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THINNING EVEN-AGED DOUGLAS-FIR STANDS: EFFECTS OF DENSITY AND STRUCTURE ON STAND VOLUME GROWTH

University of Washington Ph.D. 1987

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Thinning Even-aged Douglas-fir Stands:
Effects of Density and Structure on Stand Volume Growth

by

KEVIN LAUGHLIN O'HARA

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1987

Approved by

(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree: College of Forest Resources

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Abstract

THINNING EVEN-AGED DOUGLAS-FIR STANDS:
EFFECTS OF DENSITY AND STRUCTURE ON STAND VOLUME GROWTH

by Kevin Laughlin O'Hara

Chairperson of Supervisory Committee: Professor Chadwick D. Oliver
College of Forest Resources

The usefulness of thinning studies in Douglas-fir stands has been limited by difficulties such as the long time period required, changing study objectives, and the limited scope of these studies. An approach is presented where two baseline models -- based on volume estimates for unthinned stands from two Douglas-fir growth and yield models -- are compared to the growth of measured thinned stands. The baseline models were similar over most of their common range of age and density, but at lower densities and older ages the models indicated substantially different volumes.

Results from the 28-year Delezenne thinning study found volumes from thinned plots were comparable to, and in some cases exceeded, those of the baseline models. These high levels of production in the Delezenne plots suggest; 1) the growth and yield models are underestimating the growth of widely-spaced stands; and/or 2) an unrecognized potential exists for thinning to increase volume growth.

Gross volume increment from the Delezenne plots was unaffected by thinning in most of the lightly-thinned plots and reduced in heavily-thinned plots. Net increment was increased in some thinned plots.
Dominant and codominant trees produce more volume per tree and a greater portion of stand volume growth in thinned and unthinned stands. Average growth rates per unit of occupied growing space (growing space efficiency) were higher for dominants and codominants in unthinned stands. In thinned stands average growing space efficiency was similar among all represented crown classes. Tall trees and trees with medium-sized crowns were generally the most efficient.

The correlations between growing space efficiency and other individual tree characteristics, and between individual tree characteristics, were lower in thinned stands than in unthinned stands, suggesting these relationships do not apply after thinning.

Results suggest: 1) stand density measures do not provide similar expressions of competition in thinned stands; 2) density/growth relations are oversimplifications of a complex interaction of many variables; 3) optimal stand growth is obtained with a particular stand structure, not necessarily with a particular stand density; and 4) thinning may have the potential to increase gross stand volume growth.
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My wife Janet has assisted with all phases of this project, provided moral and financial support, and tolerated patiently my obsession for completing this dissertation. This work is dedicated to her.
CHAPTER ONE
INTRODUCTION

Thinning forest stands involves decisions based on complex biologic, sociologic, and economic variables. Stands are thinned for many reasons, but the maximization of volume growth is an underlying concern since few forest managers wish to reduce productivity, and few stands are thinned without some concern for future stand growth. Thinning reallocates available growing space to fewer trees by reducing tree numbers. While the type and the intensity of thinning varies considerably, all thinnings leave trees whose growth response is the basis for future stand vigor, growth, and yield.

Current thinning practices in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) stands in the Pacific Northwest usually remove trees from lower crown classes to various extents which are measured with stand density measures. The optimal range of density for maximum volume growth in Douglas-fir stands is uncertain. Timing of thinnings is also a critical factor since thinning too soon, too late, or too frequently may reduce stand growth.

Thinning studies have not yet produced a thorough understanding of the effects of thinning on stand growth and development. For example,
many thinning studies have attempted to quantify certain relations (such as the relation of volume growth to stand density) whose existence, or applicability to Douglas-fir stands, have not been confirmed previously. The objectives of these studies have also varied, and the objectives of several studies have not included maximization of volume growth. The variations in study objectives have led to a variety of study procedures, different methods of data analysis, and a wide range of results. The long time required for thinning studies creates logistic difficulties that are further confounded by changing knowledge, changing research needs, and inconsistent study objectives. Complex interactions of variables such as site quality, stand age, thinning intensity, stand structure, and thinning intervals have also limited the usefulness of results from thinning studies in Douglas-fir stands. Because of the limited scope of these studies, little information exists on tree or stand growth at wide spacings.

The present study takes a new approach to analyzing thinning studies. Rather than comparing incomplete sets of permanent plot data, or simulating the growth of thinned stands with growth and yield models, this study will use the simulated growth of unthinned stands to develop a baseline from which to compare the measured growth of thinned stands. This procedure will incorporate theories of volume growth/stand density changes with time. It will then attempt to explain the results of this comparison with more detailed analyses of the effect of stand density and stand structure on stand and tree volume growth.
OBJECTIVES

The primary objectives of this study are to determine:

1) If a response surface based on three variables: stand age, stand density and either mean tree volume or stand volume, can represent a baseline level of volume growth for unthinned Douglas-fir stands;
2) If the baseline model can be used to compare growth and yield models and to analyze the effects of thinning treatments on stand volume growth;
3) What relationship (if any) exists between volume growth and stand density in thinned and unthinned Douglas-fir stands; and
4) The role of individual tree growth rates, and individual tree growth rates per unit of growing space, in stand growth and productivity.
CHAPTER TWO
LITERATURE REVIEW

BASELINE VOLUME GROWTH MODEL

Competition-density theory (Kira et al. 1953; Hozumi et al. 1956; Shinozaki and Kira 1956, 1961) and the -3/2 power law of self-thinning (Yoda et al. 1963) have provided some useful relationships concerning the accumulation of biomass in plant populations. The competition-density effect, or the reciprocal yield relationship, defines the range in mean size of individual plants of a given age and site quality in relation to population density. At a given age, mean individual size is constant for a range of densities where intraspecific competition does not occur. Where intraspecific competition does occur, mean size is reduced such that when mean size and density are graphed on logarithmic axes, the slope of the relationship approaches -1 at higher densities (Figure 1). The constancy of the -1 slope at higher densities where intraspecific competition is occurring is referred to as the law of constant final yield (Hozumi et al. 1956; Shinozaki and Kira 1961; Pienaar 1965). This name is the result of biomass per unit area being constant over the range of density where the slope of this relationship equals -1 for a specific age.
Figure 1. Reciprocal yield curves (solid lines) which describe the competition-density effect, and the -3/2 self-thinning line (dashed line) for buckwheat. The reciprocal yield curves represent the maximum mean size possible for a particular age at a given density. The -3/2 power law of self-thinning limits the maximum mean size for a given density regardless of age (graph from Yoda et al. 1963).
The -3/2 power law defines an upper limit of mean individual size for a given density that is independent of age and site quality. When plotted on logarithmic axes the slope of the upper limit is approximately -3/2 (Figure 1). Together these relationships define the maximum average size of individuals at a given age for a range of densities. Successive ages have increasingly larger mean individual sizes but are limited at increasingly lower densities by mortality along the self-thinning line (Figure 1).

Incorporation of the principles of competition-density theory and the -3/2 power law into a three-dimensional model with age as a third axis has been attempted by several researchers (Sato 1983; McFadden 1985). The resulting three-dimensional surface describes the development of the mean individual size of a range of even-aged populations of various initial densities through time. A similar model has been constructed by Chang (1984), but without incorporation of the competition-density and -3/2 power law relationships.

The model described by McFadden (1985) may serve as a simplifying link between the broad range of conditions under which forest stands grow and a few causal relationships which describe the development of forest stands. Development of a three-dimensional model, such as the one described above, could be useful in representing a standard (or baseline) level of volume growth for a particular site and species. Comparing the mean tree volume of stands receiving a certain management treatment with the baseline model would then indicate the effect of that treatment on mean tree or stand volume growth.
VOLUME GROWTH AND STAND DENSITY

Volume Growth/Stand Density Relations

Many studies have attempted to document the effects of thinning on volume growth in Douglas-fir stands. These studies have analyzed various stand variables, but have used stand density (as determined by a variety of methods) as the major independent variable to gauge the effect of thinning on stand volume growth. Stand density is defined as a numerical expression of the level of space occupancy or degree of crowding per unit area.

The emphasis on stand density in these studies apparently comes from the European concept that production of cubic volume in forest stands remains relatively constant over a wide range of densities (Langsaeter 1941, from Smith 1962 and Braathe 1957; Moller 1954; Moller et al. 1954). Langsaeter and Moller found that production is optimal when growing space is fully occupied and that full occupancy of growing space can occur over a wide range of stand densities.

Another interpretation of the relationship between volume growth and density contends that maximum volume growth per unit area occurs at an intermediate density well below the upper limit of stand density (Assmann 1970). If this is true, a properly designed and implemented thinning regime may increase gross stand volume growth by thinning to an appropriate density.

Smith (1986) described a third alternative which suggests volume growth increases with increasing density to the maximum level of density for a given species. This theory receives support from studies in balsam fir (Abies balsamea (L.) Mill. - Baskerville 1965) and Douglas-
fir stands (Curtis 1967; Curtis and Marshall 1986).

The first two theories may be assumed to differ only with respect to the range of optimum density, but the third alternative represents a distinctly different interpretation of the relationship between growth and density. The differences between all three theories may be the result of trying to generalize growth/density relations over a variety of different sites, stand ages, thinning schedules, structures, and species, as well as using unstandardized approaches to measuring volume and density. For example, Nelson et al. (1961) compared growth to basal area over different site qualities in loblolly pine (Pinus taeda L.) stands and found the regions of maximal growth varied with site quality. On poor sites maximum growth occurred over a relatively wide range of density, while on high sites growth increased to nearly the highest level of density. Likewise, differences in stand age are important, and optimal levels of density vary for different species. Generally, the optimal level of density is higher for shade tolerant species, but this relationship is also affected by site quality differences (Smith 1986). Growth per unit area is reduced during the recovery period from thinning, so thinning frequency is important (Greggs 1981; Oliver et al. 1986). Stiell (1982) found that the selection of which trees to thin in red pine (Pinus resinosa Ait.) stands was more important than the residual density after thinning, suggesting stand structure is an important variable. The importance of stand structure in thinning Douglas-fir stands has also been stressed by Oliver and Murray (1983).

The Langsaeter/Moller theory has had a strong influence over density/growth silvicultural research in Douglas-fir stands in the
Pacific Northwest (Staebler 1959, 1960). Several thinning studies in Douglas-fir stands have attempted to identify the range of density where production is constant (e.g., the levels-of-growing-stock study, see Williamson and Staebler 1965, Williamson and Curtis 1984; Curtis and Marshall 1986).

Douglas-fir Thinning Studies

Some major thinning studies in Douglas-fir have shown that total production or gross increment (volume increment plus volume removed in thinnings and mortality) between thinned and unthinned stands is nearly equal. The Voight Creek thinning study (Worthington et al. 1962; Reukema 1972; King 1986) found gross increment in one of three thinned treatments to exceed the gross increment of the unthinned treatment (differences were not significant). Two other thinned treatments produced less gross increment, but were not significantly less than the unthinned treatment (King 1986). Despite the similarity between gross increment among treatments, Reukema (1972) concluded gross increment was reduced substantially by thinning, since the ratio of gross increment to pretreatment volume was lower in thinned treatments than in unthinned treatments. Net increments (gross increment less mortality) of all three thinning treatments exceeded those of the unthinned treatment.

At the Camp 6 thinning study (Oliver and Murray 1983; King 1986), gross volume increment was not significantly different among two thinned treatments and the unthinned treatment. Net increments were higher in three of four thinning treatments than in the unthinned treatments.
Warrack (1959, 1979) reported no important differences between gross production of four thinned treatments and an unthinned treatment at the Cowichan Lake thinning study. Gross increment actually varied by as much as 20% among plots, but Warrack (1979) attributed the variations to differences in site productivity and concluded that no differences in gross increment existed.

In a stand first thinned at age 60, Worthington (1966) reported gross increment from a moderately thinned treatment was only slightly reduced as compared to the unthinned treatment. A heavily thinned treatment had substantially less gross increment. Net increment was highest in the moderately thinned treatment and lowest in the heavily thinned treatment.

Reukema and Pienaar (1973) found about a 10% decrease in gross increment from a thinned treatment as compared to an unthinned treatment. Stand age was 57 years at the beginning of their 15 year study, and the initial thinning removed larger trees in favor of smaller trees. Net increment was slightly higher in the thinned treatment.

Lee and Barclay (1985) reported little difference in gross increment between unfertilized thinned and unthinned plots in a combined thinning/fertilization study in British Columbia. Net increment was higher in thinned plots.

In the levels-of-growing-stock study (Williamson and Staebler 1965, 1971), early results indicate decreased gross volume increment in thinned treatments as compared to the unthinned treatment (Tappeiner et al. 1982; Williamson and Curtis 1984; Curtis and Marshall 1986).
Little evidence of a constant level of gross volume increment is evident over the growing-stock levels represented by the treatments; however, the thinnings have removed some upper-canopy trees, and the stands were thinned at very frequent intervals.

In general, results from thinning studies in the Douglas-fir region have been mixed. Some researchers have reported substantial reductions in gross increment, especially among treatments at fairly wide spacings (Worthington 1966; Reukema 1972; Reukema and Pienaar 1973; Williamson and Curtis 1984; Curtis and Marshall 1986). Resultant thinning guidelines (Heiberg and Haddock 1955; Worthington and Staebler 1961; Reukema and Bruce 1977) have emphasized economic reasons to thin. Among these reasons are: harvesting mortality, faster individual tree growth rates, and greater merchantable yields. Most studies, however, have found comparable gross increments from thinned and unthinned stands, at least from among the more narrowly-spaced thinned stands. Williamson (1982) attributed the discrepancy in results from thinning studies to differences in initial stand density, growing-stock levels, stand structures, and "semantic ambiguities in terms such as heavy thinning and light thinning."

Stand Density Measures

Forest stands require long periods of time for development, and differential growth rates and mortality within a stand create conditions where individual trees require ever-increasing and overlapping amounts of growing space. Stand density measures express the average level of competition or crowding in a stand. Stand density
measures assume the effects of uneven spacing and stand differentiation on stand growth are proportional to growing space and can therefore be averaged. For example, if two-thirds of the trees on a given area are concentrated on half of that area, stand density measures assume the below-average individual tree growth on the crowded area will be compensated by above-average growth on the other area. While this is a gross example of the variation in density over a given area, less pronounced variations occur. Even in an evenly-spaced plantation differentiation of crown classes eventually leaves the less vigorous trees in subordinate positions to more vigorous trees. The growing space for each individual tree therefore varies, with some below and some above the average.

Stand density is expressed in many different forms which can be grouped into two categories: absolute and relative stand density measures. Absolute stand density measures are simple counts of the number of trees, or totals of basal area or volume per unit area. Number of trees, although a common ecological measure of density (Harper 1977), is of limited use because it reveals little about the stand without additional information concerning site productivity, stand age or tree size. Likewise, measures such as basal area or volume provide some information on stand development and tree size, but reveal relatively little, by themselves, about competition (Spurr 1952; Bickford et al. 1957; Curtis 1970, 1971; Ernst and Knapp 1985).

Relative stand density measures are expressions of cumulative competition effects on average tree development (Curtis 1970). They can be thought of as expressing density as a combination of number of
trees or basal area in relation to a measure of stand development or average tree development. Some relative density measures are indexed to the density of a similar stand at some standard level of competition. This standard level of competition or reference level is usually either the normal (i.e., fully stocked) stand (e.g., Reineke 1933), maximum size-density stand (e.g., Drew and Flewell 1979), or open-grown stand condition (e.g., Krajicek et al. 1961). As comparisons with normal stands or the maximum-density condition, these measures express the cumulative effects of competition. The open-grown condition assumes no prior competition but full occupancy of open-grown trees at present.

One well accepted prerequisite of a stand density measure is independence from stand age and site quality (Bickford et al. 1957; Curtis 1970; Ernst and Knapp 1985). For example, a stand density measure should provide the same value of density for a 20-year-old stand and a 100-year-old stand, regardless of site, if both stands are in the same state of competition (Bickford et al. 1957; Curtin 1964; Ernst and Knapp 1985). For this reason, relative stand density measures are preferable to absolute density measures.

The independence of site and age is achieved through the expression of density in relation to some measure of stand development. Common measures of stand development in relative stand density measures include quadratic mean diameter, mean tree volume, dominant height, and others. Stands are assumed to develop in similar patterns regardless of site quality. Although stands on different sites will grow at different rates, the measures of stand development are assumed to be
equally applicable to young and old stands, and to stands on both good and poor sites. The use of these measures of stand development, therefore, precludes the use of age as a variable in relative stand density measures.

In fully stocked even-aged stands the relationship between stand development or average tree development (using many different variables) and absolute density appears linear in logarithmic coordinates. This linearity is convenient for indexing the measure to a standard linear condition, but subsequently lower relative densities may not necessarily reflect proportionally lower levels of competition. For example, each relative density level using Drew and Flewelling's (1979) relative density index implies equal levels of competition despite widely different size-density combinations and stand ages. Curtin (1964) and Gingrich (1967) indicated the curves for average maximum and average minimum tree area (or growing space) are proportional (see Curtis 1970), but whether parallel curves between these two relationships define proportional levels of competition for thinned stands is uncertain.

Types of Relative Stand Density Measures

Relative stand density measures have been described as approximately equivalent expressions of average area -- or growing space -- available per tree (Curtis 1970, 1971). Curtis based his analysis on two assumptions: tree area (i.e., growing space) is proportional to crown projection area and to diameter; and differences in measures of stand development can be overcome by relating these measures of stand development to each other and to some common measure of tree area.
through various allometric relationships.

West (1983) compared a wide variety of stand density measures and found that density measures using a common measure of stand development varied only slightly in their expression of density. When a different measure of stand development was used, however, the variation in density was much larger. West (1983) grouped relative stand density measures into three groups based on their respective measures of stand development: a) diameter-based measures; b) volume-based measures; and c) height-based measures. Curtis (1971) divided density measures into similar groupings, but compared fewer density measures.

Diameter-based stand density measures are the most common type of relative stand density measure although the actual form of the relationship can vary considerably. Among the more common diameter-based measures are Reineke's (1933) stand density index, Chisman and Schumacher's (1940) tree area ratio, Krajicek et al.'s (1961) crown competition factor, and Curtis' (1982) relative density index. The Douglas-fir thinning guideline developed by Reukema and Bruce (1977) also uses a diameter-based measure of stand density and is similar to the density guideline developed by Gingrich (1967) for upland hardwood stands.

The most common form of a diameter-based stand density measure uses number of trees as the measure of density and stand basal area or quadratic mean diameter as the measure of stand development. Reineke's (1933) stand density index uses quadratic mean diameter as the measure of stand development, while Curtis' (1982) relative density uses the square root of quadratic mean diameter to measure stand development and
stand basal area to measure density. Other combinations of variables are also used. Sometimes these density measures are indexed to a standard reference level to make density values more comparable. For example, Reineke's stand density index is referenced (indexed) to a line which intercepts the point of 1000 trees/acre (2471 trees/ha) and 10 inches (25.4 cm) diameter (bh), and is parallel to the maximum size-density curve.

Volume-based stand density measures generally combine mean tree volume as the measure of stand development with number of trees to represent density. Drew and Flewelling (1979) developed a relative density index for Douglas-fir, similar to a system developed by Tadaki (1964), which uses mean tree volume and number of trees. Drew and Flewelling indexed their relative density measure to the maximum size-density relationship.

