajectory relies on good estimates of initial density. Therefore, the prediction of initial density through a mortality equation cannot be recommended for natural stands, especially when the average age at initial measurement was 25 years as in the data set used here.

The alternative to predicting initial density is a formulation of the size-density trajectory model which does not require initial density as input variable. As a tradeoff, the model representing the size-density trajectory had to include an adjustment parameter which was a function of the proportion of the initial density still alive at initial measurement and the relative density at which mortality starts. This parameter could be estimated for each stand and did not require the knowledge of initial density.

The practice of planting seedlings and not relying on natural regeneration of red alder has raised the question of whether the method of regeneration influences later stand growth and development. Since the red alder data set used in this study was a composite of planted and naturally regenerated stands of approximately even numbers of plots, it allowed the investigation of the influence of regeneration method on size-density patterns. After establishing the size-density trajectory for the spacing study and the natural stands, both models for planted and natural regenerated stands were combined. Disregarding the fact that age and density range for the two data sets do not fully overlap, a common size-density trajectory was shown to be sufficient to characterize the development of both natural and planted stands. The good fit of the combined model showed that the regeneration method does not influence the stand development in terms of the size-density trajectory.

A size-density trajectory was also established for Douglas-fir stands. Since initial density was not known for these plots, the influence of initial density on trajectory shape or the onset of initial density could not be examined for Douglas-fir stands. Even though the data range did not cover a density range as wide as the one used for red alder, the size of the data set used after it was screened for extreme mortality patterns gives confidence in the obtained results.

The comparison of the developed size-density trajectories for red alder and Douglas-fir indicated that both species have different trajectories and that a single asymptote was not sufficient to characterize development for both species. This did not confirm the long-held results that the slope of the self-thinning line is independent of species (e.g. Yoda et al. 1963, White 1980, Long and Smith 1983). Instead, both species had to be treated separately in the discussion of the specific characteristics of their size-density trajectories.

The asymptote of the size-density trajectory for red alder (-0.638) appears steeper than the one suggested by Reineke (1933). The different methods of analysis might partially explain the discrepancies between Reineke's lines and the size-density trajectory determined in this study. Reineke (1933) visually put a line above a number of individual stand measurements and found the slope to be -0.623 for a number of species. In this analysis, a size-density trajectory was fitted in a mathematically unbiased fashion. Reineke (1933) found two pine species which do not conform to the general slope shown to be common to a number of other species.

For Douglas-fir a shallower slope (-0.52) than the one suggested by Reineke (1933) for this species was found. This may be partially due to the different kind of analysis used to determine the maximum line and average size-density trajectory as explained for red alder. The influence of the analytical methods on the results can be shown by the results obtained by Osawa and Sugita (1989) for Douglas-fir. They selected points that lay close to the maximum and fitted a line through these using principal component analysis. They determined a slope for the maximum size-density line (-0.644) that was considerably steeper than the one found n this analysis. Other yield tables for unthinned stands use underlying self-thinning lines which vary in a similar range with the general trend of steeper trajectories for more shade tolerant species (Schnur 1937, Meyer 1942).

Analysis of a French spacing study indicated the slope of the self-thinning line of Douglas-fir was even lower than the one determined in this study (Hann, 1989). Von Gadow (1987) analyzed pine species grown in plantations in South Africa. He fit regression lines through measurements considered to be on the maximum density line and concluded that in terms of maximum density two different species groups exist. Group 1 consists of Pinus patula, P. taeda, P. elliottii, P.radiata, and Eucalyptus grandis with a slope of -0.506. The second species group consists of Pinus pinaster and P. roxburghi. Its maximum density line had the slope of -0.424. However, both the analysis by Osawa and Sugita (1988) and the work of von Gadow (1987) is subject to Weller's (1985) criticism regarding subjective selection of data points used in the analyses. An example of the data plots presented by von Gadow (1987, Figures 3.6, 3.8-3.10) indicates that stands approach the maximum density line asymptotically. Therefore the selection of data points which were on the maximum density line underlaid an arbitrary distinction, which could have influenced the results of the analysis substantially.

The maximum SDI of red alder (751) is within the range observed in the literature. For example, the SDI of the Normal Yield Table (Worthington et al. 1960) is 571, i.e.

the relative density underlying the Normal Yield Table for Red Alder (Worthington et al. 1961) is 0.77. Curtis (1982b) stated that ordinarily normal stands carry around two thirds of maximum density. The maximum red alder line is lower than the maximum line set by Hibbs and Carlton (1989). They assumed a slope of -0.623 and visually positioned a line above all data points. Thus, their line is expected to be higher than a average maximum line as determined in this study.

The SDI determined from the size-density trajectory for Douglas-fir also seems very reasonable for an average stand (1195), considering the absolute maximum for this species to be 1470 (Reineke 1933). However, due to the difference in slope, at lower densities the maximum QMD as determined in this analysis was substantially lower than the QMD calculated by Reineke (1933). The same trend was mentioned by Drew and Flewelling (1979), who found good agreement of the maximum QMD as calculated using their analysis with Reineke's at higher densities but their analysis underestimated Reineke's QMD 6% at lower densities (200 trees per hectare).

Several possible scenarios could explain a size-density trajectory with a lower slope compared to the SDI-line and the results derived by Reineke (1933). A pattern like trajectory type III (McFadden and Oliver 1988) results in individual stands following a slope less steep than

-0.623 and nonetheless agree with the results suggested by Reineke (1933) that a collection of stands are bounded by a line with the slope of -0.623. However, the analysis of the different trajectories for both red alder and Douglas-fir indicates that this scenario is not always followed. Also, the suggestion that clumping leads to lower stockability and thus to a lower maximum size-density line cannot explain the apparent discrepancy between Reineke's (1933) results and the results of this study.

Studies investigating effects of clumping on stand development indicated that stands develop toward a uniform spacing over time (Stiell 1982) and this would steepen the size-density trajectory as the stand develops. However, random mortality events, like insect attacks or windthrow would lead to increased clumping resulting in a shallower slope of the size-density trajectory. Earlier elimination of plots with extremely high mortality rates should have eliminated most of the effects of random mortality events.

The slope as determined by Reineke or -3/2 has been used in many cases because of lack of better data (Drew and Flewelling 1979, Curtis et al. 1981, DeBell and Wilcox, in prep., Hibbs and Carlton 1989). In some cases, these slopes have been used despite discrepancies. For example, Hyink et al. (1988) presented data in their Figure 5 as a confirmation of Reineke's slope for western hemlock (Tsuga heterophylla (Bar.) Sarg.). In their model the size-density relationship was represented through an M-value. An M-value of 1.01 represents the slope of -0.623 while an M-value of 1.1 would represent of slope of -0.5. Their Figures 5a and 5b showed a number of points above the M-value of 1.01. The authors might just as well have picked a slope different from -0.623 as the critical value. However, they selected -0.623 because it has been used for other species. This categorical acceptance of a paradigm perpetuates a habit which bears more careful examination.

The relative density at which competition related mortality starts is 0.44 for red alder. A value for Douglas-fir could not be computed since the data set used in this analysis did not cover the periods before the onset of density-dependent mortality in the same fashion as the red alder spacing study. The value for red alder is higher than the one found for red alder seedlings (0.31) (Smith 1984) and below the relative density at which Carlton (1989) found mortality occurring (0.5). Drew and Flewelling (1979) determined the onset of mortality for Douglas-fir to be at a relative density of 0.6.

Assuming that development of total biomass follows the -3/2 power rule, an allometric relationship can be used to interpret the results found in this study, Hughes (1973) determined the allometric relationship between biomass and diameter for European alder (Alnus glutinosa Gartn) to have the exponent 2.45. Thus if

$$b \quad n^{-1.5}$$

where b is average biomass and n is the number of trees, and

$$b \quad d^{2.45}$$

where d is the average diameter, then

$$d \quad n^{-1.5/2.45} = n^{-0.61}$$

The allometric relationship between biomass and diameter for Douglas-fir was determined to have the exponent of 2.6 (Gholz et al. 1979). In that case,

$$d \quad n^{-1.5/2.6} = n^{-0.577}$$

neither -0.61 or -0.577 fall within the confidence interval of the calculated slope of red alder and Douglas-fir, respectively. However, the allometric relationships show a slope of the self-thinning line for Douglas-fir which is lower than the slope for red alder.

Even though they are not directly comparable with the numbers found in this analysis, the results of other researchers indicate that the slope of the self-thinning line does indeed vary with species and that the magnitude as determined in this analysis is within reasonable bounds (e.g. von Gadow 1987).

The self-thinning line of red alder and Douglas-fir cross at a density of 59 trees per hectare and a QMD of 119 centimeters. This is outside the data range used to construct the red alder and Douglas-fir model. It is also outside the range in the Normal Yield Table for red alder (Worthington et al. 1960) and the Empirical Yield Table for predominantly red alder stands in western Washington (Chambers 1974). Red alder stands are in senescent condition in this region of the size-density graph. A density at which red alder can have a higher QMD than Douglas-fir is thus an extrapolation of the model and is not biologically meaningful.

The different trajectories for red alder and Douglas-fir can reveal different dynamics and yield information which can be utilized in stand density management. The self-thinning line reflects the relationship between mortality and growth, whereby growth 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). The yearly mortality rates of red alder were lower than the mortality rates of Douglas-fir, and therefore, the increase of the QMD due to mortality of the smaller trees is not likely a major contributor to the difference in slopes.

Density dependent mortality is more likely to kill the suppressed trees in a stand (Dahms 1983, Hamilton 1986), and those suppressed trees do not compete actively with the surviving portion of the stand (Ford 1975, West and Borrough 1983). Thus, a difference in slope of the self-thinning line is not simply related to a difference in competition intensity. Instead, the steeper slope of the red alder self-thinning line indicates that diameter growth of red alder seems to respond more efficiently to freed resources than diameter growth of Douglas-fir. Whether this is due to the way at which photosynthetic efficiency changes with available resources as Perry (1984) suggested, a change in patterns of carbon allocation (Waring and Schlesinger 1985), or whether other factors contribute to this effect could not be addressed in an retroactive study as this one. A study in which physiological variables are measured is necessary to answer this question.

Even though the stated results do not constitute a full stand density diagram, they still can be used to yield some guidelines for practical density management. Ignoring differences in growth rates and wood value, the difference in slope of the self-thinning line between red alder and Douglas-fir leads to some suggestions concerning thinning practices. At younger ages when the thinning material cannot be utilized and given the same stand conditions, red alder should have the higher priority for the thinning treatment. The steeper self-thinning slope indicates that there is more potential gain in thinning red alder than in thinning Douglas-fir.

In older stands where commercial thinning is feasible, the priority to thin should be on Douglas-fir stands. For the same amount of diameter growth, a higher number of trees which could be harvested and utilized in thinning will be lost due to mortality in Douglas-fir compared to red alder.

These recommendations have to be viewed with caution and by no means can be considered absolute. Instead, they imply the need to develop a dynamic growth model for red alder stands which utilizes the information about the size-density trajectory. The questions about changes of growth rates, diameter distributions, or stem quality with relative density have to be addressed to develop a usable density management tool.

Summary

The study established the size-density trajectory for red alder and Douglas-fir stands. It was confirmed that the size-density trajectory is inherent for each species. The shape of the size-density trajectory of red alder stands is independent of the initial density. The line of initial mortality is parallel to the maximum line. Red alder mortality started at a relative density of 0.44. The trajectory with a common asymptote for all stands showed superior fit to the data compared with the model allowing the intercept to vary with initial density. A common model form was sufficient for both naturally regenerated and planted red alder stands, which indicates that regeneration method does not influence the shape of the size-density trajectory.

The slope of the self-thinning lines for both red alder and Douglas-fir deviated from the parameters established by Reineke (1933) and earlier assumed to apply to a variety of species. A review of the literature indicated that a number of researchers found different slopes for different species. Other researchers found a slope of -0.623, but a close look at their analyses indicated the subjectivity which led to the choice of the specific value. The self-thinning line when defined as the asymptote of the size-density trajectory based on QMD and trees per hectare in the analysis lead to a steeper slope for red alder (-0.638) than for Douglas-fir (-0.52). The assumption of a general applicable slope for all species is not justified. When applied to thinning priorities, higher priorities for red alder stands for precommercial thinning and higher priority for Douglas-fir for commercial thinning seems appropriate.

Figure III.1: Possible size-density trajectories of stands undergoing self-thinning. A. Stands move along the self-thinning line (Type II). B. Stands approach the self-thinning line and then fall below (Type III).

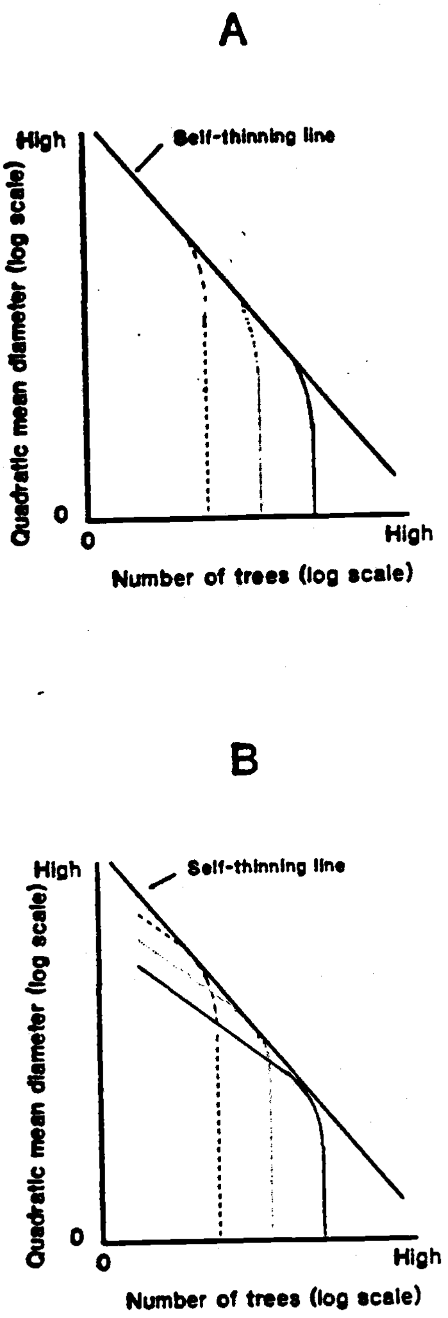

Figure III.1. (continued)

Figure III.2. Distributions for red alder stands of site index (A), age (B), density (C), quadratic mean diameter (D), and basal area (E).

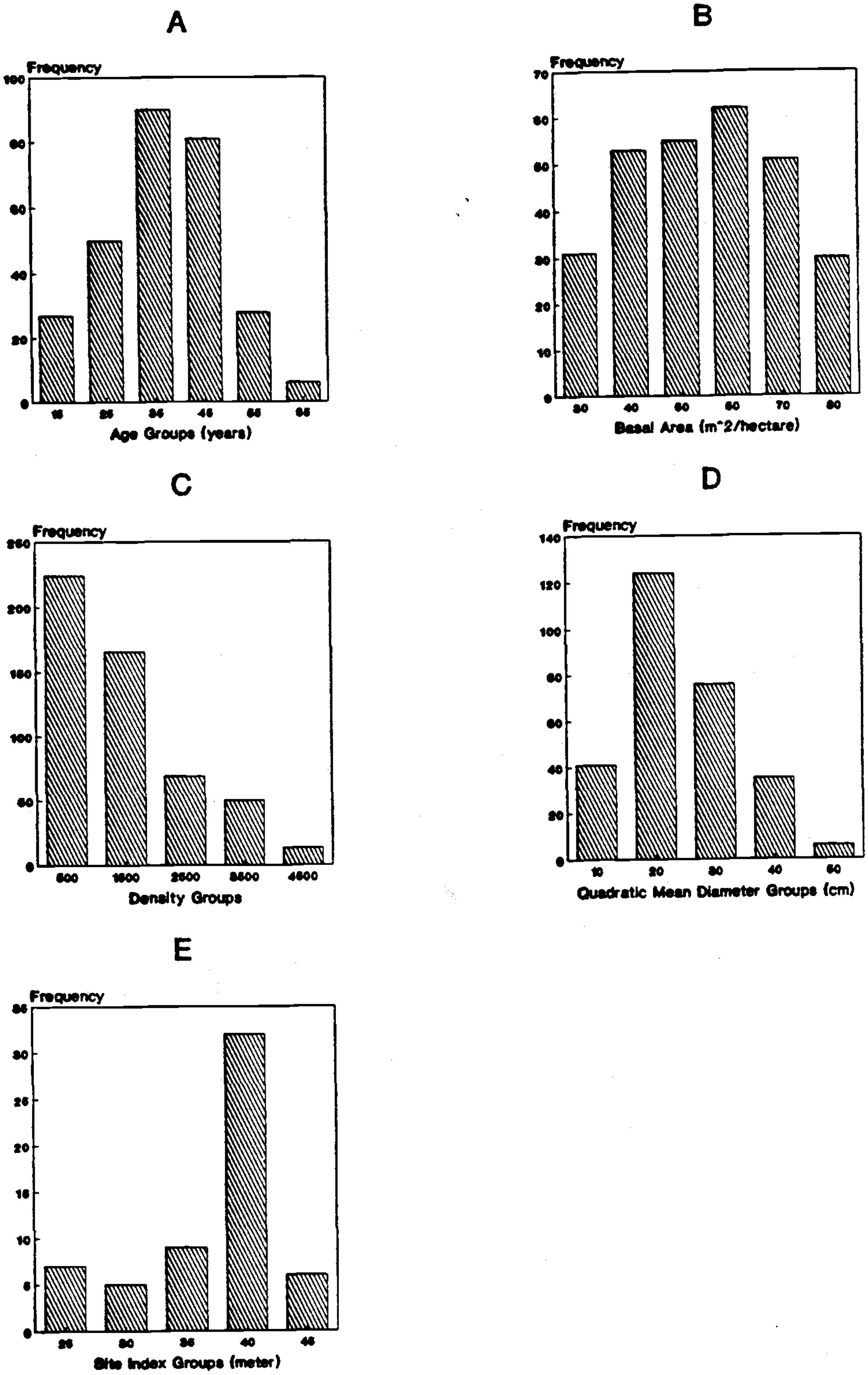

Figure III.2. (continued)

Figure III.3. Distribution for Douglas-fir stands of site index (A), age (B), density (C), quadratic mean diameter (D), and basal area (E).

