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Index selection provides an efficient means of conducting selection on multiple traits by combining information on economic value, heritability, and the genetic and phenotypic correlations between traits to improve overall merit. The use of this method in forestry has been hampered by the lack of knowledge of the relative importance of individual traits in determining tree value. Data recently made available from a lumber recovery study made it possible to a) estimate relative economic weights for individual tree traits that are important in determining lumber value of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) under two grading systems (visual and machine-stress-rated (MSR)) and b) test the implications of alternative weights under various multi-trait selection indices.

Economic weights were derived by stepwise regression of total tree value, based on either visual or MSR grading of recovered lumber, on a variety of traits measured on 164 young-growth (ages 36-66 years) Douglas-fir trees in western Washington and Oregon. Two traits were found to have a significant influence on tree value under visual grading, stem volume and branch diameter, with relative economic weights 0.06 $dm^3$ and -5.22 cm, respectively. In addition to volume and branch diameter, wood density also significantly influenced tree value under MSR grading (relative economic weights 0.06 $dm^3$, -6.69 cm, and 0.06 $kg/m^3$, respectively), where lumber strength is measured directly.

Selection indices and expected responses of volume, branch

diameter, and wood density to index selection were examined utilizing progeny test data from 20-year old trees of 85 open-pollinated families replicated on three planting sites. The derived selection indices were quite different for the two lumber grading schemes, as were the expected responses in individual traits. Under visual grading, expected response in volume is large, but because wood density was not included in the index, a large negative (unfavorable) response in wood density is also expected. Using MSR grading, a positive response is expected in both volume and wood density, but the expected response in volume is less than when visual grading is used to determine economic weights. Little response in branch diameter is expected even though branch diameter was included as a trait in both indices. This is due to the low variability of branch diameter and its adverse genetic correlation with volume.

Changes in genetic and phenotypic parameter estimates (tested by using only a portion of the progeny test data) resulted in different index coefficients and changes in expected responses of individual traits. These results emphasize the necessity of evaluating the implications of using a particular index prior to applying it to a breeding population. In one case, a desired gain index, with desired relative responses for volume and wood density equaling the MSR-based economic weights, was successful in predicting positive responses in both volume and wood density where a Smith-Hazel index had resulted in a negative response in volume. Thus, this type of restricted selection index provides a means of increasing overall merit while dictating the allowable changes in each trait.

# MULTI-TRAIT SELECTION IN COASTAL DOUGLAS-FIR

by

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## CHAPTER I

## GENERAL INTRODUCTION

Choosing the traits or characteristics that will define the best genotypes for use as parents in advanced generation breeding is a critical step in any forest tree improvement program. Many attributes of a tree can be measured, but for selection to be most effective the number of traits must be limited to those few that significantly influence the yield and quality of desired wood products. This requires a knowledge of end-use product requirements and how tree characteristics and wood properties affect these requirements. Assessing the potential for genetic improvement, however, also requires information on the genetic variability and heritability of traits. Combining information on the economic importance of traits and their genetic potential is the most effective means of selecting to improve overall merit (Hazel and Lush 1943).

The primary goal of this dissertation was to quantify the relative economic merit of stem growth and quality traits for the production of high-quality coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) lumber, and to evaluate the efficiency of multi-trait selection for improvement in these traits. An analysis of traits economically important for coastal Douglas-fir and their use in multi-trait selection is important because many Douglas-fir progeny tests are approaching the age (15-20 years) when final selections for advanced generation breeding will be made (Sniezko 1990). Douglas-fir is the primary species under intensive management on the Pacific coast of North America and its wood is valued for high-quality building and construction materials (Oswald et al. 1986, USDA 1987). The many

Douglas-fir tree improvement programs in the Pacific Northwest attest to the importance of this species in commercial forestry (Quam 1988).

Lumber quality is graded on the basis of strength and appearance (Haygreen and Bowyer 1982). Two methods of grading lumber are currently in use. Visual grading is the most common method worldwide, with grades assessed visually by inspection of individual pieces. Machine-stress-rated (MSR) grading, a more precise method for measuring wood strength, is currently restricted to assessing lumber that must meet exact design criteria, but its use is expected to grow in the future (Kellogg 1982).

Three traits are important for production of high yields and quality of Douglas-fir lumber. Stem size or volume is related to both yield and grade, while wood density and the size and frequency of knots are wood properties critical to the increased strength and improved appearance of lumber (Kellogg and Kennedy 1986). Wood density is a simple, reliable measure of the amount of cell wall material present in a piece of wood and it is the single most important physical characteristic of wood. It also indicates the size of individual cells and the thickness of cell walls; it is an excellent predictor of strength, stiffness, hardness, and paper-making capacities of wood (Megraw 1985). Knots are formed when a tree encases the base of a branch as the stem increases in diameter. The distorted grain around the knot lowers compression strength parallel to the grain and also lowers bending strength (Desch and Dinwoodie 1981). The goals of genetic improvement of Douglas-fir for lumber production, therefore, are to increase bole volume production per unit of time while limiting knot size and maintaining high wood density.

To select simultaneously for improvement in more that one trait, some type of multi-trait selection procedure is needed. The selection index approach is the most effective multi-trait selection method for improvement in overall merit (Hazel 1943, Smith 1936). Genetic gain in overall merit is maximized by placing emphasis on each trait according to its economic value, heritability, and correlations with other traits. A composite trait or index is developed for each candidate tree and trees are ranked according to their index values. Application of the selection index method in forest tree breeding has increased in recent years with the availability of computers to facilitate the extensive computations involved (Bridgwater et al. 1983, Chollet and Roman-Amat 1987, Christophe and Birot 1983, Dean et al. 1983, Dean et al. 1986), but the lack of reliable estimates of the relative economic values of individual traits has limited its use in coastal Douglas-fir. Without product-value based economic weights it is impossible to objectively tailor selection for improvement in overall merit. Lack of estimates of economic weights based on tree value has been a major barrier to the full implementation of index selection in forest tree breeding (Bridgwater and Stonecypher 1979, Cotterill and Jackson 1985, Zobel and Talbert 1984).

Product-value based economic weights cannot be developed without information on the relative influence of individual traits, as measured on standing trees, on the value of lumber. Recovery studies provide the only way to quantify the effects of individual traits on lumber value, but these studies are rarely done because they are expensive. Ideally, one would want to conduct a recovery study with rotation-age trees in the same progeny tests used for the genetic analyses, but such materials will not be available for many years to come since the oldest Douglas-fir progeny tests are only between 20 and 25 years old (Quam 1988). Although not ideal, a recently complete product recovery study (Fahey et al. 1991) provided a unique opportunity to obtain, without delay, much needed estimates of relative economic weights for traits related to lumber production in coastal Douglas-fir. These economic weights were then applied to the oldest available progeny test information in order to assess the effectiveness of multi-trait selection for high quality lumber production in this species.

The general goals of the study described in this dissertation were to: 1) determine the combination of traits that can be measured on standing trees that best predict whole-tree dollar value of lumber in young-growth Douglas-fir; 2) develop relative economic weights for these traits for application in multi-trait selection; 3) determine the extent to which relative economic weights are a function of the grading system; 4) estimate genetic and phenotypic parameters of the traits found to be significant in predicting whole-tree dollar value; 5) evaluate genetic responses in both individual traits and overall merit expected from the application of selection indices based on alternative economic weights; 6) test the sensitivity of selection indices to changes in genetic and phenotypic parameters.

To accomplish these goals, the study was divided into 2 parts, which correspond to the next 2 chapters. In Chapter II, the combinations of traits in standing trees that significantly affect whole-tree dollar value, as quantified by the value of recovered lumber, are determined for both the visual and MSR grading systems using stepwise regression. Lumber value of 164 young-growth Douglas-fir trees in western Washington and Oregon are regressed on the following candidate traits: tree height, diameter at breast height, stem volume, branch diameter, and wood density. Partial regression coefficients of the traits that have significant impact on tree value are be used in index selection as the relative economic weights (Cotterill and Jackson 1985).

In Chapter III, various selection indices are built using the two sets of economic weights based on visual and MSR grading rules, and genetic and phenotypic parameter estimates for stem volume, branch diameter, and wood density measured on 20-year old trees in 85 open-pollinated families. In order to test the sensitivity of index selection to changes in genetic and phenotypic parameter estimates, two data sets are used: one based on the data from one site alone, and the other on data for three sites pooled. The adverse correlations between volume and both branch diameter and wood density make the examination of individual trait responses a necessity, because the interaction between the economic weights and genetic parameters may result in undesirable changes in individual traits as has been found in previous studies (Dean et al. 1983, Vargus-Hernandez and Adams 1991).

General conclusions of the study are given in Chapter IV along with a discussion of potential areas of future research.

# CHAPTER II

## DETERMINATION OF RELATIVE ECONOMIC WEIGHTS FOR MULTI-TRAIT SELECTION IN COASTAL DOUGLAS-FIR


### ABSTRACT

To determine the combination of traits that best predict tree value for lumber production and to estimate relative economic weights for use in multi-trait genetic selection in coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), the relationships between tree traits and tree value were investigated. The extent to which relative economic weights are a function of the system used to grade lumber was also examined. Tree height, diameter at breast height and branch diameter were measured on each of 164 young-growth trees (ages 36-66). Increment cores from a subsample (92) of these trees were assayed by x-ray densitometry to determine wood density. Bole volume was derived by summing the log volumes of all logs from each tree. Value of lumber recovered from each tree was determined previously in a mill study using both visual and machine-stress-rated (MSR) grading rules.

Stepwise regression was used to relate each of three methods of determining tree value to individual traits measured on the same trees. These regressions revealed that under visual grading of lumber, tree value was best predicted by a model including bole volume and branch diameter, while under MSR grading, a third trait, wood density, was added to the model. For the case of tree value per unit volume, height, branch diameter, and wood density were significant independent variables in the model. In all cases, tree value was positively related to tree size (volume or height) and wood density, but was negatively related to branch diameter. For the absolute measures of tree value, the

regression models accounted for large percentages of tree value (> 89%), but for tree value per unit volume, the regression model accounted for about half (51%) of the variation.

Regression coefficients in the above models can be used directly as economic weights in selection indices. Although weights for volume and branch diameter were very similar under visual and MSR grading, the addition of wood density as a factor in predicting tree value under MSR grading makes it difficult to predict responses of individual traits when different selection indices are employed. This is due to the adverse correlations between volume and both branch diameter and wood density, and the favorable correlation between branch diameter and wood density.

The associations between volume, branch diameter and wood density would result in a correlated loss in volume if the economic weights derived for tree value per unit volume were used in index selection. This anticipated loss in volume, and the weakness of the regression model in accounting for value per unit volume, makes the economic weights based on this model of little utility in Douglas-fir breeding programs.

## Introduction

To improve the yields and quality of wood products through forest tree breeding requires an understanding of the attributes of desired products. Properties or characteristics that have a strong influence on these attributes and are measurable on standing trees can be evaluated for potential use in genetic selection. If these traits have significant levels of genetic variability and are under sufficient genetic control, as measured by narrow sense heritability, then improvement by selection and breeding may be justified. The goal of this chapter is to evaluate the relative importance of various traits on standing trees of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) in terms of their influence on overall product value.

The most common uses of Douglas-fir wood are for building and construction materials such as lumber, timbers, piling and plywood (USDA 1987) due to its superior mechanical properties (i.e., wood strength and resistance to deformation) compared to most other commercial softwood species (Haygreen and Bowyer 1982). The U.S. market for structural lumber is expected to continue to be strong well into the future (Haynes and Fight 1992). Because of the increasing availability of inexpensive wood products from other species, the high-quality lumber market is expected to provide the highest demand for Douglas-fir (Barbour and Kellogg 1990, Ernst and Fahey 1986).