Expressions relating density to height comprise the height-based stand density measures. These measures apparently originated in Europe (Day and Bennett 1962), with the first use in the United States by Wilson (1946) in red pine stands. Density is expressed as trees per unit area, and the top height or height of dominants is used as the measure of stand development. Hummel (1954) developed an index system where the reference level was represented by a spacing of 20% of height and was designated unity. Other densities were represented by the ratio of the number of trees in the stand to the number of trees in a stand of equivalent height at the 20% of height reference level. For example, a density index of 2.0 had twice as many trees for a given top height as a stand with a density index of 1.0.
With the exception of the height-based stand density measure, relative stand density measures are size-density relationships using different measures of average tree size. Density and average tree size are linear in logarithmic coordinates for these size-density relations, but the slopes of the relationships will vary with the variables used (Mohler et al. 1978). Dominant height is not a measure of average tree size, but density/dominant height relationships in Douglas-fir do appear to approach a maximum that is linear in logarithmic coordinates (King 1970).

Other types of stand density measures exist which do not fit the classification described above. These measures may combine several variables to represent stand development, but they are otherwise similar to the measures described in this study. Examples include density measures formulated by Briegleb (1952) and Curtin (1964).

Several studies have compared density measures and have indicated they do provide different values for density (Briegleb 1952; Day and Bennett 1962; Curtis 1971; Daniel et al. 1979; West 1983; Larson and Cameron 1986), especially between height, diameter, and volume-based relative density measures (Curtis 1971; West 1983). Their differences indicate some density measures probably describe competition more accurately than others.

Stand Development Measures and Stand Density

Oliver (1981) described natural, even-aged stand development as the changes occurring in forest stand structure over time and consisting of four broad stages: 1) stand initiation, 2) stem exclusion, 3) understory
reinitiation, and 4) old-growth. These changes in structure are related to stand density because stem exclusion and understory reinitiation are largely density-controlled processes. These stages are not equivalent to relative density, nor is stand development in general equivalent to relative density as has been assumed on occasion.

Stand development is more closely related to stand age or physiological age, and more closely approximates the stand development variable in a relative density measure, instead of relative density itself. It is proposed here that Oliver's (1981) stages of stand development should refer to stands undergoing density-dependent changes in structure over time, and not to comparisons of stands of equal age and widely different densities. Oliver et al. (1986) proposed three phases of growth through which stands develop: an open-grown phase; a plastic phase; and a stagnation/mortality phase. These phases of growth, or competition phases, are closely related to relative density and correspond to relative densities estimated by Drew and Flewelling (1979) to represent crown closure and the zone of imminent competition mortality. The crown closure line separates the open-grown phase from the plastic phase, while the zone of imminent competition mortality is analogous to the stagnation/mortality phase.

The measures of stand development in relative stand density measures are quite variable in regard to their independence from the effects of density and their sensitivity to site quality. Dominant height, for example, is largely independent from the effects of density in conifer stands (Sjolte-Jorgensen 1967). Its sensitivity to site quality is also well-recognized and, in combination with its
independence from density, is the basis for site index determination in forest stands. In combination with density in a relative stand density measure, height forms a measure of density which is independent from site and age.

Diameter growth (and basal area growth), in contrast to height growth, is very sensitive to changes in density. In fact, the major effects of density adjustments are to affect diameter growth rates (Assmann 1970; Smith 1986). Since diameter growth is affected by thinning, using diameter as the stand development component will lead to variable rates of development under different thinning intensities. Volume growth, being a function of both diameter and height, is intermediate between the two variables in its response to thinning.

Whether the stand development component of a stand density measure should be independent of the effects of density is uncertain. Wilson (1946, 1979) and Hummel (1954) have questioned the use of variables such as diameter and volume as gauges of stand development for comparing the effects of density, since these variables are sensitive to density. Most relative stand density measures, however, use variables to measure stand development, such as diameter and volume, which are affected by stand density.

Using average tree measurements to represent the stand development component in relative stand density measures assumes a stand instantaneously declines in development when thinned from above, or increases to a later stage of development (i.e., false increment) if thinned from below. While this assumption is justified to some extent it implies that a stand, after being thinned from below, is
further developed than before thinning despite existing at a lower level of competition. Height-based stand density measures, which use dominant height to measure stand development, are only applicable to stands thinned from below; but stands exist at the same stage of stand development before and after thinning.

STAND STRUCTURE AND GROWING SPACE EFFICIENCY

Stand structure has been defined as the distribution of tree sizes, ages, and species in a stand (Smith 1962; Assmann 1970; Husch et al. 1982) and is best indicated by the profile of the tree crowns (Smith 1962). In single-species, even-aged stands, stand structure is most often represented with a diameter frequency distribution. Diameter distributions are generally more sensitive to varying stand densities than are height distributions, another representation of stand structure, because of the relative independence of height growth to stand density. Diameter measurements are also easy to obtain, especially compared to height measurements.

The diameters of older even-aged stands (sufficiently old that the diameter distribution is in the positive range of the ordinate) are generally clustered around the mean with distributions that can be represented by a variety of distribution functions. Measures of variation, kurtosis and skewness serve as parameters from which to compare the structures of different stands. Many studies have found that these parameters are more closely related to average tree diameter than to stand age or site quality (Schumacher 1928, 1930; Meyer 1930;
Schnur 1934; Gingrich 1967). Average tree diameter has, therefore, also become a measure of stand structure.

Gingrich (1967) has described a scenario in which stands with very different stand structures (one bimodal diameter distribution, the other normal) but with equivalent stocking, average diameters, and coefficients of variation can produce equal volumes. Stands with equal stocking but with different average diameters and coefficients of variation were described as having different volume productions. Such an analysis is based on the assumption that growing space per tree is proportional to diameter, even in stands with different stand structures (but with equivalent sites, ages and species compositions). Also inherent to this analysis is the assumption that growth per unit of growing space is relatively constant, or trees of given diameter will produce the same amount of volume in stands with different structures.

Growing space refers to the availability of all of the resources needed by a tree to exist on a given site. A limitation of just one of these resources, however, may limit the growing space and also the growth of the tree (Smith 1986). The growth of the tree, therefore, may serve as an indication of its available growing space.

In thinning considerations, the role of stand structure concerns the selection of which trees to remove. Removing trees from the lower crown classes, for example, leaves the stand with a larger average tree diameter and a negatively skewed diameter distribution, while removing trees from the upper crown classes has the opposite effect.

Guidelines for thinning Douglas-fir stands treat stand structure as being of secondary importance to that of stand density. These
guidelines for thinning Douglas-fir stands usually define proper residual stand structures with the ratio of average diameter of cut trees (d) to average diameter of all trees before thinning (D) (Reukema and Bruce 1977), or simply by removing trees from lower crown classes first and trees from upper crown classes only to meet density objectives (Worthington and Staebler 1961; Harmon 1969).

Crown Classification and Stand Structure

Classification of trees into crown classes (Smith 1986) provides a means to describe the relative position and size of tree crowns, and the structure of the stand. The crown provides the photosynthetic machinery for tree growth, and the relative position and size of this crown should be related to tree growth. Assigning a tree to a crown class is a subjective decision, however, and is based on the relative level of differentiation in a particular stand. For example, Curtis and Reukema (1970) observed that mean trees of a particular crown class in Douglas-fir stands of different initial densities possessed widely different crown characteristics which were closely related to initial density. Dominant trees in narrower spacings had crown widths and lengths more similar to intermediate trees in the wider spacings than to the dominant trees.

In natural Douglas-fir stands, where stand establishment takes place over a period of several years, crown position is probably related to tree age since older trees may have larger crowns and root systems (Krueger 1967). Movement in crown class is generally downward as Douglas-fir stands develop, with increasingly fewer trees occupying each
crown class (Guillebaud and Hummel 1949; Warrack 1952; Krueger 1967; Oliver and Murray 1983). Mortality generally occurs in the smallest individuals in forest stands during any given time period (Yoda et al. 1963; White and Harper 1970; Ford 1975; Mohler et al. 1978). Warrack (1952) observed a greater stability in the dominant crown class as Douglas-fir stands develop that was manifested by high mortality in lower crown classes and increasingly greater percentages of trees in the dominant class in thinned and unthinned stands. Favoring the dominant trees during thinning may therefore be thought of as accelerating the attainment of dominance of forest trees (Warrack 1952; Smith 1986), or accelerating the process of natural stand development (Assmann 1970; Smith 1986).

In a study comparing the individual tree growth rates of different crown classes in thinned and unthinned Douglas-fir stands, Oliver and Murray (1983) found dominants and codominants produced more volume per tree and per unit of basal area than trees from lower crown classes. They concluded crown classes provided a reliable method for describing stand structure. Greater response to thinning in upper crown classes has also been observed in Douglas-fir stands by Ker (1953), Steele (1955), Staebler (1956), Krueger (1959), and Reukema (1961a).

Comparing trees of different crown classes on a per tree basis may not reflect the varying amount of growing space occupied by trees of different crown classes. A better comparison would be the ratio of volume growth per tree to some measure of growing space. For example, if two intermediate trees occupy the same amount of growing space as one dominant tree and produce the same amount of wood volume as the dominant
tree, then, with all economic considerations aside, the intermediates are just as efficient as the dominant tree.

Measures of Growing Space - Crown Projection Area

Growing space for individual trees is usually defined in horizontal dimensions such as available ground surface area or crown projection area (Spurr 1952; Assmann 1970). Crown projection area, the most common measure of growing space, is roughly proportional to spacing in single-species stands with closed canopies, since crown overlap is relatively small (especially with a species such as Douglas-fir which is relatively intermediate in shade tolerance). Some researchers have found that root extension in Douglas-fir was proportional to crown size (McMinn 1963; Smith 1964), but the greater degree of root overlap (compared to crown overlap), root grafting (Eis 1970), and differences in root biomass related to site quality (Keyes and Grier 1981) make this a questionable assumption.

Crown width has been found to be proportional to tree diameter in open-grown trees of a number of species (Krajicek et al. 1961), including Douglas-fir (Smith et al. 1961; Newnham 1964; Smith and Bailey 1964). In fact, some measures of stand density are direct efforts to relate tree area, through diameter, to some standard tree area or crown projection area such as that of the open-grown tree or a normal stand tree with an equivalent diameter (Chisman and Schumacher 1940; Krajicek et al. 1961). Curtis (1970, 1971) has described many different stand density measures as being approximately equivalent expressions of average tree area or crown projection area.
Crown projection area only describes the growing space of a tree in two dimensions without regard to crown length, crown position, or other competitive processes. It is generally assumed that trees have unlimited vertical above-ground growing space, and are limited only by horizontal or lateral competition (Assmann 1970). As stands develop and trees differentiate, however, a dominant tree can easily usurp the sunlight of a suppressed tree by increasing in height and without expanding laterally. For the suppressed tree, whose growth may be limited by a shortage of sunlight, a reduction of growth will result without a reduction in horizontal growing space. Briegleb (1952) recognized the importance of vertical crown development in assessing individual tree growing space and included both diameter and height variables in a stand density measure.

Sapwood Basal Area

Linear allometric relations between sapwood cross-sectional area at breast height and leaf biomass/leaf area (Shinozaki et al. 1964a, 1964b; Grier and Waring 1974) provide an easy method of estimating leaf area per tree for use as a measure of growing space. Leaf area provides a more three-dimensional measure of growing space than does crown projection area. On a per unit area basis in Douglas-fir stands, leaf area is sensitive to site factors (Waring et al. 1978) and to stress (Waring 1983, 1985), and it reaches and maintains a relatively constant level in undisturbed, closed stands (Turner and Long 1975).

Although leaf area apparently does reach a maximum level per unit area, use of leaf area per tree as a measure of growing space does not
translate into trees per unit area as easily as crown projection area. In the context of thinning and growing space, however, thinned trees frequently do not reclose their crowns completely and the amount of crown projection area per unit area may be substantially less than the total horizontal growing space. Leaf area may provide a better measure of crown size and photosynthetic potential, and therefore, better utilization of site resources and occupation of growing space than does crown projection area.

Brix and Mitchell (1983) questioned the applicability of the sapwood basal area/leaf area relation to thinned Douglas-fir stands, since thinned trees have greater transpiration demands and greater sapwood conductivity. Waring et al. (1982) found that sapwood cross-sectional area at the base of the crown of Douglas-fir trees provided the best estimates of leaf area, and sapwood cross-sectional area at breast height may overestimate leaf area.

Despite these shortcomings, the ratio of basal area growth to sapwood basal area (at breast height) among crown classes in an unthinned Douglas-fir stand has been used as a measure of tree vigor (Waring et al. 1980). Intermediates, codominants, and dominants had similar ratios while the suppressed crown class was significantly lower. A similar ratio has been successfully used to assess the susceptibility of lodgepole pine (Pinus contorta Dougl.) trees to bark beetle attack (Waring and Pitman 1980). These ratios have been described as indices of vigor, or measures of efficiency of use of leaf area (Waring 1983). Use as a measure of efficiency of growing space is identical, but not defined previously in these terms.
CHAPTER THREE
GENERAL PROCEDURES

BASELINE MODELS

Stand data for a variety of densities and ages for a specific site are needed to construct three-dimensional baseline models for mean tree volume and stand volume. In the present study two data sets were generated using two growth and yield models: Tree and Stand Simulator (TASS; Mitchell 1975; Mitchell and Cameron 1985), and Douglas-fir Simulator (DFSIM; Curtis et al. 1981).

These models represent two extremes of available stand simulation models for Douglas-fir. The TASS model is an individual tree, distant dependent growth and yield model which simulates the growth of individual trees within (or outside) stands. DFSIM is a whole stand growth and yield model which simulates whole-stand attributes or stand averages.

The baseline model does not provide a perfect representation of unmanaged stand growth for Douglas-fir. The lack of data for widely spaced stands and the inability of the baseline model to estimate mortality are major drawbacks. Further adjustments as additional data become available will help to construct a more accurate baseline model.
in the future.

THINNING RESPONSE

Data were required from a thinning study which represented the optimal response to thinning possible in a Douglas-fir stand. Many thinning trials exist in the Douglas-fir region; but these vary considerably with regard to study objectives, thinning methods, and length of study period. The type of thinning study which was desired would include treatments which thinned stands from below, with variable thinning intensities, over a long study period, and with an accurate record of past thinning measurements and treatments. The thinning study which best met these requirements was the Delezenne Creek thinning study.

DELEZENNE THINNING STUDY

Study Area

The Delezenne Creek thinning study was established in 1957 as a cooperative effort between Weyerhaeuser Company and the University of Washington College of Forest Resources. The study area is within the Weyerhaeuser Clemons Tree Farm (NW1/4, Sec. 25, T17N R6W, WM), south of the Chehalis River in southeastern Grays Harbor County, Washington (Figure 2). The elevation of the study area is about 60 m (200 ft.) above sea level. Slope gradients range from about 0 to 30 percent with aspects ranging from north to southwest.

The Delezenne study area lies within the Tsuga heterophylla vegetation zone (Franklin and Dyrness 1973) of the Pacific Northwest
Figure 2. Location of Delezenne study area in relation to regional and local features (insert).
that is characterized by a wet, mild, maritime climate. Precipitation in nearby Oakville (Figure 2) averages 138.6 cm (54.6 in.) per year with an average of 29.2 cm (11.5 in.) during the April through September growing season. The frost-free period averages 163 days/year with an average temperature of 15°C (59°F) (Phillips and Donaldson 1972).

The Astoria and Weikswood soil series have been identified within the study area (Steinbrenner and Duncan 1969). Both soil series are very productive for Douglas-fir, having an average site index of 42 m (140 ft. - site class I). The Astoria series is classified as a medial, mesic Andic Haplumbrepts which developed from coarse Miocene sandstones. These soils are relatively deep (total depth 100 to 150 cm - 40 to 60 in.), well-drained, and moderately fine-textured. The Weikswood series is also a well-drained, fine-textured soil developed from old alluvium overlying Miocene sandstones but exceeds the Astoria series in total depth (exceeds 150 cm - Steinbrenner and Duncan 1969).

The stand containing the study plots was of natural origin, seeding in naturally after the previous stand was harvested. The site productivity is high, with site index ranging from 41 to 45 meters (135-147 ft. - 50 year index; King 1966; Table 1).

In 1957, at the time of establishment of the study, average stand age was 36 years. The stand was nearly pure Douglas-fir but included an average of 5 red alder (Alnus rubra Bong.) per hectare. The canopy was closed, and it was noted that many trees were dying from suppression. The number of trees per hectare (based on fifth-hectare plots) ranged from about 450 to 1117 (182 to 452 trees/ac) and basal area ranged from 33.3 to 48.4 m²/ha (145 to 211 ft.²/ac - Table 1).
Table 1. Site descriptions of the 16 Delezenne study plots. Slope gradients ranged from 0 to 30% over the study area. Values in parentheses are in English units.

<table>
<thead>
<tr>
<th>PLOT</th>
<th>TREATMENT</th>
<th>ASPECT</th>
<th>SITE INDEX M - 50 YR (ft)</th>
<th>DENSITY IN 1957 TREES/HA (trees/ac)</th>
<th>BASAL AREA IN 1957 M²/HA (ft²/ac)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>CONTROL</td>
<td>NW</td>
<td>43.0 (141)</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>2</td>
<td>CONSTANT BA</td>
<td>NE</td>
<td>41.1 (135)</td>
<td>583 (236)</td>
<td>40.2 (175.1)</td>
</tr>
<tr>
<td>3</td>
<td>CONSTANT BA</td>
<td>SW</td>
<td>43.0 (141)</td>
<td>539 (218)</td>
<td>36.9 (160.7)</td>
</tr>
<tr>
<td>4</td>
<td>DECREASING-INCREASING BA</td>
<td>NE</td>
<td>41.1 (135)</td>
<td>450 (182)</td>
<td>33.3 (145.0)</td>
</tr>
<tr>
<td>5</td>
<td>DECREASING-INCREASING BA</td>
<td>SW</td>
<td>42.1 (138)</td>
<td>519 (210)</td>
<td>41.7 (181.6)</td>
</tr>
<tr>
<td>8</td>
<td>DECREASING-INCREASING BA</td>
<td>NW</td>
<td>43.9 (144)</td>
<td>870 (352)</td>
<td>40.2 (175.2)</td>
</tr>
<tr>
<td>9</td>
<td>DECREASING-INCREASING BA</td>
<td>NW</td>
<td>42.1 (138)</td>
<td>1117 (452)</td>
<td>47.6 (207.4)</td>
</tr>
<tr>
<td>10</td>
<td>CONSTANT BA</td>
<td>NW</td>
<td>43.0 (141)</td>
<td>870 (352)</td>
<td>44.1 (191.9)</td>
</tr>
<tr>
<td>11</td>
<td>CONSTANT BA</td>
<td>NW</td>
<td>43.9 (144)</td>
<td>810 (328)</td>
<td>46.0 (200.5)</td>
</tr>
<tr>
<td>12</td>
<td>INCREASING BA</td>
<td>NW</td>
<td>43.9 (144)</td>
<td>840 (340)</td>
<td>48.9 (212.9)</td>
</tr>
<tr>
<td>13</td>
<td>INCREASING BA</td>
<td>NW</td>
<td>43.9 (144)</td>
<td>850 (344)</td>
<td>45.1 (196.3)</td>
</tr>
<tr>
<td>14</td>
<td>CONTROL</td>
<td>FLAT</td>
<td>43.8 (144)</td>
<td>796 (322)</td>
<td>46.6 (203.0)</td>
</tr>
<tr>
<td>15</td>
<td>CONTROL</td>
<td>FLAT</td>
<td>44.2 (145)</td>
<td>486 (197)</td>
<td>41.4 (180.3)</td>
</tr>
<tr>
<td>16</td>
<td>CONTROL</td>
<td>FLAT</td>
<td>44.8 (147)</td>
<td>667 (270)</td>
<td>43.6 (189.9)</td>
</tr>
</tbody>
</table>
The study plots were fifth-hectare (half-acre) in size and established in two major clusters separated by about 400 m (1300 ft.) of unthinned stand (Figure 3). Plots were paired with adjoining plots of the same treatment, and treatments were separated by 10 to 12 meter-wide thinned buffer strips.