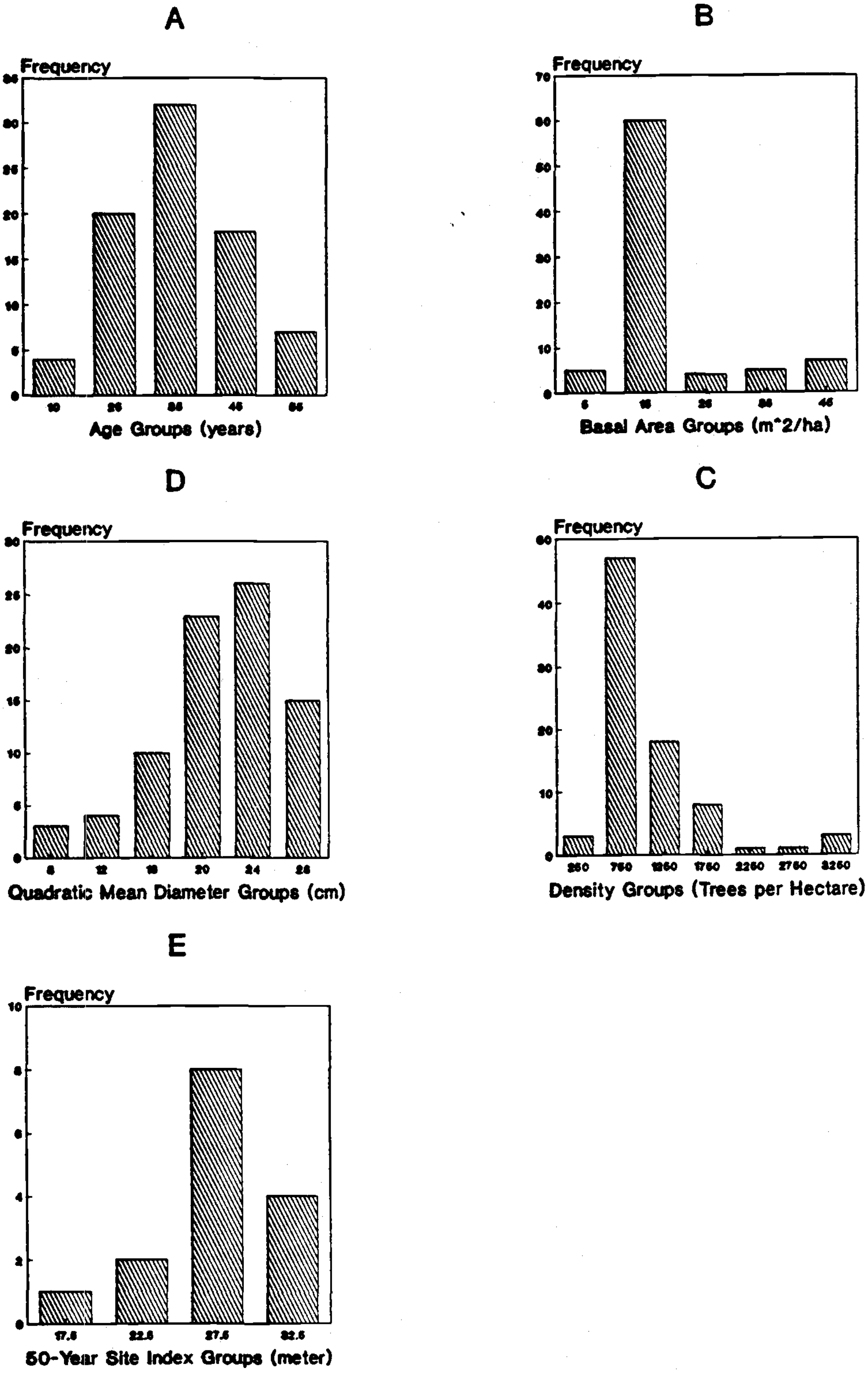

Figure III.3. (continued)

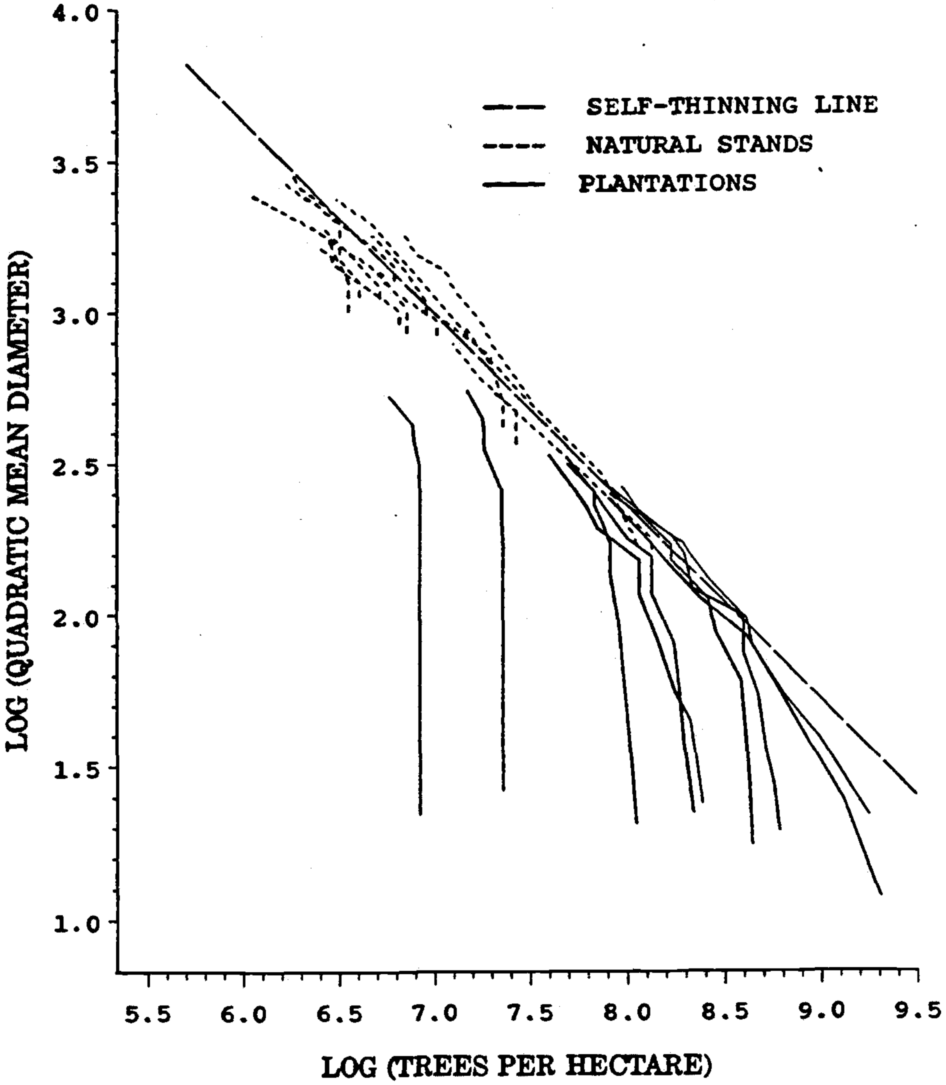

Figure III.4: Plot measurments and asymptote of the size-density trajectory for red alder stands.

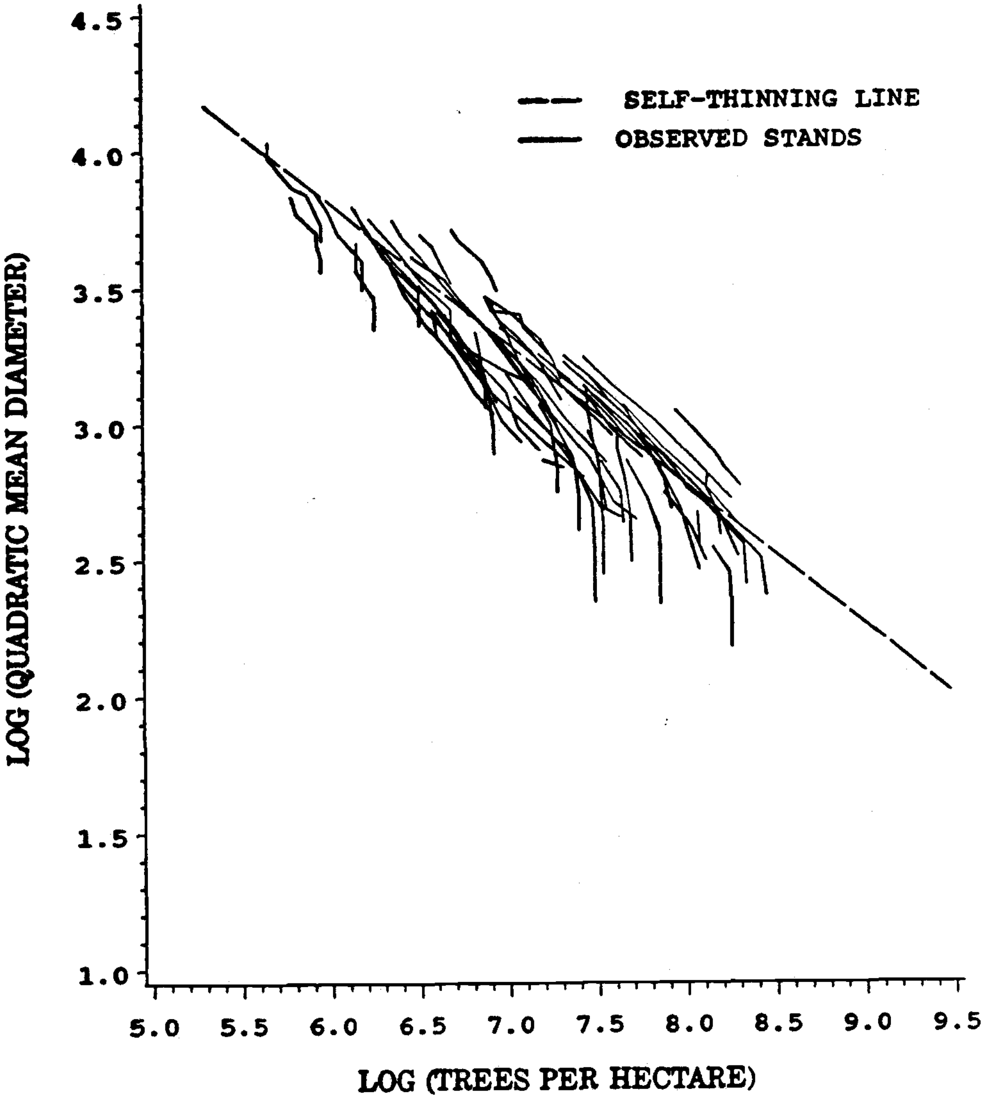

Figure III.5: Plot measurements and asymptote of the size-density trajectory for Douglas-fir stands.

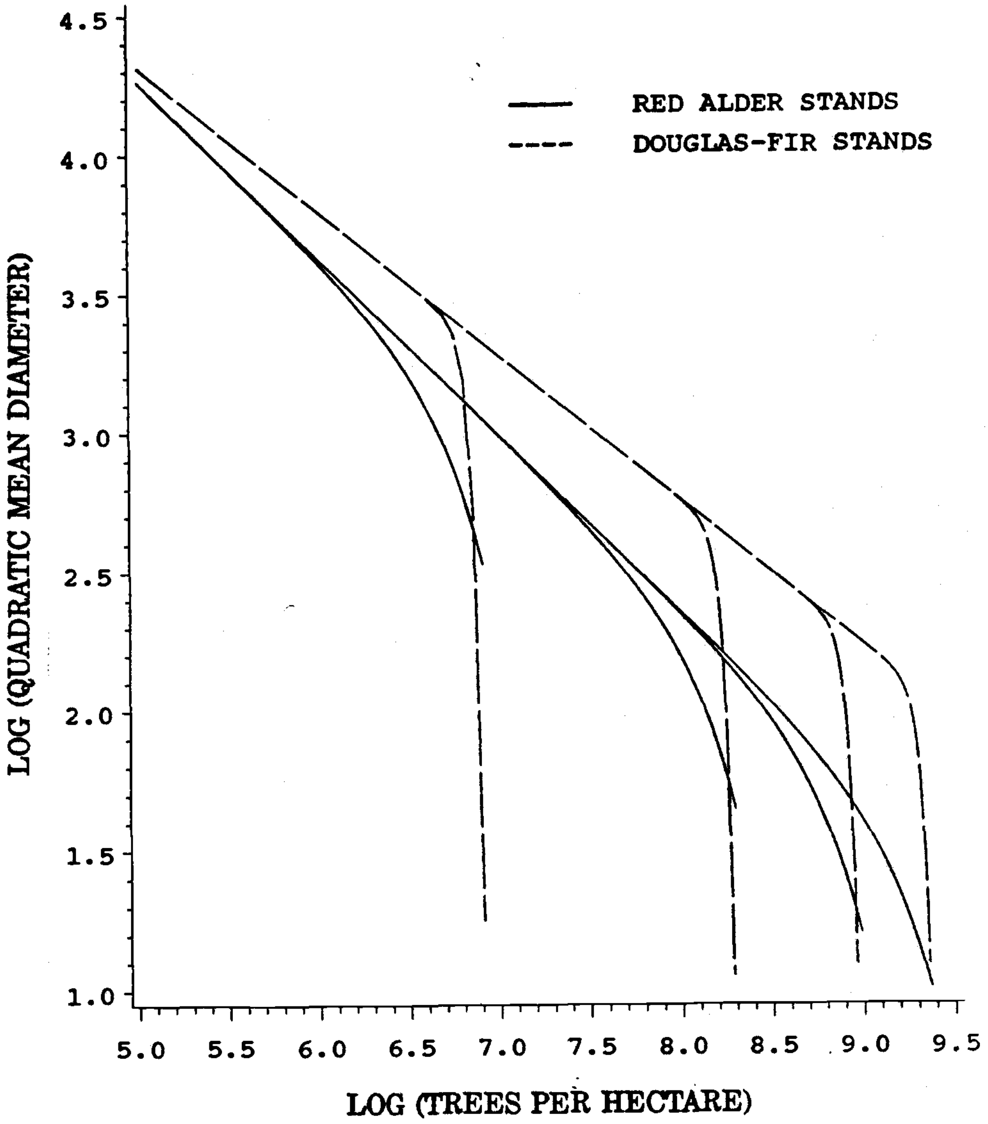

Figure III.6: Projected size-density trajectories for red alder and Douglas-fir stands for stands initiated at 1000, 4000, 8000, and 12,000 trees per hectare, projected to 100 trees per hectare.

Table III.1: Parameter estimates for pure red alder plantations, using individual a_3 and a_4 parameters. Standard errors in parentheses.

Parameter	a_1*	a_2*	a_{i3}	a_{i4}
Plot 1	6.70 (0.16)	-0.54 (0.02)	1.96 (0.58)	0.06 (0.003)
2			9.69 (1.85)	0.06 (0.002)
3			14.69 (2.73)	1.05 (0.471)
4			2.19 (0.05)	0.08 (0.009)
5			3.53 (0.06)	0.13 (0.006)
6			11.23 (0.08)	0.22 (0.006)
7			8.89 (0.51)	0.13 (0.001)
8			2.23 (0.12)	0.09 (0.005)
9			7.83 (0.05)	0.18 (0.005)

MSE=0.0006.

* Parameter common to all plots.

Table III.1: Parameter estimates for pure red alder plantations, using individual a_3 parameters. Standard errors in parentheses.

Parameter	a_1^*	a_2^*	a_3^*	a_{i4}
Plot 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.

* Parameter common to all plots.

Table III.3: Logarithm of initial stocking density and a_1 parameter using data from age 4 to 14 (a_{1a}) and 7 to 14 (a_{1b}) for estimation. Standard errors in parentheses.