What primary tree characteristics and wood properties can be used in forest tree breeding to enhance the production and quality of Douglas-fir lumber products? Some measure of stem size or volume is certainly important (Kellogg and Kennedy 1986). In addition, there are two wood properties that contribute significantly to the quality of lumber: wood density (weight per unit volume) and the size and frequency of knots (Haygreen and Bowyer 1982). Wood density is a simple, reliable index of a number of physical properties of wood, including the total amount of cell wall substance, individual cell size, and cell wall thickness; it is an excellent predictor of strength, stiffness, and hardness (Megraw 1985). Although many anatomical properties other than wood density affect wood quality, it has been suggested that breeding programs should focus on this single most important trait (Kellogg 1982). Furthermore, while wood density itself can be divided into a number of components (i.e., early wood density, latewood density, and latewood percentage), these components are highly correlated among themselves and with overall wood density in Douglas-fir, such that little additional information is obtained by its division into components (Vargas-Hernandez and Adams 1991). Knots result from tree growth encasing the branches. Knots and the distorted grain around knots are areas of discontinuity within the wood. The strength of a board is heavily dependent on the size and the position of knots (Megraw 1986).

Lumber grade, whether evaluated by visual or mechanical means, is strongly influenced by both knot size and wood density. The visual grading system is the most commonly used method of grading in North America. The Department of Commerce Product Standard PS 20-70 established national grading rules for softwood dimension lumber (Western Wood Products Association 1988). These standards, based on visible characteristics, consider knot size, knot placement, mechanical defects and biological defects in determining lumber grade. For any given width of board, grade decreases as the size of the knots increase. For higher grades of visually graded structural lumber (Select Structural, No. 1 or No. 2) both physical properties and appearance are important; acceptable knot size is limited and rings per inch must be sufficiently high (i.e., rate of growth sufficiently low) to exclude wood of low density.

In mechanical or machine-stress-rated grading (MSR), each board is visually examined for strength-limiting defects and mechanically tested for dynamic modulus of elasticity (MOE) of stiffness (Galligan, Snodgrass, and Crow 1977). The distance that knots are displaced from the edge of the board sets the upper limit of predicted fiber stress in bending, $F_b$, while MOE is used to evaluate the strength up to that limit. Wood density and knot size are correlated with MOE and $F_b$ (Grant et al. 1984, USDA 1987).

MSR grading provides a more accurate and objective assessment of wood strength, but it is more costly than visual grading and at present is used only for grading materials which must meet exact design criteria. Its use is expected to increase until most Douglas-fir structural lumber is MSR-graded by the end of the next rotation (50-100 years from now) (Kellogg 1982), while visual grading will continue to be the predominant grading system for other lumber products.

Although the importance of wood density and branch diameter to the value of wood products is well known, these traits have only recently been considered for inclusion in Douglas-fir tree improvement programs (Gonzalez and Richards 1988, King et al. 1988a, Sniezko 1991, Vargas-Hernandez and Adams 1991). Emphasis of these programs in the past has primarily been on stem volume growth alone. Increasing interest in wood quality traits has been fueled by a growing concern that the harvest of young-growth trees with larger percentages of lower-density juvenile wood will result in a lowering of wood quality and, consequently, lumber grade and value (Barbour and Kellogg 1990, Kellison et al. 1985).

Given that tree size, branch size, and wood density all affect lumber quality and quantity, the degree of emphasis placed on each trait when considered simultaneously in a selection program will depend on their relative influence on the overall merit or worth of an individual (Hazel and Lush 1943). Three approaches are available for selection on multiple traits in breeding programs: tandem, independent culling, and index selection (Lawrence 1981). In tandem selection, each trait is improved independently to the desired level before selection proceeds onto the next trait. This method is not practical for most tree breeding programs due to long generation intervals and the correlations between traits. Under the independent-culling-level method all traits are considered simultaneously, but individuals must exceed the minimum phenotypic value, i.e., independent culling level, for all traits in order to remain in the selected group (Hazel and Lush 1943).

Index selection is the most efficient method for simultaneous selection of multiple traits to improve overall merit. Information including heritabilities of all traits, genetic and phenotypic relationships between traits, and economic values of the traits are combined to produce a composite trait or single index value for each candidate tree, on the basis of which selections are made (Smith 1936, Hazel 1943). Often, this type of index is referred to as the Smith-Hazel index (Cotterill and Dean 1990, Chapter 8). In recent years, there has been increasing use of the selection index method in forest tree breeding with the availability of computers to facilitate the complex computations involved (Bridgwater et al. 1983, Chollet and Roman-Amat 1987, Christophe and Birot 1983, Dean et al. 1983, Dean et al. 1986).

The most difficult problem in the application of index selection is the lack of information on the relative worth of individual traits in influencing overall economic value of a tree (Bridgwater and Stonecypher 1979, Cotterill and Jackson 1985, Zobel and Talbert 1984). The economic weight of a trait is defined as the increase in tree value expected from a one unit increase in the trait relative to a one unit increase in other traits (Cotterill and Dean 1990, Chapter 7). In most cases, index selection in forest trees has been used without information on economic value. Index methods have been employed not to maximize gain in overall merit, per se, but to control responses in individual traits to as close to desired levels as possible. The relative economic weights, in these cases, are not based strictly on product value determination, but simply refer to the weight placed on each trait by the breeder. Among the approaches that have been utilized are to create weights to achieve maximum gains possible in all traits considered individually (King et al. in press, Magnussen 1990), to set desired levels of relative gain for each trait (Shelbourne and Low 1980), or to restrict gain on certain traits while achieving maximum gain in others (Cotterill and Jackson 1985, Adams and Morgenstern 1991, Rehfeldt 1985). Most frequently, a number of indices developed using a range of economic weights are compared to find an index which gives the best combination of preconceived responses in individual traits (Bridgwater et al. 1983, Christophe and Birot 1983, Dean et al. 1983, Dean et al. 1986, Dean et al. 1988, King et al. 1988a, Magnussen and Keith 1990).

To estimate economic weights based directly on economic value, the best sources of information are product recovery studies in which the volume and value of products milled from individual trees are recorded (Ernst and Fahey 1986). A multiple regression model can be used to relate the traits of a tree to the value of the products milled from the tree (Baker 1986, Chapter 9). The partial regression coefficients represent relative economic weights and can be used directly as components of index selection (Cotterill and Jackson 1985). There are few examples where relative economic weights based on product value have been reported for commercial tree species because product recovery studies are expensive and labor intensive (Bridgwater and Stonecypher 1979, Chollet and Roman-Amat 1987, Cotterill and Jackson 1985, Kellogg and Warren 1984, Talbert 1984). No product-value based economic weights have been reported previously for Douglas-fir.

A product recovery study conducted by the Douglas-fir Stand Management Cooperative (SMC) (Fahey et al. 1991) provided an opportunity to estimate relative economic weights based on the production of Douglas-fir lumber. The objectives of the SMC study were to model the effects of log characteristics on the recovery of lumber and veneer under both the visual and MSR grading systems. The log characteristics investigated were log diameter and taper, proportion of juvenile wood in the log, and branch diameter. Juvenile wood is an inexact term that refers to the wood in the inner stem surrounding the pith which has wood properties at undesirable levels for the production of quality wood products, notably, lower average wood density compared to mature wood (Megraw 1986). The transition from juvenile to mature wood in Douglas-fir has been estimated to occur about age 23 for wood density (Di Lucca 1989). In the SMC study, the proportion of juvenile wood in each log was estimated as the volume within the 10- and 20-year annual rings from the pith. This interval was chosen to ensure that a standard number of rings were used for each log. Total tree height, stem diameter at breast height, and branch diameter of the largest limb in the first log were measured on each tree. In addition, a wood core was taken from each tree at breast height to estimate wood density for use in other studies. Volume recovery of lumber from individual logs (of all grades) increased with log diameter and decreased with log taper, while veneer volume recovery increased with log diameter and decreased with branch diameter. Log diameter was the primary determinant of volume recovery in each case. Under visual grading, recovery of the higher grades of lumber and veneer decreased as branch diameter increased. Lumber grade recovery under the MSR grading system decreased as branch diameter and proportion of juvenile wood increased. No MSR grading system has been developed for veneer.

In the present investigation, data from the SMC study was used to estimate relative economic weights for tree traits based on tree dollar value. For genetic selection purposes, traits are measured on standing trees and, therefore, to employ index selection it is necessary to know the relative influence of these traits on whole-tree value. Whole-tree value, determined by summing the value of all logs bucked from a tree, served as the dependent variable in multiple regression models. Since most selections are made in test plantations before trees are 20-years old (Silen and Wheat 1979, Sniezko 1991), test trees consist entirely of juvenile wood. Thus, proportion of juvenile wood used in characterizing log value in the SMC study, is irrelevant in early selection. As a measure of wood strength and quality in standing trees, we replaced juvenile wood with overall wood density.

Although information was available from the SMC study on recovery of both lumber and veneer from logs, it was decided to estimate relative economic weights for only lumber products for two reasons: lumber is the major product milled from Douglas-fir timber in the Pacific northwest (Larsen and Beardon 1989), and young-growth trees that have the attributes to product high yields and quality of lumber will also produce high quality veneer (Fahey et al. 1991). The objectives of the present investigation were to:

1. Develop linear regression models that best predict whole-tree dollar value of Douglas-fir lumber as determined by the visual and MSR grading systems. Total tree height, diameter at breast height, stem volume, wood density, and branch diameter of the largest limb in the butt log were chosen as candidate independent variables because of their known effect on lumber yield and value.

2. Estimate relative economic weights for the traits in the above analysis that most influence lumber value of Douglas-fir.

3. Determine the extent to which relative economic weights are a function of lumber grading system.

The relative economic weights derived in this chapter are used in Chapter 3 to examine the consequences of applying alternative selection indices in a Douglas-fir breeding population.

# Materials and Methods

Sample trees

For the present investigation, a 164-tree subsample (from 11 stands) of the original 236 trees included in the SMC log recovery study were used. All trees were sampled from stands in western Washington and Oregon with a wide range of site attributes, growing conditions, ages, and stocking histories. Trees within stands were chosen to provide a sample of logs with a wide range of stem sizes, limb sizes and proportions of juvenile wood. Examination of scatterplots revealed a moderate correlation between age and tree value as estimated using either visual (0.60) and MSR grading (0.65) for the original sample of trees. Limiting the range of tree ages to 36 to 66 (resulting in the 164-tree subsample) removed the confounding effect of age on tree value, thus eliminating the need to use age as an independent variable in regression models.

Measurements

Trees were bucked to a top diameter of 15 cm at the logging site and were further bucked into mill-length logs at the mill (4 to 8 meters). Before felling, total tree height and diameter at breast height (DBH) were measured and 9mm wood cores were taken from each tree at breast height to estimate wood density (Table II.1). Not all core samples extended from pith to bark and cores missing more than 10% of the annual rings were discarded. This accounts for the lower sample size for wood density (92 trees). Volume was calculated by summing the inside-bark volumes of the mill-length logs. Gross cubic log volume of the butt log was computed using a butt log formula (Bruce 1982). For all other logs, the Smalian formula was used (Meyer 1953). Branch diameter was estimated by measuring the diameter of the largest limb, live or dead, in the butt log of each tree; two caliper measurements were taken at right angles to each other and averaged. Live limbs were measured just above the branch swell and dead limbs flush with the bark.

Individual ring density was estimated with the use of direct scanning x-ray densitometry (Hoag and McKimmy 1988) on extracted core samples at 9% equilibrium moisture content (Krahmer et al. 1988). Average wood density of each tree at breast height was estimated by summing the products of the mean density of each ring by its corresponding ring width and dividing by the overall length of the core.