Thinning Treatments

All thinnings in the Delezenne study were to prescribed levels of basal area, which varied with time and treatment. The treatments ranged from a severely thinned decreasing-increasing basal area treatment to unthinned controls. The decreasing-increasing treatment (treatment D) was applied to plots 4, 5, 8, and 9 (Figure 3). It consisted of relatively heavy removals during early thinnings and very light removals in later thinnings (Figure 4). The constant basal area treatment (treatment C) was applied to plots 2, 3, 10, and 11, and consisted of thinnings designed to maintain a relatively constant basal area \(2\) (approximately 32 m \(^2\)/ha) throughout the study. Plots 12 and 13 (and later plots 6 and 7) were thinned with an increasing basal area treatment (treatment B) that consisted of relatively light thinnings and increasingly higher levels of residual basal area.

Plots 6 and 7 were designated as control plots (unthinned) but some unauthorized cutting early in the study precluded their use as controls. Plots 6 and 7 were thinned subsequently with an increasing basal area treatment similar to plots 12 and 13. Since existing information on this first removal is sketchy, and since plots 6 and 7 did not follow any prescribed thinning schedule, these plots were included in this
Figure 3. Plot layout map for the Delezenne study plots. Not shown are three control plots (plots 14-16) which were located to the east of the primary study area.
Figure 4. Residual levels of basal area for the four thinning treatments in the Delezenne thinning study. Treatment A was the control treatment, B was an increasing basal area treatment, C was a constant residual basal area treatment, and D was a decreasing then increasing basal area treatment.
study only as control plots from 1957 through 1961.

Three additional control plots (treatment A) from a nearby stand of similar origin were used for control data. These plots were 0.232 ha (0.57 ac.) in size and located east of the primary study area (not shown in Figure 3). Stand age in 1957 ranged from 35 to 37 years for the three control plots. They were harvested in 1983 prior to the post-1984 growing-season measurements. These plots are designated as plots 14, 15 and 16 in this study.

Dominant and well-spaced trees were identified as crop trees and marked early in the study. All trees were numbered and larger trees were pruned to a height of approximately 5 or 6 m (16 to 20 ft.) in 1957. Thinnings removed trees in lower crown classes to promote the growth and development of crop trees and other unthinned trees. Thinnings could therefore be characterized as low thinnings, although some larger trees were removed in later thinnings in the decreasing-increasing and constant basal area treatments to meet residual basal area objectives.

Five thinning entries were made during the study: however, not every plot in the thinning treatments was thinned at each entry. Plots were measured prior to each entry and five additional times, including the last measurement after the 1984 growing season. The length of the study was, therefore, 28 years. Thinning entries were made in 1957, 1961, 1967, 1973 and 1980. Other measurements were made in 1958, 1960, 1969, 1972 and 1984. The control plots (plots 14, 15 and 16) were measured in 1957, 1964, 1969, 1974 and after the 1980 growing season.
CHAPTER FOUR

BASELINE VOLUME GROWTH MODEL

HYPOTHESES

The objectives of this chapter are to: 1) determine if a response surface based on three variables -- stand age, number of trees, and either mean tree volume or stand volume -- can represent a baseline level of volume growth for unthinned Douglas-fir stands; and 2) determine if this baseline model can be used to compare growth and yield models and to analyze the effects of thinning treatments on stand volume growth. To accomplish these objectives the following hypotheses will be tested:

1) A three-dimensional response surface based on competition-density theory and using three variables -- stand age, number of trees, and either mean tree volume or stand volume -- can represent a baseline level of volume growth for unthinned Douglas-fir stands;

2) Existing Douglas-fir growth and yield models, as represented by three-dimensional baseline models, produce similar growth estimates for even-aged stands on a particular site; and

3) Permanent plot data from thinned and unthinned Douglas-fir stands will, on the average, correspond closely with baseline models
constructed with data from growth and yield models.

METHODS

Baseline Models

Graphical representations of the three-dimensional model were produced with Surface II (Sampson 1978), a software graphics package on the University of Washington's Cyber computer system. Surface II has the ability to construct a grid matrix from non-uniform, spatially distributed data using a variety of algorithms to interpolate between data points.

Stands simulated with the TASS model in the present study were planted to a variety of densities with the exception of the most dense stand (established at 4440 trees/ha), which was assumed to be regenerated naturally. TASS replaces age in the usual North American yield table format with top height, under the assumption that stands with a given top height and density have equal volumes regardless of age and site quality (Assmann 1970). Age can be determined through site index/age relationships for a specific site quality. In the present study, tables in Mitchell and Cameron (1985) produced from the site index relationships of Bruce (1981) were used to estimate stand age, which was then converted to breast height age. Breast height age was assumed to be 6 years less than total age for site index 44 meters (144 feet) at 50 years (King 1966; Bruce 1981; Mitchell and Cameron 1985). The three-dimensional model constructed with the TASS data therefore corresponded in site quality to that of the Delezenne study site.
DFSIM can generate yield tables both for managed and unmanaged, and for planted and natural stands. In the present study, yield tables were produced for stands planted to a variety of densities with no subsequent treatments thereafter. Site index was assumed to be 44 meters (144 feet) at 50 years (Bruce 1981), the same site index as the Delezenne study site.

Two grid matrices were generated from each of the TASS and DFSIM data sets: one each for mean tree volume and whole stand volume. The data sets consisted of simulation runs from the growth and yield models for stands of various initial densities. The simulation runs provided the number of trees, age, and stand volume for the simulated stands. A grid matrix consisted of number of trees or density (the $x$ variable) and age (the $y$ variable) with either mean tree volume or stand volume on the $z$ axis. Number of trees, mean tree volume, and whole stand volume were transformed with natural-log transformations in all grid matrices.

The TASS data set ranged in density from 50 to 4440 trees/ha, and in breast height age from 0 to 79 years. The grid matrix generated for mean tree volume ranged from about 55 to 4915 trees/ha and from 0 to 80 years, breast height age. The DFSIM data set ranged from 247 to 7413 trees/ha and from 9 to 94 years old at breast height. Both the DFSIM mean tree volume and the DFSIM whole stand grid matrices ranged from 245 to 8100 trees/ha, and in breast height age from 10 to 90 years for the mean tree matrix and 10 to 100 years for the whole stand matrix. Density values from the grid matrices were rounded to the nearest whole multiple of 5 after an inverse-logarithmic transformation from the log-density values used in the grid matrix generation (e.g., $\log^{-1} 4 = 54.6$
55 trees/ha).

The grid matrices were constructed by interpolating from a specific age and density (a grid node) to the nearest data points to determine the value of the z variable (either mean tree volume or whole stand volume). An algorithm was used to calculate the grid nodes using a weighted average of the four nearest data points from the grid node. Inverse distance to the 6th power (1/d) was used as the weighing function to weigh most heavily those points closest to the grid node.

The decline in density with age in the simulated stands left a major void in the rectangular grid matrices at high densities and older ages (Figure 5). While the simulated stands did not occupy this area, it is theoretically possible for stands in a stagnated condition to occur with high densities and at older ages, but relatively low volumes. Therefore, data were added to the TASS and DFSIM data sets for stands at high densities and older ages to complete the grid matrices. These data included stand volumes for a specific density which were equal to the largest stand volume observed in the simulated stands for that density. The stands that these data represented were assumed to exist at constant densities and constant stand volumes (and therefore constant mean tree volumes) and to change only in age.

Delezenne Study

Measurements taken in the Delezenne study included diameter breast height (dbh) of all plot trees and total tree heights of a subsample of trees in each plot. The number of height trees per plot ranged from 7% to 39% of the total number of trees in each plot during the 28 year
Figure 5. Simulated DFSIM stands and their decline in density with stand age (at breast height).
study period. Heights of remaining trees were then estimated from dbh using fitted regression equations of the form:

\[ \text{height} = a - b \times (\text{dbh}^{-.5}) \]

Equations were fitted from groups of neighboring plots such that a single height/dbh equation for each measurement represented plots 2 through 5, 6 through 9, and plots 10 through 13, respectively. These height/dbh equations were used to predict tree height for individual plot volume totals.

Individual tree cubic foot volumes were estimated using a volume equation for second-growth Douglas-fir developed by Bruce and DeMars (1974) and converted to cubic meters. The crown-class of each tree was also recorded at each measurement, as were descriptions of the condition of the bole (e.g., forks, crooks, etc.) and the amount and type of tree injury (e.g., logging, weather, etc.), if any.

RESULTS  
Mean Tree Baseline Models

The three-dimensional baseline models for mean tree volume for the TASS and DFSIM data sets are shown in Figures 6 and 7. The models are similar in many respects, but differ in the range of spacings included in the models. The TASS mean tree model (Figure 6) indicates lower mean tree volumes at older ages than the DFSIM model, reflecting the wider spacings represented by the TASS data. The mean tree volumes indicated by the DFSIM mean tree volume model (Figure 7) increase with decreasing density throughout the entire range of data; however, densities below
Figure 6. TASS mean tree volume baseline model. The density and volume axes have a logarithmic scale while the age axis is linear.
Figure 7. DFSIM mean tree volume baseline model. The density and volume axes have a logarithmic scale while the age axis is linear. The DFSIM baseline model showed no evidence of leveling-off within the range of density of the model.
approximately 250 trees/ha are not included in this model. Both data
sets conform to the self-thinning rule (Yoda et al. 1963) and,
therefore, so do the baseline models. The similarities of these figures
and their conformance to the self-thinning rule support the first
hypothesis that a three dimensional response surface based on
competition-density theory and using three variables -- stand age,
number of trees, and either mean tree volume or stand volume -- can
represent a baseline level of volume growth for unthinned Douglas-fir
stands.

The broad area with the constant slope at higher densities and
older ages has approximately a -1.5 slope relative to the density and
mean tree volume axes. While it is unlikely that any stand would exist
at the combination of age, density, and mean tree volume that is
represented by this broad area of constant slope, stands in a stagnated
condition could exist with these characteristics. The mean tree volume
of these stands, and the size of any individual tree, would
theoretically only increase with a decrease in stand density.

On both baseline models, the lines running in the same direction as
the density axis represent the range of mean tree volume/density
combinations possible for a particular stand age (hence they are called
constant-age lines). These lines are shown as viewed from the side for
both the TASS mean tree model (Figure 8) and the DFSIM mean tree model
(Figure 9). The lines running in the same direction as the age axis
(constant-density lines) represent the range of mean tree volume/age
combinations possible for a specific stand density. A stand growing
without mortality would theoretically follow these constant-density
Figure 8. Constant-age (left) and constant-density lines (right) for the TASS mean tree volume baseline model.
Figure 9. Constant-age (left) and constant-density lines (right) for the DFSIM mean tree volume baseline model.
lines. This stand would become stagnant relatively soon at a narrow spacing and later, if at all, at a wider spacing.

The mean tree volumes indicated by the two mean tree models are similar throughout most of the range of ages and density in which the two baseline models coincide. At the lower densities and older ages, however, the DFSIM baseline model (Figure 6) indicates higher mean tree volumes than the TASS baseline model (Figure 7). The difference between the baseline models at lower densities and older ages is somewhat masked by the logarithmic transformations performed on the data. For example, at 80 years and at a density of 245 trees/ha, the DFSIM baseline model indicates a mean tree volume of \(3^{3} 6.05 \text{ m}^3\) (213.8 ft\(^3\)), while TASS indicates a mean tree volume of \(3^{3} 4.81 \text{ m}^3\) (170.0 ft\(^3\)) for the same age and density. At 40 years of age and a density of 400 trees/ha DFSIM indicates a mean tree volume of \(3^{3} 1.65 \text{ m}^3\) (58.2 ft\(^3\)) while TASS indicates \(3^{3} 1.66 \text{ m}^3\) (58.6 ft\(^3\)).

Whole Stand Baseline Models

The general appearances of the whole stand models for the TASS and DFSIM data sets are quite different, in part because of the different ranges of stand density in each data set. The TASS baseline model indicates a peak in stand volume of \(3^{3} 1383 \text{ m}^3/\text{ha}\) (19771 ft\(^3\)/ac) at about 400 trees/ha from about age 55 and older (Figure 10). A sharp decline in stand volume occurs at densities lower than 400 trees/ha with a stand volume of \(3^{3} 275 \text{ m}^3/\text{ha}\) (3937 ft\(^3\)/ac) at a density of 55 trees/ha at 80 years. Several of the constant-age and constant-density curves for the TASS whole stand model are shown in Figure 11. The constant-age curves
Figure 10. Two views of the TASS whole stand volume baseline model. The density and volume axes are logarithmic while the age axis has a linear scale.
Figure 11. Constant-age (left) and constant-density (right) lines for the TASS whole stand volume baseline model. Note the stand volume scale is logarithmic.
for younger stands generally decline with decreasing density, but at older ages they peak at lower than maximum densities. The shape of the constant-density curves varies with density. The narrowly spaced stands increase in volume rapidly, and then level off abruptly if they become stagnated. The widest spaced stands increase in volume relatively slowly but appear as if they will eventually surpass the narrowly spaced stands in total volume. The 400 tree/ha stand density surpasses the higher densities when the higher densities become stagnated, and the lower densities do not reach the level of the 400 trees/ha stand within the age range of the model.

The DFSIM whole stand model peaks in stand volume at $1677 \text{ m}^3/\text{ha}$ (23966 ft$^3$/ac) at age 100 and a density of approximately 245 trees/ha (100 trees/ac - Figure 12). Unlike the TASS whole stand model, the DFSIM model shows no appreciable decrease in volume with decreasing densities at older ages. This difference between the models is largely the result of the TASS data encompassing much lower densities than the DFSIM data. Widely spaced stands will have less volume than narrow spacings at younger stand ages. Constant-age lines for the DFSIM whole stand model (Figure 13) range from decreasing stand volume with decreasing density at young ages to increasing stand volume with declining density at older ages. Much of the range of density in the older stands shown in Figure 13 does not come from the simulated stands, but is from the data added to complete the grid matrix. For example, the simulated stands in the DFSIM data set range in density from just 193 to 526 trees/ha (78 to 213 trees/ac) at age 70 (Figure 5).

The large differences between the TASS and DFSIM baseline models at
Figure 12. DFSIM whole stand volume baseline model. The density and volume axes are logarithmic while the age axis is linear.
Figure 13. Constant-age (left) and constant-density (right) lines for the DFSIM whole stand volume baseline model. Note the stand volume scale is linear.
low densities and older ages do not support the second hypothesis that existing Douglas-fir growth and yield models, as represented by three-dimensional baseline models, produce similar growth estimates for even-aged stands on a particular site. At least one of the growth and yield models is forecasting incorrectly the growth and development of Douglas-fir stands under the conditions tested in this study.

Delezenne - Baseline Model Comparisons

Comparisons between the baseline models and the Delezenne study control plots showed some similarity. The three Delezenne control plots grew at different densities throughout the study period but were all relatively close to the surface of the mean tree volume models (Figures 14 and 15). Plot 15, the least dense of the control plots, had a mean tree volume of 0.95 m$^3$ (33.5 ft$^3$) at age 32 compared to 0.99 and 0.93 m$^3$ (35.0 and 32.8 ft$^3$) as indicated by DFSIM and TASS mean tree models for stands of the same age and density. At age 56 plot 15 had a mean tree volume of 3.05 m$^3$ (107.7 ft$^3$) compared to 3.05 m$^3$ (107.7 ft$^3$) for DFSIM and 2.76 m$^3$ (97.5 ft$^3$) for TASS. Plot 14, the most dense of the control plots, had a mean tree volume of 0.64 m$^3$ (22.6 ft$^3$) at age 33 compared to 0.72 and 0.74 m$^3$ (25.4 and 26.1 ft$^3$) for the DFSIM and TASS models, respectively. At age 57, plot 14 had a mean tree volume of 2.47 m$^3$ (87.2 ft$^3$), while DFSIM and TASS indicated mean tree volumes of 2.37 and 2.30 m$^3$ (83.7 and 81.2 ft$^3$), respectively.

The thinned Delezenne study plots were very close initially to the surface of the mean tree volume baseline models (Figures 16 and 17), but subsequent thinning reduced density without an appreciable increase in
Figure 14. Development of the three Delezenne control plots in relation to the TASS mean tree volume baseline model. The mean tree volumes of the three control plots were very close to the surface of the TASS baseline model. All three plots were slightly higher than the constant-age curve for 60 years in the left-hand graph, and at similar mean tree volumes they closely coincided with the constant-density lines in the right-hand graph.
Figure 15. Development of the three Delezenne control plots in relation to the DFSIM mean tree volume baseline model. The mean tree volumes of the three control plots were very close to the surface of the DFSIM baseline model. All three plots were slightly higher than the constant-age curve for 60 years in the left-hand graph, and at similar mean tree volumes they closely coincided with the constant-density lines in the right-hand graph.
Figure 16. Development of three thinned plots from the Delezenne study in relation to the TASS mean tree volume baseline model. The thinned plots were below the surface of the baseline model at younger ages, but after repeated thinnings some of the thinned plots exceeded the mean tree volumes indicated by the model. Plot 5 was well above the constant-age line for 60 years in the left-hand graph, although the stand was only 59 years of age at breast height.
Figure 17. Development of three thinned plots from the Delezenne study in relation to the DFSIM mean tree volume baseline model. The thinned plots were below the surface of the baseline model at younger ages, but after repeated thinnings some of the thinned plots had mean tree volumes very similar to those indicated by the model. Complete comparisons were not possible because of the limited range of the DFSIM data.
mean tree volume, so that these stands were below the surface after the early thinnings. Repeated thinnings, however, increased mean tree volume by removing smaller trees and promoting the growth of the most vigorous residual trees, so that some of these stands eventually exceeded the indicated mean tree volumes of the unthinned stands of similar densities represented by the TASS mean tree volume model (Figure 16). Direct comparisons with the DFSIM mean tree volume model for the entire development of the thinned stands was not possible since the DFSIM model did not include densities below 245 trees/ha (99 trees/ac).

Comparisons between the Delezenne study plots and the whole stand models were very similar to those with the mean tree volume models. Figures 18 through 21 show the relationship of the Delezenne plots to the whole stand models without the logarithmic transformations of stand volume. Without the transformation, differences between the model and the study plots are more apparent.