Log(obs. density)	a_{1a}	a_{1b}
6.92***	6.91 (0.014)	6.91 (0.014)
7.36***	7.45 (0.145)	7.45 (0.145)
8.80	8.76 (0.088)	12.88 (0.543)**
9.44	9.90 (0.356)	9.34 (0.659)
8.43	8.70 (0.195)	9.79 (4.35)
8.08	8.07 (0.039)	7.96 (0.031)**
8.81	8.78 (0.029)	8.74 (0.085)
9.33	10.06 (0.406)	12.21 (*)
8.38	8.42 (0.067)	9.18 (1.48)

* Jacobian singular

** The asymptotic 95% confidence interval of the parameter estimate does not include the logarithm of the initial density.

*** Mortality started after age 7.

Table III.4: Parameter estimates for naturally regenerated red alder plantations, using common a_3 and a_4 parameters. Standard errors in parentheses.

Parameter	a_1*	a_2*	a_3	a_4
Plot 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.

* Parameter common to all plots.

Table III.5: Parameter estimates for pure red alder stands with indicator variables for origin (Nat. B= Natural stands, Plant. = Plantation). Standard errors in parentheses.

Parameter	a_1	a_2	a_3	a_4
Nat.	6.98 (0.09)	0.56 (0.01)	6.01 (2.03)	0.02 (0.002)
Plant.	7.82 (0.01)	0.68 (0.01)	3.92 (0.31)	0.08 (0.004)

MSE=0.0005.

Chapter IV

Development of an Analytical Model for the Size-Density Surface for Pure and Mixed Red Alder/Douglas-fir stands

Introduction

Intensive forest management has generally focused on single species stands. Mixed species stands have received little attention for both economic and management reasons. Loggers and log users prefer a product uniform in species and size to reduce the costs of handling and manufacturing. Foresters have been very successful providing this kind of product.

Mixed species stands have been perceived as undergoing a complicated, unpredictable development with an infinite number of possible stand conditions, but Oliver (1980) indicated a generalized growth pattern of mixed species stands. He stressed that for given soil conditions and with given species combination, stands follow a predictable development pattern.

Mixed stands are always contrasted with pure species stands. Therefore, research in development of mixed forests must incorporate a number of additional factors. These include: 1) development of a simple and accurate indicator of species proportion, site index, stand structure and density (Assmann 1961) 2) assessment of growth and yield of pure stands of each species on similar site conditions (Wierman and Oliver 1979), 3) characterization of the different development phases of individual trees (Assmann 1961), and 4) assessment of the effect of mixture on stem quality (Mitscherlich 1978).

Recently, broadening of forest management objectives increased the interest in management of mixed forest stands. Mixed stands can have several advantages over pure species stands. Mixtures can yield greater volume and better quality products than pure species stands. For example, Wierman and Oliver (1979) indicated that mixtures of Douglas-fir (Pseudotsuga menziesii Mirb. Franco) and western hemlock (Tsuga heterophylla (Bar.) Sarg.) can contain higher basal area than pure stands of either species. Mitscherlich (1978) stressed the advantage of higher product value in mixed oak-beech and beech-spruce stands that outweighed the reduction in volume production.

Mixed species stands may be more resistant to insect attacks (Schwertfeger 1981) and microbial pathogens (Nelson et al. 1978). Compared to pure species stands, they may also constitute better habitat for wildlife species (Hall et al. 1985). Mixed species stands may also result in soil improvement (Perry et al. 1987). A continuous monoculture might reduce soil fertility while establishing a second species can improve soil conditions. The greatest gains in overall productivity can be reached, when one of the species in mixture has the ability to fix atmospheric nitrogen(e.g. Miller and Murray 1978). Circumstances which might lead to existence of mixed species stands also exist when the monetary loss due to the mixture is too low to justify the cost to eradicate an invading species (Walstad et al. 1986).

All of the above mentioned advantages of mixed stands depend on the particular stand and forest conditions. For example, the advantages of a mixture of red alder (Alnus rubra Bong.) and Douglas-fir was detectable on a site which was nitrogen deficient (Tarrant 1961, Miller and Murray 1978). Other research on these two species disclosed that on higher nitrogen sites the benefit for Douglas-fir due to nitrogen fixation was offset by other competitive interactions with red alder (Berntsen 1961, Binkley 1983, Cole and Newton 1987).

To make a complete assessment of advantages and disadvantages of mixed stands, the growth and yield of pure and mixed stands has to be known. The lack of data comparing the yield of pure and mixed stands over a rotation has limited the comparison of mixed and pure stands (Assmann 1961) and so has prevented the evaluation of the full spectrum of management options (Franz 1986).

Even though growth and yield information for certain species mixtures have been developed, mixed stands have not been given very much attention. For example, the textbook "Timber Management: A Quantitative Approach" (Clutter et al. 1983) do not mention mixed stands at all. Other examples include publications in which researchers are discouraged from pursuit of modeling of mixed species stands (Hyink et al. 1988)

Approaches used to Analyze Mixed Stands

Different approaches have been used to develop yield tables or simulation models for mixed species stands. In the following, a summary of techniques used to represent species mixtures in prediction tools is presented.

Dunning and Reineke (1933) developed a yield table for mixed conifer stands. For lack of better knowledge, they established the concept of the maximum Stand Density Index (SDI), with a reference value of 1000 for stand comparison. The SDIs for individual stands were calculated by adding the SDI of all species in the stand. SDI is a major driver in growth equations. The authors recognized that stand SDI was not sufficient to characterize the stands and therefore included adjustments based on species proportions to their growth equations.

Mulloy (1944, 1947) developed yield tables for mixed species stands in Canada. He grouped the species into two species groups based on shade tolerance and split the mixture range into four classes. He also treated the mixture as additive, i.e. the SDI was calculated for both species groups separately and then summed to compute the SDI for the mixed stand.

A number of mixed-stand yield tables were developed in Germany. These include an oak-beech yield table and a pine-beech yield table (Wiedemann 1949). Two yield tables were developed for beech-spruce stands, one for sites with a medium site quality for beech, and a second for sites with low site quality for beech (Wiedemann 1942). The German yield tables assume a specific management regime, which includes control of basal area and species proportion. However, even with this restriction, the yield tables are not accurate enough to be recommended as a basis for management decisions (Assmann 1961, Franz 1987). In a theoretical paper, Abetz (1979) expanded the density management guides he developed earlier (Abetz 1975) for pure species stands to address mixed stands. He suggested treating mixed stands as pure stands of the different species and scale the density values by desired proportion of each species. To accommodate for mixture of species with different growth patterns, Abetz recommended a reduction in the calculated density values, but did not include any estimates of the possible sizes of this reduction.

A stand management guide for mixed stands in the Allegheny Hardwood region (Stout et al. 1987) was based on the concept of tree area ratio (Chisman and Schumacher 1940). Stout and Nyland (1986) also compared the SDI (Reineke 1933) with the tree-area ratio. To incorporate information about species mixture, they modified the SDI by adding the basal area of a species as a variable. In their comparison, the modified SDI did not perform as well as the index based on the concept of tree-area-ratio. Brooks (1979) developed a yield model for three species groups in eastern red-cedar forest type using the tree-area ratio. However, the author concluded that the model did not show an improvement over a model using only average stand growth rates.

Leary (1979) used differential equations to model stand containing two or more species. Moser (1974) and Lynch and Moser (1986) used a system of differential equations to construct stand tables. The effects of interspecific competition were incorporated by Lynch and Moser (1986) solely through an interaction term of both species in the basal area growth equation. The mortality equations included interspecific competition only indirectly through incorporation of predicted basal area growth.

Solomon et al. (1986) used a two-stage matrix model to model multi-species stands. The transition probabilities of diameter classes for individual species were determined using stand level variables without acknowledging species mixture as independent variables. Also Moser (1972) and Ek (1974) did not distinguish species in their growth models. Their predictions are therefore only limited to the specific species mixes in their data sets.

Leak et al. (1969) developed a management guide for northern hardwoods, but did not incorporate the effect of species composition. However, Stout and Nyland (1986) stated that a revised guide will exhibit an increase in the reference basal area with increasing proportion of conifers in a stand. A similar concept was applied by Tubbs (1977) who varied maximum density with the species composition in northern hardwood stands.

Arney (1985a, b) developed the Stand Projection System (SPS) growth and yield simulator which models both pure and mixed stands of a variety of species. Mixed species stands are modeled as separate pure species stands and the effect of mixture is brought into the model through cumulative crown competition indices. A comparison of predicted and actual density, basal area and trees per acre for mixed red alder/Douglas-fir stands showed the inaccuracies associated with this approach. (Puettmann 1990, Chapter II). SW-ORGANON (Hester et al. 1989) is a growth model for mixed conifer stands in southwest Oregon. The species were treated separately by developing individual equations for each species (e.g. Walters and Hann 1986). Differences in growth patterns were reflected in different equation form and/or parameters.

Self-thinning of Mixed Stands

For accurate simulation of mixed species stands a prediction model has to accommodate for the full complexity of mixed stands. The architecture of a growth simulator and all its components have to allow for species mixture. One of the major components of growth simulation models is the size-density relationship or self-thinning concept (Curtis et al. 1981, Hyink et al. 1988, Hann and Wang 1990). The size-density relationship describes the concomitant changes in plant size or weight and density in even-aged plant populations (for review, see White 1980); relationship bounded by the self-thinning line (Yoda et al. 1963).

The self-thinning line has been under intensive investigation for pure species stands (White 1980). Harper (1967) questioned the possibility of expanding it to mixed-species plant populations, but few experiments have been carried out to address this question. A review of the use of the self-thinning concept for mixed stands was presented by White (1985). The first experimental investigations used two-species populations of herbaceous plants (White and Harper 1970, Bazzaz and Harper 1976). In both cases, the investigators found that the common self-thinning line, calculated by combining both species, followed a self-thinning line with the slope of -3/2, the value expected for pure species populations (White 1980). The individual species, however, showed striking differences between their self-thinning lines. The authors suggested that a stratification into different canopy layers resulted in one species behaving like small individuals in a single-species population. This would explain why one species contributed more to mortality while the other species contributed most of the growth. Being aware of the results by White and Harper (1970) and Bazzaz and Harper (1976), Malmberg and Smith (1982) used two rather similar species (<u>Trifolium pratense</u> L. and <u>Medicago sativa</u> L.) in an experiment. In their experiment, the development of distinct canopy strata was prevented which resulted in the same mortality rate for both species. Consequently, the self-thinning line had a slope of -3/2 when it was calculated for the two species combined but also when it was calculated for each individual species.

The above mentioned pattern (combined species self-thinning line having the slope expected for each component species, but the self-thinning lines of the component species having a different slope) has also been reported for forest stands. Analysis of forest stands generally used quadratic mean diameter (QMD)and trees per hectare as size and density variables, respectively, resulting in the self-thinning line having a slope of about -0.623 (Reineke 1933, Long 1985).

A study in the Harvard Black Rock Forest (Cornwall, New York) analyzed a multi-species stand. The combined species self-thinning line had a slope of -0.67 (White 1985). A study in the Harvard Forest (Petersham, Massachusetts) indicated a combined self-thinning line with a slope of -0.54 (White 1985). Within each stand, the individual species showed striking differences in their self-thinning lines. For both stands, the species differences could be explained by the growth rates and shade tolerance of the individual species. Also, research by Spurr and Barns (1980) and Stephens and Waggoner (1980) indicate also that the common self-thinning lines in mixed stands showed values very similar to pure species stands both in intercept and slope.

Binkley (1984) assumed a slope of -3/2 and used the self-thinning line to compare pure Douglas-fir and mixed red alder/Douglas-fir stands on sites with low and high fertility. On fertile sites, the self-thinning lines of mixed stands were lower than the self-thinning line of pure Douglas-fir stands and on infertile sites the trend was reversed. Binkley attributed the effect of site quality to the interaction of nitrogen fixation and competition of red alder. Binkley described his work as preliminary analysis and declared that planting trials were needed to confirm his conclusions.

The results of his analysis have to be viewed with caution for several reasons. First, the assumption of a slope of -3/2 for all species is not necessarily true (Puettmann 1990, Chapter III). Second, Binkley used only four pairs of stands in his analysis. For two pairs of stands only a single measurement was available. The asymptotic approach of the size-density trajectory to the maximum line (Stiell and Berry 1973, White 1980, Puettmann 1990, Chapter III) makes it difficult to establish the self-thinning line from a single measurement. This determination can only be done when it is certain that self-thinning is the main factor determining stand development at the time of measurement. Finally, two of the remaining stands used for comparisons also had problems associated with them. The red alder and Douglas-fir at the Wind River Study Experimental Forest site were grown from an off-site seed source. The Cascade Head Experimental Forest site includes both thinned and unthinned plots. In addition, the proportion of sitka spruce (<u>Picea sitchensis</u> Bong.) and western hemlock in the stand was substantial (greater than 20% in some plots). All these factors have an effect on growth and mortality pattern but were not considered in analysis and interpretation of the results.

Effect of Species Proportion on Self-thinning

In the above described experiments and investigations, the exact proportion of the species in mixture has not been given attention. Instead plant populations have simply been classified as mixed. This is a simplified view. Even a scenario where the self-thinning line of two species have the same slope but a different intercept implies that a shift in species proportion results in different slopes and intercepts of the self-thinning line for the mixed-species populations. Some authors do not give any information about species proportions (e.g. Binkley 1984). Others specify only the mixture at seeding time (e.g. Bazzaz and Harper 1976, Malmberg and Smith 1980). Even though differential mortality for each species was acknowledged, the change in species proportion during the time of self-thinning has been ignored. The self-thinning in mixed stands must be viewed as a surface over which species proportion can change (Figure IV.1). The boundaries of the surface are represented by the pure species and the mixtures connect the pure species lines.

This thesis has the major focus of modeling the size-density trajectory, as defined by White (1981), of red alder and Douglas-fir in pure and mixed stands. The establishment of a model for the size-density trajectory instead of the self-thinning line has several advantages.

First, it avoids the problem of deciding which stands are in the linear stage of self-thinning (Weller 1987). Second, stands in all stages of self-thinning can be utilized. Third, using a model as developed by Smith (1984) and Smith and Hann (1984), the self-thinning line can be determined and is defined as the asymptote of the size-density trajectory. Fourth, since a size-density trajectory also characterizes the development an average stand follows, it can be expanded to a dynamic growth model by including a mortality equation (Smith and Hann 1986).

Red alder and Douglas-fir were chosen because of their wide overlapping distributions in the Pacific Northwest (Fowells 1966) and because interest in management of mixed red alder/Douglas-fir stands has recently increased (Tarrant et al. 1983). Red alder has been demonstrated to fix substantial amounts of nitrogen (>80 kg/ha/year) (Borman and Gordon 1984). This is especially important in a region where nitrogen is limiting Douglas-fir growth on 60% of the forest sites (Steinbrenner 1975).

The size-density trajectory for both red alder and Douglas-fir stands have been analyzed by Puettmann (1990, Chapter III). The size-density trajectory of Douglas-fir had an asymptote with a steeper slope than the asymptote for red alder, a different intercept, and a different approach to the maximum line. The trajectories for pure stands are part of the size-density relationship, but in order to accommodate the complexity of mixed stands, both pure and mixed stands have to be included in the analysis to cover the full range of species proportions.

Objectives

The objective of this study was to develop an analytical model representing the size-density surface for red alder and Douglas-fir in pure and mixed stands. Within this general objective, the following specific objectives were established:

1. Determine whether parameters of the size-density trajectory for pure red alder and Douglas-fir stands can be combined.
2. Determine whether a linear connection of the pure species models is sufficient to characterize the size-density surface for pure and mixed stands.

Methods

Data Set

The data used in this analysis consisted of a number of long term remeasurement plots from pure red alder and Douglas-fir and mixed red alder/Douglas-fir stands in northwestern Oregon, western Washington and southwestern

British Columbia. The data quality criteria and the data for pure red alder and Douglas-fir were described in detail by Puettmann (1990, Chapter III). In addition to these, data from mixed stands were added to the data base to cover the continuum of species proportion. Mixed stands were defined as stands where the Douglas-fir and red alder individuals constitute more than 80% of the stand basal area. However, none of the species individually contributed more than 80% to the total basal area. The distinction of 80% is commonly used in forest management to classify pure and mixed stands (e.g. Worthington et al. 1960, King 1966). However, species proportion has to be viewed as a continuum. Stands can traverse the 80% line during their development due to differential growth patterns of the species, thereby changing their category without any recruitment or death.

For calculation of proportion, the species were grouped into conifers and broadleaf trees. This ensured that the sum of the proportions always equaled 1. Since all other species combined (besides red alder and Douglas-fir) constituted only a minor proportion in the stands (less than 20%), stands which contained more than 80% of its basal area in hardwoods or conifers were labeled a pure red alder or Douglas-fir stand, respectively.

Data came from 106 stands with a total of 544 measurements, 487 measurement in pure and 57 in mixed stands. The mean age of the stands was 33 years (one standard deviation = 14 years). The average QMD of all measurements was 21 centimeters (one standard deviation = 9 centimeters), the average density was 1729 trees per hectare (one standard deviation = 1520), and the average basal area was 39 square meters per hectare (one standard deviation = 15 square meters per hectare).