Lumber processing

All logs were sawn into 2 by 4 and 2 by 6 dimensional lumber at a state of the art sawmill in western Washington (Fahey et al. 1991). This product mix was used to help ensure that lumber recovery would reflect the inherent quality of the wood, not the skill of the sawyer in offsetting the effect of branch size on log quality by sawing logs with larger knots into wider boards. Also, the majority of MSR-graded lumber is marketed in this product mix. Recovery of chips and sawdust was measured in the log study, but was not considered in the present analysis since the contribution of chips and sawdust to log value was found to vary little within the limited range of tree sizes used.

Logs were graded both visually and under the MSR grading system. Under the visual system, 2 by 4s were graded by the structural light framing rules and 2 by 6s were graded by the rules for structural joists and planks (Western Wood Products Association 1988). To set the MSR grade, each board was first assigned an Fb (extreme fiber stress in bending) class by a lumber grader using the MSR visual grading requirements (Western Wood Products Association 1988). Those boards meeting minimum visual grade criteria for MSR were machine-tested and both average and low point of modulus of elasticity (MOE) were recorded. Boards not meeting minimum MSR criteria retained the dollar value that had been assigned during visual grading, and this value was used in the summation of board values to estimate MSR tree dollar value.

In setting prices for individual lumber grades, the price of No. 2

and Better grade (No. 1, No. 2, and Select structural grades combined) was used as a base. Combining these 3 grades for sales purposes is a common practice in the Douglas-fir lumber industry. More lumber is sold in this expanded grade than any other. A reasonable index price was $200/thousand board feet in 1989. (Board feet is the conventional measurement used in the region and no metric equivalent is available.) This price was used for No. 2 grade and other grades were priced as ratios of this price using Western Wood Products Association (WWPA) reports of sales for lower grades, and WWPA reports plus discussions with producers of MSR-graded lumber to estimate the price premiums for the higher grades (Table II.2)(Western Wood Products Association 1989). This type of pricing was used to gain a generalized picture of the premium for quality without undue attachment to the current pricing structure where No. 2 grade and above are combined, and to reflect the expectation that premiums for superior quality structural items will increase slightly over the next 40 years (Haynes et al. 1988). A similar approach was taken by the British Columbia Ministry of Forests in a recent financial study of the genetic improvement of wood quality in Douglas-fir (Jefferson, undated) and in the development of the pricing structure for TREEVAL2, a computer model designed to estimate net product value of individual Douglas-fir trees (Briggs and Fight 1992).

Analysis

To build a regression model that best predicts whole-tree dollar value, and to estimate partial regression coefficients for use as relative economic weights in genetic selection, a stepwise multiple regression procedure (Neter et al. 1983, Chapter 12) was applied using the tree traits measured in the log recovery study: total tree height, DBH (diameter at breast height), stem volume, branch diameter and wood density. The multiple regression equation takes the general form:

$$Y = c + a_1X_1 + a_2X_2 + a_jX_j + \ldots + a_nX_n ,$$

where $Y$ = dollar value of individual trees

$c$ = Y intercept (a constant)

$X_j$ = phenotypic value of the $j^{th}$ trait

$a_j$ = partial regression coefficients (economic weights)

The economic weights, $a_j$, estimate the amount that the dollar value of a tree changes when the phenotypic value of the $j^{th}$ trait is increased by one unit of measure and the other traits are held constant. A sequence of regression models were built and at each step an independent variable was automatically added or dropped using the F-statistic at $P < 0.05$ to test the hypothesis $H_0$: $a_j = 0$, where $a_j$ is the regression coefficient for the independent variable, $X_j$. Height, DBH, volume, branch diameter, wood density and the two-way interactions between these traits were tested as independent variables. Testing for lack of fit revealed that linear regression functions adequately fit the data as measured by the appropriate F-statistic and, therefore, polynomials were not tested as independent variables because they would not add to the amount of variation explained by the models (Neter et al. 1983, Chapter 4).

Three response variables were created:

1. Dollar value of an individual tree based on the visual grading system ($VSL).
2. Dollar value of an individual tree based on the MSR grading system ($MSR).
3. Dollar value per gross cubic meter ($\$/m^3$).

In each case, the summed dollar value of all boards milled from an individual tree was used to estimate the value of the tree; manufacturing costs were not subtracted from the dollar value. As in the SMC study, the rationale was to formulate a generalized picture of the role of measured traits in determining tree value without the influence of the harvesting or manufacturing costs of a particular company. This is consistent with the approach used in the development of relative economic weights for loblolly pine (Talbert 1984).

Tree size was such a dominant factor in the models using \$VSL and \$MSR as response variables, that a third response variable ($\$/m^3$) was created employing MSR grading rules to investigate the effects of quality traits (branch size and wood density) on tree dollar value when the strong impact of volume is removed. A similar approach was taken in a mill study of interior Douglas-fir (Middleton et al. 1985).

Using \$VSL and \$MSR response variables, inspection of residual plots revealed that error variance increased with increasing volume. Therefore, the residual terms in the \$VSL and \$MSR models were weighted by $1/(\text{volume})^2$ following the method of weighted least squares (Neter et al. 1983, Chapter 5).

The adjusted coefficient of multiple determination ($R_a^2$), was used to measure the amount of variation in tree value explained by each model. $R_a^2$ quantifies the proportion of the total variation in the independent variable, Y, accounted for by the set of X variables included in the model (Neter et al. 1983, Chapter 7). It is defined as:

$$R_a^2 = 1 - \left[\frac{n-1}{n-p}\right] \frac{SSE}{SSTO}$$

where, SSE = sums of squares error,

SSTO = sums of squares total,

n-1 = degrees of freedom associated with SSTO,

n-p = degrees of freedom associated with SSE.

The ratio of the degrees of freedom associated with SSE and SSTO adjusts for the increase in the coefficient of multiple determination, $R^2$, that automatically occurs with the addition of independent variables to the model.

## Results and Discussion

Relative economic weights

For all three measures of tree value, once individual traits were included in regression models, interaction effects did not explain significant additional information. Tree dollar value based on visual grading analysis ($VSL) was best predicted by volume and branch diameter (model 1, Table II.3) and most of the variation in whole-tree dollar value was explained by this model ($R_a^2$ = .92). Volume explained most of the variation in $VSL as shown by an examination of the cumulative $R_a^2$ (Table III.4). In the log recovery study, percent visual grade recovery of individual logs was entirely dependent on branch diameter; log volume was not tested as a dependent variable (Fahey et al. 1991).

Volume, branch diameter, and wood density best predicted tree dollar value determined by MSR grading (model 2, Table II.4), and the total amount of variation explained was comparable to that of model 1 ($R_a^2$ = .89). Similarly, in the log recovery study, juvenile wood proportion, which is negatively correlated with overall wood density, and branch diameter determined MSR grade recovery (again log volume was not tested). As in the $VSL model, volume was by far the best single predictor of $MSR, followed by branch diameter, as revealed by cumulative $R_a^2$ (Table III.4). Wood density explained a small, though still statistically significant, percentage of the variation in $MSR. This may be due in part to the low coefficient of variation of wood density in this study compared to the other traits (Table II.1). Or perhaps, using the average whole core density at breast height did not adequately reflect the variation in wood density within a tree and subsequently, in the boards milled from that tree, since wood density increases with increasing ring age after about age 10, and decreases with height in the bole (Megraw 1986). This illustrates the complexities involved in relating the importance of traits measured on standing trees to the attributes of the end-product, in this case, individual boards. Because height and DBH are both highly correlated with volume (Table II.4), these variables accounted for little additional variation in either $VSL or $MSR with volume already in the model; thus, neither height nor DBH were selected as dependent variables by stepwise regression.

In model 3 (Table II.3), height, branch diameter, and wood density explained significant amounts of variation in the response variable, $\$/m^3$. This model explained slightly more than half the variation in tree value, much less than models 1 and 2. The largest proportion of variation in $\$/m^3$ was accounted for by branch diameter in the model, with a much smaller percentage by wood density and height. Since the effect of volume on dollar value was removed from the response variable, the omission of volume as a significant predictor of $\$/m^3$ was expected. For all three models, standard errors of the partial regression coefficients, except for wood density, were low compared to the coefficients themselves, and confidence intervals for the coefficients were relatively narrow.

The fact that volume was a significant predictor of whole-tree dollar value under both the visual and MSR grading systems (models 1 and 2, Table II.4), illustrates the effect that tree size has on the number of pieces, and therefore the value, of lumber that is milled from each tree. Volume is a composite trait of height and DBH, and the size of the stem determines the number of logs per tree (height effect) and the number of boards per log (diameter effect). Both numbers of logs and number of boards per log varied considerably among trees in this study: 1 to 6 (mean = 4) and 6 to 97 (mean = 36), respectively. Clearly, this variation had a major impact on tree value.

Branch diameter was important in predicting the value of trees for all three response variables. This is to be expected considering the direct impact that branch diameter has on lumber grade.

The inclusion of wood density in the model predicting $MSR but not in the model predicting $VSL reflects the way that wood strength is assessed in these two grading systems. Lumber strength is measured directly by machine testing in MSR grading and strength is positively correlated with wood density. In visual grading, wood density is considered indirectly by limiting growth rate to four rings/inch in the higher grades, but in this study almost all of the logs met this growth rate criteria, so lumber value was determined entirely by branch diameter alone. It is possible that if the study had included trees with higher growth rates, as would be expected when trees are grown at wide spacings, that wood density might have proven to be a significant predictor of tree value under visual grading as well.

Relative economic weights based on product value have been reported for various combinations of stem size and quality traits in a few forest tree species, including, stem height, diameter, volume, and straightness in loblolly pine (Bridgwater and Stonecypher 1979, Talbert 1984); stem height, diameter, straightness, and branch diameter in radiata pine (Cotterill and Jackson 1981); and log diameter and basal sweep in maritime pine (Chollet and Roman-Amat 1987). A common feature of all these studies, and the results presented here, is the inclusion of a trait representing tree size or yield and at least one quality trait in models developed to estimate economic weights. But other than this general statement, contrasts or comparisons between the results of this investigation and former studies estimating economic weights is not possible due to differences in species, tree age, traits, formulation of response variables and the type of product modeled.

<u>Application of product-value based economic weights</u>

Since only one of the three sets of economic weights developed in this study would be used in any one breeding program, it is of interest to compare the implications of using each of the models. Tree breeders would be expected to employ the economic weights in model 3, rarely, if ever, since the implied breeding goal is improvement in quality traits alone, with no interest in improving stem volume. Since the genetic correlation between wood density and volume is negative in Douglas-fir (Chapter III, this thesis, King et al. 1988a, Vargas-Hernandez and Adams 1991), employing model 3 in a selection index would likely result in loss of mean volume in the next generation which would be unacceptable to the majority of forest managers.

Choosing between the economic weights in model 1 and model 2 represents a decision whether to include wood density in a selection program. The partial regression coefficients for volume and branch diameter are similar in the two models, but responses to multi-trait selection using these two sets of weights may not be similar because wood density is genetically correlated with both volume and branch diameter (Chapter III, this thesis, King 1992 in prep). Previous studies have shown that selection for volume alone will reduce wood density in coastal Douglas-fir (King et al. 1988a, Vargas-Hernandez and Adams 1991). However, no information is available on the effects of simultaneous selection for improvement in volume, branch diameter and wood density. Application of economic weight equations to actual genetic data sets is needed to evaluate the implications of using these two models in multi-trait selection systems.

