

AN ABSTRACT OF THE THESIS OF

Jesus Vargas-Hernandez for the degree of Doctor of Philosophy  
in Forest Science presented on June 8, 1990

Title: Genetic Variation of Wood Density Components in Coastal  
Douglas-Fir and their Relationships to Growth Rhythm

Signature redacted for privacy.

Abstract approved: \_\_\_\_\_  
W. Thomas Adams

Overall wood density is a complex trait resulting from the interaction of three components: average earlywood density, average latewood density, and latewood proportion. In order to better understand the genetic control of wood density in juvenile Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and to assess the utility of information on its components for improving the efficiency of selection for overall wood density, wood density components were examined in 15-year-old trees of 60 open-pollinated families. Wood density traits were obtained on a ring-by-ring basis by X-ray densitometry of increment cores. In addition to providing information on overall wood density traits over the entire cores, these data made it possible to examine changes in wood density traits with increasing distance from the pith. Relationships between wood density traits and growth phenology, and their implications for tree breeding, were also examined.

Overall core density showed strong genetic control ( $h_1^2 = 0.59$ ) and a negative genetic correlation with bole volume ( $r_A = -0.52$ ). Wood density components were strongly genetically related with overall core density, but they were also strongly related among themselves and had lower heritability than overall core density. Therefore, information on

density components would not be useful for improving the efficiency of selection for overall core density, or for reducing the negative correlated response on volume growth. It is possible, however, to substantially increase volume growth without loss in wood density, or even while slightly increasing wood density, when both traits are included in selection indices. Genetic control of overall core density and its components increased with age (ages 7 to 15). Overall core density and its components at age 15 were also strongly genetically correlated with their respective traits at all younger ages examined. Thus, early selection for overall core density at age 15 would be very effective. Including density components as secondary traits did not enhance the efficiency of early selection for overall core density.

Ring density and its components (adjusted by ring size) followed different age trends, but the slopes of the trends did not differ significantly among families. A plateau in the earlywood density trend was observed around age 12 in some trees, and families varied in the proportion of trees having this plateau. This proportion was not correlated with overall core density or with growth traits at age 15. It is hypothesized that the plateau in earlywood density trend might be related to an earlier juvenile-mature transition age.

Overall core density and all its components were negatively correlated with dates of cambial growth initiation and latewood transition, and positively correlated with date of cambial growth cessation. Thus, selection for higher wood density would cause a slight extension in the cambial growth period, and an earlier transition to latewood formation. Wood density was not genetically correlated with the date of budburst.

GENETIC VARIATION OF WOOD DENSITY COMPONENTS IN COASTAL  
DOUGLAS-FIR AND THEIR RELATIONSHIPS TO GROWTH RHYTHM

by

Jesus Vargas-Hernandez

A THESIS

submitted to

Oregon State University

In partial fulfillment of  
the requirements for the  
degree of

Doctor of Philosophy

Completed June 8, 1990

Commencement June 1991

## ACKNOWLEDGEMENTS

I wish to thank the National Council of Science and Technology (CONACYT) in Mexico, for granting me a graduate scholarship. The financial support received from this Institution made it possible to complete my graduate studies at Oregon State University.

I would also like to acknowledge the members of the Pacific Northwest Tree Improvement Research Cooperative and the Department of Forest Products, O.S.U., for the financial support provided to this research project.

Thanks are due to all the people who contributed to the completion of this study. My sincere appreciation goes to the members of my committee, Drs. Tom Adams, Jim Boyle, Bob Krahmer, Steve Strauss, and Don Zobel, for their advise during my graduate program and their critical review of the thesis. I am especially grateful to Dr. Tom Adams, my major professor, for his patience, guidance, and encouragement during all my graduate studies, and his valuable help and comments for improving the quality of this manuscript. I am also indebted to Dr. Bob Krahmer for sharing his expertise and allowing me the full use of his laboratory and equipment.

I also wish to express my gratitude to Mike Hoag and Eini Lowell, Department of Forest Products, for training me in the use of the X-ray densitometer, and helping me to solve all the problems during the processing of wood samples. Thanks also to Peng Li and Brad St. Clair, graduate students in the Department of Forest Science, for sharing data and computer programs with me. I am grateful to Dr. Bob Campbell, U.S.D.A. Forest Service, Forest Science Laboratory, for his assistance and comments on the analysis of data.

To all my friends in the Department of Forest Science, especially Alejandro Velazquez and Nestor Rojas, who contributed in various ways to make my stay here in Corvallis a pleasant experience, I thank all of you.

Finally, I would like to give special thanks to my parents for their love and moral support, and to my wife, Silvia, and my son, Ivan, for providing me with love, encouragement, and understanding during all these years.