One aspect of the third hypothesis of this chapter -- permanent plot data from thinned and unthinned Douglas-fir stands will, on the average, correspond closely with baseline models constructed with data from growth and yield models -- is supported by the similarity of the Delezenne control plot volumes and the baseline models. The high volumes of the thinned plots in relation to the baseline models, however, does not support the third hypothesis, and suggests the potential growth of thinned stands may exceed the growth of unthinned stands at similar spacings as estimated by the TASS and DFSIM growth models.
Figure 18. Development of the three Delezenne control plots in relation to the TASS whole stand volume baseline model. The mean tree volumes of the three control plots were very close to the surface of the TASS baseline model.
Figure 19. Development of the three Delezenne control plots in relation to the DFSIM whole stand volume baseline model. The stand volumes of the three control plots were very close to the surface of the DFSIM baseline model.
Figure 20. Development of three thinned plots from the Delezenne study in relation to the TASS whole stand volume baseline model. The thinned plots were below the surface of the baseline model at younger ages, but after repeated thinnings some of the thinned plots exceeded the stand volumes indicated by the model. Note the stand volume scale is linear.
Figure 21. Development of three thinned plots from the Delezenne study in relation to the DFSIM whole stand volume baseline model. The thinned plots were below the surface of the baseline model at younger ages, but after repeated thinnings some of the thinned plots had stand volumes which were very similar to those indicated by the model. Complete comparisons were not possible because of the limited range of the DFSIM data. Note the stand volume scale is linear.
DISCUSSION

Baseline Models

The three-dimensional baseline models provide a visual representation of a range of developmental patterns for even-aged Douglas-fir stands on site quality 44 meters (144 ft.). The data from which these baseline models were developed were produced with growth and yield models which simulate the growth of Douglas-fir stands established at a variety of densities. The actual growth of a stand established at a particular density will differ from the simulated stand depending on factors which are beyond the simulation capabilities of the growth model. The simulated stands can therefore be assumed to represent the average development of a stand, and the baseline models used in this study can be assumed to represent the range of average developmental patterns for stands from a range of densities on site index 44 meters (144 ft.).

The Tree and Stand Simulator (TASS; Mitchell and Cameron 1985) simulates the development of individual trees in a stand and can therefore simulate the development of stands at very low densities. The Douglas-fir Simulator (DFSIM; Curtis et al. 1981) simulates whole stand attributes or stand averages. A shortage of existing data for widely spaced stands prevents DFSIM from simulating stands at initial densities lower than 247 trees/ha (100 trees/ac). The range of densities included in the TASS baseline models extends to lower densities than those for the DFSIM baseline models, which included higher densities. The TASS baseline models also have a more limited age range than the DFSIM
baseline models.

Comparisons between the TASS and DFSIM baseline models are limited to the range of density/age combinations they have in common. Within this range the models indicate similar mean tree volumes (and whole stand volumes) except at lower densities and older ages. In this region the DFSIM baseline models indicate substantially higher mean tree volumes than the TASS baseline models. The TASS mean tree model at 80 years old indicates only slightly increasing mean tree volume at densities wider than 245 trees/ha (99 trees/ac - Figure 6), and implies that stands at these densities are experiencing little, if any, intraspecific competition. The rapid increase in mean tree volume with declining density indicated by the DFSIM mean tree volume model implies little decrease in the amount of intraspecific competition within the age/density range encountered by the model. The small decrease in intraspecific competition is evident from the upward slope of the constant-age curves with decreasing density for every age in the DFSIM mean tree volume model (Figure 7).

The whole stand baseline models provide a similar comparison between the TASS and DFSIM growth models. The TASS baseline model includes low densities which indicate substantially less volume per hectare than higher densities throughout the age range (Figure 10). The DFSIM baseline model indicates increasingly larger stand volumes as age increases and density decreases (Figure 12).

The constant-density curves for the TASS whole stand baseline model (Figure 11) indicate maximum stand volumes when density is approximately 400 trees/ha. Volume at higher densities are shown to be substantially
less, but this is the result of data added to represent the stagnated condition of stands at these densities. Mortality actually reduces stand density as mean tree volume increases, especially near the self-thinning line. Stands can only travel along the constant-density lines without mortality. Stands undergoing mortality move across the surface of the baseline models diagonally with respect to both the density and age axes (Figure 5).

It is uncertain if a stand which begins development at a high density and is reduced to a given density through mortality (self-thinning) will have a mean tree volume or standing volume equal to an equal-aged stand which has always existed at this lower density. Competition-density theory implies that equal aged stands with different density histories will self-thin at the same rate (Yoda et al. 1963; Hutchings and Budd 1981). Figure 1 shows the development of buckwheat (*Fagopyrum sagittatum*) from different initial densities. Solid lines represent reciprocal yield curves while the dashed-line represents the -3/2 self-thinning line. Once a stand reaches the self-thinning line its development converges with that of other stands along the self-thinning line. A stand at the self-thinning line has a lower mean tree weight (or volume) than an equal-aged stand at a lower density, but, according to competition-density theory, will have an approximately equal mean tree volume when these two stands converge on the self-thinning line. The manner in which the dense stand overtakes the less dense stand in mean tree volume is probably the result of two factors: the surviving individuals in both stands are increasing in size, and the decrease in density in the dense stand creates "false increment"
(Warrack 1959) where mean tree size increases because of the mortality of smaller individuals.

Rates of increase in mean tree volume of the simulated stands used in the present study found that DFSIM indicates an initially dense stand will have a lower mean tree volume than a stand growing at a lower density, when the stands reach age 100 (Figure 22). At age 86 TASS indicates the stands will have approximately equal volumes (Figure 22). It is possible that the large size attained by forest trees creates a situation where they do not react the same as annual plants to self-thinning. If this is the case, less dense stands may actually be capable of producing more, or less, volume than initially dense stands when they have self-thinned to the same density. That some forest stands may stagnate, even slightly, implies that different time trajectories do exist in some circumstances.

The baseline models have the potential to be standardized so that a single three-dimensional surface represents a broad range of site qualities. This standardization is predicated on the assumption that the -3/2 self-thinning line is the same for all site qualities (Yoda et al. 1963), and that stands with a given top-height and number of trees have equal stand volumes regardless of age and site quality (Assmann 1970). Replacement of the age axis with top height would accomplish this standardization over site quality, but would lead to other changes. One change would remove the broad flat areas in the three-dimensional baseline models that represent stagnated stands. While a stand could increase in age without increasing in mean tree volume (or stand volume), it could not increase in top height without increasing in mean
Figure 22. Development of mean tree volume (expressed in cubic meters) for simulated stands of different initial densities from DFSIM (left) and TASS (right). The development of all the stands in the DFSIM graph is through age 100 while the development of the TASS stands is through age 86. The DFSIM stands developed at different rates along the self-thinning line, while the TASS stands developed at similar rates.
tree volume. This part of the baseline model would therefore become blank. Such a change would standardize the baseline models so that if stands of different initial densities do self-thin at different rates, one three-dimensional surface would apply to all. Some recent studies, however, have indicated that the -3/2 self-thinning line may vary over different site qualities (Perry 1984; McFadden 1985).

Delezene - Baseline Model Comparisons

Competition-density theory dictates that stands with different density histories will self-thin at the same rate and along the same trajectory (Yoda et al. 1963; Hutchins and Budd 1981). The mean size of the individual trees within a stand undergoing self-thinning will theoretically equal the mean size of trees in another stand when the latter stand reaches the self-thinning line from a much lower initial density. For this to occur, the increase in mean tree size of the dense stand cannot be accomplished entirely by mortality of smaller individuals. If competition-density theory is applicable to forest stands, a number of the largest individuals, equal to the number of individuals in the less dense stand, must be increasing in mean size at the same rate as all the individuals in the less dense stand.

In a forest stand whose density is reduced artificially by thinning, mean tree size can either increase or decrease depending on whether the larger or smaller trees are favored. If tree size is the only thinning criterion and large trees are favored (i.e., smallest trees are removed first without regard to form, spatial organization, or other factors), then competition-density theory dictates that the stand
will stay along the same constant-age curve (Tadaki 1963; Ando 1968). If the stand were thinned to a density equal to an open-grown stand located on the horizontal part of the constant-age curve, then, according to competition-density theory, the thinned stand would also be on the horizontal part of the constant-age curve. The net volume increment of the thinned stand will exceed that of other unthinned stands on the self-thinning line since the thinned stand had its future mortality removed during thinning while the unthinned stand’s mortality was not recovered. The total gross increment (including mortality) of the thinned stand should be less than that of unthinned stands on the self-thinning line since the unthinned trees which died subsequently must have had some increment prior to their death. The thinned stand will have greater gross and net increment than the unthinned open-grown stand because the open-grown stand has a history of unused growing space. How and if the largest trees growing in a stand undergoing competition-induced mortality could be as large as open-grown trees of the same age is unclear. Perhaps the dominant tree in a dense stand is a more efficient user of its limited growing space than is an open-grown tree with relatively unlimited growing space. Or possibly, this aspect of competition-density theory may not apply to the above-ground stem volume of forest stands.

Ando (1968) assumed thinning from below would not invalidate competition-density theory and Peet and Christensen (1980) found unthinned loblolly pine stands to conform to competition-density theory. Pienaar’s (1965) analysis of slash pine (Pinus elliottii Engelm.), however, concluded that once a stand began to compete intraspecifically,
subsequent thinning would not increase stand growth to the level of a stand of a similar density which had never experienced competition. Aiba (1975) and Drew and Flewelling (1977) also concluded competition-density theory could not account for the effects of thinning in forest stands.

Comparisons of the Delezenne study plots to the baseline models found some of the thinned plots with greater mean tree volumes (and stand volumes) than the TASS baseline models, and approximately equal to the DFSIM baseline models. The other thinned plots were only slightly lower. These thinned plots were thinned from below to favor larger trees, but tree form and spatial patterns were also considered. The thinned stands would be expected to be equal to or lie beneath the surface of the baseline models. Although there was some variation in site quality among the Delezenne study plots, the baseline models were constructed for a site quality at the more productive end of this range to avoid any biases. The high level of conformity between the control plots and the baseline models gives credibility to these models.

The relatively high volumes of the thinned Delezenne plots in relation to the volumes indicated by the baseline models could be the result of:
1) The TASS and DFSIM growth and yield models underestimate volumes from widely-spaced Douglas-fir stands for the site index used in this study. This underestimation would appear to exist if it is assumed the thinned Delezenne plots should be below the yields predicted by the growth models for unthinned stands of similar densities. In this case, the TASS model is apparently in greater error than the DFSIM model, but
the limited density range of the DFSIM model makes complete comparisons impossible;

2) The trees in thinned stands might be able to grow faster than open-grown trees. Possibly the selection of genetically superior and/or physiologically vigorous trees during thinning produces bigger trees than found in open-grown conditions where genetically inferior trees, or trees on suboptimal micro-sites, might survive. The processes of competition might also force trees to grow more efficiently with relatively limited resources than in open-grown conditions; or

3) A combination of 1 and 2; the growth models may underestimate the yield of widely-spaced stands, and the practice of thinning from below may select the fastest-growing trees whose growth nearly approaches that of unthinned stands of similar densities.

The limited existing growth data for widely-spaced Douglas-fir stands from which to develop growth models and the general disagreement between the baseline models tends to favor the first explanation.

SUMMARY

Three-dimensional representations of the volumes estimated for various ages and densities by the TASS and DFSIM growth and yield models provided a means to compare these growth models for site index 44 m (144 ft.). Over most of the range of age and density in which the models coincide, the estimated volumes are similar. At low densities and older ages, however, the DFSIM growth and yield model predicts substantially higher volumes than the TASS growth and yield model. Both
baseline models correspond quite well to theories concerning the competition-density effect and the -3/2 power law.

Comparisons of the observed development of the control plots in the Delezenne thinning study and the baseline models found the baseline models to be reasonably accurate representations of Douglas-fir stand development in relatively dense stands without thinning. The thinned plots, however, had greater mean tree and stand volumes in some cases than similarly spaced unthinned stands indicated by the TASS baseline models and, where comparable, volumes that were similar to those indicated by the DFSIM baseline models. While competition-density theory implies that stands thinned to a low density should have mean tree or stand volumes similar to stands which always existed at the lower density, it has usually been assumed that the thinned stands would have much lower mean tree or stand volumes. Explanations for the relationships observed in the present study include: a substantial underestimation of volume for widely-spaced stands by the TASS and DFSIM growth models; a previously unrecognized ability of thinning to improve the average growth rates or form of individual trees; or a combination of the above. It is possible that the growth of widely-spaced stands has been underestimated in the past and that a potential may exist for these stands to equal, or possibly exceed, the volume production of more closely-spaced stands.
CHAPTER FIVE
VOLUME GROWTH AND STAND DENSITY

HYPOTHESES

This chapter will attempt to determine what relationship (if any) exists between volume growth and stand density in thinned and unthinned Douglas-fir stands by testing the following hypotheses:

1) Mean periodic gross increment is not reduced by thinning in the Delezenne study plots; and

2) A strong, consistent relationship does not exist between stand growth and stand density in the Delezenne thinning plots.

RESULTS

Volume Growth Response in the Delezenne Study

Gross volume increment from the thinned Delezenne study plots ranged from 437.9 cubic meters/hectare (6258.6 ft/ac) in plot 4 to 733.5 m/ha (10483.0 ft/ac) in plot 12 between 1957 and 1984 (Table 2). These gross increment totals do not include mortality prior to 1957 or the volume removed in the initial thinning and, therefore, only describe gross production since the inception of this study. Those
Table 2. Gross and net increments, and gross and net periodic annual increments for the Delezenne thinning study. Values in parentheses are English unit equivalents (expressed in cubic feet/acre).

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<td>(8434.6)</td>
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</table>

1 Period length for plots 8 - 13 was 22.8 years instead of 23.
plots with the higher densities and those in the eastern cluster of plots (plots 8 through 13) generally produced the highest gross volume increment. The plots in the eastern cluster had more trees per hectare than the western cluster at the beginning of the study (Table 1), and they maintained this advantage throughout the study in plots of the same treatment.

Gross volume increment from the control plots ranged from $606.4 \text{ to } 706.8 \text{ m }^3/\text{ha (8666.4 to 10101.3 ft }^3/\text{ac})$ from 1957 through 1980 (Table 2). Periodic annual gross increment for the 24-year period ranged from $25.3 \text{ to } 29.5 \text{ m }^3/\text{ha yr} (361.1 \text{ to } 420.9 \text{ ft }^3/\text{ac yr})$ for the control plots. From 1957 through 1979 (a 23 year period) the thinned plots had periodic annual gross increments ranging from $16.4 \text{ to } 27.9 \text{ m }^3/\text{ha yr} (234.1 \text{ to } 399.3 \text{ ft }^3/\text{ac yr})$. The average gross periodic annual increment of the highest four thinned plots (plots 10 through 13) was $26.3 \text{ m }^3/\text{ha yr}$ compared to 27.5 for the three control plots. Three of the thinned plots had higher gross periodic annual increments for the 1957 through 1979 period than did the lowest yielding control plot (plot 15) for the 1957 through 1980 period.

Net volume increment for thinned plots exhibited trends which were similar to those for gross volume increment, since these thinned plots had little mortality during the study period. Both mortality and net volume increment were higher in the eastern cluster of plots (Table 2) and mortality was highest in plot 9. The high mortality in plot 9 was unexplained and led to the exclusion of this plot from the more detailed analyses of the 1980 through 1984 growth data that are described in subsequent chapters.
Net volume increments from the control plots were substantially lower than their gross increments because of their relatively high losses to mortality (Table 2). Periodic annual losses to mortality averaged 3.7 m³/ha/yr from 1957 through 1980 in the control plots compared to 0.8 m³/ha/yr from 1957 through 1979 in the thinned plots. The highest yielding thinned plots (plots 10 through 13) had an average periodic annual net increment of 25.5 m³/ha/yr compared to 23.7 m³/ha/yr for the three control plots.

Treatment means were calculated for adjoining plots of the same treatment instead of combining all plots of each treatment because of the large variation between the eastern and western cluster of plots (Table 2). For example, a single group represented plots 2 and 3, or plots 12 and 13. One group included all three control plots. A one-way analysis of variance found significant differences between group means for both net and gross periodic annual increment (Table 3). A Newman-Keuls multiple range test found mean periodic annual gross increment not significantly different (p = .05) for the three groups representing plots 10 and 11, plots 12 and 13, and plots 14, 15 and 16 (Table 3). These results support the first hypothesis that mean periodic gross increment is not reduced by thinning in the Delezenne study plots. Mean net periodic annual increment from the group representing plots 12 and 13 was significantly greater than the control group mean, and the control group mean was not significantly higher than the group representing plot 10 and 11 (Table 3).
Table 3. One-way analysis of variance tables for gross and net mean periodic annual increment between groups of adjoining Delezenne study plots. Group means were found to be significantly different in both cases. Non-significantly different group means (Newman-Keuls multiple range test, p = .05) are indicated by corresponding letters below the group means.

### ONE-WAY ANALYSIS OF VARIANCE TABLE FOR MEAN GROSS PERIODIC ANNUAL INCREMENT

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<thead>
<tr>
<th>SOURCE</th>
<th>df</th>
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<th>MS</th>
<th>F RATIO</th>
<th>P Prob.</th>
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<td>TOTAL</td>
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### ONE-WAY ANALYSIS OF VARIANCE TABLE FOR MEAN NET PERIODIC ANNUAL INCREMENT

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### MULTIPLE RANGE TEST

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<td>D</td>
<td>D</td>
<td>C</td>
<td>B</td>
<td>A</td>
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<td>10,11</td>
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<td>14,15,16</td>
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<td>25.4</td>
<td>27.3</td>
<td>27.5</td>
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<td>16.8</td>
<td>19.8</td>
<td>24.7</td>
<td>26.4</td>
<td>23.7</td>
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</table>

Letters indicate non-significantly different group means.
Stand Growth/Density Relations in the Delezenne Study

Figures 23, 24, and 25 show the relationship of periodic annual increment to density among the thinned Delezenne plots for three measurement periods. Data from unthinned stands were not available since the control plots were measured at different times. Four different measures of density are shown: basal area per hectare, the density measure used in the Delezenne study to specify thinning intensities; percent of height (Wilson 1946, 1979); relative density (Curtis 1982); and relative density index (Drew and Flewelling 1979). The three measurement intervals chosen represented three different periods of stand development and were thought to exhibit sufficient recovery from thinning to show the effect of density on subsequent stand volume growth. Densities used are averages of the density at the beginning and the end of the measurement period.

Volume increment generally increased with increasing density, but a strong, consistent volume growth/density relation is not evident in the measurement intervals shown (Figures 23 through 25). The age 38-40, and the age 48-51 measurement intervals had increasing increment with increasing density while in the age 59-64 measurement interval increment leveled off at higher densities. In the six measurement intervals not shown, the relationship of periodic annual increment to density varied from an increasing relationship, as is shown in Figures 23 through 25, to no visible trend at all. Intervals with no visible trend were generally preceded by thinnings and/or were less than two growing seasons in length. These results support the second hypothesis that a strong, consistent relationship does not exist between stand
Figure 23. Periodic annual increment/stand density graphs of the Delezenne data for stand age 38 through 40 using four different measures of stand density. Symbols represent treatments: crosses = increasing basal area treatment; circles = constant basal area treatment; and squares = decreasing-increasing basal area treatment.
Figure 24. Periodic annual increment/stand density graphs of the Delezenne data for stand age 48 through 51 using four different measures of stand density. Symbols represent treatments: crosses = increasing basal area treatment; circles = constant basal area treatment; and squares = decreasing-increasing basal area treatment.
Figure 25. Periodic annual increment/stand density graphs of the Delezenne data for stand age 59 through 64 using four different measures of stand density. Symbols represent treatments: crosses = increasing basal area treatment; circles = constant basal area treatment; and squares = decreasing-increasing basal area treatment.
growth and stand density in the Delezenne thinning plots.