A study based on a collection of different data sets must be considered exploratory because of several restrictions. First, only mixed stands could be analyzed which still contained both species at the time of the first measurement. This phenomena limited the range of conditions sampled in regard to site, timing of establishment and spatial distribution of species.

Mixed stands with ages greater than 20 years are probably not found on extreme site conditions. For example, sites which have rapid alder growth and slow Douglas-fir growth will probably be dominated by red alder within the first two decades.

Timing of establishment may also limit the conditions of proportions, site quality, and age. Even though red alder can invade up to several years after establishment of Douglas-fir (Stubblefield and Oliver 1978) a longer time delay will necessarily reduce its chances for establishment in the stand (Ross and Harper 1972).

A third factor which has to be assumed to be constant or not to have an influence on the size-density trajectory is the spatial distribution of both species within a plot. This assumption could not be tested.

Model Derivation

The model used for the analysis of the size-density relationships was based on the work by Smith (1984). He modeled the size-density trajectory as a linear component which is approached asymptotically. The analysis herein started with the size-density trajectory as determined for pure red alder and Douglas-fir stands by Puettmann (1990, Chapter III):

$$Y_i = a_1 + a_2*X_i - a_1* (a_4+ IO*a_5)*\exp(a_3*(X_1 - X_i)) \quad (1)$$

where Y_i = logarithm of the average QMD

X_1 = logarithm of the initial stocking density

X_i = logarithm of actual stocking density

a_1 = intercept of the asymptote

a_2 = slope parameter of the asymptote

a_3 = intercept of the exponential function

a_4 = adjustment for the relative density at the onset of mortality

a_5 = correction the proportion of initial density still present at first measurement

IO = Indicator variable, IO=0 if the initial density is known, else IO=1.

i = total stand age

To combine the pure stands of red alder and Douglas-fir in a single equation (Objective 1), equation 1 was used and a modification was added to the parameters using indicator variables to accommodate for Douglas-fir. Since the initial density for Douglas-fir was not known, no adjustment for the a_4 parameter could be calculated. Instead this adjustment was contained in the correction on the a_5 parameter. The combined equation for pure stands of both red alder and Douglas-fir stands was

$$Y_i = a_1 + I*b_1 + (a_2+I * b_2) * X_i - ((a_i + I*b_1) \\ +(a4+IO*a_5+I*b_5))*\exp ((a_3+I*b_3)*(X_1-X_i)) \qquad (2)$$

where parameters are as in Equation 1 and

b_1 = intercept correction for Douglas-fir

b_2 = slope correction for Douglas-fir

b_3 = exponential curvature correction for Douglas-fir

b_5 = correction for proportion of initial density alive at first measurement and relative density at onset of mortality

I = species indicator variables, I = 0, if species = red alder, else I = 1.

To incorporate mixed stands, the indicator variable for the species (I) was replaced by a continuous variable representing basal area proportion (P) of Douglas-fir. To investigate objective 2, the proportion variable was incorporated untransformed, constituting a linear adjustment for species proportion. In the next step, P was used as a basis for an exponent (C_m), which results in equation 3. This transformation allowed more flexibility in determining the surface but only required the estimation of one additional parameter.

$$\begin{aligned} Y_i &= a_1 + P\hat{}C_1*b_1 + a_2*X_i + P\hat{}C_2*b_2*X_i - \\ &\quad ((a_i + P\hat{}C_1*b_1)+(a_4+IO*a_5+P\hat{}C_5*b_5)) \\ &\quad *\exp\ ((a_3+P\hat{}C_3*b_3)*(X_1- X_i)) \end{aligned} \tag{3}$$

where parameters are as in Equation 2 and

C_m = exponent to the species proportion for the i^{th} parameter.

m = parameter indicator, m=1, 2, 3 and 5.

Fitting Method

To develop a biologically meaningful model with significant parameters, the significance of the parameter estimates were evaluated at $p<=0.05$. The F-tests for the comparisons of sums of squares of full and reduced models used $p<=0.01$. The approach used in model fitting is outlined in Puettmann (1990, Chapter III).

Model Development and Results

To test whether the model of the size-density trajectory of pure red alder and Douglas-fir stands can be simplified (Objective 1), the model as presented in equation 2 was fit to the pure stand data. The values as presented by Puettmann (1990, Chapter III, Equation 22) were used as initial parameter estimates for the algorithm. The parameters were estimated to be

$$Y_i = \underset{(0.18)}{7.33} - \underset{(0.23)}{I*0.41} - (\underset{(0.02)}{0.61} + \underset{(0.03)}{I*0.09})*X_i$$

$$- (\underset{(0.01)}{0.08} - \underset{(0.01)}{IO*0.07} + \underset{(0.01)}{I*0.02})*\exp((\underset{(1.14)}{-3.48}\underset{(7.91)}{-I*13.55})*(X_1 - X_i)) \qquad (4)$$

MSE=0.0008. Standard errors in parentheses.

The species adjustment for the intercept (b_1) and the curvature of the size-density trajectory (b_2) as well as the adjustment for the proportion of the initial density present at the time of first measurement (b_5) were not significantly different from 0.

To test whether a model without adjustment for the species was sufficient for both species, I solved equation 1 using the above presented parameter values as initial estimates for the nonlinear fitting process. The equation solved to

$$Y_i = \underset{(0.06)}{7.14} - \underset{(0.01)}{0.55} * X_i - (\underset{(0.006)}{0.12} - IO*\underset{(0.005)}{0.09})$$

$$* \exp(\underset{(0.22)}{-1.31} *(X_1 - X_i) \tag{5}$$

MSE=0.0014. Standard errors in parentheses.

The F-test comparing the sums of squares of both models (equations 4 and 5) was highly significant and indicated a model without adjustment parameters for species is not sufficient.

Since a one species model was not sufficient and since the correction on the slope of the asymptote b_2 was the only significant modifier parameter in equation 4, b_1, b_2, and b_5 were dropped out of equation 2 and this reduced model was fitted to the data of pure red alder and Douglas-fir stands. The parameters as presented in equation 4 were used as initial estimates. The algorithm estimated the parameters to be

$$Y_i = \underset{(0.13)}{7.21} - (\underset{(0.01)}{0.59} + I*\underset{(0.003)}{0.03})*X_i - (\underset{(0.01)}{0.10} - IO*\underset{(0.01)}{0.07})$$

$$* \exp ((\underset{(0.97)}{-2.63} *(X_1 - X_i) \tag{6}$$

MSE=0.0009782. Standard errors in parentheses.

All parameters in equation 6 were significant. In addition, the F-test of the sums of squares of both models (equations 4 and 6) indicated that the equation with a correction on the slope of the asymptote (b_2) was sufficient to represent the size-density relationships of pure red alder and Douglas-fir stands.

To fit this model to the full data set containing data from pure and from mixed stands (Objective 2), the indicator variable was replaced by a continuous variable representing the percent of the total basal area in Douglas-fir (P). A linear connection between the pure stands was used as an initial model. Using initial estimates as presented in equation 6 yielded

$$Y_i = \underset{(0.11)}{7.12} - (\underset{(0.02)}{0.58} + P*\underset{(0.004)}{0.03})*X_i - (\underset{(0.01)}{0.09} - IO*\underset{(0.01)}{0.07}) *\exp\,(-\underset{(0.79)}{2.62}*(X_1 - X_i)) \qquad (7)$$

MSE=0.0009. Standard errors in parentheses.

Analysis of the residual indicated a trend when plotted over proportion of basal area in red alder. The QMDs of mixed stands with a high proportion of red alder were underestimated while the QMDs of mixed stands with a high proportion of Douglas-fir were overestimated. This suggested a correction by using a parameter as an exponent on the proportion of basal area in Douglas-fir (P^C). Using initial parameter estimates as presented in equation 7, the parameters were estimated to be

$$Y_1 = \underset{(0.15)}{7.07} - (\underset{(0.007)}{0.57} + (P\hat{}\,\underset{(1.20)}{3.09})*\underset{(0.003)}{0.03})*X_i - (\underset{(0.003)}{0.10} - IO*\underset{(0.006)}{0.08})$$

$$*\exp(\underset{(0.07)}{-2.57})*(X_1 - X_i) \qquad (8)$$

MSE=0.0009. Standard errors in parentheses.

The exponent (C_2) on the Douglas-fir proportion parameter (P) was significantly different from 0, but not from 1. However, the analysis of residuals indicated the trend over proportion of basal area was eliminated. For illustration, a surface is presented in Figure IV.2 which represents the development of stands of the full range of species proportions initiated at 10000 trees per hectare.

Discussion

The approach used to model the size-density relationship allowed a detailed analysis of the size-density relationship of pure and mixed red alder (hardwoods)/Douglas-fir (conifer) stands. Unlike earlier models, the model used in this analysis permitted the proportion of the species in plant populations to change through stand development. Compared to the work by Puettmann (1990, Chapter III), the definition of pure species stands was changed to include all species in either a hardwood or conifer group. Since these stands were dominated by red alder and Douglas-fir, respectively, they are labeled after the dominant species. The more liberal definition of pure stands was necessary for the proportion parameter to always add up to 1. The changed definition allowed the size-density relationship for both species to be combined in a simplified model. The size-density trajectory for both species could be represented by a common model in which the size-density trajectory for pure red alder has only a modifier on the slope of the asymptote to adjust for pure Douglas-fir. The inclusion of additional stands in the pure stand category influenced the location of the size-density trajectory for red alder stands compared the size-density trajectories as determined by Puettmann (1990, Chapter III). The size-density trajectory for red alder was changed such that it had a shallower slope and lower intercept. This might indicate that a minor proportion of a third species has a strong impact on the size-density trajectory of red alder. If so, this indicates that it is necessary to exclude additional species when studying species mixtures.

The values for the Douglas-fir size-density trajectory model were not changed due to the new definition of pure stands. The new definition did not add stands to the pure Douglas-fir category, because the range of mixtures with a higher proportion of Douglas-fir was limited to 90% and more in conifers.

An adjustment only on the slope parameter does not imply that both pure red alder (hardwoods) and Douglas-fir (conifers) stands followed the same size-density trajectory with the only difference in steepness of the asymptote. It merely indicated that keeping other parameters constant and changing the slope was a sufficient modification to represent the size-density trajectory of pure hardwood and conifer stands. The intercept of the size-density trajectory itself with the Y-axis is an extrapolation of the model since no stand with 0 trees can be analyzed. The "biological meaningful" intercept lies at the lower density end which can be considered a full stocked stand. Because of the different slope, the maximum QMD at the lowest biological meaningful density of the Douglas-fir stands was higher than the maximum QMD for red alder stands. The difference in slope also accommodated for the different curvatures, which eliminated the need for an adjustment parameter on a_3.

Compared to the number of measurements in pure stands (n=487) the number of measurements in mixed stands (n=57) was very low. Thus the fit of a model, as optimized in the least squares procedure, was dominated by the pure stands. This suggested caution in the evaluation of the parameters indicating the mixture. As long as the form of the parameter representing species proportion equaled 0 and 1 for pure red alder and Douglas-fir stands, respectively, the fit statistic indicated good fit. This was shown as the linear correction is modeled (Equation 7, asymptotic adjusted R-square = 0.916). To circumvent this problem, a residual analysis was performed. When plotted over the proportion, a trend in the residuals indicated that a linear parameter representing species proportion was insufficient. The addition of an exponent (c_2) to the species proportion (P) resulted in elimination of the residual trend, even though the exponent was not significantly different from 1. However, the unequal sample size of the mixed stands compared to the pure stands in the data base in combination with the elimination of the residual trends justified to keep this parameter in the model. The absolute improvement in fit was reflected in the increased asymptotic adjusted R-squares when adding the exponent in the size-density relationship ($r^2 = 0.916$ vs. $r^2 = 0.921$). For assessment of this gain, it had to be considered that the improvement was mainly in the mixed stands.

The resulting size-density relationship, an example of which is shown in Figure IV.2 indicated that the maximum size-density surface for pure and mixed stands was close to the red alder level for stands with lower proportions of Douglas-fir. In these ranges it showed a stable, almost planar region. Up to a mixture of 80 % conifers, stands have a maximum size for a given density closer to the pure red alder maximum level. This might be partially due to the change in parameter values when changing the definition of pure and mixed stands. The pure red alder line might have been influenced by a third species, and therefore, an additional mixture of Douglas-fir had only a minor effect. It might also indicate that stands with a lower to medium proportion of red alder can only exist when red alder is in a dominant position in the stand. At higher Douglas-fir proportions, this dominance is not assured anymore and the surface has a curvilinear increase towards the pure Douglas-fir level.

The size-density relationship for mixed red alder/Douglas-fir stands in the fashion as presented in equation 8 and figure IV.2 differs considerably from the size-density trajectory for single species stands. The size-density trajectory for single species stands not only yields the maximum size-density line but it also predicts the development which an average stand follows towards this maximum. In mixed stands, the prediction of the development to the maximum surface as well as along the maximum surface cannot be predicted from the size-density relationship because of the possibility of a shift in species proportion. To analyze the size-density development of mixed stands requires analysis of dynamics of mixed stand development.

Development and dynamics of individual stands vary with different stand conditions even though the basal area proportions might be similar. Three possible scenarios are presented in Figure IV.3 for illustration. The stands began on a maximum self-thinning surface with a 50/50 mix of red alder and Douglas-fir by basal area. Scenario 1 represents a stand in which red alder is dominating Douglas-fir and the mortality and growth patterns lead to an increased dominance of red alder. This might occur on a good red alder site, as seen in the Cascade Head Study (Berntsen 1961). Scenario 2 shows a stand where the species proportions remain fairly stable until red alder senescence. Scenario 3 symbolizes a dominant Douglas-fir proportion, the basal area proportion of which is constantly increasing. Scenario 2 and 3 could occur on sites favoring Douglas-fir to differing degrees.

Figure IV.4 shows the size-density trajectories of these scenarios when analyzed in a "two dimensional" way used by White (1985) Only one of the three scenarios ever reaches a linear portion on its size-density trajectory (Scenario 2). Until development into a pure stand, scenario 1 had a constantly decreasing and scenario 3 a constantly increasing slope until they develop into pure stands. It can easily be seen, that self-thinning lines based on observations of individual stands (e.g. White 1985, Spurr and Barns 1980, Stephens and Waggoner 1980) can only represent a single trajectory out of numerous scenarios. Inference based on these kinds of studies are restricted to the specific stand and site conditions. A reliable estimate of a self-thinning model for mixed stands requires the analysis of the full spectrum of species proportion in mixed species stands.

Conclusions

The investigation through the expansion of trajectories for pure stands allowed the development of an analytical model of the size-density relationship of pure and mixed red alder/Douglas-fir stands. The maximum size-density surface showed a near-planar region for stands consisting mainly of red alder. At high proportions of Douglas-fir, the surface showed a curvilinear increase towards the level of pure Douglas-fir stands. This brings into question the usefulness of self-thinning lines for mixed stands developed solely through analysis of individual stands. The complexity of the surface indicated the need for a more thorough exploration of the underlying dynamics.

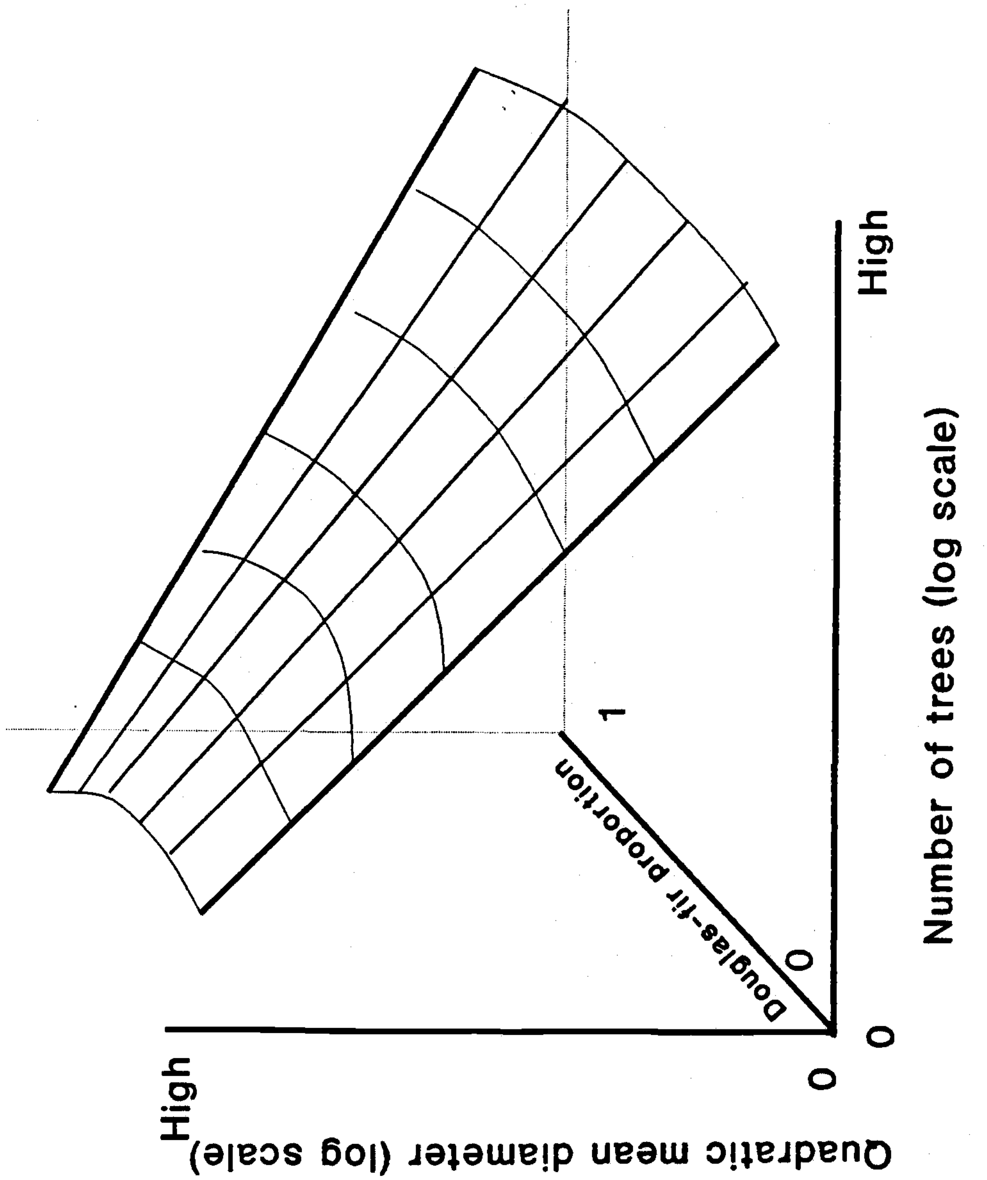

Figure IV.1: Expansion of the self-thinning line to a self-thinning surface for pure and mixed stands.