Several factors need to be considered when contemplating application of economic weights developed in this study for use in Douglas-fir breeding programs (Cotterill and Jackson 1981, Lin 1978). One concern is that the weights will change with the definition of the product. If the product mix was vastly different than the 2 by 4 and 2 by 6 combination described here, the economic weights developed in this study would probably not be applicable. If the goal of Douglas-fir management was changed to maximization of fibre production, for example, changes in the weights might be expected. In this chapter, however, it was assumed that coastal Douglas-fir is primarily used for structural lumber and other building materials; an assumption certainly true for today and expected to be the trend in the future.

There is also the concern that the pricing structure used in this study may not reflect that of future markets. Although absolute lumber values may rise or fall, relative values are expected to remain the same (Haynes and Fight 1992). Changes in lumber prices over time did not change the relative value of tree quality classes in a log study of interior Douglas-fir (Middleton et al.1985). Also, since the values of all the boards milled from a tree are added to calculate tree value, only large changes in the relative value of each grade would alter the outcome of this study.

Another concern is that the relative economic weights might change with the combination of traits in the model. This is expected due to multicollinearity (high correlations) among traits which cause changes in the partial regression coefficients as traits enter or are removed from the multiple regression model (Neter et al. 1983, Chapter 8). The significance of this effect was explored by building a series of multiple regression models with $MSR as the response variable and by changing the number of independent variables (Table II.5). Model 2 (Table II.3) is used as a baseline for comparison. Models 4, 5, and 6 show the effects of the addition of the rejected variables, height and DBH. The coefficients for volume, branch diameter, and wood density, which had significant impact on tree dollar value, varied little among these models.

Models 7, 8, and 9 show the effects of removing one of the three variables in model 2: volume, branch diameter, and wood density. The coefficients for branch diameter and wood density increased when each was included individually in the regression model with volume (models 7 and 8). When a model was built without volume (model 9), the coefficients for branch diameter and wood density changed dramatically. In this case, the coefficient for branch diameter is positive because in the absence of volume as an independent variable, branch diameter is a surrogate for tree size due to the positive correlation between branch diameter and volume ($r^2 = .51$); tree size is much more important in determining tree value than decreasing lumber quality due to large knots.

Relative economic weights, therefore, did change as highly correlated traits enter or are removed from the model. Use of stepwise regression to select traits in the final model eliminated highly correlated traits that added little additional information (in this case, height and diameter). These traits had little impact on the coefficients of the significant independent variables whether they were included in the model or not. Elimination of traits found by stepwise regression to significantly influence tree dollar value did lead to appreciable changes in the coefficients of the remaining traits in the model. Thus, it is important to recognize and include all traits that significantly impact tree value when estimating relative economic weights for genetic selection. But, responses of individual traits can only be assessed when genetic and phenotypic parameter estimates are combined with economic weights to predict the outcome of utilizing multi-trait selection indices in breeding programs. This is the subject of the next chapter.

Table II.1. Means, standard deviations and coefficients of variation for traits measured on individual young-growth (ages 36 to 66) Douglas-fir trees.

| Trait | Description | Sample Size | $\bar{X}^a$ | Coefficient of Variation |
|---|---|---|---|---|
| Height | Total tree height (m) | 164 | 32.5 ± 4.6 (20.8 - 45.5) | 14.2 |
| Diameter | Diameter of bole at breast height (cm) | 164 | 45.6 ± 12.7 (22.9 - 71.1) | 27.9 |
| Volume | Volume of bole ($dm^3$) | 164 | 1877.1 ± 1041.3 (303.0 - 4431.6) | 55.5 |
| Wood Density | Wood density, whole core (all rings) ($kg/m^3$) | 92 | 493 ± 44.9 (404 - 658) | 9.1 |
| Branch diameter | Diameter of largest limb in buttlog (cm) | 159 | 3.5 ± 1.8 (1.3 - 9.6) | 52.1 |

[a] Range is shown in parentheses.

Table II.2. Dollar values of 2 by 4 and 2 by 6 dimensional lumber by grading system.

| Visual Grade | $/thousand board feet |
|---|---|
| Select structural | 240 |
| #1 | 220 |
| #2 | 200 |
| #3 | 140 |
| economy | 80 |
| MSR Grade | |
| 2100f[a] | 280 |
| 1650f | 240 |
| 1450f | 200 |

[a] f = fiber stress in bending

Table II.3. Partial regression coefficients (with SE in parentheses) for Douglas-fir as determined by multiple regression for three response variables.

| Model | Response Variable | Trait | Partial Regression Coefficients | 95% Confidence Interval | $R_A^2$ [a] | Cumulative $R_A^2$ [b] |
|---|---|---|---|---|---|---|
| 1 | Dollar value, whole tree, visual grading ($VSL) | Intercept | 11.77 | | .92 | |
| | | volume | 0.06 (0.01) | 0.05 to 0.06 | | 0.89 |
| | | branch diameter | - 5.22 (0.89) | -7.14 to -3.61 | | 0.92 |
| 2 | Dollar value, whole tree, MSR grading ($MSR) | Intercept | -14.56 | | .89 | |
| | | volume | 0.06 (0.01) | 0.05 to 0.06 | | 0.83 |
| | | branch diameter | - 6.69 (1.03) | -8.75 to -4.64 | | 0.88 |
| | | wood density | 0.06 (0.03) | 0.00 to 0.12 | | 0.89 |
| 3 | Dollar value per gross cubic meter, MSR grading ($/m³) | Intercept | 16.82 | | .51 | |
| | | branch diameter | - 4.23 (0.56) | -5.34 to -3.12 | | 0.40 |
| | | wood density | 0.07 (0.02) | 0.02 to 0.12 | | 0.47 |
| | | height | 0.63 (0.22) | 0.19 to 1.07 | | 0.51 |

[a] Adjusted coefficient of multiple determination.

[b] Cumulative adjusted coefficient of multiple determination for variable and any variables proceeding it in the model, i.e., the cumulative $R^2$ due to volume and branch diameter in Model 2 is 0.88.

Table II.4. Estimated Pearson product-moment correlations among traits measured in coastal Douglas-fir (ages 36-66).

| Trait | Diameter | Volume | Branch diameter | Wood density |
|---|---|---|---|---|
| Height | 0.42 * | 0.62 * | -0.08 | 0.26 * |
| Diameter | | 0.92 * | 0.71 * | -0.16 |
| Volume | | | 0.51 * | -0.09 |
| Branch diameter | | | | -0.18 |

* Correlation coefficients significantly different from zero (P < .05).

Table II.5. Partial regression coefficients for whole tree dollar value ($MSR) with a varying number of independent variables.

| Model Number<br>Trait | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|
| Volume | 0.06 | 0.06 | 0.07 | 0.05 | 0.06 | -- |
| Height | 0.11 | -- | 0.13 | -- | -- | -- |
| DBH | 0.09 | 0.10 | -- | -- | -- | -- |
| Branch diameter | -6.67 | -6.96 | -6.52 | -- | -7.15 | 4.81 |
| Wood density | 0.06 | 0.06 | 0.06 | 0.11 | -- | 0.27 |

# CHAPTER III

## EXPECTED RESPONSES OF STEM VOLUME, BRANCH DIAMETER, AND WOOD DENSITY UNDER INDEX SELECTION IN COASTAL DOUGLAS-FIR

### ABSTRACT

The responses of stem volume, branch diameter, and wood density to index selection were examined to evaluate the utility of multi-trait selection in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) for improving lumber value. Data on these three traits in 20-year old trees of 85 open-pollinated families were obtained from a progeny test in western Oregon. Economic weights for these traits under 2 different lumber grading systems (visual and machine-stress-rated (MSR)) was estimated previously (Chapter II, this thesis) based on the results of a separate lumber recovery study. Selection indices for family selection were derived by applying these economic weights to the genetic and phenotypic variance-covariance matrices estimated from the progeny test data.

Under visual grading, wood density had zero economic weight, thus only volume and branch diameter were included in the selection index. Application of this index is expected to result in large gains in stem volume, but because of the negative genetic correlation between volume and wood density ($r_A$ = -0.49), a negative (unfavorable) correlated response in wood density is also expected.

Under MSR grading, all three traits have non-zero weights and are included in the index. Positive responses are expected in both volume and wood density, although the expected response of volume is less than that predicted using visual grading. The low phenotypic variability of branch diameter and its adverse genetic correlation with volume ($r_A$ = 0.55) resulted in little expected change in this trait using either

index.

Changes in genetic and phenotypic parameters used in index selection resulted in substantially different expected responses in individual traits. Application of the selection index with MSR-based economic weights to parameter estimates derived from a portion of the progeny test data (data from only one of the three test sites) resulted in a negative expected response in volume and a large positive response in wood density. In contrast, using the same portion of the progeny test data, a positive response in both volume and wood density is expected when a desired gain index was used and desired relative responses set equal to the MSR-based economic weights. Thus, it is important to evaluate the impact on individual traits before using a particular index in a breeding program. In some cases, a desired gain index may provide an effective means to increase overall merit while restricting changes in individual traits.

# INTRODUCTION

Coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) is the primary forest tree species under intensive management in the Pacific coast region of North America (Oswald et al. 1986). In this region, Douglas-fir tree improvement programs have been established by most private timber companies and government agencies (Silen and Wheat 1979). Most of these programs have progeny tests approaching 15-20 years old, ages at which selection for second generation breeding is usually anticipated (Sniezko 1991). Determining the most effective combinations of traits to be included in selections is essential for the efficient use of these tests.

To compare methods of multi-trait selection and the relative importance of candidate traits for selection, three types of information are needed: the relative economic value of each trait (how phenotypic variation in a trait affects commercial or practical value), the heritability of each trait, and the genetic and phenotypic correlations between traits (Hazel and Lush 1943). Of these three, information on relative economic weights is the most difficult to obtain.

Bole volume, branch diameter, and wood density are the primary determinants of grade, quality, and dollar value of Douglas-fir solid wood products (Fahey et al. 1991, Harris 1965, Haygreen and Bowyer 1982, Kellogg and Kennedy 1986, USDA 1987). Recently, data from a lumber recovery study was used in multiple regression analysis to assess the relative influence of these traits on whole-tree dollar value of young-growth trees (mean age 50 years) from western Washington and Oregon (Chapter II, this thesis). Partial regression coefficients of these traits in regression models predicting whole-tree value, estimate their relative economic weights (Cotterill and Jackson 1984). Stem volume and branch diameter were found to be significant contributors to whole-tree value under visual grading of lumber, while under machine-stress-rated

(MSR) grading, stem volume, branch diameter and wood density all had significant partial regression coefficients. As yet, the impact of employing of these economic weights in multi-trait selection has not been explored. The goal of this study is to combine economic weights derived under each system of lumber grading with genetic and phenotypic parameter estimates obtained in a 20-year progeny test in western Oregon to examine the implications of using multi-trait selection in Douglas-fir breeding.

Simultaneous selection in Douglas-fir for improvement in stem volume, branch diameter and wood density provides a challenge to the tree breeder because of adverse genetic correlations between these traits. Strong negative genetic correlations have been reported between stem volume and wood density (King et al. 1988a, Vargas-Hernandez and Adams 1991). In addition, a strong positive correlation exists between stem volume and branch diameter (King et al. in press). These unfavorable correlations make it impossible to maximize gain in all three traits at the same time.