Plots from the lower cluster had lower periodic increments than plots of the same treatment from the upper cluster in nearly all measurement intervals during the study period. Differences between the upper and lower clusters of plots occurred despite these plots being thinned to similar levels of residual basal area and despite relatively constant site quality over the study area. These results suggest differences in initial (pretreatment) density between the upper and lower clusters (Table 1) may have affected their future productivity.

DISCUSSION

Thinning Response in the Delezenne Study

Given the relatively high gross and net increments of the thinned Delezenne study plots (Table 2), and the similarity of results obtained elsewhere in the Douglas-fir region, it is probable that proper thinning will not necessarily lower the productive potential (i.e., gross increment) of the stand and can increase recoverable (net) volume. Defining a proper, much less an optimal, thinning regime is a very difficult task given the wide array of variables which influence stand growth. Site quality, stand density, stand structure, tree vigor, genetic potential, thinning interval, and others are all important; but silviculturists have generally attempted to hold site quality constant and concentrate their efforts towards studying the effects of variations in density on stand growth. Stand density is much easier to quantify and measure than the other variables, and is one of the easiest stand
characteristics for the silviculturist to manipulate. It seems logical, however, that the variation in gross increment (or even net increment) reported in this study and elsewhere cannot be explained completely by stand density (regardless of how it is measured) alone.

Opportunities to increase recoverable volumes through thinning do seem to exist. Light thinnings seem to have the most potential to increase yields, but widespread thinning practices in the Douglas-fir region will probably require further information on the mechanisms of increased volume growth in thinned stands.

Stand Density Measures

Curtis (1970) concluded that most relative stand density measures are approximately equivalent expressions of crowding, and choosing one density measure over another should be based on "information available, convenience of computation, and ready understanding and visualization rather than fundamental differences in meaning or precision." Several studies, however, have compared density measures and found the different types do provide different values for density (Briegleb 1952; Day and Bennett 1962; Curtis 1971; Daniel et al. 1979; West 1983; Larson and Cameron 1986), especially between height, diameter, and volume-based relative density measures (Curtis 1971; West 1983). Their differences indicate some density measures may describe competition more accurately than others.

It is thought here that expressing density in relation to dominant height, or site height, is easier to understand than expressing density in relation to an average tree measurement such as mean tree volume or
quadratic mean diameter. Computationally, expressing spacing as a percentage of height is simple and easily convertible to trees per unit area. Dominant height information for this density measure is usually available from site index information. Furthermore, dominant height growth patterns are better understood than the growth patterns of average tree characteristics such as diameter or volume, especially in non-normal stands. Another advantage is that thinning intervals can be based on dominant height growth and therefore can be prescheduled relatively accurately with the percent of height method.

The best comparative test of stand density measures would probably be correlations between density and periodic growth over a range of densities and ages. This proposition is based on the assumption that periodic growth per unit area is indicative of competition. Other concerns include holding stand structure constant to measure just the effects of density and not comparing stands at different stages of recovery from past thinnings.

Comparisons of these density measures using the Delezenne data has not been attempted because of the small data base, and unthinned control plot data do not exist for corresponding measurement periods. It is also believed that comparing the relationships between volume growth and various density measures would describe the merits of the various transformations on these basically curvilinear relationships rather than the density measures themselves.

Stand Growth/Stand Density Relations

The effects of thinning make growth/density comparisons difficult
in thinned stands. Immediately after thinning, while individual trees expand into unoccupied space, stand volume growth is reduced. Response to thinning can vary among stands thinned to identical levels of density because of differences in stand vigor and stand structure. Shock from thinning may also reduce growth temporarily, especially on poor sites (Harrington and Reukema 1983).

Comparisons of simulated unthinned stands offer one way of comparing growth at different densities and avoiding the difficulties of comparing the growth of thinned stands. The two growth and yield models described in Chapters Three and Four, TASS and DFSIM, simulate the growth and development of even-aged Douglas-fir stands of different initial densities. The relationship of periodic annual increment to density (trees per hectare) in simulated unthinned stands of different initial densities ranges from an increasing relationship in younger ages, to a relatively distinct peak in periodic annual increment at an intermediate density in stands over age 20 to 25 (Figures 26 and 27). The peak moves to lower densities and to lower periodic annual increments at older ages. One might infer an increasing growth/density relationship for the younger ages, and a relationship which peaks at an intermediate density for the older ages, but no consistent growth/density relationship is evident from these simulated data.

A consistent relationship between stand growth and density is not evident among the thinned Delezenne plots (Figures 23 through 25). The generally increasing relationship observed with increasing stand density in most of the Delezenne plots may be nothing more than the lower density stands undergoing more severe thinning treatments and a much
Figure 26. The relation of periodic annual increment and number of trees per hectare for stands of different ages as simulated by the TASS growth and yield model. Each line represents the periodic annual increment of stands of a specific age over a range of stand density. At young ages increment increased with increasing density. At older ages increment peaked at an intermediate density.
Figure 27. The relation of current annual increment and number of trees per hectare for stands of different ages as simulated by the DFSIM growth and yield model. Each line represents the periodic annual increment of stands of a specific age over a range of stand density. At young ages increment increased with increasing density. At older ages increment peaked at the lowest density, and in stands of intermediate ages the peak was at an intermediate density.
longer recovery period, than higher density stands. Although thinning tends to disrupt comparisons of growth and density, thinned stand data are frequently used to identify growth/density relationships. For example, the Levels-of-Growing-Stock (LOGS) study have used very strict control of stand density to identify growth/density relationships (Williamson and Curtis 1984; Curtis and Marshall 1986). They have found an increasing growth trend throughout their range of density, but have thinned very frequently and removed larger trees in their more severe treatments than would be removed under a strict low thinning regime. The reduction in growth at wide spacings and the growth/density relationship reported from the LOGS study may therefore be the result of the thinning techniques used rather than an interaction between volume growth and density.

**SUMMARY**

Comparisons of gross and net periodic increment from the Delezenne study plots indicated net increment can be increased by thinning, and that proper thinning has only a slight effect on gross increment. Similar results have been reported in most other thinning studies in Douglas-fir stands in the Pacific Northwest. Little effort has been expended towards determining the effects of other variables such as stand structure or thinning interval on stand yield.

Relative stand density measures are described as a combination of an absolute density measure and a measure of stand development. The various measures of stand development separate these relative density
measures into three categories: volume-based, diameter-based, and height-based density measures (West 1983).

These different types of density measures are assumed to provide equivalent measures of competition in forest stands. Differences between them have been observed and are largely the result of their formulation (i.e., their absolute density and stand development components). Height-based density measures are most desirable because 1) dominant height is a preferable measure of stand development since it is independent of site and age; 2) dominant height is relatively unaffected by density; 3) they are not affected by the phenomena of "false-increment"; and 4) they are simple to understand and use.

A strong, consistent stand growth/density relationship was not evident among either unthinned stands simulated with two growth and yield models or the thinned Delezenne plots. Differences in stand structure, thinning intervals, thinning severity, or stand age may explain the lack of a relationship among the Delezenne plots. Stand growth/density relationships may be oversimplifications of a complex model which includes more variables than just density.
CHAPTER SIX

STAND STRUCTURE AND GROWING SPACE EFFICIENCY

HYPOTHESES

This chapter will examine the growth and development of the Delezenne thinning plots on an individual-tree basis. Specifically, this chapter will attempt to determine the role of individual tree growth rates, and individual tree growth rates per unit of growing space, in stand growth and productivity by testing the following hypotheses:

1) Trees in upper crown classes in thinned and unthinned stands have higher growth rates than trees in lower crown classes;

2) Trees in upper crown classes in thinned and unthinned stands have higher rates of growth per unit of growing space than trees in lower crown classes; and

3) Individual tree characteristics, such as diameter and height, are related to individual tree productivity and growing space efficiency.

METHODS

In addition to the measurements of the Delezenne study plots
described in previous chapters, additional measurements were made after the 1984 growing season to examine individual tree growth for the 1980 through 1984 measurement interval.

Volume Measurements

Since no control plots existed for the 1980 through 1984 measurement period, an additional fifth-hectare (half-acre) control plot (designated plot 1) was established after the 1984 growing season in an unthinned area near plot 13 (Figure 3). Plot 1 had a northwest aspect and site index of 43 meters (141 ft. - 50 year index). The dbh of all trees in the plot were measured, as were the heights of 10 of the 91 trees in this plot. Heights of the remaining trees were estimated with the equation:

\[ \text{height} = 75.48 - 207.18 \times (\text{dbh}^{-.5}) \]

which was derived from the height trees from this plot and 16 more trees measured the following year.

Additional height/dbh equations were used to estimate tree heights for the thinned plots in the individual tree analyses of the data. This latter set of equations differed from those described in earlier chapters since each equation represented only plots of the same treatment (e.g., plots 12 and 13, or plots 3 and 10), while the earlier equations represented nearly adjacent plots but of different treatments (e.g., plots 2, 3, 4, and 5 - Figure 3). This additional step was taken to avoid any bias associated with estimating height based on diameter over different treatments when the major effect of the treatments was to affect diameter growth rates.
Increment cores, taken on the north and south sides of each tree, provided diameter growth measurements for the previous 5 years. Bark thickness and sapwood radius were also measured on both increment cores from all trees. Outside bark dbh prior to the 1980 growing season was estimated from the 5-year growth measurements obtained from the increment cores by assuming bark thickness increased from 1980 through 1984 by the same relative percentage as did dbh (inside bark) over the same period.

A regression equation:

\[(1980 \text{ height}) = 3.408 + 0.883 \times (1984 \text{ height}),\]

was derived from the 1980 and 1984 height measurements of individual trees in the thinned plots (plots 2 through 13) to predict the 1980 height of trees measured only in 1984. Heights in 1980 of the trees in plot 1 which were not measured in 1984 were estimated with the height/dbh equation:

\[(1980 \text{ height}) = 72.69 - 196.49 \times (\text{dbh}^{-.5}),\]

derived from 1980 measurements in control plot 14, which was harvested in 1983.

To improve the precision of individual tree volume estimates, additional measurements of height were made after the 1985 growing season. Approximately 15 trees, randomly chosen, from each of plots 1, 8, 10 and 12 were measured to the top of the first whorl of branches (i.e., the height after the 1984 growing season). Heights of these trees after the 1979 growing season were estimated using the following equation based on 1984 heights:

\[(1980 \text{ height}) = 3.408 + 0.883 \times 1984 \text{ height}.\]
These additional height measurements, along with those taken previously, provided 100 relatively accurate measurements of height from which to calculate volume growth for trees in plots 1, 8, 10, 12, and 13. The 8 height trees from plot 13 were added to this group because of the close proximity of plots 12 and 13 and the similarity of their treatments.

Sapwood Basal Area

Sapwood radius was measured on all trees from plots 1, 3, 5, 8, 10, 12, and 13 during the winter of 1984-85. Plots 1, 12 and 13 were selected because they were the only existing plots of their respective treatments in 1984. Plots 3, 5, 8, and 10 were selected because they appeared to be the most evenly stocked plots of their respective treatments and relatively free from outside influences.

Twenty trees representing a range of crown classes and treatments were selected to assess the variability in sapwood radius in individual trees. Each of these 20 trees was cored from all four cardinal directions. The sapwood-heartwood boundary was delineated visually. Sapwood radius was measured on each increment core to the nearest 0.5 mm with a metric caliper with vernier scale. From this sample of trees it was determined that coring the north and south sides of each tree provided a reasonable estimate of the average sapwood radius as indicated by the four-core mean (ratio of north-south mean to four-core mean equaled 1.006, with a standard deviation of 5.8%). During the subsequent coring of the trees, if the north and south side cores showed a large amount of variablity, additional cores were taken on the east and west sides. While no measurements of the relation of crown shape to
sapwood radius were made, above-average sapwood radii usually were found on the same side as the larger part of lopsided crowns.

The sapwood radius was measured with 2 to 4 cores from each of 312 trees in 7 plots. Since the increment cores were started in the outermost, flat sections of the bark, bark thickness measurements were also taken on each core. Sapwood basal area was calculated as the difference between the calculated basal area inside bark and the heartwood basal area of each tree. Although sapwood basal area is assumed to indicate leaf area (Grier and Waring 1974), sapwood basal area values were used in all analyses to avoid the additional source of error associated with sapwood/leaf area conversions.

Crown Projection Area

Crown projection area of these selected trees from plots 1, 8, 10, 12, and 13 was also measured after the 1985 growing season (the crown projection areas of only 99 trees were measured since one tree was windthrown prior to measurement). The inflections of the crown profile were projected to the ground with a clinometer held at 90 degrees and marked with pin flags. The distance from these points to the tree center was measured, as was the bearing from these points to the tree. The number of points per tree ranged from 5 to 11 with an average of 7.25 points per tree. The crown profiles were then mapped for each tree and digitized, and the crown projection area was calculated with an area calculation program from a Hewlett Packard 9874A digitizer.
RESULTS

Size Class Distributions

Diameter frequency distributions for the four treatments show relatively normal stand structures, but there is a shift to the larger diameter classes for the most heavily thinned treatments (Figure 28). The diameter distribution of the control plot (treatment A) was bimodal, possibly the result of the different growth rates of large and small trees which are in the upper and lower canopy, respectively (Ford and Newbould 1970; Ford 1975). The upper range of the height frequency distributions was similar in all four treatments (Figure 29). This reflects the independence of dominant height growth to stand density. The wider range of heights in the control plots was the result of the other stands being thinned from below, thereby removing the shorter trees.

Growth by Crown Classes

The average volume growth of individual trees from 1957 through 1961 in plots 6 through 13 are listed by crown class and treatment in Table 4 (plots 6 and 7 were still controls during this period). Crown class was identified at the beginning of the measurement period. Average tree growth rates are also shown for the 1980 through 1984 measurement period. Treatment A results reflect the 1980 - 1984 data from plot 1, where crown class was identified at the end of the growth period, since the crown class at the beginning of the period was not known. Comparisons between crown classes from growth periods between
Figure 28. Frequency distributions for 1984 tree diameters from the four treatments in the Delezenne study. Data for treatment A, the control treatment, were from one fifth-hectare (half-acre) plot. Data from treatments B, C and D were from two fifth-hectare plots apiece.
Figure 29. Frequency distributions for 1984 tree heights from the four treatments in the Delezenne study. The data represents only trees whose height was measured, not predicted. Data for treatment A, the control treatment, were from one fifth-hectare (half-acre) plot. Data from treatments B, C and D were from two fifth-hectare plots apiece.
Table 4. Mean individual tree periodic increment for measurement periods from 1957 through 1961 and from 1980 through 1984 with standard error and sample size. Treatments B, C and D were thinned at the beginning of both measurement periods. The 1980-84 data from Treatment A are from just one fifth-hectare plot, while data from Treatments B, C and D are from two fifth-hectare plots. All means were significantly different within treatments (one-way analysis of variance). Values in parentheses are English unit equivalents expressed in ft³/tree.

<table>
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<th>Treatment</th>
<th>Crown Class</th>
<th>1957-61 Mean (M³/TREE)</th>
<th>1980-84 Mean (M³/TREE)</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>D</td>
<td>.317±.013 (11.19±0.46)</td>
<td>.666±.058 (23.52±2.05)</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>.156±.006 (5.51±0.21)</td>
<td>.407±.027 (14.37±0.95)</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>.050±.003 (1.77±0.11)</td>
<td>.102±.010 (3.60±0.35)</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>.028±.002 (0.99±0.07)</td>
<td>.011±.005 (0.39±0.18)</td>
<td>16</td>
</tr>
<tr>
<td>B</td>
<td>D</td>
<td>.297±.013 (10.49±0.46)</td>
<td>.622±.035 (21.97±1.24)</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>.142±.008 (5.01±0.28)</td>
<td>.369±.012 (13.03±0.42)</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>.052±.007 (1.84±0.24)</td>
<td>.198±.012 (6.99±0.42)</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>.003±.002 (0.11±0.07)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>D</td>
<td>.325±.014 (11.48±0.49)</td>
<td>.656±.042 (23.17±1.48)</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>.213±.008 (7.52±0.28)</td>
<td>.448±.019 (15.82±0.67)</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>.095±.008 (3.35±0.28)</td>
<td>.277±.008 (9.78±0.28)</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>.024±.003 (0.84±0.11)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>D</td>
<td>.303±.018 (10.70±0.64)</td>
<td>.774±.037 (27.33±1.31)</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>.163±.008 (5.76±0.28)</td>
<td>.459±.017 (16.21±0.60)</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>.031±.005 (1.09±0.18)</td>
<td>.217 (7.66)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>.006±.003 (0.21±0.11)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
1961 and 1980 were not possible since the measurement of the control plots did not coincide with those of the thinned plots.

Results indicate that the average growth from each treatment during both periods was highest in the dominant trees and lowest in the suppressed and intermediates, where present (Table 4). One-way analyses of variance found differences in mean growth rates to be highly significant in all treatments in both measurement periods. During both measurement periods the dominant and codominant trees contributed the most to total stand production. The small numbers of suppressed and intermediate trees, with their relatively low growth rates, contributed very little to total stand production. These results support the first hypothesis that trees in upper crown classes in thinned and unthinned stands have higher growth rates than trees in lower crown classes.

Growing Space Efficiency

The crown projection areas, measured on the height trees (i.e., those trees whose heights were measured, not predicted) in plots 1, 8, 10, 12, and 13, exhibited a worsening relationship to cubic volume increment with increasing thinning intensity (Table 5). For example, in the constant basal area treatment, the most severe of the thinning treatments in 1980 (Figure 4), crown projection area and individual tree volume increment (from the 1980 through 1984) had a correlation coefficient of just .512 (Table 5). The poor relationships between crown projection area and growth are probably not attributable to comparing 1980 through 1984 volume growth to crown projection area measured after the 1985 growing-season. Large changes in crown width
Table 5. Correlation coefficients ($r$) for periodic volume growth from 1980-84 with sapwood basal area and crown projection area, sapwood basal area with crown projection area, and crown projection area with basal area in 1985 and diameter to the 1.6 power. Correlations coefficients for periodic volume increment/sapwood basal area were significantly greater than for periodic volume increment/crown projection area in Treatments A and C at the .01 level (Fisher's Z transformation).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>PI/CPA</th>
<th>PI/SBA</th>
<th>SBA/CPA</th>
<th>CPA/BA(85)</th>
<th>CPA/DBH(85)\textsuperscript{1.6}</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>.797</td>
<td>.967</td>
<td>.716</td>
<td>.784</td>
<td>.797</td>
</tr>
<tr>
<td>B</td>
<td>.792</td>
<td>.806</td>
<td>.682</td>
<td>.786</td>
<td>.777</td>
</tr>
<tr>
<td>C</td>
<td>.512</td>
<td>.893</td>
<td>.606</td>
<td>.595</td>
<td>.593</td>
</tr>
<tr>
<td>D</td>
<td>.705</td>
<td>.840</td>
<td>.627</td>
<td>.721</td>
<td>.722</td>
</tr>
</tbody>
</table>

Abbreviations:
- PI = periodic increment from 1980 through 1984
- SBA = sapwood basal area in 1984
- CPA = crown projection area in 1985
- BA(85) = basal area in 1985
- DBH(85) = diameter in 1985
- Treatment A = Control
- Treatment B = Increasing Basal Area Treatment
- Treatment C = Constant Basal Area Treatment
- Treatment D = Decreasing-Increasing Basal Area Treatment
during this one year were not expected, especially in the thinned plots where the released crowns were probably changing primarily in length and not width (Reukema 1964).