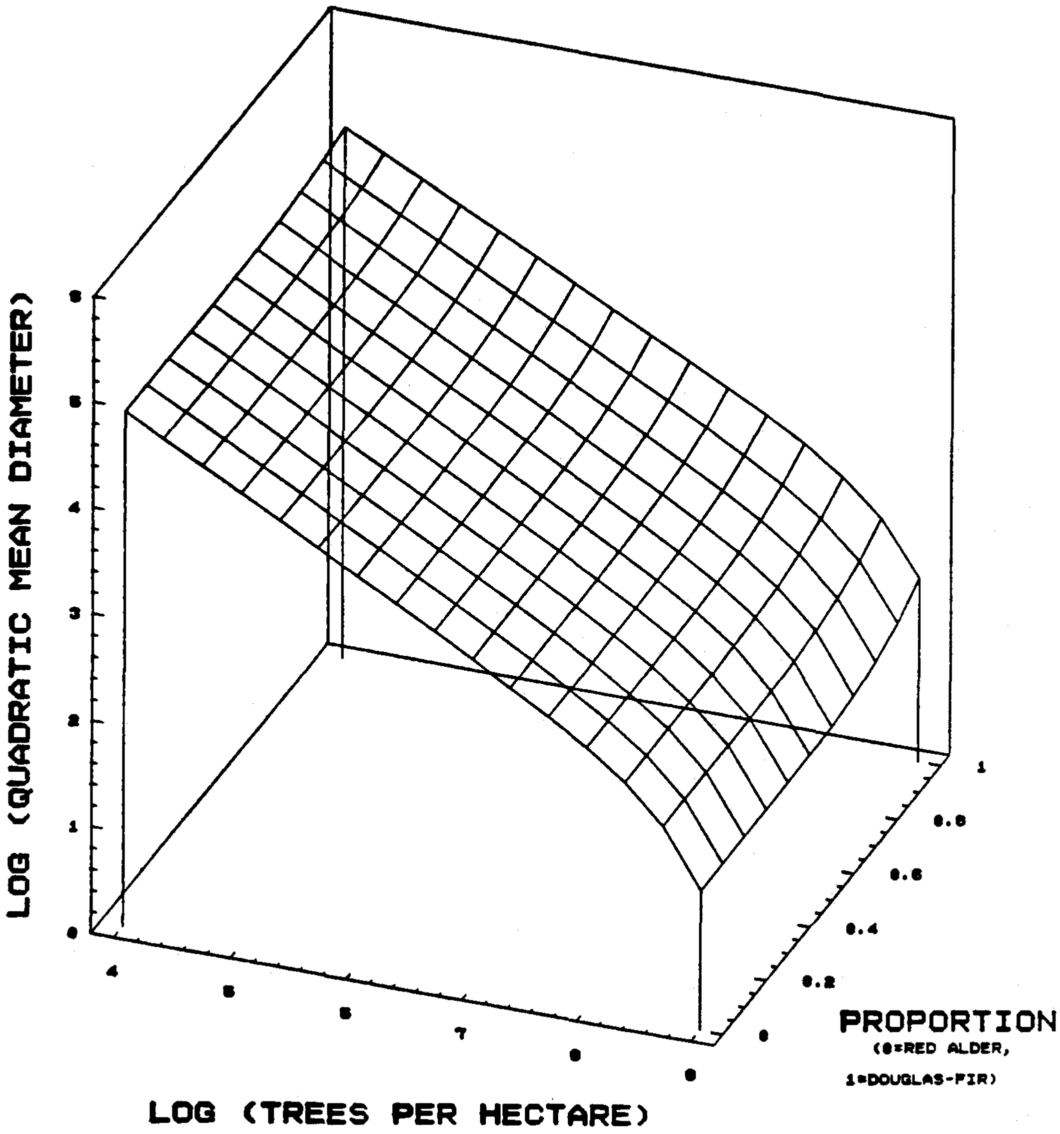

Figure IV.2: Size-density surface for pure and mixed red alder Douglas-fir stands simulated from equation 8. Stands were initiated at 10000 trees per and simulated to 100 trees per hectare.

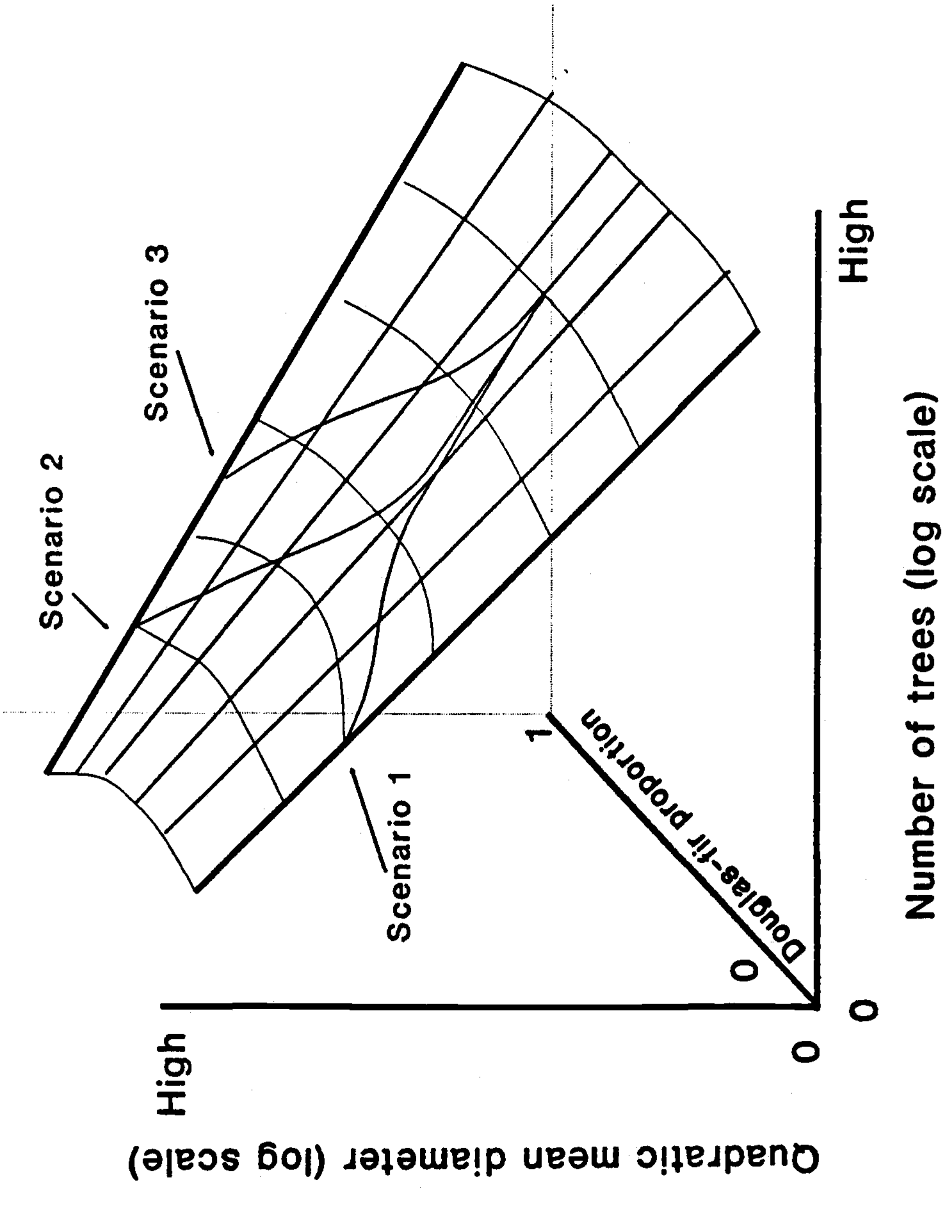

Figure IV.3: Conceptual self-thinning surface for a two species mixture. Plotted on the surface are three possible trajectories for developing stands.

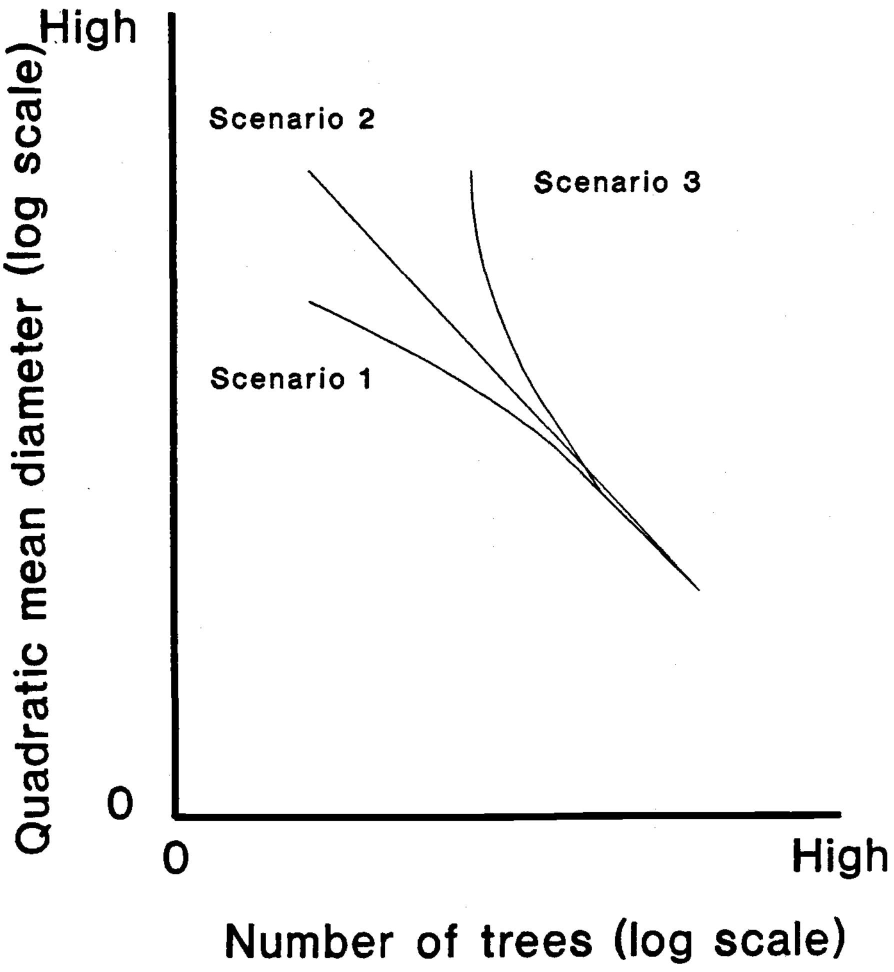

Figure IV.4: Self-thinning lines from mixed stands. Differences in the lines are due to the change is species proportions (see Figure IV.3).

Chapter V

Development of a Growth Model for Pure and Mixed Red Alder/Douglas-fir Stands Based on the Size-Density Relationship

Introduction

To fully investigate development of mixed species populations requires an investigation into stand dynamics. This can be done through modeling of the change in stand density and species proportion. These components can then be integrated with the size-density relationship into a growth model. Smith and Hann (1986) developed a growth model based on the size-density relationship for red alder (*Alnus rubra* Bong.) seedlings and red pine (*Pinus retinosa* Ait.) stands by incorporating a mortality equation as a driver of density. A growth model for mixed stands also needs a component predicting the change in proportion. Since basal area proportion is generally used for categorizing pure and mixed stands (Worthington et al. 1960, King 1966), it was used in this study to represent species proportion. By incorporating mortality and proportion the size-density relationship can be developed into a growth model which predicts future development of stands. Such a growth model can be a useful tool in the investigation of stand dynamics and at the same time provide help in planning future research activities.

To model mixed stands requires a common variable representing site quality. This required either a new site index variable or a conversion of red alder to Douglas-fir site index. Harrington and Curtis (1986) stated that generally a better red alder site is also a better Douglas-fir site, but did not give a conversion equation. Hoyer (1978) presented the conversion from several different Douglas-fir site indices to the 50-year red alder site index. The range of data used by Hoyer (1972) for the conversion of site index by King (1966) was limited to stands with a lower site index. In order to cover the range in this data set, a conversion equation had to be developed which allowed site index to be converted for a wider range of site qualities.

Objectives

The general objective was to investigate the dynamics of pure and mixed red alder/Douglas-fir (<u>Pseudotsuge menziesii</u> (Mirb.) Franco) stands utilizing size-density relationships. To accomplish this, the following specific objectives were addressed:

1. Model the stand mortality for pure and mixed red alder/Douglas-fir stands.

2. Model the shifting proportions in mixed red alder/Douglas-fir stands utilizing basal area as a unit of measure.
3. Use the relationships developed in objectives 2 and 3 and the size-density relationship (Puettmann 1990, Chapter IV) to develop a growth model for pure and mixed red alder/Douglas-fir stands.

Methods

The data set as described in Chapter III and IV was used for this analysis. Relative size or sociological position of a species in a stand is assumed to be of importance for stand development. Since height information was not available for all stands, relative quadratic mean diameter (quadratic mean diameter of the Douglas-fir divided by quadratic mean diameter of the whole stand) was used as a surrogate for size differences or position of species within a stands. Relative density was based on the size-density surface as developed by Puettmann (1990, Chapter IV). It is expressed in a manner described by Drew and Flewelling (1979) as actual density divided by maximum density for given diameter and proportion.

The Douglas-fir site index was estimated from red alder site index for stands for which this variable was not measured. Utilizing the predicted site index, equations for the annual overall stand mortality rate, the proportion of dying trees in Douglas-fir, and the annual shift in basal area proportion were developed.

The selection criteria for the models was to maximize the adjusted R-square. The parameters had to be significant ($p<=0.05$) and have variance inflation factors less than ten.

The data set contained 10 stands which had information about red alder and Douglas-fir site index. The restricted conditions which allowed the coexistence of both species eliminated sites where both species were not compatible. Therefore the general relationship as described by Harrington and Curtis (1986) was assumed in which better red alder sites are better Douglas-fir sites. A linear equation was fitted to obtain an conversion from red alder to Douglas-fir site index in stands for which it was not measured. First, second, and third order polynomials of red alder site index were used as potential independent variables. The predicted site indices were then used in further analyses.

To accomplish the three objectives the current stand density, species proportion, quadratic mean diameter, relative quadratic mean diameter, age and Douglas-fir site index were used as independent variables.

Annual stand mortality rate was predicted from current stand conditions. The proportion of the initial number of trees dying followed a binomial distribution and was bounded by 0 and 1. A logistic equation was used to model the proportion and ensure that the proportion was limited by 0 and 1 and asymptotically approaches these values. It also had the advantage of easy interpretation: an increase in the transformed variable reflects in increase in the untransformed variable. For stands with no mortality occurring, the value of 0 was replaced by 25/n, where n is the sample size (Bartlett 1947) ($n=438$ for stand mortality equation, $n=200$ for equation of Douglas-fir mortality and species proportion). Because a binomial distribution does not fulfill the assumption that the errors are normally distributed, weighted regression was applied with the weight (Neter et al. 1983)

$$w = n * p * (1-p)$$

where, w = weight

n = sample size

p = proportion.