Of the methods that have been developed for simultaneous selection of multiple traits, index selection is the most effective for improving overall value or merit (Hazel 1943, Hazel and Lush 1943, Smith 1936); for this reason, this method will be used in this study. When applying index selection, genetic gain in overall merit is maximized by placing weight on each trait according to its economic value, its heritability, and the genetic and phenotypic correlations between traits. The index used in this manner is frequently referred to as a Smith-Hazel index (Cotterill and Dean 1990, Chapter 8, Lin 1978). A single measure, the combined weighted performance across all traits, or index value, is calculated for each candidate tree and selection is done on the index value. In recent years, application of the selection index method in forest tree breeding has increased with the availability of computers to facilitate computation (Bridgwater et al. 1983, Chollet and Roman-Amat

1987, Christophe and Birot 1983, Dean et al. 1983, Dean et al. 1986). Without product-value based economic weights, however, it is impossible to objectively tailor selection for maximum improvement in overall value of wood products. Lack of estimates of economic weights based on tree value has been a major barrier to the implementation of selection indices in forest tree breeding (Bridgwater and Stonecypher 1979, Cotterill and Jackson 1985, Zobel and Talbert 1984).

Several modifications of the Smith-Hazel index have been developed to meet objectives other than maximizing gain in the overall merit (see review by Lin 1978). In one modification, the restricted selection index, a desired response is set for each trait. Originally, the restricted index was designed to preclude changes in one or more traits while achieving as much genetic improvement in the remaining traits as possible (Kempthorne and Nordskog 1959). In forest tree breeding, this technique has been used to maximize gain in growth traits, while maintaining the mean values of what authors consider to be secondary traits (i.e., wood density, stem form, branch diameter) at the levels found in the parental population (Dean et al. 1986, Rehfeldt 1985, Vargas-Hernandez and Adams 1991).

One assumption of the index procedure is that genetic and phenotypic parameters are estimated without error. The efficiency of an index to predict the true genetic worth of an individual is sensitive to failure of this assumption (Lawrence 1981, Talbert 1984). In the present study, the sensitivity of indices to variation in parameter estimates was explored by using two empirically determined sets of estimates: one based on data from a single progeny test site, the other from the combined analysis of data over three progeny test sites containing the same families.

The goals of this investigation were to: 1. determine the implications of applying selection indices based on product-value determined economic weights in terms of expected responses in overall merit and individual traits; 2. determine how responses differ when economic weights based on visually graded versus MSR graded lumber are utilized; 3. evaluate the sensitivity of expected responses to changes in genetic and phenotypic parameter estimates; and 4. compare the responses under index selection to responses expected when traits are selected individually.

# MATERIALS AND METHODS

## Plant material

Trees from eighty-five families were measured in three test plantations (Gershman 1, Gershman 2, and Religion Creek) just north of Corvallis, Oregon. These families comprise sets 1, 2, and 3 (28-29 families each) in the Phase I breeding zone of the Burnt Woods Cooperative Douglas-fir Progressive Tree Improvement program which encompasses about 27,000 hectares (Quam 1988). Parent trees were phenotypically selected in natural stands between elevations of 183 and 518 m, based on above average growth, stem form, and evidence of cone production. Open-pollinated progenies of the parent trees were formed into the three family sets by grouping them according to geographic proximity of parent trees within the breeding zone; each group of parent trees covered about 5,000 hectares. Seeds were sown in the spring of 1969 and plantations Gershman 1 and 2 were planted in the spring of 1971 with 2-0 bareroot stock on adjacent sites at 250 m elevation. Survival at age 5 was 93.6% and 96.5%, respectively. These sites were in meadow grass and were treeless before planting. Religion Creek, located within 14 km of the Gershman sites, was planted in the spring of 1972 with 2-1 bareroot stock at 230 m elevation. This site was forested prior to logging and planting. Records indicate the presence of several competing hardwood species during early years which may account for the lower survival (85.5% at age 5) compared to the Gershman sites. The seedlings were planted at 3.0 x 3.0 m spacing on all sites. Religion Creek was fenced to protect the trees from possible damage from large animals; the Gershman sites were not fenced, but animal damage has been slight. The experimental design on each site was a randomized split plot with four replicates, with sets as whole plots and families within sets as subplots, often referred to as sets-in-reps. Families were represented in each subplot by a 3-tree noncontiguous plot. Mortality was replaced in the first 2 years after planting by replacement stock of the same family, but these trees were not included in the analysis.

Measurements

Total tree height (dm), breast height (1.37m) diameter (DBH,mm), and branch diameter (3 cm from bole of tree) (mm) were recorded on all three sites when the trees were 20 years old from seed. Branch diameter was measured on the thickest branch in the first main whorl above breast height. This data was collected for a previous study (Sniezko 1991). Individual tree bole volume ($dm^3$, hereafter referred to as "volume") was calculated using the volume equations developed by Bruce and Demars (1974).

For the purposes of estimating wood density, a single pith to bark (5 mm diameter) increment core was extracted at breast height from each tree at the Gershman 1 site in the summer of 1990. All cores were processed at the Weyerhauser Technical Center, Tacoma, Washington. Core samples were sawn into flat strips approximately 5 mm wide on the transverse surface and were analyzed by direct scanning x-ray densitometry at 9% moisture content after chemical extraction (Hoag and McKimmy 1988).

The calendar year corresponding to the year each ring was formed was determined to ensure that the average core density calculated for each tree was made for the same time period. The largest number of rings found in all wood cores corresponded to tree ages 10-19; this set of rings was used to estimate overall average wood density for each tree. Width-weighted average core density was calculated by dividing the sum of the products of the average density of each ring and ring width by the length of the core between ages 10-19. Wood density information was collected on only the Gershman 1 site. Since wood density is expensive to measure, has high individual heritability and low family-by-site interaction, it has been suggested that selection based on family means from a single site is an efficient and effective way to select for this trait (Cotterill and Dean 1990, Chapter 10).

Statistical analysis

To provide estimates of genetic and phenotypic parameters to use in individual trait and index selection, analyses of variance and covariance were done for volume, branch diameter, and wood density on the Gershman 1 site. To provide separate estimates to test the sensitivity of index selection to changes in these parameters, analyses of variance and covariance was also done for volume and branch diameter on the combined data for the three sites (Table III.1). Form of analyses of variance and covariance for the Gershman 1 site is similar to that shown in Table III.1, but with all terms involving site as a factor removed.

Using a random effects model on an individual tree basis, components of variance and covariance were estimated from the appropriate mean squares and cross products (Table III.1) by the Procedure VARCOMP in the Statistical Analysis System (SAS Institute Inc, 1991). The few missing plots were not estimated. Standard errors of variance components were calculated according to Becker (1984). Appropriate F-tests were used to test the significance of family and family-by-site effects (Zar 1974). All effects were tested at the $P < 0.05$ level.

Individual, $h^2_i$, and family heritabilities, $h^2_f$, were estimated according to Falconer (1981), using terms as defined in Table III.1.

For one site...

$$h^2_i = \frac{4\sigma^2_{f(s)}}{\sigma^2_{f(s)} + \sigma^2_p + \sigma^2_w}$$

$$h_f^2 = \frac{\sigma^2_{f(s)}}{\sigma^2_{f(s)} + \frac{\sigma^2_p}{r} + \frac{\sigma^2_w}{rn}}$$

For three sites pooled...

$$h_i^2 = \frac{4\sigma^2_{f(s)}}{\sigma^2_{f(s)} + \sigma^2_{tf(s)} + \sigma^2_p + \sigma^2_w}$$

$$h_f^2 = \frac{\sigma^2_{f(s)}}{\sigma^2_{f(s)} + \frac{\sigma^2_{tf(s)}}{t} + \frac{\sigma^2_p}{rt} + \frac{\sigma^2_w}{nrt}}$$

Standard errors of heritability estimates were calculated as described by Becker (1984) as were phenotypic and genetic correlations and their standard errors.

Economic weights

The product-value based relative economic weights used in this study (Chapter II, this thesis) represent partial regression coefficients for traits that contributed significantly to tree value based on visual and machine-stress-rated (MSR) grades and pricing structures. Using stepwise regression, linear models were built with whole-tree dollar value (the sum of the value of all boards milled from a tree) as a function of whole-tree volume ($dm^3$), branch diameter (cm), and whole core wood density ($kg/m^3$) as measured on 164 young-growth trees (mean age 50 years). The product mix was 2 by 4 and 2 by 6 dimensional lumber.

The following relative economic weights were estimated (SE in parentheses):

| | volume | branch diameter | wood density |
|---|---|---|---|
| Visual grading: | 0.06 (0.01) | -5.22 (0.89) | --- |
| MSR grading: | 0.06 (0.01) | -6.69 (1.03) | 0.06 (0.03) |

The main difference between these sets of economic weights is that wood density is included as a trait when MSR grading of lumber is used to assess whole tree value, but has no weight when visual grading is applied. Although several factors are involved, the major reason for this difference is that wood strength, of which wood density is a primary determinant, is measured directly under MSR grading (Grant et al. 1984, USDA 1987) but is evaluated only indirectly under visual grading, by counting the number of rings per inch. Since knot size is the primary determinant of visual grade (Kellogg and Kennedy 1986), and wood density and branch diameter were positively correlated ($r = 0.51$, Chapter 2), it appears that with branch diameter already in the regression model, the addition of wood density did not provide enough additional information on tree value under visual grading of lumber to be significant.

<u>Selection methods</u>

**Individual traits**

All calculations of selection response in this chapter are for gains expected in the offspring of randomly mated seed orchard clones of the top parent trees as determined from the performance of their open-pollinated progeny. Expected responses (genetic gain) of individual traits under direct parent tree selection were calculated by:

$$\Delta G/i = 2\, h_f^2\, \sigma_{pf}$$

where

$\Delta G/i$ is the expected response per unit of selection intensity (i)

$h_f^2$ is the family heritability

$\sigma_{pf}$ is the phenotypic standard deviation calculated on family means

In order to evaluate the effect of individual trait selection on traits of interest not being directly selected, correlated responses were estimated as (Falconer 1981):

$$CR_y/i = h_x\, h_y\, r_A\, \sigma_{py}$$

where $CR_y/i$ is the correlated response of trait y to selection for trait x, per unit of selection intensity

$h_x$ is the square root of family heritability for trait x

$h_y$ is the square root of family heritability for trait y

$r_A$ is the genetic correlation between traits x and y

$\sigma_{py}$ is the phenotypic standard deviation (based on families) for trait y

**Index selection**

To evaluate responses to index selection using different economic weights, several indices were constructed following index theory as outlined by Lin (1978) and the methodology described by Wilcox et al. (1975). Calculations were done using the Lotus 1-2-3 computer software (Lotus Development Corporation 1991).