Ratios of individual tree volume growth to crown projection area were used as a measure of the efficiency of a tree's use of crown projection area or growing space. Mean efficiency values (Table 6) were significantly different between crown classes in the control treatment at less than the .0005 level (one-way analysis of variance). In the thinned treatments mean efficiency values were not significantly different at the .05 level (Newman-Keuls test – Table 6). The dominant trees in the control treatment were the most efficient single group of trees in this analysis.

The correlation between volume increment and sapwood basal area was highest in the control treatment (treatment A) and somewhat less in the three thinned treatments (Table 5). In all four treatments, the correlation between volume increment and sapwood basal area was larger than for volume increment and crown projection area (Table 5). In two of the four treatments, the simple correlation coefficient (r) for volume increment/sapwood basal area was significantly greater than for volume increment/crown projection area at the .01 level (Table 5).

Expressing efficiency as growth per unit of sapwood basal area produced results similar to those using crown projection area (Table 6). Mean efficiencies were significantly different between crown classes at less than .0005 and at the .001 levels, respectively (one-way analysis of variance), in treatments A and B. Mean crown class efficiencies in treatments C and D were not significantly different at
Table 6. Variation in mean periodic increment from 1980 through 1984 per unit of crown projection area (CPA), and per unit of sapwood basal area (SBA), with standard error and sample size. Letters denote non-significantly different means within treatments at the .05 level.

<table>
<thead>
<tr>
<th>TREATMENT</th>
<th>CROWN CLASS</th>
<th>PER. INC./ CPA (M³/M²×10²)</th>
<th>SAMPLE SIZE</th>
<th>PER. INC./ SBA (M³/M²)</th>
<th>SAMPLE SIZE</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>D</td>
<td>2.20±.47</td>
<td>3</td>
<td>9.03±.57</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>1.47±.11</td>
<td>12</td>
<td>7.47±.24</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.70±.10</td>
<td>10</td>
<td>3.98±.28</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>0.39</td>
<td>1</td>
<td>0.67±.31</td>
<td>16</td>
</tr>
<tr>
<td>B</td>
<td>D</td>
<td>1.39±.19 a</td>
<td>4</td>
<td>8.17±.53</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>1.32±.07 a</td>
<td>23</td>
<td>7.10±.17</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>1.10±.29 a</td>
<td>3</td>
<td>6.07±.33</td>
<td>17</td>
</tr>
<tr>
<td>C</td>
<td>D</td>
<td>1.37±.14 b</td>
<td>5</td>
<td>7.33±.45 d</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>1.30±.13 b</td>
<td>14</td>
<td>7.90±.34 d</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.99±.14 b</td>
<td>2</td>
<td>6.88±.17 d</td>
<td>4</td>
</tr>
<tr>
<td>D</td>
<td>D</td>
<td>1.36±.10 c</td>
<td>8</td>
<td>7.28±.44 e</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>CD</td>
<td>1.10±.09 c</td>
<td>13</td>
<td>6.99±.22 e</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.70</td>
<td>1</td>
<td>5.91</td>
<td>1</td>
</tr>
</tbody>
</table>
the .05 level (Newman-Keuls test) for crown classes where sample size was greater than 1. The most efficient group of trees were the dominants in the control treatment (treatment A).

The relatively similar growing space efficiencies from different crown classes in thinned stands -- using both measures of growing space -- is in contrast to the results from unthinned stands. These similar rates of growing space efficiency in thinned stands do not support the second hypothesis: trees in upper crown classes in thinned and unthinned stands have higher rates of growth per unit of growing space than trees in lower crown classes.

Efficiency and Individual Tree Characteristics Within Treatments

Attempts were made to relate tree efficiency (using both measures of growing space) to a number of individual tree characteristics such as sapwood basal area (as a measure of crown size), basal area, volume, diameter, height and crown projection area. Correlation coefficients (Table 7) were higher for all variables in the control treatment than in any of the thinned treatments. The similarity between correlation coefficients within the control treatment is the result of the allometric relationships which exist between individual tree characteristics in unthinned Douglas-fir stands. For example, height and diameter are frequently highly correlated in unthinned, even-aged stands, and diameter will always be closely related to basal area (Table 8). Individual tree volume, being the product of height and basal area, is highly correlated to both, as well as to diameter. In the thinned treatments, however, very little similarity is evident between any of
Table 7. Correlation coefficients for a number of individual tree characteristics in relation to tree efficiency (volume increment from 1980 through 1984 per unit of crown projection area and sapwood basal area). These correlation coefficients are meant to imply a degree of association between the variables and the direction of that association (either positive or negative), not necessarily any causal relationships.

<table>
<thead>
<tr>
<th>Growth per Unit of Crown Projection Area on:</th>
<th>CORRELATION COEFFICIENTS (r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sapwood Basal Area</td>
<td>.914  .044  .375  .327</td>
</tr>
<tr>
<td>Crown Projection Area</td>
<td>.473  -.387  -.298  -.315</td>
</tr>
<tr>
<td>Height</td>
<td>.829  .243  .660  .497</td>
</tr>
<tr>
<td>Diameter</td>
<td>.872  .131  .478  .248</td>
</tr>
<tr>
<td>Basal Area</td>
<td>.870  .101  .461  .247</td>
</tr>
<tr>
<td>Cubic Volume</td>
<td>.875  .136  .514  .298</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Growth per Unit of Sapwood Basal Area on:</th>
<th>CORRELATION COEFFICIENTS (r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crown Projection Area</td>
<td>.861  .273  -.199  .316</td>
</tr>
<tr>
<td>Sapwood Basal Area</td>
<td>.767  -.116  -.171  .074</td>
</tr>
<tr>
<td>Height</td>
<td>.861  .509  .473  .677</td>
</tr>
<tr>
<td>Diameter</td>
<td>.867  .315  .056  .397</td>
</tr>
<tr>
<td>Basal Area</td>
<td>.845  .300  .019  .393</td>
</tr>
<tr>
<td>Cubic Volume</td>
<td>.859  .364  .090  .467</td>
</tr>
</tbody>
</table>
Table 8. Correlation matrices for Treatments A through D. SAPBA represents sapwood basal area, and CPA represents crown projection area. All measurements were made in 1984 except crown projection area which was measured in 1985.

### TREATMENT A - CORRELATION MATRIX

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>SAPBA</th>
<th>HEIGHT</th>
<th>BASAL AREA</th>
<th>DBH</th>
<th>VOLUME</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>.862</td>
<td>.865</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BASAL AREA</td>
<td>.964</td>
<td>.965</td>
<td>.993</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH</td>
<td></td>
<td>.884</td>
<td></td>
<td>.991</td>
<td></td>
</tr>
<tr>
<td>VOLUME</td>
<td>.963</td>
<td>.904</td>
<td>.996</td>
<td>.991</td>
<td></td>
</tr>
<tr>
<td>CPA</td>
<td>.716</td>
<td>.698</td>
<td>.788</td>
<td>.806</td>
<td>.787</td>
</tr>
</tbody>
</table>

### TREATMENT B - CORRELATION MATRIX

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>SAPBA</th>
<th>HEIGHT</th>
<th>BASAL AREA</th>
<th>DBH</th>
<th>VOLUME</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>.432</td>
<td>.583</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BASAL AREA</td>
<td>.811</td>
<td>.590</td>
<td>.996</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH</td>
<td></td>
<td>.685</td>
<td></td>
<td>.989</td>
<td></td>
</tr>
<tr>
<td>VOLUME</td>
<td>.788</td>
<td>.784</td>
<td>.765</td>
<td>.788</td>
<td></td>
</tr>
<tr>
<td>CPA</td>
<td>.682</td>
<td>.528</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### TREATMENT C - CORRELATION MATRIX

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>SAPBA</th>
<th>HEIGHT</th>
<th>BASAL AREA</th>
<th>DBH</th>
<th>VOLUME</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>.544</td>
<td>.655</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BASAL AREA</td>
<td>.939</td>
<td>.683</td>
<td>.997</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH</td>
<td>.923</td>
<td>.734</td>
<td>.994</td>
<td>.996</td>
<td></td>
</tr>
<tr>
<td>VOLUME</td>
<td>.921</td>
<td>.592</td>
<td>.594</td>
<td>.559</td>
<td></td>
</tr>
<tr>
<td>CPA</td>
<td>.606</td>
<td>.191</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### TREATMENT D - CORRELATION MATRIX

<table>
<thead>
<tr>
<th>VARIABLES</th>
<th>SAPBA</th>
<th>HEIGHT</th>
<th>BASAL AREA</th>
<th>DBH</th>
<th>VOLUME</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>.660</td>
<td>.721</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BASAL AREA</td>
<td>.845</td>
<td>.729</td>
<td>.997</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH</td>
<td>.854</td>
<td>.799</td>
<td>.992</td>
<td>.991</td>
<td></td>
</tr>
<tr>
<td>VOLUME</td>
<td>.842</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
the variables except diameter, basal area and volume (Table 7).

The relationships between the individual tree variables (including both measures of efficiency) were analyzed with principal components analysis, which examines patterns of correlation between variables to suggest possible groupings of variables. In treatment A, only one principal component had an eigenvalue greater than unity, suggesting high levels of correlation between all variables (Figure 30). This principal component explained 87.2% of the variation in the data. Although crown projection area is removed slightly from most of the variables, a large amount of grouping of all variables is apparent (Figure 30).

In the thinned treatments, two principal components were identified as explaining significant amounts of variation in the data. Patterns of groupings varied with treatment, but diameter, basal area, and volume were strongly associated with each other by both principal components in all three treatments (Figure 30). In contrast to the unthinned treatment, height and crown projection area showed little association with diameter or basal area in any of the thinned treatments, indicating a decrease in the usefulness of linear allometric relationships between these variables (e.g., diameter and height, or basal area and crown projection area) in thinned stands. Both measures of efficiency were relatively independent from the diameter-based variables (e.g., basal area, volume). The measures of efficiency and the diameter-based variables were somewhat related to height, indicating the importance of height and crown position.

In the thinned treatments, height generally had the strongest
KEY
b = basal area
c = crown projection area
d = diameter
e = efficiency (CPA)
E = efficiency (SBA)
h = height
s = sapwood basal area
v = volume

Figure 30. Factor loadings for the principal components identified in the analysis performed on the individual tree variable correlation matrix from each treatment. Letters denote variables as indicated in the key. Only one principal component was identified in treatment A reflecting the high levels of correlation between all variables. Two principal components were identified in each of treatments B, C and D.
correlation with tree efficiency of the six variables using both measures of growing space (Table 7). The two measures of crown size -- sapwood basal area and crown projection area -- varied from both positive and negative correlation coefficients with efficiency. When efficiency was based on growth per unit of crown projection area, crown projection area was correlated negatively with efficiency in the thinned treatments. In treatment B, crown projection area had the highest correlation coefficient of the six variables.

Stepwise multiple regression equations using all individual tree variables were used to test their relative contribution towards explaining the within-treatment variation in tree efficiency using both measures of growing space. Variables were entered into the equations based on the size of their squared partial correlation coefficient (i.e., the amount of previously unexplained variation explained by that variable). Variables were excluded if the F ratio of bringing that variable into the equation was less than 1.0, and if its tolerance (i.e., the amount of variance explained by an independent variable not explained by previously entered variables) was less than 0.02%.

Results using growth per unit of crown projection area as the measure of efficiency were rather inconclusive (Table 9). In the unthinned treatment, sapwood basal area entered the equation first and explained most of the variation in tree efficiency. Had sapwood basal area not been included, the equation would have explained about the same amount of variation, since all variables in the unthinned treatment were so closely correlated with each other (Table 8, Figure 30).

In the thinned treatments, crown projection area and height were
Table 9. Summary tables for stepwise regressions to predict individual tree efficiency (growth per unit of crown projection area * 10^2) for Treatments A through D. Only significant variables (see text) are included in these tables.

### TREATMENT A - STEPWISE REGRESSION - SUMMARY TABLE

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>SAPBA</td>
<td>121.76</td>
<td>.000</td>
<td>15.943</td>
<td>.835</td>
<td>121.76</td>
<td>.000</td>
</tr>
<tr>
<td>CPA</td>
<td>16.00</td>
<td>.001</td>
<td>-0.038</td>
<td>.903</td>
<td>106.93</td>
<td>.000</td>
</tr>
<tr>
<td>DIAMETER</td>
<td>8.38</td>
<td>.008</td>
<td>0.048</td>
<td>.930</td>
<td>96.95</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -0.607, Sy|x = 0.185 m³/m²*10²
EXCLUDED VARIABLES: HEIGHT, VOLUME, BASAL AREA

### TREATMENT B - STEPWISE REGRESSION - SUMMARY TABLE

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>CPA</td>
<td>4.92</td>
<td>.035</td>
<td>-0.031</td>
<td>.149</td>
<td>4.92</td>
<td>.035</td>
</tr>
<tr>
<td>VOLUME</td>
<td>40.74</td>
<td>.000</td>
<td>0.288</td>
<td>.661</td>
<td>26.32</td>
<td>.000</td>
</tr>
<tr>
<td>HEIGHT</td>
<td>2.95</td>
<td>.098</td>
<td>0.039</td>
<td>.695</td>
<td>19.79</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -0.514, Sy|x = 0.197 m³/m²*10²
EXCLUDED VARIABLES: SAPWOOD BASAL AREA, BASAL AREA, DIAMETER

### TREATMENT C - STEPWISE REGRESSION - SUMMARY TABLE

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>14.63</td>
<td>.001</td>
<td>0.068</td>
<td>.435</td>
<td>14.63</td>
<td>.001</td>
</tr>
<tr>
<td>CPA</td>
<td>8.84</td>
<td>.008</td>
<td>-0.035</td>
<td>.621</td>
<td>14.75</td>
<td>.000</td>
</tr>
<tr>
<td>DIAMETER</td>
<td>14.19</td>
<td>.002</td>
<td>0.046</td>
<td>.793</td>
<td>21.77</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -2.76, Sy|x = 0.213 m³/m²*10²
EXCLUDED VARIABLES: SAPWOOD BASAL AREA, VOLUME

### TREATMENT D - STEPWISE REGRESSION - SUMMARY TABLE

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>6.56</td>
<td>.019</td>
<td>0.090</td>
<td>.247</td>
<td>6.56</td>
<td>.019</td>
</tr>
<tr>
<td>CPA</td>
<td>36.73</td>
<td>.000</td>
<td>-0.018</td>
<td>.743</td>
<td>27.51</td>
<td>.000</td>
</tr>
<tr>
<td>SAPBA</td>
<td>12.59</td>
<td>.002</td>
<td>7.025</td>
<td>.849</td>
<td>33.73</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -2.60, Sy|x = 0.141 m³/m²*10²
EXCLUDED VARIABLES: VOLUME, DIAMETER, BASAL AREA
two of the first variables to enter the equations (Table 9). In treatment B, crown projection area entered first, followed by volume. In treatments C and D, height entered first, and crown projection area was the second variable to enter. In all three thinned treatment equations, crown projection area had a negative coefficient indicating that increased crown size decreased individual tree growing space efficiency.

When efficiency was based on growth per unit of sapwood basal area, diameter was the first variable to enter the equation, followed by crown projection area, height, and sapwood basal area in the unthinned treatment (Table 10). Volume and basal area did not contribute significantly to the equation.

In all three thinned treatments, height entered first followed by sapwood basal area (Table 10). The other independent variables entering into the thinned equations varied with treatment. In each thinned treatment, sapwood basal area had a negative coefficient meaning increased sapwood basal area decreased the growing space efficiency of the tree. The interaction between height and sapwood basal area is apparent in these equations, where together these variables account for more variation in tree efficiency than their individual coefficients of determination together, and where sapwood basal area, by itself, showed little relationship to efficiency (Table 7).

Efficiency and Individual Tree Characteristics in All Treatments

A similar analysis was performed on all trees, regardless of treatment, from which height and crown projection area measurements were
Table 10. Summary tables for stepwise regressions to predict individual tree efficiency (growth per unit of sapwood basal area) for Treatments A through D. Only significant variables (see text) are included in tables.

**TREATMENT A - STEPWISE REGRESSION - SUMMARY TABLE**

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIAMETER</td>
<td>72.76</td>
<td>.000</td>
<td>0.174</td>
<td>.752</td>
<td>72.76</td>
<td>.000</td>
</tr>
<tr>
<td>CPA</td>
<td>9.92</td>
<td>.004</td>
<td>0.079</td>
<td>.827</td>
<td>54.86</td>
<td>.000</td>
</tr>
<tr>
<td>HEIGHT</td>
<td>8.28</td>
<td>.009</td>
<td>0.226</td>
<td>.874</td>
<td>50.92</td>
<td>.000</td>
</tr>
<tr>
<td>SAPBA</td>
<td>7.36</td>
<td>.013</td>
<td>-72.792</td>
<td>.907</td>
<td>51.08</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -9.435, $Sy|x = 0.73 \text{ m}^3/\text{m}^2$

EXCLUDED VARIABLES: VOLUME, BASAL AREA

**TREATMENT B - STEPWISE REGRESSION - SUMMARY TABLE**

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>9.80</td>
<td>.004</td>
<td>0.297</td>
<td>.259</td>
<td>9.80</td>
<td>.004</td>
</tr>
<tr>
<td>SAPBA</td>
<td>6.19</td>
<td>.019</td>
<td>-83.527</td>
<td>.397</td>
<td>8.90</td>
<td>.001</td>
</tr>
<tr>
<td>DIAMETER</td>
<td>14.61</td>
<td>.001</td>
<td>0.173</td>
<td>.614</td>
<td>13.79</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -10.479, $Sy|x = 1.02 \text{ m}^3/\text{m}^2$

EXCLUDED VARIABLES: CROWN PROJECTION AREA, BASAL AREA, VOLUME

**TREATMENT C - STEPWISE REGRESSION - SUMMARY TABLE**

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEIGHT</td>
<td>5.47</td>
<td>.030</td>
<td>0.455</td>
<td>.223</td>
<td>5.47</td>
<td>.030</td>
</tr>
<tr>
<td>SAPBA</td>
<td>9.10</td>
<td>.007</td>
<td>-83.555</td>
<td>.484</td>
<td>8.45</td>
<td>.003</td>
</tr>
<tr>
<td>VOLUME</td>
<td>1.82</td>
<td>.195</td>
<td>1.312</td>
<td>.534</td>
<td>6.49</td>
<td>.004</td>
</tr>
</tbody>
</table>

CONSTANT = -12.090, $Sy|x = 1.21 \text{ m}^3/\text{m}^2$

EXCLUDED VARIABLES: CROWN PROJECTION AREA, BASAL AREA, DIAMETER

**TREATMENT D - STEPWISE REGRESSION - SUMMARY TABLE**

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>F RATIO</th>
<th>SIGNIF.</th>
<th>COEF.(B)</th>
<th>R SQUARE</th>
<th>OVERALL F</th>
<th>SIGNIF.</th>
</tr>
</thead>
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<tr>
<td>HEIGHT</td>
<td>16.89</td>
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<td>0.513</td>
<td>.458</td>
<td>16.89</td>
<td>.001</td>
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<tr>
<td>SAPBA</td>
<td>15.67</td>
<td>.001</td>
<td>-75.844</td>
<td>.703</td>
<td>22.48</td>
<td>.000</td>
</tr>
<tr>
<td>DIAMETER</td>
<td>9.21</td>
<td>.007</td>
<td>0.115</td>
<td>.803</td>
<td>24.53</td>
<td>.000</td>
</tr>
</tbody>
</table>

CONSTANT = -16.949, $Sy|x = 0.75 \text{ m}^3/\text{m}^2$

EXCLUDED VARIABLES: CROWN PROJECTION AREA, BASAL AREA, VOLUME
taken. The relationship between growing space efficiency (volume growth from 1980-1984 per unit of crown projection area in 1984) and crown projection area is shown in Figure 31. While no linear relationship is visible, the peak in efficiency among trees with medium-sized crowns is apparent. The trees with smaller crowns at the lower left-corner of Figure 31 are the relatively suppressed trees from the control treatment. The trees with the large crown projection areas are the heavily-released trees with large crowns from the thinned treatments.