## TABLE OF CONTENTS

CHAPTER I. GENERAL INTRODUCTION	1
CHAPTER II. GENETIC VARIATION OF WOOD DENSITY COMPONENTS IN YOUNG COASTAL DOUGLAS-FIR: IMPLICATIONS FOR TREE BREEDING	7
Abstract	7
Introduction	9
Materials and Methods	13
Results and Discussion	20
Conclusions	30
CHAPTER III. AGE-AGE CORRELATIONS AND EARLY SELECTION FOR WOOD DENSITY IN YOUNG COASTAL DOUGLAS-FIR	40
Abstract	40
Introduction	42
Materials and Methods	45
Results and Discussion	50
Conclusions	58
CHAPTER IV. FAMILY VARIATION IN AGE TRENDS OF WOOD DENSITY TRAITS IN YOUNG COASTAL DOUGLAS-FIR	68
Abstract	68
Introduction	70
Materials and Methods	73
Results and Discussion	79
CHAPTER V. GENETIC RELATIONSHIPS BETWEEN WOOD DENSITY COMPONENTS AND GROWTH RHYTHM TRAITS IN YOUNG COASTAL DOUGLAS-FIR	86
Abstract	86
Introduction	88
Materials and Methods	91
Results and Discussion	96
CHAPTER VI. GENERAL CONCLUSIONS	110
LITERATURE CITED	115

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>	
Chapter I		
I.1	Density profile of an increment core sample as obtained by X-ray densitometry analysis. The earlywood-latewood boundary in each ring is defined here as the point where density equals the average of the minimum and the maximum densities in the ring	6
Chapter II		
II.1.	Model of path coefficient analysis of the genetic relationships between wood density components and overall core density.	32
Chapter III		
III.1.	Age-associated changes in population means for overall density and its components.	60
III.2.	Age trends in phenotypic, environmental, and additive variance components (expressed as coefficients of variation), and individual-tree heritability for overall core density and its components.	61
III.3.	Age-associated changes in individual-tree heritability for overall core density and its components.	62
III.4.	Genetic and phenotypic correlations for overall core density and its components at different ages, with their respective values at age 15.	63
III.5.	Mean genetic and phenotypic correlations between annual rings of different ages for ring density and its components, plotted over the difference in years of the two ring ages involved.	64
III.6.	Age-associated changes in the direct effect of individual density components on overall core density, as estimated by path coefficient analysis.	65
Chapter IV		
IV.1.	Age trends of relative ring density (RRD) traits and latewood proportion (LP) in a representative sample of six open-pollinated families of coastal Douglas-fir.	83

Chapter V.

- V.1. Comparison of a diameter growth curve and wood density profile for an individual tree in the 1987 growing season, illustrating the method of estimating the date of earlywood-latewood transition and duration of the earlywood and latewood formation periods.

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
Chapter II		
II.1.	Form of the variance and covariance analyses for wood density and growth traits at age 15.	33
II.2.	Estimates of population means, phenotypic and genetic coefficients of variation, and narrow sense heritabilities for overall core density and its components, and intra-ring density variation at age 15.	34
II.3.	Estimates of genetic correlations between wood density components and intra-ring density variation at age 15.	35
II.4.	Path-coefficient analysis of direct and indirect genetic effects of wood density components on overall density at age 15.	36
II.5.	Expected response in overall core density and correlated response in intra-ring density variation at age 15 when different wood density components are used as selection criteria.	37
II.6.	Estimates of genetic correlations between core density components and growth traits at age 15.	38
II.7.	Expected response in intra-ring density variation, overall core density, bole volume, and bole weight at age 15 when different selection criteria are used.	39
Chapter III		
III.1.	Form of the variance and covariance analyses for overall core density and its components measured at different ages.	66
III.2.	Relative efficiencies (%) of early selection for overall core density when different selection criteria are used.	67
Chapter IV		
IV.1.	Form of the variance and covariance analyses for age trends of wood density traits.	84
IV.2.	Estimates of genetic correlations between the proportion of trees with earlywood RRD (relative ring density) plateau by age 12 and overall core density and growth traits at age 15.	85



TablePage

## Chapter V

V.1.	Form of the variance and covariance analyses for wood density, growth phenology, and wood formation traits.	106
V.2.	Estimates of population means, phenotypic and genetic coefficients of variation, and individual-tree heritabilities for wood formation traits in the 1987 annual ring.	107
V.3.	Estimates of genetic correlations between overall wood density traits at age 15 and cambial (diameter) growth phenology and wood formation traits in the 1987 growing season.	108
V.4.	Estimates of genetic correlations between overall wood density traits at age 15 and date of budburst in the terminal shoot in the 1987 growing season.	109

GENETIC VARIATION OF WOOD DENSITY COMPONENTS IN COASTAL  
DOUGLAS-FIR AND THEIR RELATIONSHIPS TO GROWTH RHYTHM

CHAPTER I

GENERAL INTRODUCTION

Increasing demands for wood products, coupled with intensive management practices, is resulting in the harvest of younger and faster grown trees. Due to the greater proportion of low-density juvenile wood in these trees at rotation age, wood quality has become a major concern. Increasing the density of juvenile wood, or reducing the length of the juvenile wood formation phase through selection and breeding, might help offset some of the expected losses from utilizing young trees. Efficient application of tree breeding principles to improve these characteristics in Douglas-fir, however, is hampered by lack of knowledge of the genetic control of wood density in this species and its relationships with other growth and adaptive traits.