The Smith-Hazel index is defined as,

$$I = b_1 P_1 + b_2 P_2 + \ldots + b_n P_n,$$

where I = single index value on which selection is based,

$P_j$ = phenotypic value of an individual or a group of individuals

$b_j$ = weight given to $P_j$

The best values of the b's, the factors by which each of the measurements will be weighted, are those that maximize the correlation between the index and the aggregate breeding value (overall merit) of an individual, H. This is defined as,

$$H = a_1 G_1 + a_2 G_2 + \ldots + a_n G_n,$$

where $a_i$ = weight factors which express the relative importance attached by the breeder to each trait (i.e., economic weights)

$G_i$ = breeding value for each trait

The index weights (b's) were estimated by solving (in matrix notation),

$$\underline{b} = \underline{P}^{-1} \underline{G} \, \underline{a}$$

where $\underline{b}$ = a column vector of index coefficients

$\underline{P}$ = the phenotypic variance-covariance matrix of traits in I

$\underline{G}$ = the genetic covariance matrix between the phenotypic values in I and the genetic values in H

$\underline{a}$ = a column vector of economic weights

For example, an index for volume, branch diameter, and wood density is defined as

$$I = b_1 \text{ volume} + b_2 \text{ branch diameter} + b_3 \text{ wood density}$$

and aggregate breeding value (when economic weights are based on MSR grading) is

$$H = 0.06 \text{ volume} - 5.22 \text{ branch diameter} + 0.06 \text{ wood density.}$$

Since genetic selection takes place at younger ages and economic value is determined at rotation, the traits included in I and H are rarely the same. In this study, the traits in I are the measured traits on which the selection criteria are based (i.e., volume, branch diameter, and wood density at age 20 years). The traits in H are the goal traits defining the breeding objective, and the economic weights for these traits are based on traits measured at age 50 years. Indirect selection on juvenile traits for improvement in mature traits involves a specialized type of index selection (Binet 1965, Burdon 1989); estimates of juvenile-mature genetic covariances are needed to build matrix $\underline{G}$, the genetic covariance matrix between the traits in I and H. However, since all progeny tests of Douglas-fir are much younger than harvest age, no estimates of juvenile-mature genetic covariances are available. A model has been developed for predicting juvenile-mature correlations in Pinaceae but only for height (Lambeth 1980). It is generally agreed that the benefits of early selection outweigh the potential benefits of more reliable data at older ages and thus, that forest tree breeders are forced to make simplifying assumptions in order to proceed (Burdon 1989). Without reliable estimates of the covariances between the traits in I and H, juvenile-mature correlations were assumed to be 1 in this study, and the genetic variances and covariances estimated in the 20-year old progeny test supplied the elements of $\underline{G}$. This follows the approach of a previous study on loblolly pine (Talbert 1984). Although a loss in efficiency in realizing genetic gain is expected, studies of early selection for height and wood density indicate that, at least for these traits, this loss would be minimal and outweighs delaying selection until rotation (Gonzalez and Richards 1988, Lambeth 1980).

To evaluate the efficiency of an index to achieve genetic gain compared to a perfect index based on unknowable breeding values, the correlation between I and H, $r_{IH}$, was estimated:

$$r_{IH} = \sigma_I/\sigma_H$$

where $\sigma^2_I = \underline{b}'\ \underline{P}\ \underline{b}$, the variance of the index, I,

$\underline{b}'$ = transpose of $\underline{b}$,

$\sigma^2_H = \underline{a}'\ \underline{G}\ \underline{a}$, the variance of the breeding value, H,

$\underline{a}'$ = transpose of $\underline{a}$

The expected genetic response in overall merit from index selection is

$$\Delta G_I/i = r_{IH}\ \sigma_H$$

The expected genetic gain in the $i^{th}$ trait in the index is the correlated response in that trait when selection is based on the index values (Falconer 1981):

$$\Delta G_i/i = \frac{\sigma^2_{A(i)I}}{\sigma_I}$$

where $\sigma^2_{A(i)I}$ = the covariance of the breeding value of the $i^{th}$ trait and the index

After the index coefficients, $b_j$'s, were estimated for the traits under direct selection, correlated responses of traits not included in the index were estimated using a Binet-type restriction (Binet 1965). The index coefficient of the trait under indirect selection was set to zero and the genetic response equations given above were then calculated. This was used, for example, when volume and branch diameter were used in an index and it was of interest to know the indirect response to selection in wood density.

It was of interest to evaluate the implications of applying a modification of the Smith-Hazel index in which the genetic responses of the traits in an index can be set to desired levels using a restricted selection index (Lin 1978). The coefficients (b's) are equal to the product of the genetic variance-covariance matrix, $\underline{G}$, and the vector of desired gains for each trait, $\underline{\Delta}$, (Tallis 1962)

$$\underline{b} = \underline{G}^{-1}\ \underline{\Delta}$$

Relative desired gains in this case were set equal to the economic weights for each trait. In this way, the goal of index selection was changed from maximizing response in overall merit as used in a Smith-Hazel index, to setting certain levels of genetic gain in each trait. Economic weights implied by these coefficients can be calculated for comparison purposes as,

$$\underline{a} = \underline{G}^{-1}\ \underline{P}\ \underline{b}$$ (Cotterill and Jackson 1984).

# RESULTS AND DISCUSSION

## Genetic and phenotypic parameter estimates

Site by families-within-sets interaction was not significant for volume and branch diameter indicating family stability across the three test sites (Table III.2). The variance due to families-within-sets, however, was significant for all traits in both data sets (Table III.2 and III.3). Set effects, as evaluated by the F-statistic, were not significant for any of the three traits in either data set and, therefore, in both the single site and the pooled data sets, families were pooled across sets in all scenarios of selection. The percentage of total phenotypic variance due to families-within-sets was 4-8% for volume and branch diameter while the within-plot variance was at least 90% in both the single site and combined analyses (Tables III.2 and III.3). This very large within-plot variance component is commonly found in open-pollinated progeny tests (Adams and Joyce 1990, Adams and Morgenstern 1991, Magnussen and Keith 1990). For wood density, the families-within-sets variance was much higher than for volume or branch diameter, contributing 16.6% to the total phenotypic variance.

The high proportion of total phenotypic variance in wood density due to families is reflected in the high individual heritability estimate for this trait ($h_i^2$ = 0.66, Table III.4), a result consistent with previous findings in this species (Bastien et al. 1985, King et al. 1988a, Vargas-Hernandez and Adams 1991). Heritabilities for the Gershman 1 site were low for volume ($h_i^2$ = 0.16) and branch diameter ($h_i^2$ = 0.24) which is also consistent with earlier estimates in coastal Douglas-fir, based on data from single test sites (Adams and Joyce 1990, Joyce and Adams, Department of Forest Science, Oregon State University, in prep, King in press, King et al. 1988b). The combined-sites analysis yielded higher estimates for both individual and family heritabilities of volume ($h_i^2$ = 0.30, $h_f^2$ = 0.70, Table III.5), but heritability of branch diameter increased substantially only for families ($h_i^2$ = 0.22, $h_f^2$ = 0.63).

Based on data from Gershman 1 only, volume and branch diameter were estimated to have a perfect positive genetic correlation ($r_A$ = 1.00) (Table III.6). The reliability of this estimate, however cannot be quantified since when the correlation is 1.00, the estimator for the standard error is zero which is obviously meaningless. The estimated genetic correlation between volume and branch diameter based on data for the three sites pooled ($r_A$ = 0.55 ± 0.11) is higher than reported in previous studies: $r_A$ = 0.29 (King et al. in press), $r_A$ = 0.44 (Joyce and Adams in prep). These results suggest that the value of $r_A$ = 1.00 at Gershman 1 considerably overestimates the true correlation between these traits. The phenotypic correlation between volume and branch diameter for the pooled analysis ($r_p$ = 0.37) was similar to that for the single site ($r_p$ = 0.33). Wood density had moderate negative correlations with both volume ($r_A$ = -0.49) and branch diameter ($r_A$ = -0.43); the negative correlation between wood density and branch diameter provides the only favorable relationship among the three traits.

Individual trait selection

Parent tree selection for any one of the three traits measured at Gershman 1 is expected to result in considerable response in the trait selected (Table III.7A). Although volume had the lowest heritability, it had the highest phenotypic variation (Table III.3), so the expected response expected in this trait is the highest of the three.

Since the current emphasis in Douglas-fir tree improvement programs is on volume improvement, correlated responses in quality traits (branch diameter and wood density) when volume is selected, are of primary interest. Selection for volume alone is expected to result in increased branch diameter and decreased wood density (Table III.7), both of which will lower the value of lumber in the next generation (Chapter II, this thesis). Although the percent correlated response per selection intensity in wood density appears small in this case (-1.5%), this reduction in wood density could have a serious effect on lumber value. It has been estimated that a 2.41% decrease in Douglas-fir wood density would result in a loss of 11,000 kg of dry fiber per hectare in a 60 year rotation (Vargus-Hernandez and Adams 1991). Kellogg (1982) predicted that a 2% decrease in western hemlock wood density would result in a loss in product value of almost $5 million/year.

Parent tree selection for volume or branch diameter across all three sites followed the same trends as for the single site with the exception of a doubling in the expected response in volume (Table III.7B). This increase was due to the greater phenotypic variance and increased heritability for volume in the pooled analysis.

Index selection

For selection indices based on the data from Gershman 1, the estimated correlation between branch diameter and volume ($r_A$ = 1.00) was used even though this probably overestimates the true value. This was done because it was desirable to use empirically estimated phenotypic and genetic covariances and because it provides a contrast to the parameter estimates obtained from the pooled analysis. For selection indices applied to data for the three sites pooled, the information on wood density, is available from the Gershman 1 site only. Thus, all phenotypic and genetic covariances involving wood density are based on data from this one site.

Applying Index 1 (economic weights based on visually-graded lumber) to the Gershman 1 site is expected to result in nearly 10% gain in volume with every unit of selection intensity (Table III.8). Branch diameter is also expected to increase (5.98%), despite the negative economic weight given this trait, because the index coefficient for branch diameter is positive. There is no way to increase volume in this situation without also increasing branch diameter, since the genetic correlation between these traits is 1.00. It is interesting that Index

1 was more efficient for improving volume than selection for volume alone (9.54% versus 7.3% expected response, Table III.7A). Because $h_f^2$ for branch diameter is greater than for volume (Table III.4), the efficiency of indirect selection for volume based on branch diameter is greater that direct selection for this trait; thus, having branch diameter in the index increases overall response in volume. As when selection is practiced on volume alone (Table III.7A), application of Index 1 is expected to result in a negative indirect response in wood density (Table III.8).

Applying Index 1 to the data pooled over all sites makes it possible to examine the implications of the index when genetic and phenotypic parameters differ. Because of the greater phenotypic variation of traits across the three sites and the higher estimated heritabilities of volume and branch diameter (Table III.5), expected response in overall merit, $\Delta G_I$, was two and one-half times greater that when selection was applied to Gershman 1 alone (Table III.8). Response in volume was about 60% greater. In this case, the estimated genetic correlation between volume and branch diameter is only 0.55 and the index coefficient for branch diameter takes on a negative value. Because of the negative index weight for branch diameter and the low phenotypic variation in this trait (Table III.5), the expected response in branch diameter is now nearly zero (0.02). Furthermore, due to the favorable, negative correlation between branch diameter and wood density, and the negative economic weight given to branch diameter, the unfavorable correlated response in wood density is expected to be only about one-half that in Gershman 1 alone. Large differences in expected responses from index selection, due to changes in genetic and phenotypic parameter estimates were also observed in a study on loblolly pine (Talbert 1984).

The expected responses are quite different when Index 2 with economic weights based on MSR lumber grading rules, is applied to the two data sets. The main differences are that gains in volume are reduced relative to Index 1, especially when Gershman 1 is considered by itself, and wood density is expected to increase in magnitude rather than decrease. Including wood density in the overall merit equation, with its moderate negative correlation with volume, limits the potential gain in volume. For all three traits, the responses to index selection were lower than expected if selection were practiced on each trait individually (Table III.7). In particular, the changes in branch diameter are expected to be near zero. Relative volume gains were not nearly as impacted in the pooled data set, although gain in wood density was only about one-half that expected when only Gershman 1 data is utilized. This is probably due to the greater balance between the family heritabilities of volume and wood density in the pooled data set (0.70 and 0.68, respectively), relative to those for Gershman 1 alone (0.29 and 0.68, respectively). The finding that moderate genetic gains in both volume and wood density can be achieved when both traits are included in selection indices, despite the negative correlation between them, supports results in earlier studies (Dean et al. 1983, King et al. 1988a, Vargas-Hernandez and Adams 1991).