Growing space efficiency (growth per unit of crown projection area) in relation to tree height is shown in Figure 32. Taller trees are generally more efficient, as is the case within the individual treatments. The tallest measured tree in the entire study area, from plot 3, produced only about 0.012 m per m of crown projection area. Displaying growing space efficiency on a continuous scale, such as with crown size (Figure 31) or height (Figure 32), avoids the subjectivity of classifying trees by crown classes, since crown class is largely a function of crown size and height (Smith 1986). Combining treatments in these graphs assumes, however, that the growth to growing space ratio is constant over different treatments. Spurr (1962) found growth to growing space relations were similar in three thinning treatments in Douglas-fir stands in New Zealand.

Figures 33 and 34 show the same relationships as do Figures 31 and 32, except symbols denote the crown class of the individual trees rather than their treatment. The most efficient trees are a combination of dominants and codominants. Dominant trees with a given efficiency are generally taller and have larger crowns (i.e., crown
Figure 31. Growth per unit of crown projection area in relation to crown projection area for individual trees by treatments (denoted by symbols) in the Delezenne study. Trees with larger crowns (larger crown projection areas) were not as efficient users of growing space as some trees with smaller crowns.
Figure 32. Growth per unit of crown projection area in relation to tree height for individual trees by treatments (denoted by symbols) in the Delezenne study. Taller trees were generally more efficient users of growing space than shorter trees, but the tallest trees were among the most inefficient trees in the study.
Figure 33. Efficiency of growing space (crown projection area) in relation to crown projection area for individual trees by crown class (denoted by different symbols).
Figure 34. Efficiency of growing space (crown projection area) in relation to tree height for individual trees by crown class (denoted by different symbols). Dominants were generally taller than lower crown classes, but ranged from among the most inefficient to the most efficient trees in the study.
projection areas) than equally efficient codominants. Dominant trees
range in efficiency from about 0.008 to 0.032 m$^3$/m$^2$, while codominants
have a similar range from about 0.006 to .022 m$^3$/m$^2$. The large range in
efficiencies for dominants and codominants occurs over a small range in
height (Figure 34) and for codominants also over a narrow range of crown
projection area (Figure 33). Of the 16 intermediate trees shown in
Figures 33 and 34, only 6 are from thinned treatments. Although the
mean efficiencies for intermediate trees in the thinned treatments were
not much lower than the mean efficiencies for dominants and codominants,
the intermediates did not range nearly as high in efficiency as the
dominants and codominants.

Efficiency per unit of sapwood basal area displays similar trends
as efficiency per unit of crown projection area when plotted over
sapwood basal area and height (Figures 35 and 36). This analysis also
indicated the most efficient trees were relatively tall with small
crowns. Figures 37 and 38, which denote crown classes, also indicate
dominants and codominants encompass a wide range of efficiencies. These
results support the third hypothesis: individual tree characteristics,
such as diameter and height, are related to individual tree productivity
and growing space efficiency.

Although the two measures of growing space efficiency generally
indicate the same trees are efficient, some variation exists between the
two measures of growing space (Figure 39). Since sapwood basal area
explained a higher percentage of the variation in cubic volume growth,
it is probably the better measure of growing space.
Figure 35. Growth per unit of sapwood basal area in relation to sapwood basal area for individual trees by treatments (denoted by symbols) in the Delezenne study. Trees with larger crowns (larger sapwood basal areas) were not as efficient users of growing space as most trees with smaller crowns.
Figure 36. Growth per unit of sapwood basal area in relation to tree height for individual trees by treatments (denoted by symbols) in the Delezenne study. Taller trees were generally more efficient users of growing space than shorter trees, but the tallest trees were among the most inefficient trees in the study.
Figure 37. Efficiency of growing space (sapwood basal area) in relation to sapwood basal area for individual trees by crown class (denoted by different symbols).
Figure 38. Efficiency of growing space (sapwood basal area) in relation to tree height for individual trees by crown class (denoted by different symbols). Dominants were generally taller than lower crown classes, but ranged from among the most inefficient to the most efficient trees in the study.
Figure 39. Relationship between sapwood basal area and crown projection area among all treatments combined. Symbols denote efficiency classes based on growth per unit of sapwood basal area and are expressed in cubic meters of volume growth per square meter of sapwood basal area.
Stand Efficiency

Plot totals for sapwood basal area ranged from 9.96 m²/ha for the constant basal area treatment to 16.83 m²/ha for the control treatment (Table 11). Since the plots in the Delezenne thinning study were thinned to prescribed levels of basal area, the 1984 levels of basal area varied little between plots of the same treatment. Sapwood basal area totals for the plots of the same treatment were also very similar (Table 11), suggesting a strong relationship between basal area and sapwood basal area (Figure 40).

Basal area and standing volume were closely related to sapwood basal area and basal area among the Delezenne thinning plots, but basal area growth and volume growth from 1980 through 1984 were not strongly related to either (Table 11). In the present study, the ratio of periodic volume increment from 1980 through 1984 to sapwood basal area in 1984 was used as a measure of stand efficiency. Individual plot efficiency ratios exhibited no distinct patterns for either sapwood basal area or treatment (Figure 41). Efficiencies for plots in the constant basal area treatment and the decreasing-increasing basal area treatment differed by 41.5% and 29.2%, respectively, from the lower value. In both cases, the less efficient plot from each treatment (plots 3 and 5) was in the western cluster of plots (Figure 3).

Similar productivity differences existed in general between plots in the western and eastern clusters. Plots of the same treatment in the eastern cluster had net periodic annual volume increments which on the average were 4.2 m³/ha/yr higher for the entire study period than those from the western cluster of plots (Table 2). Since the site
Table 11. Totals in 1984 for number of trees per plot, sapwood basal area, basal area, and volume. Plot size was 0.202 hectare (0.50 acre). Basal area growth and volume growth are periodic annual increments from 1980 through 1984. Treatments are indicated by the letter following the plot number. A is the control treatment, B the increasing basal area treatment, C the constant basal area treatment, and D the decreasing-increasing basal area treatment. Values in parentheses are English unit equivalents.

<table>
<thead>
<tr>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M²/Ha (ft²/ac)</td>
<td>M²/Ha (ft²/ac)</td>
<td>M²/Ha/yr (ft²/ac/yr)</td>
<td>M³/Ha (ft³/ac)</td>
<td>M³/Ha/yr (ft³/ac/yr)</td>
</tr>
<tr>
<td>1(A)</td>
<td>91</td>
<td>16.83 (73.31)</td>
<td>64.0 (278.8)</td>
<td>1.07 (4.66)</td>
<td>1090.7 (15588)</td>
<td>22.2 (317.3)</td>
</tr>
<tr>
<td>3(C)</td>
<td>28</td>
<td>9.96 (43.39)</td>
<td>35.9 (156.3)</td>
<td>0.57 (2.48)</td>
<td>585.5 (8368)</td>
<td>12.2 (174.4)</td>
</tr>
<tr>
<td>5(D)</td>
<td>24</td>
<td>11.04 (48.09)</td>
<td>36.9 (160.7)</td>
<td>0.63 (2.74)</td>
<td>580.9 (8302)</td>
<td>13.4 (179.6)</td>
</tr>
<tr>
<td>8(D)</td>
<td>31</td>
<td>10.99 (47.87)</td>
<td>36.4 (158.5)</td>
<td>0.81 (3.52)</td>
<td>618.9 (8845)</td>
<td>17.2 (245.8)</td>
</tr>
<tr>
<td>10(C)</td>
<td>34</td>
<td>10.18 (44.35)</td>
<td>36.5 (158.8)</td>
<td>0.76 (3.31)</td>
<td>625.4 (8938)</td>
<td>17.7 (253.0)</td>
</tr>
<tr>
<td>12(B)</td>
<td>49</td>
<td>13.84 (60.29)</td>
<td>50.9 (221.6)</td>
<td>0.83 (3.62)</td>
<td>875.0 (12505)</td>
<td>19.2 (274.4)</td>
</tr>
<tr>
<td>13(B)</td>
<td>55</td>
<td>13.34 (58.11)</td>
<td>51.0 (221.9)</td>
<td>0.85 (3.70)</td>
<td>879.6 (12571)</td>
<td>19.1 (273.0)</td>
</tr>
</tbody>
</table>
Figure 40. Stand totals for sapwood basal area per hectare in relation to basal area per hectare by treatment.
Figure 41. Stand volume increment (from 1980 through 1984) per unit of sapwood basal area per hectare in relation to sapwood basal area in 1984. Widely different rates of growth per unit of sapwood basal area, and therefore density (basal area), were evident in treatments C and D.
quality over the entire study area was relatively constant, varying from just 41 to 44 m (135 to 144 ft.), the differences between these plots may be the result of more than just site related factors.

DISCUSSION

Individual Tree Growth Rates and Efficiencies

Comparisons of mean tree growth rates for different crown classes (Table 4) indicate trees in upper crown classes grow more volume per tree, and contribute more towards stand volume than their counterparts in lower crown classes. Lower crown classes grow at very slow rates, even in thinned stands. Similar results have been reported by Oliver and Murray (1983).

Rates of growth per unit of growing space indicate dominants are not necessarily more desirable than lower crown classes in thinned stands if maximizing stand volume growth is the only concern. Differences between crown classes were small and usually not significant in thinned stands. In unthinned stands, the upper crown classes were more efficient than lower crown classes.

Both measures of growing space used in this study are cursory measures of crown size. Differences in efficiency, as defined here, result from variation in net photosynthesis between trees and variation in carbohydrate allocation to stem volume growth. While not reflecting photosynthetic efficiency or relative contribution of carbohydrates to stemwood volume, these measures of efficiency do describe efficiency of growing space in terms of the desired product: stemwood volume. These
measures of efficiency may not be applicable where other values -- such as total tree biomass -- are considered the desired product.

Efficiencies, using both measures of growing space, ranged considerably within crown classes (Figures 33, 34, 37 and 38), possibly reflecting the subjectivity of classifying trees into crown classes (Smith 1986). Growing space efficiency in relation to crown size (using either crown projection area or sapwood basal area) and tree height indicated tall trees and trees with relatively small crowns were the most efficient in thinned stands. In unthinned stands, tall trees with relatively large crowns were the most efficient. The trees in the control treatment were all stand grown, and those with large crowns were also trees with the large diameters and tall heights. Sapwood basal area, therefore, added little to an equation that already included these other variables. In an unthinned stand an efficient tree is apparently just a big tree: a tree whose dimensions place it in a favorable position in the upper canopy. A large-crowned tree in an unthinned stand is comparable in size to a small-crowned tree in a thinned stand. Figure 42 shows the three-way relationship of height, crown size (sapwood basal area) and growing space efficiency for all treatments combined. Efficiency generally increases with increasing height, but peaks at an intermediate crown size. For any given crown size, the tallest trees were the most efficient.

Applicability of Results

These results were obtained in a 64-year-old stand on a high site. They may not be applicable to younger stands or to stands of similar
Figure 42. Three-way relationship between tree height, sapwood basal area (as a measure of crown size) and growing space efficiency (growth per unit of sapwood basal area) for all treatments combined. The most efficient trees were tall trees with intermediate-sized crowns.
age but with a less intensive thinning history. Other studies have produced similar results, however. For example, Waring et al. (1980) found non-significantly different efficiencies, based on basal area growth per unit of sapwood basal area, across the three upper crown classes in an unthinned 40-year-old Douglas-fir stand. Efficiencies based on volume increment would have probably produced results more like those of the present study, since the height component of volume increment would have been greater in upper canopy trees. Waring et al. (1980) also reported similar standard errors around their mean efficiencies as those in the present study, suggesting they may also have had a wide range of tree efficiencies within a single crown class. Reanalysis of data from Greggs (1981) indicates a slight peak in efficiency in unthinned dominant and codominant Douglas-fir trees at less than maximum crown size in the two older stands studied (Figure 43). Ford (1975) attributed the bimodal diameter distribution frequently observed in unthinned stands (Figure 28) to differential rates of growth and efficiency, with those trees in the upper canopy being more efficient than those in the lower canopy. Studies of a number of other forest tree species have also found a decrease in efficiency in larger-crowned trees using a variety of measures of crown-size (Moller 1947; Senda et al. 1952; Satoo et al. 1955, 1959; Senda and Satoo 1956; Baskerville 1965; Kramer 1966; Hamilton 1969, 1981; Assmann 1970).

Explanations for Results

The relatively inefficient trees with large crowns in the present
Figure 43. Relation of growth per unit of sapwood basal area (efficiency) to sapwood basal area (as a measure of crown size) for dominant and codominant Douglas-fir trees in unthinned stands of three different ages. Growing space efficiency peaked at less than the maximum crown size in the two older stands (data from Greggs 1981).
study are trees which were heavily released at an early thinning and allowed to grow in a relatively open-grown condition for many years. They have large diameters and large live-crown ratios. As can be seen in Figure 39, trees with the largest sapwood basal areas did not have the largest crown projection areas. Perhaps this represents a different mechanism of crown expansion between early-released and late-released trees. The early-released trees are trees released at a relatively young age that expand their crowns vertically as the tree increases in height. Late-released trees are trees released later in the thinning regime, when height growth has slowed and crown expansion occurs through branch elongation. Information on the release history of individual trees during the Delezenne study was not available. Tree crowns do vary in shape because of a number of factors, only one of which is crowding. Measuring growing space with sapwood basal area (because of its relation to leaf biomass) would therefore seem preferable to crown projection area because leaf biomass is more closely related to photosynthetic capacity.

Identifying the mechanisms which make large-crowned trees inefficient was beyond the scope of this study, but several possible explanations will be offered. It can be assumed that the major structural difference between a small-crowned tree and a large-crowned tree of the same age and height is the retention of lower branches by the larger tree. Woodman (1968) described the lower branches of a codominant, forest-grown Douglas-fir as having increasingly lower rates of net photosynthesis towards the base of the crown. Underwood (1967) found the lower branches on forest-grown Douglas-fir trees to be "non-
functional" in terms of their contribution to stem growth (based on the number of growth rings at the base of the branch compared to branch age). Brix (1983) observed an accumulation of foliage in the lower crown of released codominant Douglas-fir trees and found the efficiency (both annual aboveground dry matter production per unit of foliage mass, and annual stemwood production per unit of foliage mass) of these trees fell below that of similar unreleased trees by the seventh year following release. The lower branches on the large inefficient trees in the present study may also be non-functional, although their sunlight environment is superior to that of the lower branches on forest-grown trees. The relatively large size of these inefficient trees may also contribute to their inefficiency because of relatively high rates of respiration needed to support the large amount of living tissues.

Sapwood/Leaf Area Assumptions

Using sapwood basal area as a measure of growing space assumes the sapwood basal area/leaf area relation is constant over different stand histories. This assumption has been questioned by Brix and Mitchell (1983), and the use of sapwood cross-sectional area at breast height has been questioned by Waring et al. (1982). For lack of better information, however, the measurements of individual tree sapwood basal area in the present study were assumed to approximate leaf biomass or leaf area per tree. The apparent superiority of the periodic growth/sapwood basal area relation, as compared to the periodic growth/crown projection area relation (Table 5), tends to support this
assumption.

The assumption that the sapwood/leaf biomass relation is valid could lead to a number of sources of error in this analysis. For example, if thinned trees have higher rates of sapwood conductivity than unthinned trees because of larger ratios of earlywood to latewood, heavily released trees would have greater sapwood conductivity than unreleased trees. If this is the case, the large inefficient trees in the present study will probably have high sapwood conductivity, a low sapwood to leaf biomass ratio, and the results presented here overestimate their efficiency. Increased transpiration in released trees would have the opposite effect on efficiency since these trees require greater sapwood area to support a given amount of leaf biomass. Brix and Mitchell (1983) found no unique relationships between sapwood and leaf biomass for thinned and fertilized treatments in their study. They cited Granier (1981) as having observed greater foliage per unit of sapwood area for thinned stands, suggesting efficiencies in the present study may be overestimated in released trees.

Estimating leaf biomass based on sapwood cross-sectional area at breast height (instead of the base of the crown) also indicates efficiencies of large trees in the present study may be overestimated. Since variation in height of thinned trees was relatively small (Figure 29), differences in crown size were largely differences in crown length, with larger-crowned trees reaching closer to the ground than smaller-crowned trees. If sapwood cross-sectional area decreases with increasing height towards the base of the crown (Waring et al. 1982), then trees with lower crowns would have more leaf biomass than trees.
with higher crowns but with equivalent sapwood cross-sectional area at breast height. This would lead to overestimation of efficiency of trees with larger crowns and underestimation of efficiency of trees with smaller crowns.

The individual tree analyses of this study were based entirely on trees whose diameter and height were measured, but did not consider differences in tree-form caused by treatment. Released Douglas-fir trees generally have greater taper than unreleased trees (Reukema 1964; Brix 1983; Thomson and Barclay 1984). This greater taper in the most heavily released trees in the present study would lead to overestimation of their volume relative to unreleased trees, and overestimation of their efficiency.

The magnitudes of the sources of error in estimations of growing space efficiency in this study are impossible to estimate, and there is also some doubt about the effect of these errors on the direction of change in efficiency. Nevertheless, it would appear that the larger-crowned trees are at least as inefficient as is indicated in this study.

Measures of Growing Space

Both measures of growing space used in the present study are useful. The stronger relationship between periodic volume increment and sapwood basal area (Table 5), especially in the more heavily thinned treatments, suggests sapwood basal area is the better measure. Measurement of sapwood cross-sectional area at the base of the crown would probably provide even better results. Measurement of sapwood basal area at the beginning of the measurement interval, during the
measurement interval, or during one of the growing seasons (Blanche et al. 1985), may also have improved results.