The annual shift in proportion of basal area and mortality in Douglas-fir were calculated only for stands which contained both species ($n=200$). In single species stands, species proportion is constant and proportion of mortality in Douglas-fir is 0 or 1 for stands solely consisting of red alder or Douglas-fir, respectively. For stands with both species present the shift in species proportion can be negative, zero or positive. A linear equation was used in the estimation process.

In order to simulate development of the relative quadratic mean diameter (RQMD), Douglas-fir mortality had to be estimated. The proportion of dying trees, which are Douglas-fir, follows a binomial distribution, which can be modeled through a logistic equation as presented for stand mortality. These equations constitute a seemingly unrelated system, i.e. their error terms are not independent.

To utilize the size-density relationships as developed by Puettmann (1990, Chapter IV) and to predict future stand development from current stand conditions, the initial density before the onset of density dependent mortality must be known. The equation for the size-density surface (Puettmann 1990, Chapter IV) was solved for initial density. This allowed the calculation of the initial density from current stand conditions. The calculated initial density was then used to predict the future development of the size-density relationship. The equations predicting stand and Douglas-fir mortality, the shifting species proportion, and the model for the size-density relationship (Puettmann 1990, Chapter IV) were then combined in a growth simulator.

The accuracy and benefits of the simulation model were tested using three stands out of the data set. These stands had a Douglas-fir basal area component of one third, one half and two thirds. A detailed stand description of these three stands is presented in table V.1. Stand 1, was a younger, high density stand, where Douglas-fir and red alder averaged approximately the same size. Stand 2 was older and had a high number of small trees. The Douglas-fir were on average smaller than the average red alder. Stand 3 was a similar age as stand 2, but had fewer, bigger trees. The average sizes of Douglas-fir and red alder were very similar.

To simulate the development of these stands, the initial stand conditions (stand density, Douglas-fir density, basal area proportion, stand quadratic mean diameter) were used as input, and the stands were projected for the length of the measurement period. The simulated stand and Douglas-fir densities, stand basal area, basal area proportions and stand quadratic mean diameters were then compared with the observed values for each stand.

Results

The equation for the conversion of red alder site index to Douglas-fir site index was

$$\begin{array}{rl} \mathrm{DFSI} = & \underset{(8.8)}{-4.60} + \underset{(0.33)}{1.55} * \mathrm{RASI} \end{array} \qquad (1)$$

adj. $R^2 = 0.70$, MSE=10.2. Standard errors in parentheses.

where DFSI = 50-year site index for Douglas-fir (King 1966)

RASI = 50-year red alder site index (Worthington et al. 1960).

Using the logistic transformation and the equation for the annual stand mortality rate yielded

$$Y_t = \underset{(0.16)}{-3.46} - \underset{(0.11)}{0.41}*RQMD_t + \underset{(0.00002)}{0.00015}*N_t - \underset{(0.004)}{0.022}*t_i$$

$$+ \underset{(0.18)}{1.1} * RD_t \qquad (2)$$

adj. R^2 = 0.54, MSE=2.53. Standard errors in parentheses.

where $Y_t = \log(M_{s,t}/(1-M_{s,t}))$

$M_{s,t}$ = proportion of trees dying or $((N_t-N_{t+1})/N_t)$

$RQMD_t$ = relative quadratic mean diameter (Douglas-fir quadratic mean diameter/stand quadratic mean diameter)

N_t = number of trees per hectare

RD_t = relative density (actual density/maximal density for given diameter and proportion)

t = total stand age.

Fitting of the equation predicting the annual change in basal area proportion lead to

$$P_{Df,t+1} - P_{Df,t} = \underset{(0.0013)}{-0.004} + \underset{(0.000026)}{0.00007*t} + \underset{(0.0009)}{0.0045*RQMD_t}$$

$$- \underset{(0.0001)}{0.0016*P_{Df,t}} \qquad (3)$$

R^2 = 0.14. MSE=0.00001. Standard errors in parentheses.

where variables as in equation 2 and

$P_{Df,t}$ = proportion of basal area in Douglas-fir

The proportion of the mortality which is contributed from the Douglas-fir components was modeled through

$$Z_t = \underset{(1.04)}{-1.59} + \underset{(1.23)}{2.32*P_{Df,t}} + \underset{(0.027)}{0.09*QMD_t} + \underset{(0.0003)}{0.0008*N_t}$$

$$- \underset{(0.024)}{0.073*DFSI} \qquad (4)$$

R^2=0.49 MSE=34. Standard error in parentheses.

where parameters as in equation 1,2 and

Z_t = $\log(PM_{Df,t}/1-PM_{Df,t})$

$PM_{Df,t}$ = proportion trees dying, which are Douglas-fir

QMD = quadratic mean diameter (cm).

These three equation were combined with the size-density surface as developed by Puettmann (1990, Chapter IV) to construct a growth model which allowed simulation of development of pure and mixed red alder/Douglas-fir stands. The results of the comparison of the predicted and observed stand development of three stands are presented in Figures V.1, V.2 and V.3.

Stand 1 started with a basal area proportion of one third in Douglas-fir. The simulated proportion shifted faster towards Douglas-fir than the actual stand (Figure V.1D). Also the overall stand mortality was overpredicted, which led to overestimation of quadratic mean diameter (Figures V.1A, V.1B). These discrepancies originated in the overestimation of Douglas-fir mortality. The actual stand did not experience Douglas-fir mortality between ages 21 and 26, while the simulation predicted substantial mortality during this period (Figure V.1E).

Stand 2 started with 50% of its basal area in Douglas-fir. The shift in basal area proportion was irregular, but the simulation seemed to reflect the long term trends accurately for all components (Figure V.2A through V.2E), with the exception of basal area (Figure V.2C).

The shift in basal area proportion of stand 3 was very erratic (Figure V.3D). However, the simulated basal area proportion represented the general trend. As with stand 1, the lack of Douglas-fir mortality in the stand during the first measurement period (Figure V.3E) led to an underestimation of stand density (Figure V.3A). The resulting overestimation of the quadratic mean diameter offset this effect (Figure V.3B), so that basal area development was simulated very accurately (Figure IVB.3C).

Discussion

Inferences from the results must be carefully limited to the range of conditions represented in the data set. The data set represented only a limited window of the conditions leading to development of mixed red alder/Douglas-fir stands.

A common variable representing site quality was needed to model mixed stands. This required either a new site index variable or a conversion of red alder to Douglas-fir site index. The estimated Douglas-fir site index conversion equation confirmed the trend proposed by Harrington and Curtis (1986) and by Hoyer (1978). It was verified that better red alder sites are also better Douglas-fir sites. While Harrington and Curtis (1986) determined that some of the best red alder sites were not suitable for Douglas-fir, such sites are probably not represented in this data set. On these sites, Douglas-fir probably does not become established or else dies out before the stand reaches the ages of the stands in the data set used in this analysis.

This simple conversion of equation 1 cannot not be fully satisfactory as interest increases in red alder and mixed red alder/Douglas-fir stands. The concept of dominant height as a site indicator is especially problematic in mixed species stands. It requires height measurements of trees which could have been previously overtopped by the trees of the other species. The question of site index conversion has to be investigated more thoroughly. Approaches, utilizing geographic and topographic information, soil moisture, aeration and fertility information have been used for Douglas-fir (Steinbrenner 1975) and red alder (Harrington 1986). These approaches are of special interest for mixed stands because the results are not influenced by specific stand conditions. Also, other site indicators like plant communities have been shown to be useful either alone (Cajander 1926) or in combination with physiographic factors and soil information (Moosmayer 1957) and should be considered for usage in mixed stands.

From the growth information in the yield tables (Worthington et al. 1960, McArdle et al. 1961), a generalized pattern of shift in species proportion can be hypothesized. Due to its faster initial growth rate, red alder will increase its basal area faster than Douglas-fir. In cases of complete dominance, red alder can kill all Douglas-fir, and the stand will develop into a pure red alder stand. If Douglas-fir survives, its growth pattern suggests that it will eventually overtop the red alder and its basal area proportion will increase (e.g. Berntsen

1961, Miller and Murray 1978). In some cases, this might lead to a pure Douglas-fir stand. In other cases, only very few Douglas-fir might survive, not enough to fully occupy the site and red alder will constitute the majority of the stand until senescence. Most of the stands in the data set were in the stage where the Douglas-fir proportion was increasing.

Interpreting the growth model allowed insight into the relative importance of different aspects of stand development. The equation predicting annual stand mortality rates indicated that mortality rates were determined largely by stand density. All else being equal, stand mortality rates decreased with age and with increased dominance of Douglas-fir.

The equation for the shift in basal proportion indicated that Douglas-fir basal area proportion increased faster at older ages and at higher relative quadratic mean diameter. Stands in which the basal area proportion shifted towards red alder were not represented in the data set. Shifts towards red alder are more common in stands that are younger than those included here.

The model predicting the proportion of the mortality in Douglas-fir showed that in stands where Douglas-fir contributed a major basal area proportion of the stand, it also contributed a higher percentage of the mortality. In addition, the proportion of Douglas-fir mortality increased with higher stand densities. This might indicate that the mixed stands had a component of suppressed Douglas-fir in the understory, which can better survive in low density stands than in high density stands.

Comparisons of the growth model predictions with actual development of three stands showed some of the strengths and weaknesses of the growth model. Not all components of each stand were simulated with high accuracy. The growth model predicts average stand development and consequently discrepancies with individual stands have to be expected. However, the general dynamics of stand development were reflected well. This suggested its usefulness as a research tool with potential for guidance in setting research priorities. A few examples are discussed here.

The first research area concerns the development of young stands. This is of special interest considering that a typical red alder rotation is around 40 years. Since these stands were not represented in the data set, the periods when red alder has a potential growth advantage are not represented in the growth model. Measurement in mixed plantation should be taken from establishment to allow complete representation of these stages. The yield table information suggests that a peaking function which shows flexibility in shape, for example a Weibull distribution, might be a good candidate to model the increase and subsequent decrease of the red alder proportion.

Another area needing research is the effect of initial size difference between the two species. The growth model suggests that a stand with dominant red alder has higher overall stand as well as Douglas-fir mortality rates. This implies that red alder is a more severe competitor of either species than Douglas-fir. This agrees with the results of Shainski (1988) for young, high density plantations. A more detailed investigation about these effects might lead to silvicultural implications about delayed planting, or precommerical or commercial thinnings to reach a desired stand composition (Newton et al. 1968).

Another related aspect which was not sufficiently reflected in the growth model is the effect of silvicultural treatments. Thinnings can change the proportion and relative position of the species. The effects of the instant change in stand conditions need to be tested and incorportated into the growth model. This should be given special consideration when installing a thinning study by adequately characterizing the stand conditions before thinning.

The stand simulations also indicated the complexity of factors influencing stand development. Mortality patterns were not regular, rather there were periods of high and low mortality. This could not be reflected in a simulation of average stand conditions. It appears that only an individual tree model can characterize stand conditions accurately enough to model the full complexity of mixed stands and give reliable yield estimates at the stand level.

Conclusions

The development of a growth model allowed investigation of mixed-stand development. This model identified stand density, relative dominance and species proportions as important factors driving stand development. The growth model also allowed projection of different stands forward in time, thus determining the relative importance of several factors. It can also be helpful in setting research priorities. For examples, it showed the necessity to investigate development of young stands, the effect of relative size, and the need to study the effects of management practices on stand development.

Figure V.1: Simulated and actual development of stand density (A), quadratic mean diameter (B), basal area (C), Douglas-fir proportion (D), and Douglas-fir density of stand 1 (for description of initial stand conditions see Table V.1).

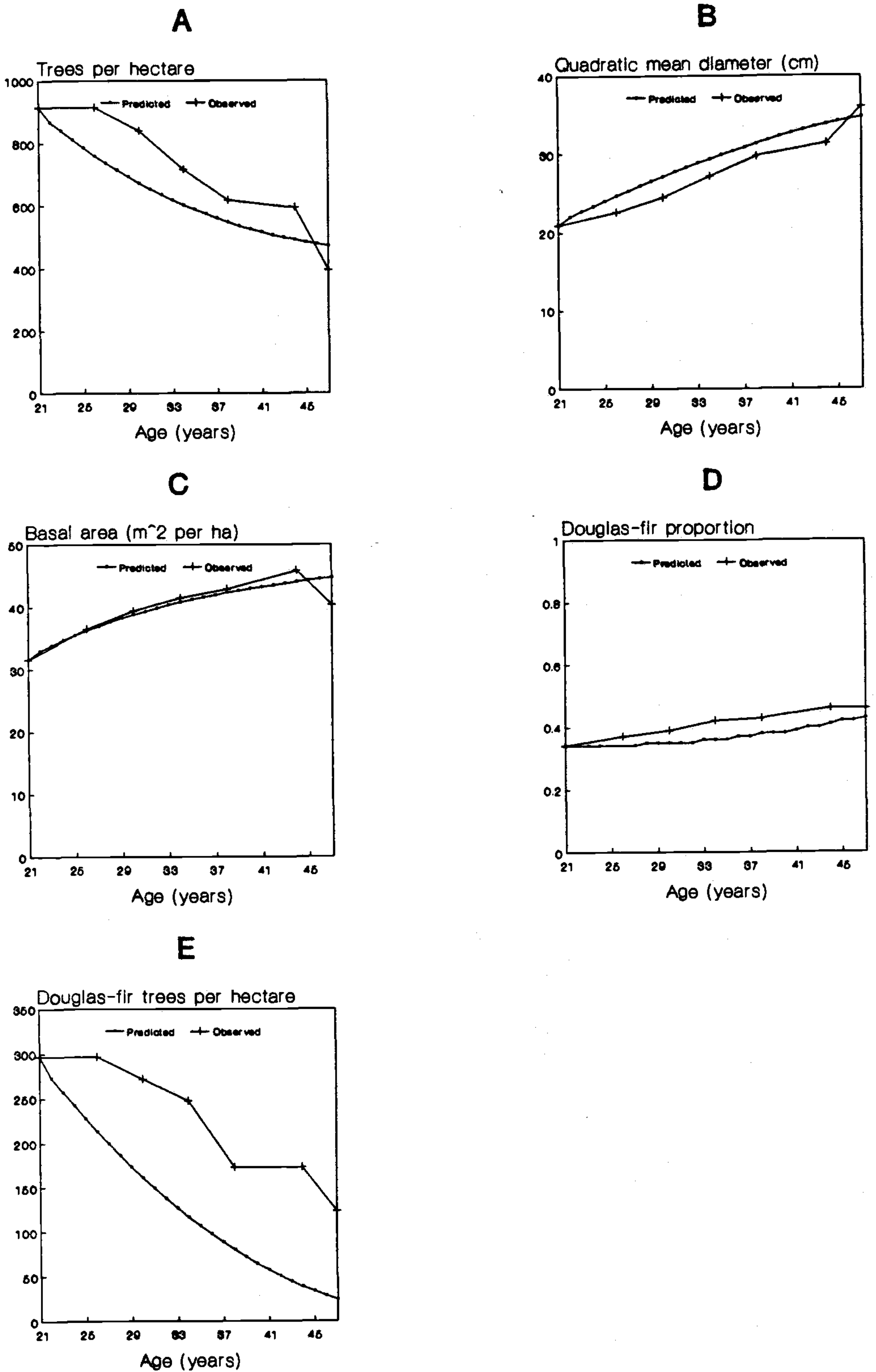

Figure V.1. (continued)

Figure V.2: Simulated and actual development of stand density (A), quadratic mean diameter (B), basal area (C), Douglas-fir proportion (D), and Douglas-fir density of stand 2 (for description of initial stand conditions see Table V.1).