Since a low response in branch diameter is expected in three of four cases involving Indices 1 and 2 (Table III.8), it was of interest to test an index containing volume and wood density, but not branch diameter. If the response in branch diameter remains low, it might be possible to eliminate measurement of branch diameter in progeny tests, with a cost savings realized. Such an index (Index 3) was created by using economic weights derived from the regression of tree value (based on MSR grading of lumber) on only volume and wood density (Table III.8). Application of Index 3 to Gershman 1 is expected to result in nearly no response in volume and branch diameter, but a relatively strong response in wood density. Application of this index to the data pooled over 3 sites is expected to lead to responses of the three traits similar to those found when Index 2 is used. Thus, the decision to include branch diameter or not in an index is heavily dependent on the genetic and phenotypic parameter estimates of the population.

Index 4 is a desired gain index in which the relative desired response for each trait is set equal to the economic weights used in Index 3 (Cotterill and Jackson 1985, Lin 1978, Pesak and Baker 1969, Tallis 1962). The objective in this case is to maximize the genetic gain in each trait corresponding to the empirically-determined economic weights. Both the economic weights and the index ($b_j$) coefficients are smaller than those in Index 3, but the economic weights are more evenly balanced. Applying Index 4 to the Gershman 1 data results in a positive expected response in both volume and wood density, whereas in Index 3 there was a negative (or little) response expected in volume, but less gain in wood density. Using the pooled data set, application of Index 4 is expected to nearly double the response in wood density relative to Index 3, but at the price of a greatly reduced response in volume. The expected responses for volume and wood density expressed as a ratio should closely approximate the ratio of desired responses. Thus, the ratio of relative economic weights .11/.05 = 2.20 (wood density/volume) equalled or nearly equaled the ratio of expected responses in both cases (2.20 and 2.24, respectively).

Even though the merit equations among the four indices are dissimilar, one can compare the correlations between the index and the overall merit, $r_{IH}$, at least in the sense that they show how well each index predicts breeding value for overall merit. Using either data set, Index 2 is the most efficient as judged by $r_{IH}$, although Index 1 does well also. Adding more traits to the index can increase the value of $r_{IH}$ (James 1981) and this may account for the higher values of $r_{IH}$ for Index 2. Lower $r_{IH}$ and $\Delta G$ close to zero, for Index 4 reflect the shift in selection goals from maximizing response in overall merit (Indices 1, 2, and 3) to achieving desired responses in individual traits.

# CONCLUSIONS

The results of this study clearly demonstrate the impossibility of simultaneously maximizing genetic improvement of both volume and wood quality traits (branch diameter and wood density) in coastal Douglas-fir. Whether selection is based on volume alone or on an index including volume and branch diameter (Index 1), a loss in wood density, and hence wood strength, is expected in the next generation. Although the goal of Index 1 is to maximize gain in overall tree merit based on currently practiced (visual) grading rules, it is unlikely that forest managers will want to achieve the volume gain possible using this index at the price of lower wood density.

With the inclusion of wood density in the index, and using relative economic weights based on MSR lumber grading rules, it would be possible to achieve gain in both volume and wood density, although for Gershman 1 data set, this depended on whether branch diameter was included in the index. When branch diameter was included in the index (Index 2), a positive response in both volume and branch diameter is expected, but when branch diameter was omitted, the estimated response in volume is expected to slightly negative. This was due to the strong genetic correlation between volume and branch diameter which aided selection for volume in Index 2. This indicates the need to examine individual trait responses before applying index selection.

Expected responses of all three traits using economic weights based on MSR grading were similar in the pooled data set regardless of whether branch diameter was included in the index (Index 2) or not (Index 3). Given that the lower genetic correlation between branch diameter and volume as estimated for the pooled data set is more realistic, that the inclusion of branch diameter had only marginal impact on the response in volume and wood density, and that branch diameter itself changed very little, it is probably unnecessary to include branch diameter in Douglas-fir breeding programs. Since pruning and other silvicultural activities are effective in reducing the impact of limb size on wood quality (Cahill 1986, Maguire et al. 1991), it appears more efficient to concentrate selection on increasing volume and wood density alone.

Using a desired gain index (Index 4) with desired relative responses for volume and wood density equaling the MSR economic weights is expected to result in positive gains in both volume and wood density for both data sets. This is in contrast to the responses to Index 3 which varied considerably between the two data sets. Index 3 gave the most desirable result for the pooled data set, in terms of responses in both overall merit and individual traits, but resulted in a loss in volume when applied to the Gershman 1 site data only. The desired gain index used in this fashion provides a means of dictating genetic responses in individual traits that mirror relative economic weights, and can be useful when responses of individual traits predicted by the application of the Smith-Hazel index are unfavorable.

Table III.1. Structure of variance and covariance analyses for branch diameter and volume at age 20 across three sites pooled.[a]

| Source of variation | Degrees of freedom | Expected mean squares[b] |
|---|---|---|
| Sites | t-1 | $\sigma^2_w+k_{22}\sigma^2_p+k_{23}\sigma^2_{tf(s)}+k_{24}\sigma^2_{r(t)s}+k_{25}\sigma^2_{r(t)}+k_{26}\sigma^2_{ts}+k_{27}\sigma^2_t$ |
| Sets | s-1 | $\sigma^2_w+k_{16}\sigma^2_p+k_{17}\sigma^2_{tf(s)}+k_{18}\sigma^2_{f(s)}+k_{19}\sigma^2_{r(t)s}+k_{20}\sigma^2_{ts}+k_{21}\sigma^2_s$ |
| Sites x Sets | (s-1)(t-1) | $\sigma^2_w+k_{12}\sigma^2_p+k_{13}\sigma^2_{tf(s)}+k_{14}\sigma^2_{r(t)s}+k_{15}\sigma^2_{ts}$ |
| Replications/Sites | t(r-1) | $\sigma^2_w+k_9\sigma^2_p+k_{10}\sigma^2_{r(t)s}+k_{11}\sigma^2_{r(t)}$ |
| Replications/Sites x Sets | t(r-1)(s-1) | $\sigma^2_w+k_7\sigma^2_p+k_8\sigma^2_{r(t)s}$ |
| Families/Sets | s(f-1) | $\sigma^2_w+k_4\sigma^2_p+k_5\sigma^2_{tf(s)}+k_6\sigma^2_{f(s)}$ |
| Families/Sets x Sites | s(f-1)(t-1) | $\sigma^2_w+k_2\sigma^2_p+k_3\sigma^2_{tf(s)}$ |
| Replications/Sites x Families/Sets (plot error) | t(r-1)s(f-1) | $\sigma^2_w+k_1\sigma^2_p$ |
| Error (within-plot) | $\sum_i^t(n_i-1)$ | $\sigma^2_w$ |

[a] modified from Stonecypher *et al.*, 1973.

[b] For covariance analysis, cross products are used instead of mean squares.
t = number of sites; s = number of sets; r = number of replications per sites; f = number of families per set; k = coefficient of variance component; nt = total number of plots in all sets; $n_i$ = number of trees in the $i^{th}$ plot.

$\sigma^2_w$ = within-plot variance;

$\sigma^2_p$ = plot-to-plot variance;

$\sigma^2_{tf(s)}$ = variance due to families-in-sets by site interaction;

$\sigma^2_{f(s)}$ = variance due to differences among families-in-sets;

$\sigma^2_{r(t)}$ = variance due to differences among replications in sites;

$\sigma^2_{r(t)s}$ = variance due to replications in sites by set interactions;

$\sigma^2_{ts}$ = variance due to site by set interactions;

$\sigma^2_s$ = variance due to differences among sets;

$\sigma^2_t$ = variance due to differences among sites.

Table III.2. Estimates of variance components (SE in parentheses) for stem volume ($dm^3$) and branch diameter (cm) in 20-year-old coastal Douglas-fir across three sites pooled.

| Variance Component | Volume Estimate | Volume %[a] | Branch diameter Estimate | Branch diameter %[a] |
|---|---|---|---|---|
| Families/Sets ($\sigma^2_{f(s)}$) | 777.823*** (175.895) | 7.6 | 0.012*** (0.003) | 5.5 |
| Families/ Sets x Sites ($\sigma^2_{tf(s)}$) | 95.063 (122.765) | 0.9 | 0.001 (0.003) | 0.5 |
| Plot Error ($\sigma^2_{p}$) | 138.885 (222.031) | 1.4 | 0.005 (0.005) | 2.3 |
| Within-plot Error ($\sigma^2_{w}$) | 9195.950 (314.036) | 90.1 | 0.201 (0.007) | 91.8 |
| Total ($\sigma^2_{ph}$) | 10207.721 | 100.0 | 0.219 | 100.0 |

Note: ***, Significant at the 0.1% level.

[a] Percent of total phenotypic variance ($\sigma^2_{ph}$).

Table III.3. Estimates of variance components (SE in parentheses) for stem volume ($dm^3$), branch diameter (cm), and wood density ($kg/m^3$) in 20 year-old Douglas-fir from analysis of the Gershman 1 site only.

| Variance Component | Volume | | Branch diameter | | Average wood density | |
|---|---|---|---|---|---|---|
| | Estimate | % | Estimate | % | Estimate | % |
| Families/Sets ($\sigma^2_{f(s)}$) | 376.418* (217.937) | 4.0 | 0.011* (0.005) | 6.0 | 112.135*** (25.998) | 16.6 |
| Plot Error ($\sigma^2_p$) | 448.409 (375.154) | 4.8 | 0.005 (0.007) | 2.7 | 0.726 (22.685) | 0.1 |
| Within-plot Error ($\sigma^2_w$) | 8474.078 (497.615) | 91.1 | 0.168 (0.010) | 91.3 | 562.720 (33.044) | 83.3 |
| Total ($\sigma^2_{ph}$) | 9299.905 | 100.0 | 0.184 | 100.0 | 675.581 | 100.0 |

Note: *, Significant at the 5% level; ***, Significant at the 0.1% level.

Table III.4. Estimates of population means, additive variances ($\sigma^2_{ai}$, $\sigma^s_{af}$) (± SE), phenotypic variances ($\sigma^2_{pi}$, $\sigma^2_{pf}$), heritabilities ($h^2_i$, $h^2_f$) (± SE), and coefficients of variation ($CV_{pi}$, $CV_{pf}$) on both individual (subscript i) and family mean bases (subscript f), for 20-year volume ($dm^3$), branch diameter (cm), and whole core wood density ($kg/m^3$) for the Gershman 1 test site.

| Parameter | Traits | | |
|---|---|---|---|
| | Volume | Branch diameter | Average wood density |
| Mean[a] | 289 (203-373) | 2.34 (1.87-2.74) | 382.85 (343-422) |
| $\sigma^2_{ai}$ | 1506 ± 872 | 0.04 ± 0.02 | 449 ± 104 |
| $\sigma^2_{pi}$ | 9299 | 0.18 | 676 |
| $h^2_i$ | 0.16 ± 0.09 | 0.24 ± 0.10 | 0.66 ± 0.15 |
| $CV_{pi}$ | 33.41 | 18.33 | 6.79 |
| $\sigma^2_{af}$ | 376 ± 218 | 0.01 ± 0.005 | 112 ± 26 |
| $\sigma^2_{pf}$ | 1278 | 0.03 | 164 |
| $h^2_f$ | 0.29 ± 0.17 | 0.39 ± 0.17 | 0.68 ± 0.16 |
| $CV_{pf}$ | 12.39 | 7.14 | 3.35 |

[a] Range over 84 family means shown in parentheses.
[b] Note: $\sigma^2_{af} = \sigma^2_{f(s)}$ (Table III.1).