Measures of point density also offer the potential to represent the growing space per tree (Staebler 1951; Spurr 1962; Bella 1971; Arney 1973; Daniels 1976). These measures generally express the growing space of a tree as being related to tree size, and the size of and distance to the tree’s nearest competitors. Since these measures of point density are based on the assumption that growing space is related to present tree size, regardless of stand history, they were not used in this study. Individual tree characteristics such as diameter or volume are the result of a tree’s entire history of growth to growing space relationships, not just those of the present (Reukema 1961b). Such relationships will probably be satisfactory in unthinned, undisturbed stands where growing space is consistently proportional to crown position and to tree size. When stands are thinned or otherwise disturbed to redistribute growing space, allometric relationships -- such as between diameter and height, or diameter and crown projection area -- fail to apply.

The lower correlation between periodic increment and crown projection area observed in thinned stands (Table 5) may also be attributed to redistribution of growing space and failure of crown projection area to reflect the tree’s response. Douglas-fir tree crowns have a parabolic shape that is unlikely to change dramatically in response to an increase in growing space. A lack of a branch elongation response following release has been observed in Douglas-fir by Reukema (1964) and Brix (1981). If a tree is to increase its foliage mass to
receive an increase in sunlight, vertical expansion is probably more
physiologically "economical" than horizontal branch elongation. Upon
release a tree may increase its crown size vertically through greater
height growth, horizontally through branch elongation, or do both.
Horizontal expansion in lower branches involves a considerable
structural and respiratory system to support foliage at the end of a
branch. Vertical expansion involves additional foliage at the top of
the crown where it is supported by relatively small branches. Crown
projection area is still a useful measure of growing space, but the
assumption that it is related to tree diameter does not appear to be
valid in thinned stands (Table 8, Figure 30).

Efficiency of Released Trees

In Chapter Four, one explanation for the relatively high mean tree
volumes of the thinned Delezenne study plots in comparison to the mean
tree volumes predicted by two growth models for open-grown trees, was
that thinned trees exhibit greater growth efficiencies than do open-
grown trees. This implies a thinned tree will be larger than an open-
grown tree of the same age and currently growing at the same density,
despite the relatively limited growing space environment in which the
thinned tree has developed.

The results of this segment of the present study are inconclusive
on this point. While the relatively open-grown trees of the present
study did exist at lower efficiencies per unit of growing space than
smaller-crowned trees, their actual rates of growth were among the
greatest of any tree studied. These trees were all thinned trees,
however, and only represent a gradient to, but not including, the open-grown tree. As crown size (as measured by sapwood basal area) increases, an increasingly large amount of variability in volume increment can be observed (Figure 44). The volume increment for the trees with the largest crowns is no greater than for trees with half the crown size, possibly indicating a decline in volume increment with increasing crown size in these thinned trees. With larger crown sizes in open-grown trees, volume increment may remain constant, or perhaps it will decrease. For it to decrease, the additional leaf biomass (or the additional sapwood basal area) must make a negative contribution (i.e., net loss) to growth. Because the difference between an open-grown tree and a stand-grown tree is largely in retention of lower branches, it is these lower branches which would be net drains for photosynthates.

Several studies have shown that the lowermost branches of stand-grown Douglas-fir are basically non-functional in that they make no, or very little, contribution to stem growth (Underwood 1967; Woodman 1968, 1971); however, little information exists concerning the role of lower branches in open-grown trees. Some evidence exists in the Danish literature that indicates lower branches may have a negative effect on stem growth (Bavngaard 1946); however these results have been questioned by other researchers (Moller 1946; Larsen 1951).

Stand Efficiency

The ratio of stand periodic increment to stand leaf area has been used as an expression of stand vigor or efficiency in other studies (Waring et al. 1980, 1981; Binkley and Reid 1984; Waring 1985). A
Figure 44. Volume growth from 1980 through 1984 in relation to sapwood basal area in 1984 for individual trees from all treatments combined (treatments denoted by symbols). Increasing variability in volume growth with increasing sapwood basal area led to some trees having equal volume growth as larger trees despite having half the crown size.
strong, decreasing relationship of stand efficiency with increasing leaf area was not evident among the Delezenne study plots (Figure 41). These results resemble those reported by Binkley and Reid (1984), but differ from those reported by Waring et al. (1981). The differences may be attributed to the procedure used by Waring et al. (1981), which reduced growth by the high amounts of mortality which occurred on the study plots during the year preceding their measurements.

The differences between the efficiency of plots of the same treatment (Figure 41), basal area, and sapwood basal area (Figure 40) in this study may be attributed to structural differences between these stands. The diameter distributions of the plots are shown in Figure 45. In both treatments, the plots in the western cluster (i.e., plots 3 and 5) had fewer trees but these trees were larger than in the corresponding plots in the eastern cluster. Since larger trees are generally less efficient than smaller trees, plots 3 and 5 are less efficient despite having nearly identical levels of basal area and sapwood basal area as plots 8 and 10.

Thinning treatments which reduce leaf area, but keep stand structure constant (i.e., leaving similar structures) would probably produce an efficiency/leaf area relationship with less noise. However, attempts to ascertain volume/leaf area relationships, or efficiency/leaf area relationships for entire stands will encounter many of the same difficulties as volume/density relationships. Leaf area is a form of space occupancy or site utilization measure, and therefore resembles measures of stand density. What is more important than space occupancy is the distribution or arrangement of leaf area in a stand. As this
Figure 45. Diameter frequency distributions from plots 3 and 10 (treatment C), and plots 5 and 8 (treatment D) in 1984. Plots 3 and 5 had fewer trees than plots 8 and 10, but these trees were generally larger and had lower rates of growing space efficiency.
study has indicated, leaf area can exist at widely different efficiencies depending on crown position and size; and the arrangement of these tree crowns should override concerns over the amount of leaf area over a given area.

SUMMARY

Comparisons of periodic increments of individual trees in 64-year-old thinned and unthinned stands indicate dominants and codominants produce the most volume per tree and make the greatest contribution to stand volume increment. Comparisons on a per unit of growing space basis produced similar results, except differences in average efficiency between crown classes were smaller, or nonexistent, in more heavily thinned treatments.

Two measures of growing space were used: crown projection area and sapwood basal area. Both are cursory measures of crown size, but sapwood basal area reflects total crown size while crown projection area reflects crown area on a horizontal plane. Sapwood basal area was the better measure of growing space because of its higher correlation with periodic increment in thinned stands.

In thinned stands, tall trees with relatively small crowns were found to be the most efficient users of growing space. In unthinned stands, tall trees with relatively large crowns were most efficient, but a large crown in an unthinned stand was found to be comparable in size to a small crown in a thinned stand.
CHAPTER SEVEN
CONCLUSIONS

BASELINE VOLUME GROWTH MODEL

The three-dimensional baseline model of volume growth provides a method to compare the growth of dissimilar stands which otherwise may not be comparable. The baseline model facilitates these comparisons of stands of different densities or different ages by using known relationships of even-aged stand growth to create a broad, all-encompassing three-dimensional surface. This surface represents the standing volume of unmanaged stands of a range of densities and ages. In the present study, baseline models were constructed with, and used to compare, two growth and yield models for Douglas-fir stands in the Pacific Northwest. The predicted volumes from these models were in agreement over most of the range of ages and densities in which they coincided. At lower densities and older ages, however, the volumes predicted by the Douglas-fir Stand Simulator (DFSIM) exceeded those of the Tree and Stand Simulator (TASS).

Comparisons of the baseline models with the plot data from the Deleuzenne study found the baseline models to be in relatively close agreement with the control plots. The thinned plots, which represented
much lower densities than the control plots, exceeded the TASS baseline model in some cases at lower densities, and were similar to the DFSIM baseline model where densities and ages were comparable.

Explanations for these observations include: the TASS and DFSIM growth models may underestimate the growth of widely-spaced stands; a previously unrecognized response to thinning which permits properly thinned stands to grow faster than unthinned stands of similar densities; or a combination of both explanations.

The baseline model serves a purpose that can be met by existing growth and yield models, or other methods of comparison. For example, Staebler (1954, 1955) developed gross volume yield tables -- which represented maximal possible production -- as a standard for defining thinning treatments (Staebler 1960). Staebler assumed a constant growth/density relationship over a relatively wide range of density, and so this procedure has limited applicability to managed stands. Existing growth and yield models can also simulate the growth of stands for use in comparisons with observed managed stands. A baseline model, as described in this study, can be constructed which integrates simulated growth model data, competition-density theory, and permanent plot data into a graphical representation of stand growth. Unlike Staebler's procedure, this baseline model represents standing volume instead of gross volume production. The major advantage of this three-dimensional baseline model is that it provides a visual representation of the interaction between age, density, and self-thinning, and their effect on stand volume growth. Further development may allow formulation of a series of baseline models to represent different site productivities.
The approach to analyzing thinning data used in this study can be used to overcome the ambiguities of a limited data base frequently encountered in thinning studies. As more information becomes available, and the shape of the surface of the baseline model becomes better defined, this technique can be used to analyze the effects of various stand treatments on volume growth with very small data bases. Different treatments can be compared to a predefined volume/density relationship, rather than just strict comparisons between treatments.

VOLUME GROWTH AND STAND DENSITY

Results from the Delezenne study indicated recoverable (net) volume increment from some thinned plots exceeded the net increment from comparable unthinned plots. Thinning produced gross increments (net increments plus mortality) from some plots which were approximately equal to those of unthinned stands. Net increment in this study and in other cited studies was generally highest in thinned stands at relatively high densities.

Stand density measures can be separated into absolute and relative stand density measures, depending on whether they are independent from site and age. Relative stand density measures achieve independence from site and age by expressing density in relation to a measure of stand development. The various measures of stand development, such as mean tree volume or dominant height, separate relative density measures into different measures of competition.

Relative stand density measures which use height as the measure of
stand development, such as Wilson's (1946) percent of height, are considered to be the most useful density measures because: 1) dominant height is independent of site and age; 2) dominant height growth is largely unaffected by density; 3) thinning does not cause instant changes in dominant height (e.g., false increment) because it is not a measure of average tree development like mean tree volume or quadratic mean diameter; and 4) height-based stand density measures are simple, easy to conceptualize, and permit easy estimation of thinning intervals.

The Levels-of-Growing-Stock (LOGS) study, the most extensive thinning study to date in the Douglas-fir region, has attempted to identify stand growth/density relationships through strict control of density levels in thinned stands. Results reported to date from the LOGS study come from installations on high-quality sites where thinning intervals were very frequent. Methodologies do not resemble normal management practices in Douglas-fir stands; and, by minimizing the importance of variables such as thinning interval and stand structure, these studies are unlikely to represent the full potential of thinning in Douglas-fir stands. Since the primary objective of the LOGS study is to study growth/growing stock relationships, the strict control of density necessitated by this objective has led to short thinning intervals and some compromises over thinning methods (such as thinning to certain d/D ratios rather than a strict low thinning). Other, less extensive, thinning studies in Douglas-fir stands, such as the Delezenne study, have found nearly equal gross volume growth among unthinned and some thinned treatments. These results are in contrast to the results of the LOGS study and indicate some potential for thinned stands to
produce volumes at least as great as from comparable, unthinned stands.

It is concluded that stand growth/stand density relations are attempts to generalize a complex array of interacting variables into a single-variable model. Many studies have attempted to identify a growth/density relationship but no consistent relationship is discernible, especially among thinned stands (Davis 1956; Baskerville 1965; Clutter et al. 1983; Smith 1986). Many variables, including stand structure, thinning interval, stand vigor, site, age, and species, in addition to density, affect stand volume growth.

STAND STRUCTURE AND GROWING SPACE EFFICIENCY

Stand density has traditionally been the most important thinning variable, but it has been suggested that thinning to a particular stand structure in Douglas-fir stands may describe a proper thinning treatment more accurately than do measures of stand density (Oliver and Murray 1983; Larson and Cameron 1986). Stand structure has long been recognized as an important stand variable, but difficulties in its quantification have prevented it from becoming a major consideration in thinning guidelines. For example, Douglas-fir thinning guidelines generally define proper stand structures with a d/D ratio (average diameter of cut trees/average diameter of all trees prior to cutting), or simply by thinning from below (Worthington and Staebler 1961; Harmon 1969; Reukema and Bruce 1977), but stand structure is only of secondary importance to density in these guidelines.

A wide range in efficiency in use of growing space was observed in
individual trees in thinned and unthinned stands from the Delezenne study. These rates of efficiency were most closely related to canopy position (tree height) and crown size and imply a considerable range of possible yields from stands of a given density. This range is dependent on the combination and arrangement of tree sizes (i.e., the structure) of the stand. For example, two stands can be thinned to identical levels of density (using any measure of density) and have very different yield potentials (Stiell 1982). Thinning these two stands to a specific structure would produce very similar yields since trees of similar growing space efficiency would be left in both stands. The level of density may or may not be the same in these two stands, but coincidentally could be the same frequently enough for researchers to hypothesize all-encompassing growth/density relationships from such data.

Density measures represent average competition in a stand and assume trees with average characteristics are representative of the entire stand. Stand differentiation leads to a gradient in tree sizes, and the range of this gradient depends on many factors, of which density is only one. Although a differentiated stand consists of trees of a range of efficiencies, the relationship between growing space efficiency and tree size is not strong. In thinned stands the average tree in size may actually represent the maximum in efficiency, not the mean. Averaging these trees in an effort to gauge competition, or even stand development, produces results that are less than desirable and probably contribute to the confusion in growth/density relations.
It is concluded that optimal stand growth is obtained with a particular stand structure, or a particular combination and arrangement of tree sizes, and not necessarily with a particular stand density. An optimal stand structure at one point during stand development may or may not lead to optimal stand structures in the future. For example, a stand with an optimal structure may develop into a stand with a preponderance of inefficient trees and a suboptimal structure. The silviculturist can enhance the structural development of a stand with proper thinnings which anticipate the growth patterns of individual trees within the stand. This information can be obtained by more detailed studies which trace the growth and development of individual trees in thinned stands.

The high levels of gross production of the Delezenne thinned plots and of thinned treatments reported elsewhere may indicate thinning improves the growth rates of individual trees over that of open-grown trees of similar densities. Competition-density theory implies that gross production would be less in thinned stands than in unthinned stands, and the Langsaeter/Moller theory assumes the reduction from full-occupancy of growing space caused by thinning lowers gross production. Both of these theories assume the open-grown tree represents the optimum in individual tree growth rates, but optimal stand growth is obtained with full-occupancy of growing space. The high levels of gross production in thinned stands, where occupancy of growing space has been reduced by thinning, may be the result of increased tree efficiencies in thinned stands. Perhaps the lower efficiencies of
heavily released trees observed in the present study can be extrapolated to imply open-grown trees have even lower efficiencies and lower rates of growth than trees at similar densities in thinned stands. Unfortunately, there is a shortage of growth data for open-grown Douglas-fir trees to compare to the Delezenne plots.

The assumptions that tree area (i.e., growing space) is proportional to crown projection area, and that the stand development components of relative stand density measures can be related allometrically -- the assumptions which Curtis (1970) used to compare density measures as expressions of average area available per tree -- are apparently not valid in thinned Douglas-fir stands. Results from the Delezenne thinning plots indicate crown projection area is an increasingly poor measure of growing space in thinned stands as thinning intensity increases (Table 5). Other linear allometric relationships which exist between tree characteristics in unthinned stands or for open-grown trees -- such as between height and diameter, or basal area and crown projection area -- apparently break-down in thinned stands (Table 8, Figure 30). Transforming diameter to the 1.6th power (Bruce 1965; Curtis 1970) also fails to improve upon the relationship between basal area and crown projection area (Table 5). Other transformations of these variables are not expected to improve these relationships. Leak (1981) expressed similar concerns over the assumption that horizontal crown dimensions represent growing space as used in stocking guides in the eastern United States.
THINNING RECOMMENDATIONS

If maximizing recoverable stand volume is the management objective, the goal of thinning should not be full occupancy of growing space, but rather maximum efficiency of all growing space. Full occupancy of growing space and maximum efficiency of growing space are not always mutually exclusive alternatives, however. It is not suggested that all inefficient trees should be removed in a thinning operation. Inefficient trees can be either very large trees, or small suppressed trees. The inefficient large trees occupy large areas of growing space, and in the case of the most inefficient trees in the present study, they have few competitors. Removing these large trees would result in a short-term increase in average tree efficiency, but would result in large amounts of unoccupied growing space and substantial reductions in stand volume growth. Removing inefficient suppressed trees would increase average tree efficiency without a substantial loss of stand increment.

A more judicious thinning regime would be designed to prevent trees from becoming large, inefficient, relatively open-grown trees, such as those found in the present study. Several codominant trees could occupy the same growing space more efficiently than one large, open-grown dominant. Light thinnings which release larger intermediates and codominants, but not dominants, are recommended. The unreleased dominant trees in the unthinned treatment in the present study were more efficient, by both measures of growing space, than any other group of trees (Table 6). Thinnings should continue to thin from below,
anticipate and harvest future mortality, and space leave trees appropriately. When choosing leave trees, tree height should override crown size, although both are important. With other management objectives, thinning methods should be adjusted accordingly.

The results of this study imply light thinnings are most desirable in older stands, but these results are not necessarily applicable to younger stands. Younger Douglas-fir stands have a greater capacity to reclose their crowns following thinning, and can exhibit a greater response to heavy thinning than older stands (Staebler 1960). Hamilton (1976, 1981) reached this conclusion based on thinning trials with a number of species in Great Britain. Hamilton suggested that high intensity thinnings stimulated volume production in younger stands, but had the opposite effect in older stands. Wiley and Murray (1974) also found early thinning in Douglas-fir stands increased merchantable yields over later thinnings.

In order to maximize volume growth, thinning treatments should leave a sufficient number of trees to expand into and occupy the available growing space prior to subsequent thinnings, or within the expected rotation. Excessive removals reduce stand growth by creating unused growing space and producing inefficient trees. Results from the Delezenne study and in other thinning trials in the Douglas-fir region, where volume increments are highest in the less severe thinning treatments, support these conclusions. If trees become inefficient by existing in a relatively open-grown state for a prolonged period, then excessively heavy thinnings will reduce average tree efficiency.
Unfortunately, data on individual tree efficiency from this study does not exist for the entire study period so complete rotation-length comparisons are not possible. It is hypothesized, however, that light thinnings might increase the efficiency of unthinned intermediates and codominants and, coupled with the efficiency of the unreleased dominants in the thinned stands, result in periodic increments significantly greater than in unthinned stands. Such a thinning regime would probably create some unoccupied growing space, but may also increase the efficiency of occupied growing space resulting in increased stand growth. Binkley and Reid (1984) observed an increased efficiency in thinned Douglas-fir stands that produced nearly equal volume growth as similar unthinned stands, despite having less leaf area.

Stand density measures should remain an important part of thinning, but not without incorporating stand structure as at least an equally important part of a thinning treatment. Further study may provide more definitive guidelines for thinning Douglas-fir stands.

In summary, if maximizing recoverable volume is the management objective, thinning regimes are encouraged which:

1) Thin from below, removing inefficient suppressed and intermediate trees. Taller trees should be favored over shorter trees, and large-crowned trees should be favored in lower crown classes while small-crowned trees are preferable in upper crown classes;

2) Release larger intermediate, and codominant crop trees, but leave dominant trees unreleased. Release apparently decreases the efficiency of these large trees;
3) Leave a sufficient number of trees which are capable of reoccupying available growing space prior to subsequent thinnings or the final harvest; and
4) Thin heavily only in young stands, and thin relatively lightly in older stands.
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