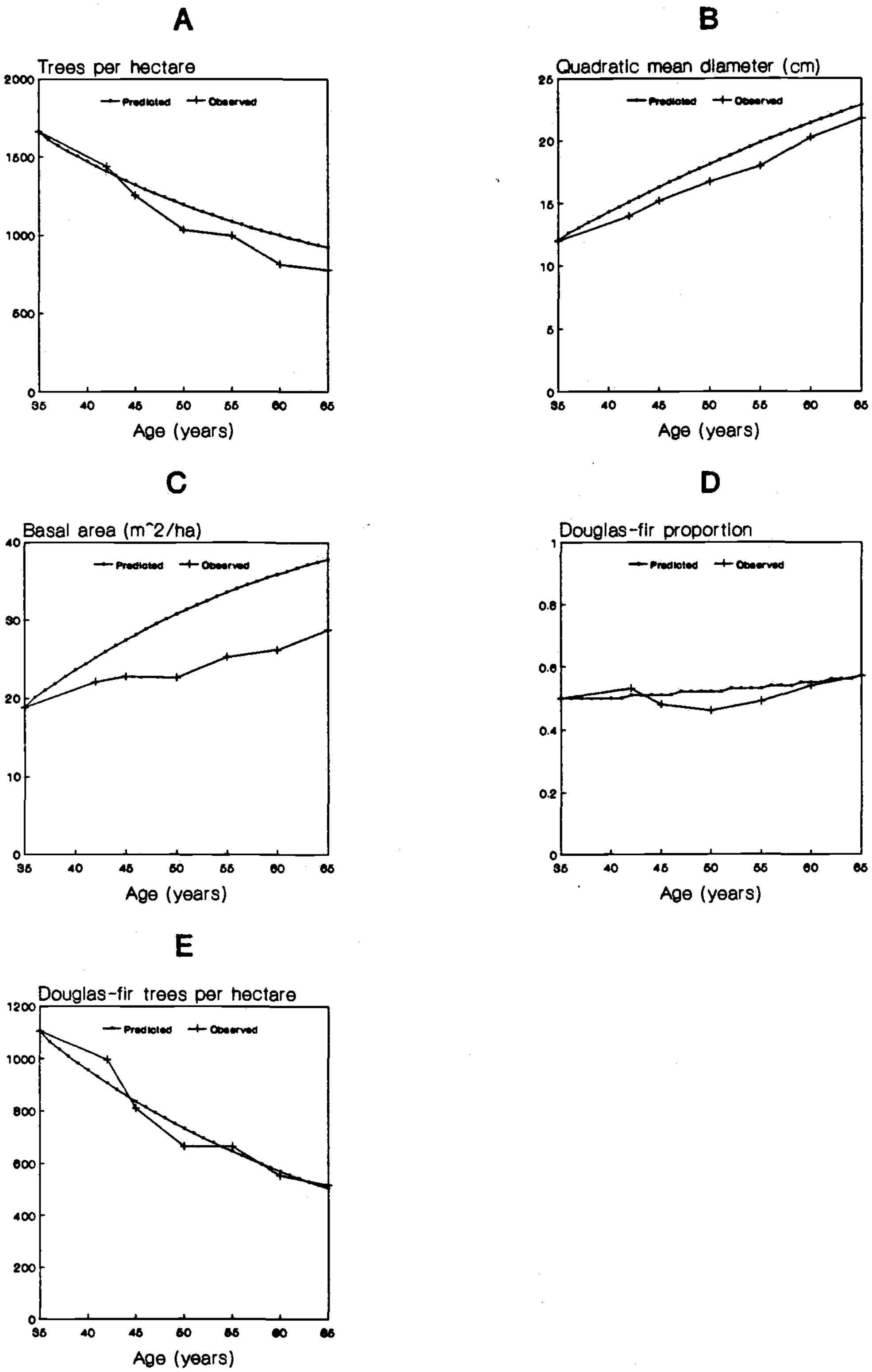

Figure V.2. (continued)

Figure V.3: Simulated and actual development of stand density (A), quadratic mean diameter (B), basal area (C), Douglas-fir proportion (D), and Douglas-fir density of stand 3 (for description of initial stand conditions see Table V.1).

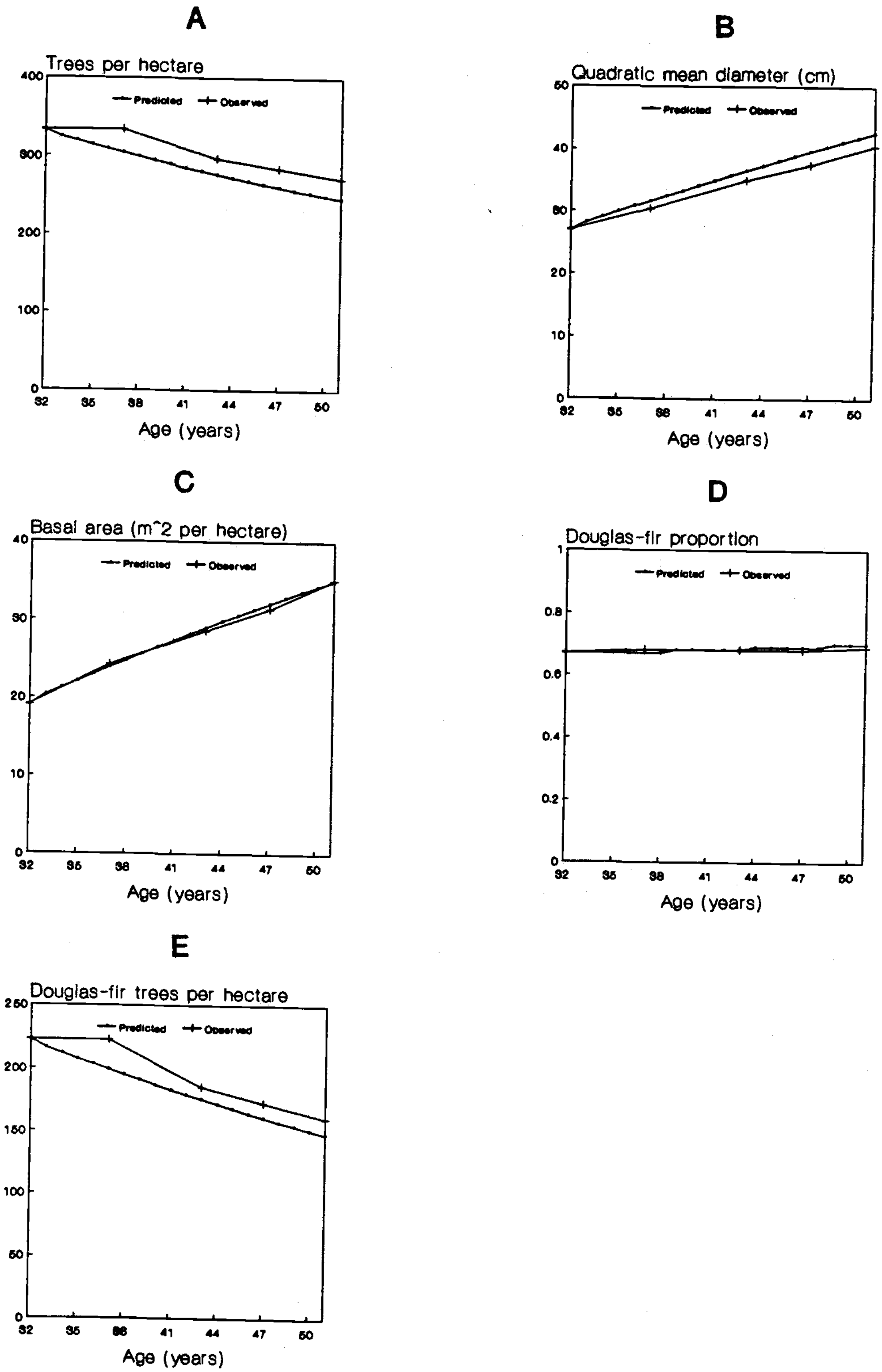

Figure V.3. (continued)

Table V.1: Initial conditions for 3 stands used for comparisons of the growth model .

Stand	Age	Duration	Stand		Basal		Douglas-fir	
	(yrs)	(yrs)	Density (tpha)	QMD (cm)	Area (m^2/ha)	Proportion	density (tpha)	QMD (cm)
1 2	35	30	1660	12.0	18.85	0.50	1106	10.4
2 3	32	19	333	26.9	19.03	0.67	222	27.0
3 1	21	26	913	21.0	31.56	0.34	297	21.4

where:

Age = stand age at initial measurement in years (yrs)
Duration = length of measurement period in years (yrs)
Density = trees per hectare (tpha)
QMD = quadratic mean diameter in centimeter (cm)
Douglas-fir Proportion = proportion of basal area in Douglas-fir
Douglas-fir density = Douglas-fir per hectare
Douglas-fir QMD = quadratic mean diameter of Douglas-fir proportion

Bibliography

Abetz, P. 1975. Eine Entscheidungshilfe fuer die Durchforstung der Fichte. AFZ-M 30.

Abetz, P. 1979. Brauchen wir Durchforstungshilfen? Schw. Forstz. f. Forstw. 130: 945-961.

Aiba, Y. 1975. Effects of cultural system on the stand growth of sugi plantations (Cryptomeria japonica). III. Estimate of stem volume yield under actual stand density. (H-D-V diagram). J. Jap. For. Soc. Tokyo, Japan. 57: 67-73.

Aikman, D. P., and A. R. Watkinson. 1980. A model for growth and self-thinning in evenaged monocultures of plants. Ann. Bot. 45:419-427.

Ando, T. 1968. Ecological studies on the stand density control in even-aged stands. Bull. Gov. for. Exp. Stn. Tokyo, Japan. 210:1-153.

Arney, J. D. 1985a. A modeling strategy for the growth projection for managed stands. Can. J. For. Res. 15:511-518.

Arney, J. D. 1985b. SPS: Stand projection system for mini- and micro-computers. J. For. 83:378.

Arney, J. D. 1989. SPS-Guide for the Stand Projection System Version 2.1. (revised January 1989) including the Stand Appraisal system (SAS).

Assmann, E. 1961. Waldertragskunde. BLV Muenchen. 490 p.

Atkinson, W. A., and W. I. Hamilton. 1978. The value of red alder as source of nitrogen in Douglas-fir alder mixed stands. IN: Utilization and Management of Alder. USDA forest Service Gen. Tech. Rep. PNW-70.

Bartlett, M. S. 1947. The use of transformations. Biometrics 3:39-52.

Bazzaz, F. A., and J. L. Harper. 1976. Relationship between plant weight and numbers in mixed populations of Sinapsis alba(L.) RABENH. and Lepidium sativum L. J. Appl. Ecol. 13:211-216.

Berntsen, C. M. 1961. Growth and development of red alder compared with conifers in a 30-year old stand. USDA For. Serv. Pac. Northw. For. and Range. Exp. Stn. Res. Pap. 38. 20 p.

Binkley, D. 1983. Ecosystem production in Douglas-fir plantations: interaction of red alder and site fertility. For.Ecol. Manage. 5:215-227.

Binkley, D. 1984. Importance of size-density relationship in mixed stands of Douglas-fir and red alder. For. Ecol. Manage. 9:81-85.

Bormann, B. T., and D. S. DeBell. 1981. Nitrogen content and other soil properties related to age of red alder stands. Soil Sci. Soc. Am. J. 45:428-432.

Borman, B. T., and J. C. Gordon, 1984. Stand density effects in young red alder plantations: Production, photosynthate partitioning, and nitrogen fixation. Ecol. 65:394-402.

Brigleb, P. A. 1942. Progress in estimating trend of normality percentage in second-growth Douglas-fir. J. For. 40:785-793.

Brigleb, P. A. 1952. An approach to density measurements in Douglas-fir. J. For. 50:529-536.

Brooks, S. D. 1979. Compatible growth and yield equations for eastern redcedar forest types. M.S. Thesis. Univ. Tenn., Knoxville, TN. 90 p.

Burkhart, H. E., J. P. Barrett, and H. G. Lund. 1984. Timber Inventory. P. 361-412 IN: Forestry Handbook. 2nd edition. K. J. Wenger (ed.) J. Wiley and Sons, New York.

Cajander, A. K. 1926. The theory of forest types. Acta For. Fenn. 29. 108 p.

Carlton, G. C. 1989. The structure and dynamics of red alder communities in the central Coast Range of western Oregon. Master Thesis. Oregon State University, Corvallis, OR. 173 p.

Chambers, C. J. 1974. Empirical yield tables for predominantly alder stands in western Washington. State of Washington, Department of Natural Resources DNR Report No.
Chisman, H. H., and F. X. Schumacher. 1940. On the tree-area ratio and certain of its applications. J. For. 38:311-317.

Clutter, J. L., F. C. Fortson, L. V. Pienaar, G. H. Brister, and R. L. Bailey. 1983. Timber Management: A Quantitative Approach. Wiley and Sons, New York.

Cole, E. C. 1984. Fifth-year response of Douglas-fir to crowding and other competition. Master Thesis. Oregon State University.

Cole, E., and M. Newton. 1987. Fifth-year response of Douglas-fir to crowding and nonconiferous competition. Can. J. For. Res. 17:181-186.

Cunia, T. 1973. Dummy variables and some of their uses in regression analysis. IN: Cunia, T., Kuusela K., and A. Nash (eds.). Proceedings of the June 1973 IUFRO meeting, Nancy, France.

Curtis, R. O. 1972. Yield tables past and present. J. For. 70:28-32.

Curtis, R.O. 1982a. A simple index of stand density for Douglas-fir. For. Sci. 28:92-94.

Curtis, R. O. 1982b. Stand density presentation for Silviculture Institute, Module IV/4. Unpublished Notes. College of Forest Resources, University of Washington.

Curtis, R. O. 1987. Levels-of-Growing-Stock Cooperative Study in Douglas-fir: Report No. 9 - Some comparisons of DFSIM Estimates With Growth in the Levels-of-Growing-Stock Study. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Research Paper PNW-RP-376.

Curtis, R. O., G. W. Clendenen, and D. L. Reukema. 1981. A new stand simulator for coast Douglas-fir. USDA For. Serv. Ge. Tech. Rep. PNW-135.

Curtis, R. O., and D. D. Marshall. 1986. Report No. 8. The LOGS-Study: Twenty year results. USDA For. Serv. Res. Pap. PNW-356. 113 p.

Dahms, W. G. 1983. Growth-simulation model for lodgepole pine in central Oregon. USDA For. Serv.. Pacific Northwest Forest and Range Experiment Station. Portland, Oregon. Research Paper PNW-302. 22 p.

Daniel, T. W., J. A. Helms, and F. S. Baker. 1979. Principles of Silviculture. McGraw-Hill, New-York. 500 p.

DeBell, D. S., W. R. Harms, and C. D. Whitesell. 1989. Stockability: A major factor in productivity differences between Pinus taeda in Hawaii and the southeastern United States. For. Sci. 35:708-719.

DeBell, D. S., R. F. Strand, and D. L. Reukema. 1978. Short rotation production of red alder: some options for future management. P. 221-232 IN: Utilization and Management of Alder. USDA forest Service Gen. Tech. Rep. PNW-70.

DeBell, D. S., and T. C. Turpin. 1989. Control of red alder by cutting. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Res. Pap. PNW-RP-414.

DeBell D. S., and J. E. Wilcox. in preparation. Spacing effects on stand structure and development in a 12-year-old red alder plantation. In preparation for WJAF.

Draper, N. R., and H. Smith. 1981. Applied Regression Analysis. 2nd edition. Wiley and Sons, N. Y. 706 p.

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

Dunning, D., and L. H. Reineke. 1933. Preliminary yield tables for second-growth stands in the California pine region. USDA, Pacific Southwest Research Station Technical Bulletin No. 354.

Ek, A. R. 1974. Nonlinear models for stand table projections in northern hardwood stands. Can. J. For. Res. 4:23-27.

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

Fowells, H. A. (ed.) 1965. Silvics of forest trees of the United States. USDA Agricultural Handbook No. 271. 762 p.

Franz, F. 1987. Zum Aufbau eines neuzeitlichen Informationssystems fuer die Forstwirtschaft. Forstarchiv 58: 131-137.

Gedney, D. R. 1982,. The timber resources of western Oregon-highlights and statistics. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Resource Bulletin PNW-138. 84 p.

Gedney, D. R., P. M. Bassett, and M. A. Mel. 1986a. Timber resouece statistic for non-federal forest land in southwest Oregon. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Resource Bulletin PNW-138. 26 p.

Gedney, D. R., P. M. Bassett, and M. A. Mel. 1986b. Timber resource statistic for non-federal forest land in southwest Oregon. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Resource Bulletin PNW-RB-140. 26 p.

Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. For. Res. Lab. Oregon State University. Corvallis, OR. 39 p.

Gorham, E. 1979. Shoot height, weight and standing crop in relation to density of monospecific plant stands. Nature. 279:148-150.

Hall, F. C., L. W. Breser, J. F. Franklin, and R. L. Werner. 1985. Plant communities and stand conditions. IN Management of wildlife and fish habitat in forests of western Oregon and Washington. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. pg. 17-31.

Hamilton, D. A., Jr. 1986. A logistic model of mortality of thinned and unthinned mixed conifer stands of northern Idaho. Forest Science 32:989-1000.

Hann, D. W. 1989. Personal communication. Department of Forest Management, College of Forestry. Oregon State University, Corvallis, OR.

Hann, D. W., and C.-H. Wang. 1990. Individual tree mortality equations for the mixed conifer zone of southwest Oregon. Forest Research Laboratory, Oregon State University, Corvallis, OR. Research Bulletin 67.

Hann, D. W., and K. Riitters. 1982. A key to literature on forest growth and yield in the Pacific Northwest: 1910-1981. Forest Research Laboratory, Oregon State University, Corvallis, OR. Research Bulletin 39.

Hansen, E., and E. E. Nelson. 1975. Study Plan No. EN 75-1. Red alder as a control for Poria weirii root rot of Douglas-fir. A cooperative study with International Paper Company, Longview Fiber Company, Crown Zellerbach Corporation, Oregon State University, and United States For. Serv.. Plan is on file at Pacific Northwest Research Station, Corvallis, OR.

Hara, T. 1984. Modeling the time course of self-thinning in crowded plant populations. Ann. Bot. 55:181-188.

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

Harrington, C. A. 1986. A method of site quality evaluation for red alder. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn. General Technical Report. PNW-192.

Harrington, C. A., and R. O. Curtis. 1986. Height growth and site index curves for red alder. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Res. Pap. PNW-358.

Hebner, C. F., and M. J. Bergener. 1982. Red alder: a bibliography with abstracts. USDA For. Serv. Pac. Northw. For. and Range Exp. Stn. Gen. Tech. Rep. PNW-161.