Table III.5. Estimates of population means, additive variances ($\sigma^2_{ai}$, $\sigma^s_{af}$) (± SE), phenotypic variances ($\sigma^2_{pi}$, $\sigma^2_{pf}$), heritabilities ($h^2_i$, $h^2_f$) (± SE), and coefficients of variation ($CV_{pi}$, $CV_{pf}$) on both individual (subscript i) and family mean bases (subscript f), for 20-year stem volume ($dm^3$) and branch diameter (cm) across three sites pooled.

| | Traits | |
|---|---|---|
| Parameter | Volume | Branch diameter |
| Mean[a] | 277 $dm^3$ (198-363) | 2.48 cm (2.14-2.77) |
| $\sigma^2_{ai}$ | 3111 ± 703.58 | 0.05 ± 0.01 |
| $\sigma^2_{pi}$ | 10207 | 0.22 |
| $h^2_i$ | 0.30 ± 0.07 | 0.22 ± 0.06 |
| $CV_{pi}$ | 36.43 | 18.87 |
| $\sigma^2_{af}$ | 777 ± 175 | 0.01 ± 0.003 |
| $\sigma^2_{pf}$ | 1109 | 0.02 |
| $h^2_f$ | 0.70 ± 0.16 | 0.63 ± 0.16 |
| $CV_{pf}$ | 12.00 | 5.54 |

[a] Range over 84 family means shown in parentheses.
[b] Note: $\sigma^2_{af} = \sigma^2_{f(s)}$ (Table III.1).

Table III.6. Estimates of genetic correlations (upper triangle, standard errors in parentheses) and phenotypic correlations (lower triangle) among three traits of 20 year-old Douglas-fir measured on the Gershman 1 site.

| | Bole volume | Branch Diameter | Wood Density |
|---|---|---|---|
| Bole volume | | 1.00 (0.00) | -0.49 (0.19) |
| Branch Diameter | 0.33 | | -0.43 (0.17) |
| Wood density | -0.31 | -0.14 | |

Table III.7. Estimated direct (on diagonal) and indirect (off diagonal) responses (per unit of selection intensity, i) to parent tree selection for each of three individual traits: A) in the Gershman 1 site only; B) pooled across three test sites. Percent responses (relative to population mean) are given in parentheses.

| A | Response trait | | |
|---|---|---|---|
| Selected trait | Volume | Branch diameter | Wood density |
| Volume | 21.09 (7.3) | 0.12 (4.9) | -5.63 (-1.5) |
| Branch diameter[a] | -24.38 (-8.4) | -0.13 (-5.6) | 5.71 (1.5) |
| Wood density | -15.71 (-5.4) | -0.08 (-2.1) | 17.47 (4.6) |

| B | Response trait | |
|---|---|---|
| Selected trait | Volume | Branch diameter |
| Volume | 46.62 (16.8) | 0.10 (4.0) |
| Branch diameter[a] | -24.34 (8.8) | -0.18 (-6.98) |

[a] Selection for branch diameter is in the negative direction (i.e., smaller branches)

Table III.8. Expected responses in overall merit ($\Delta G_I/i$) and in bole volume, branch diameter, and wood density ($\Delta G_i/i$) (with percent response in parentheses) from parent tree selection using index selection.

| Trait Code[a] | Economic weight[b] | Index coefficient | $r_{IH}$[c] | $\Delta G_I/i$[d] | $\Delta G_i/i$[d] | |
|---|---|---|---|---|---|---|
| Index 1 | | | | | | |
| Selection at Gershman 1 | | | | | | |
| | | | 0.81 | 0.98 | | |
| VOL | 0.06 | 0.004 | | | 27.58 | (9.54) |
| BD | -5.22 | 2.135 | | | 0.14 | (5.98) |
| WD | -- | -- | | | -6.48 | (-1.68)[e] |
| Selection across three sites pooled | | | | | | |
| | | | 0.89 | 2.58 | | |
| VOL | 0.06 | 0.049 | | | 44.78 | (16.16) |
| BD | -5.22 | -5.485 | | | 0.02 | (0.80) |
| WD | -- | -- | | | -3.58 | (-0.94)[e] |
| Index 2 | | | | | | |
| Selection at Gershman 1 | | | | | | |
| | | | 0.95 | 0.80 | | |
| VOL | 0.06 | 0.003 | | | 3.92 | (1.36) |
| BD | -6.69 | 1.270 | | | 0.02 | (0.86) |
| WD | 0.06 | 0.032 | | | 12.86 | (3.36) |
| Selection across three sites pooled | | | | | | |
| | | | 0.96 | 2.74 | | |
| VOL | 0.06 | 0.055 | | | 35.96 | (12.98) |
| BD | -6.69 | -7.066 | | | -0.02 | (-0.80) |
| WD | 0.06 | 0.058 | | | 6.44 | (1.68) |
| Index 3 | | | | | | |
| Selection at Gershman 1 | | | | | | |
| | | | 0.68 | 1.48 | | |
| VOL | 0.05 | 0.014 | | | -1.68 | (-0.58) |

| | | | | | | |
|---|---|---|---|---|---|---|
| BD | -- | -- | | | 0.02 | (0.86)[e] |
| WD | 0.11 | 0.060 | | | 14.24 | (3.72) |
| Selection across three sites pooled | | | | | | |
| | | | 0.89 | 2.62 | | |
| VOL | 0.05 | 0.039 | | | 33.04 | (11.92) |
| BD | -- | -- | | | 0.04 | (1.62)[e] |
| WD | 0.11 | 0.087 | | | 8.84 | (2.30) |
| Index 4 | | | | | | |
| Selection at Gershman 1 | | | | | | |
| | | | 0.59 | 0.04 | | |
| VOL | 0.002 | $0.52\times10^{-3}$ | | | 4.86 | (1.68) |
| BD | -- | -- | | | 0.04 | (1.62)[e] |
| WD | 0.003 | $1.45\times10^{-3}$ | | | 10.70 | (2.80) |
| Selection across three sites pooled | | | | | | |
| | | | 0.01 | 0.01 | | |
| VOL | 0.001 | $1.75\times10^{-4}$ | | | 7.16 | (2.58) |
| BD | -- | -- | | | -0.02 | (-0.80)[e] |
| WD | 0.001 | $1.58\times10^{-4}$ | | | 16.06 | (4.06) |

[a] VOL = bole volume ($dm^3$);
BD = branch diameter (cm);
WD = wood density ($kg/m^3$);

[b] Economic weights in Index 1 based on visual grading system;

Economic weights in Index 2 and 3 based on MSR grading system.

Economic weights in Index 4 are implied weights based on setting desired relative responses of volume and wood density to MSR economic weights as follows: $\Delta G_i/i$ (VOL): $G_i/i$ (WD) = 0.05: 0.11.

[c] $r_{IH}$ = correlation of the index with breeding value for overall merit.

[d] Expected responses per unit of selection intensity.

[e] Expected responses to indirect selection for trait not in index.

# CHAPTER IV

## GENERAL CONCLUSIONS

Maintaining or increasing the quality of Douglas-fir lumber is imperative if this species is to continue its dominance in the structural and building product market. Because of the negative correlation between bole volume and wood density, losses in wood strength are inevitable if increased volume is the only criteria for genetic selection. It is predicted that the use of MSR grading will become more widespread in the future and that all structural lumber may be stress-rated by the turn of the century, because it provides an accurate, objective evaluation of wood strength (Kellogg 1982). Wood density had little bearing on tree value as determined by visual grading, but wood density is critical to wood strength, and this was reflected in the economic weights based on MSR grading. The results of this study demonstrate the importance of including wood density along with volume in selection programs for coastal Douglas-fir and the economic weights based on MSR grading utilized in selection indices result in positive expected responses in both volume and wood density.

Expected genetic response in branch diameter under index selection was low regardless of the economic weights used. This is due to the low phenotypic variation for this trait and its adverse correlation with volume. Thus, little potential for genetic improvement in branch diameter was found regardless of the selection index tested. This does not negate the importance of branch diameter in determining tree, log or board dollar value. It simply illustrates the low impact that can be made by genetic selection. However, branch diameter may have some value in improving the efficiency of index selection by increasing the correlation between the index and overall merit, $r_{IH}$. Silvicultural activities provide opportunities to mitigate the impact of branch diameter on lumber quality. For example, pruning has proven to be an effective technique in reducing the adverse effect of knots on wood quality. If wider initial tree spacings are used in the future as some researchers have proposed, larger limbs will result and pruning might be essential to preserve the supply of knot-free Douglas-fir wood products (Cahill et al. 1986, Smith and Reukema 1986).

One limitation of the lumber recovery study, from which information was derived in this dissertation to estimate relative economic weights, was the production of only two lumber sizes: 2 by 4 and 2 by 6. Although this product mix was considered quite adequate for evaluating the effects of quality traits on tree value, it would be of interest to model volume, branch diameter, wood density on other piece sizes. Fahey et al. (1991) predicted that cubic recovery (from logs) would have increased by about 2 percent if 1-inch width lumber had also been manufactured. In addition, production of large structural timber production could have reduced the effect of large knots on grade because the higher grades of these larger board sizes accommodate larger knots. However, logs used to produce larger board sizes would also produce lower-quality smaller dimension lumber from the periphery of the log. Since each tree produces a variety of log sizes with varying limb sizes, it is difficult to predict the effects of milling different products on tree value. It may be that summing the values of all the boards produced from a tree to estimate whole-tree value tends to negate the impact made by changing the product mix.

In this study, gross value (yield x price) was used to estimate whole-tree value. The cost of harvesting and milling were not included. It would be informative to use net value of the products in a future study to evaluate the effects of these additional costs, if any, on the economic weights that are derived.

Varying the genetic and phenotypic parameter estimates gave very different expected responses in individual traits. This supports earlier reports that selection indices are sensitive to changes in genetic and phenotypic parameter estimates (Lawrence 1981, Talbert 1984). This makes it imperative to evaluate the expected responses of individual traits before applying an index to a breeding population. Because of the effect of varying parameter estimates on individual trait responses, it would be informative to apply the relative economic weights reported here to different progeny test data sets, perhaps including information for the same families measured over more sites.

Further study is also needed on the potential of family selection for wood density. It has been suggested that for traits of high heritability like wood density, family selection can be very cost effective (Cotterill and Dean, Chapter 10, 1990). As few as 10 trees per family may be needed to produce reliable family means (Cotterill and James 1984). The wood density parameter estimates used in this study came from only one site, and the question remains whether one site is adequate, and if not, how many trees per site must be measured for accurate estimation of family means for wood density .

The Smith-Hazel selection index emphasizes improvement in overall merit without regard to how this may change individual traits, and thus, may result in shifts of trait means in undesirable directions (Hogsett and Nordskog 1958). Expected responses of individual traits as well as overall merit must be evaluated to determine whether changes in all traits are acceptable. The desired gain index method provides an alternative to the Smith-Hazel index, whereby changes in individual traits can be limited to reflect their relative importance to product value. Although the Smith-Hazel index is the always the most effective for improvement in overall merit, restricting changes in any one trait may be necessary in order to meet breeding program objectives.

Another alternative to index selection that could be explored is multiple trait truncation selection. Minimum levels are set for each trait and all individuals below those levels are rejected, regardless of their values for any other trait (Hazel and Lush 1943). Although less effective in maximizing improvement in overall merit, truncation selection provides the advantage of additional flexibility. For example, selection for wood density, which is expensive to measure, could be limited to a subset of trees with acceptable performance in stem volume. Examination of the costs per unit of time, plus the response in individual traits, is needed to evaluate the relative merits of index and truncation selection.

To summarize, four areas of additional research are needed:

1. The influence of other product mixes and other economic factors (e.g., harvesting and milling costs) on relative economic weights.
2. The implications of applying indices to populations with different parameter estimates.
3. Ways to make selection for wood density as efficient as possible.
4. The merits of multi-trait truncation selection as compared to index selection and how these two methods might be combined to maximize the efficiency of selection programs.

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