Helgerson, O.T., J. C. Gordon, and D. A. Perry 1984. N_2 fixation by red alder (Alnus rubra) and scotch broom (Cytisus scoparius) planted under precommercially thinned Douglas-fir (Pseudotsuga menziesii). Plant and Soil. 78:221-233.

Hester, A. S., D. W. Hann, and D. R. Larsen. 1989. ORGANON: Southwest Oregon growth and yield model user manual. Version 2.0. For. Res. Lab. Oregon State University. Corvallis, OR. 59 p.

Hibbs, D. E. 1987. The self-thinning rule and red alder management. For. Ecol. Manage. 18:273-281.

Hibbs, D. E., and G. D. Carlton. 1989. A comparison of volume-and diameter-based stocking guides using red alder. W. J. Appl. For. 4:113-115.

Hoyer, G. 1978. Relative site index. P. 176-177. IN: Briggs, D. G., DeBell, D. S. and W. A. Attkinson (eds.) Utilization and Management of Red Alder. USDA For. Serv. Gen. Tech. Rep. PNW-70.

Hozumi, K. 1980. Ecological and mathematical considerations of self-thinning in even-aged pure stands. II. Growth analysis of self-thinning. Bot. Mag., Tokyo, Japan. 93:149-166.

Hughes, M. K. 1971. Tree biocontent, net production and litter fall in a deciduous woodland. Oikos 22:62-73.

Hundeshagen, J. C. 1826. Die Forstschaetzung auf neuen wissenschaftlichen Grundlagen. Heinrich Lapp Verlag, Tuebingen.

Hutchings, M. J., and C. S. J. Budd. 1981. Plant competition and its course through time. BioScience. 31:640-645.

Hyink, D. M., W. Scott, and R. M. Leon. 1988. Some important aspects in the development of a managed stand growth model for western hemlock. IN: Ek. A. R., Shifley, S. R. and T. E. Burk (eds.). Forest Growth Modelling and Prediction. Proceedings of the IUFRO Conference August 23-27, 1987, Minneapolis, MN. USDA For. Serv. Gen. Tech. Rep. NC-120.

King. J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser For. Pap. No. 8. Weyerhaeuser For. Res. Cent., Centralia, WA. 49 p.

King. J. E. 1973. Principals of growing stock classification for even-aged stands and an application to natural Douglas-fir stands. Ph.D. Thesis. University of Washington. 91 p.

Leak, W. B., D. S. Solomon, and S. M. Filip. 1969. A silvicultural guide for northern hardwoods in the northeast. USDA For. Serv. Res. Pap. NE-143.

Leary, R. A. 1979. Design. p. 5-15. IN: A generalized forest growth projection system applied to the Lake States Region. USDA For. Serv. Gen. Tech. Rep. NC-49.

Long, J. N. 1985. A practical approach to density management. Forestry Chronicle. 23-26.

Long, J. N., J. B. McCarter, and S. B. Jack. 1988. A modified density management diagram for coastal Douglas-fir. WJAF. 3:88-89.

Long, J. N., and F. W. Smith. 1983. Relation between size and density in developing stands: a description and possible mechanisms. For. Ecol. and Management. 7:191-206.

Lloyd, F. T., and W. R. Harms. 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Annals of Botany 57:681-688.

Lynch, T. B., and J. W. Moser. 1986. A growth model for mixed species stands. Forest Sci. 32:697-706.

Marquardt, D. W. 1963. An algorithm for least squares estimation of nonlinear parameters. S.I.A.M. J. Appl. Math. 11:431-441.

Malmberg, C., and H. Smith. 1982. Relationship between plant weight and density in mixed populations *Medicago sativa* and *Trifolium pratense*. Oikos 38:365-368.

McArdle, R. F., W. H. Meyer, and D. Bruce. 1961. The Yield of Douglas-fir in the Pacific Northwest. USDA Technical Bulletin No. 201.

Meyer, W. H. 1942. Yield of even-aged stands of loblolly pine in northern Louisiana. Yale Univ. Sch. For. Bull. 51. 39 p.

McCarter, J. B. 1984. Density management of lodgepole pine. Thesis. Utah State Univ., Logan, Utah. 37 p.

McFadden, G., and C. D. Oliver. 1988. Three-dimensional forest growth model relating tree size, tree number, and stand age: Relation to previous growth models and to self-thinning. For. Science 34:662-676.

Meyer, W. H. 1933. Approach of abnormally stocked forest stands of Douglas-fir to normal condition. J. For. 31:400-406.

Miller R. A., and M. D. Murray, 1978. The effect of red alder on growth of Douglas-fir. P. 283-306. <u>IN</u>: Briggs, D. G., DeBell, D. S. and W. A. Attkinson (eds.) Utilization and Management of Red Alder. USDA For. Serv. Gen. Tech. Rep. PNW-70.

Mitchell, K. J. 1986. Comparison of McArdle, DFSIM, and TASS growth and yield models. P. 350-359. <u>IN</u>: Douglas-fir: Stand Management for the Future. C.D. Oliver, D.P. Hanley, and J. A. Johnson (eds.). University of Washington, Seattle, WA. 388 p.

Mitscherlich, G. 1978. Wald, Wachstum und Umwelt. Band 1. Form und Wachstum von Baum und Bestand. 2. Auflage. J. Sauerlaender Verlag. Frankfurt a. M. 144 p.

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. 66:559-614.

Moser, J. W. 1972. Dynamics of an uneven-aged forest stand. Forest Sci. 18:184-191.

Moser, J. W. 1974. A system of equations for the components of forest growth. <u>IN</u>: Growth models for tree and stand simulation. C. J. Fries (ed.). Dep. For. Yield Res., Royal Coll. For. Stockholm. Res. Note 30: 260-287.

Moosmayer, H. U. 1957. Zur ertragkundlichen Auswertung der Standortsgliederung im Ostteil der Schwaebischen Alb. Mitt. Vereins forstl. Standortsk. Forstpflz. 7:3-41.

Mulloy, G. A. 1944. Empirical stand density yield tables. Canada Department of Mines and Resources. Lands, Parks and Forestry Branch. Dominion Forest Service, Ottawa, Canada Silvicultural Research Note No. 73.

Mulloy, G. A. 1947. Empirical stand density yield (II). Canada Department of Mines and Resources. Lands, Parks and Forestry Branch. Dominion Forest Service, Ottawa, Canada Silvicultural Research Note No. 82.

Munro, D. D. 1974. Forest growth models - a prognosis. P. 7-21 IN: Growth models for tree and stand simulation. J. Fries (ed.). Department of Forest Yield Research. Royal College of Forestry, Stockholm, Research Note 30.

Nelson, E. E., E. N. Hansen, C. Y. Li, and J. M. Trappe. 1978. The role of red alder in reducing losses from laminated root rot. P. 273-282. IN: Briggs, D. G., DeBell, D. S. and W. A. Attkinson (eds.) Utilization and Management of Red Alder. USDA For. Serv. Gen. Tech. Rep. PNW-70.

Neter, J., W. Wassermann, and M. H. Kutner. 1983. Applied linear regression models. Irwin Inc. Homewood, IL. 547 p.

Newton, M., B. A. El Hassan, and J. Zavitkowski. 1968. Role of red alder in forest succession in western Oregon. pg. 75-84. IN: Biology of red alder. Trappe, J. M, Franklin, J. F., Tarrant, R. F., and G. M. Hansen (eds.). USDA For. Serv. Pac. Northw. For. and Range Exp. Stn.

O'Hara, K. L., and C. D. Oliver. 1988. Three-dimensional representation of Douglas-fir volume growth: Comparison of growth and yield models with stand data. For. Sci. 34:724-743.

Oliver, C. D. 1980. Even-aged development of mixed-species stands. J. For. 78:201-203.

Osawa, A., and S. Sugita. 1989. The self-thinning rule: another interpretation of Weller's results. Ecol. 70:279-283.

Opalach, D. 1988. Development of a diameter distribution projection model. Ph.D. Thesis. University of Washington. 296 p.

Peet, R. K., and N. L. Christensen. 1987. Competition and tree death. BioScience 37:586-595.

Perry, D. A. 1984. A model of physiological and allometric factors in the self-thinning curve. J. theor. Biol. 106:383-401.

Perry, D. A., C. Choquette, and P. Schroeder. 1987. Nitrogen dynamics in conifer-dominated forests with and without hardwoods. Can. J. For. Res. 17:1434-1441.

Petersen, W. C., and D. E. Hibbs. 1989. Adjusting stand density management guides for sites with low stocking potential. WJAF 4:62-65.

Pickard, W. F. 1983. Three interpretations of the self-thinning rule. Ann. Bot. 51:749-757.

Pienaar, L. V. 1965. Quantitative theory and forest growth. Ph.D. Thesis, Univ. of Wash. Seattle, WA. 177 p.

Puettmann, K. J., D. E. Hibbs, and B. Yoder. 1988. Permanent Plot Data Base for red alder. Unpublished Report to the Hardwood Silviculture Cooperative. Corvallis, OR. 44 p.

Radkowski, D. A. 1978. Nonlinear regression modeling. Marcel Dekker. NY. 276 p.

Ralston, M. L., and R. L. Jenrich. 1978. DUD, A derivative free algorithm for nonlinear least squares. Technometrics 20:7-14.

Reineke, L. H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Resch, H. 1980. Utilization of red alder in the Pacific Northwest. Forest Products Journal. 30:21-26.

Resch, H. 1988. Red alder: Opportunities for better utilization of a resource. Forest Research Laboratory, Oregon State University, Corvallis. Special Publication 16. 13 p.

Reineke, L. H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627-638.

Ross, M. A., and J. L. Harper. 1972. Occupation of biological space during seedling establishment. J. Ecol. 60:77-88.

SAS Institute. 1987. SAS/STAT Guide for Personal Computers, Version 6 Edition. SAS Institute Inc. Cary, N.C.

Schnurr, G. L. 1937. Yield, stand, and volume tables for even-aged upland oak forests. USDA Tech. Bull. 560. 88p

Schwertfeger, F. 1981. Die Waldkrankheiten. Parey Verlag. Hamburg. 486 p.

Scott, W. 1987. Personal communication. Weyerhaeuser Company, Western Forestry Research Center, Tacoma, WA.

Shainsky, L. J. 1988. Competitive Interaction between Douglas-fir and red alder: growth analysis, resource use, and physiology. Ph.D. Thesis. Oregon State University. Corvallis, OR. 221 p.

Smith, D. M. 1986. The practice of silviculture. 7th edition. Wiley and Sons, New York. 527 p.

Smith, J. H. G. 1968. Growth and yield of red alder in British Columbia. P. 271-286. IN: Biology of alder. Trappe, J. M, Franklin, J. F., Tarrant, R. F., and G. M. Hansen (eds.). USDA For. Serv. Pac. Northw. For. and Range Exp. Stn.

Smith, N. J. 1984. Effects of density stress and soil productivity on size, mortality and nitrogen fixation in artificial populations of seedling red alder. Ph.D. Thesis. Oregon State University. Corvallis, OR. 143 p.

Smith, N. J. 1989. A stand-density control diagram for western redcedar (Thuja plicata). For. Ecol. Mmgt. 27:235-244.

Smith, N. J., and D. W. Hann. 1984. A new analytical model based on the -3/2 power rule of self-thinning. Can. J. For. Res. 14:605-609.

Smith, N. J., and D. W. Hann. 1986. A growth model based on the self-thinning rule. Can. J. For. Res. 16:330-334.

Solomon, D. S., R. A. Hosmer, and H. T. Jr. Hayslett. 1987. FIBER handbook: a growth model for spruce and northern hardwood types. USDA For. Serv., Northeastern For. Exp. Stn. NE-RP-602.

Spurr, S. H., and B. V. Barns, 1980. Forest Ecology. 3rd edition. Wiley, New York. 687 p.

Steinbrenner, E. C. 1975. Mapping soils on Weyerhaeuser lands in the Pacific Northwest. IN: Forest soils and forest land management. Bernier B., and Ch. H. Winget (eds.). Laval University Press. Quebec.

Stephens G. R., and P. E. Waggoneer, 1980. A half-century of natural transitions in mixed hardwood forests. Bulletin. Connecticut Agric. Exp. Stn. New Haven. 783:1-43.

Stiell, W. M. 1982. Growth of clumped vs. equally spaced trees. The Forest Chronicle. 23-25.

Stiell, W. M., and A. B. Berry. 1973. Yield of unthinned red pine plantations at the Petawawa Forest Experimental Station. Publ. Can. For. Serv. No. 1320.

Stout, S. L., D. A. Marquis, and R. L. Ernst. 1987. A relative density measure for mixed-species stands. J. For. July: 45-47.

Stout, S. L., and R. D. Nyland. 1986. Role of species composition in relative density measurement in Allegheny hardwoods. Can. J. For. Res. 16:574-579.

Stubblefield, G., and C. D. Oliver. 1978. Silvicultural implication to the reconstruction of mixed alder/conifer stands. P. 307-320. IN: Briggs, D. G., DeBell, D. S. and W. A. Attkinson (eds.) Utilization and Management of Red Alder. USDA For. Serv. Gen. Tech. Rep. PNW-70.

Tadaki, Y. 1963. The pre-estimating of yield based on the competition density effect. Gov. For. Exp. Stn. Tokyo, Japan. Bulletin 154:1-19

Tadaki, Y. 1964. Effect of thinning on stem volume yield studied with the competition-density effect. Gov. For. Exp. Stn. Tokyo, Japan. Bulletin 166:1-22.

Tarrant, R. F. 1961. Stand development and soil fertility in a Douglas-fir - red alder plantation. Forest Sci. 1:238-246.

Tarrant, R. F., B. T. Bormann, D. S. DeBell, and W. A. Atkinson. 1983. Managing red alder in the Douglas-fir region: some possibilities. J. For. 81:787-792.

Tubbs, C. H. 1977. Manager's handbook for northern hardwoods in the north central states. USDA For. Serv. Gen. Tech. Rep. NC-39.

Von Gadow, K. 1987. Untersuchungen zur Konstruktion von Wuchsmodellen fuer schnellwuechsige Plantagenbaumarten. Forstliche Forschungsberichte. Schriftenreihe der Forstwissenschaflichen Fakultaet der Universitaet Muenchen und der Bayer. Forstlichen Versuchs-und Forschungsanstalt. Nr. 77. 160 p.

Walters D. K., and D. W. Hann. 1986. Taper equations for six-conifer species in southwest Oregon. Forest Research Laboratory, Oregon State University, Corvallis. Research Bulletin 56. 41 p.

Walstad J. D., J. D. Brodie, B. C. McGinley, and C. A. Roberts. 1986. Silvicultural value of chemical brush control in the management of Douglas-fir. West. J. Appl. For. 1:69-73.

Walstad, J. D., and P. J. Kuch. (eds.). 1987. Forest vegetation management for conifer production. Wiley and Sons, New York. 523 p.

Waring, R. H., and W. H. Schlesinger. 1985. Forest Ecosystems Concepts and Management. Academic Press, Orlando, FL. 340 p.

Weller, D. E., R. H. Gardner, and H. H. Shugart, Jr. 1985. A mathematical and statistical analysis of the -3/2 power rule of self-thinning in even-aged plant populations. ORNL/TM-9548, Oak Ridge National Laboratory, Oak Ridge, TN.

Weller, D. E. 1987a. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monograph. 57:23-41.

Weller, D. E. 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. Ecology. 68:813-821.

West, P. W., and C. J. Borough. 1983. Tree suppression and the self-thinning rule in a monoculture of <u>Pinus</u> <u>radiata</u> D.Don. Ann. Bot. 52:149-158.

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

White, J. 1980. Demographic factors in populations of plants. <u>IN</u>: Demography and evolution in plant populations. O. T. Solbrig (ed.). P. 28-48. Oxford: Blackwell.

White, J. 1981. The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89:475-500.

White, J. 1985. The thinning rule and its application to mixtures of plant populations. P. 291-309. <u>IN</u>: Studies on plant demography: A Festschrift for John L. Harper. J. White (ed.). Academic Press, Orlando, FL. 393 p.

White, J., and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. J. Ecol.58:467-485.

Wiedemann, E. 1942. Der gleichaltrige Fichten-Buchen Mischbestand. Mitteilungen aus der Forstwirtschaft und Forstwissenschaft. 13: 1-88.

Wiedemann, E. 1949. Ertragstafeln der wichtigsten Holzarten. Schaper Verlag. Hannover. 98 p.

Wierman, C. A., and C. D. Oliver. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir - western hemlock. Can. J. For. Res. 9:1-9.

Worthington, N. P., F. R. Johnson, G. R. Staebler, and W. S. Lloyd. 1960. Normal yield tables for red alder. USDA Pac. Northwest For. and Range Exp.Stn. Research Paper 36.

Yoda, K., T. Kira, H. Ogawa, and H. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants XI). J. of Biol., Osaka City Univ., Series D. 14:107-129

Zeide, B. 1988. Analysis of the 3/2 power law of self-thinning. Forest Sci. 33:517-537.