Wood density is a complex trait resulting from several interacting components. If, for example, an increment core is extracted from a tree, wood density can be considered at two levels: at the level of individual rings and over the entire core. At the individual ring level, mean ring density (RD) is determined by the average of earlywood (ED) and latewood densities (LD) weighted by their proportional contribution to the total ring width. That is,

$$\begin{aligned}RD &= ED (1 - LP) + LD (LP) \\ &= ED + LP (LD - ED)\end{aligned}\tag{I.1}$$

where LP is the latewood proportion in the ring.

Similarly, at the core level, overall density can be expressed in terms of overall earlywood density, overall latewood density, and overall latewood proportion, which are the averages over the entire core of the three ring density components. Although wood density is assessed in only a specific portion of the stem (normally breast height) when increment cores are utilized, this is the only means of non-destructively sampling stems. Fortunately, density of the entire stem usually is strongly related to breast height density determined from increment cores, especially in young trees (Cown, 1976).

The general goals of the study described in this dissertation were to: 1) determine the degree of genetic control of wood density components in young coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco); 2) determine the extent to which individual density components influence overall density in this species; and 3) assess the genetic relationships between wood density components and annual growth rhythm traits. X-ray densitometry was employed to measure, on a ring-by-ring basis, each density component on increment cores taken from 15-year-old open-pollinated progenies of 60 parent trees (Figure I.1). In addition to estimating mean ring density and its components over the entire core, changes in ring density components with increasing distance from the pith were investigated.

To accomplish the general goals, the study has been separated into four parts, which correspond to the next four Chapters. In Chapter II, the utility of wood density components for improving selection efficiency of overall wood density at age 15 is examined. Because a

particular value of overall density can result from different combinations of its components, it was hypothesized that genetic gain in overall density can be improved when information on individual density components is utilized in selection programs. The potential usefulness of the individual components will depend on the magnitude of their heritabilities and their interrelationships with each other and with overall density. Genetic relationships between wood density components and intra-ring density variation and volume growth, two traits previously identified as having undesirable (negative) genetic correlations with wood density in Douglas-fir, are also examined in this Chapter. If individual density components are less negatively correlated with these traits than is overall core density, they may be useful for increasing the efficiency of multi-trait selection. It might be possible, for example, to emphasize selection on particular wood density components that increase overall wood density, yet have the least negative impact on other traits. This possibility was explored by comparing several multi-trait selection criteria using index-selection methods.

In Chapter III, age-age correlations in overall wood density and the potential for early selection of wood density are investigated. The feasibility of early selection is largely determined by the strength of age-age genetic correlations and age-associated changes in the genetic control (heritability) of the selected trait. It was hypothesized that information on individual density components in younger trees might be useful for predicting overall wood density at older ages and, therefore, increasing the efficiency of early selection for this trait. To better

understand the genetic control of wood density over time, changes associated with age in the genetic interrelationships between overall wood density and its components were also examined.

In Chapter IV, genetic variation in age trends of wood density and its components, and their genetic correlations with overall wood density traits, are investigated. Age trends refer to the pattern of variation of ring density components in the radial direction (i.e., with increasing distance from the pith). Differences in age trends among the components will affect the level of inter- and intra-ring density variation across the stem, and the relative influence of the components on overall wood density. Age trends for each density component were described for each tree by using linear regression. The slope of the regression line, therefore, measures the rate of change in the component with increasing age. If genetic differences in the slopes are present, it might be possible to increase uniformity of wood density across the stem by selecting trees or families with smaller slopes. The possibility of selecting for a shorter juvenile wood formation phase is also explored in this Chapter. Selecting for an earlier age of transition to mature wood formation would improve overall wood quality by reducing the proportion of low-density juvenile wood in the stem. Genetic differences in the age of transition to mature wood have been associated in loblolly pine with family differences in the age at which the age trend in ring density reaches a plateau or otherwise shows a sharp decrease in slope (Loo et al. 1985, Bendtsen and Senft 1986). Since a plateau in the ring density trend must be correlated with associated changes in the density components, age trends in one or more

of the individual components might prove to be more sensitive indices of the transition from juvenile to mature wood.

In Chapter V, the genetic relationships between wood density and growth rhythm traits are explored. These relationships are of interest because wood formation is controlled to a large extent by physiological processes associated with the annual growth cycle in both the cambium and shoot. By comparing the diameter growth curve for a particular year, for which growth phenology is known, to a plot of wood density across the annual ring formed the same growing season, it is possible to derive several traits related to the process of wood formation (i.e., timing of latewood transition, lengths and rates of early and latewood formation) for that year. It was expected that individual density components would have strong genetic associations with these derived wood formation traits. It was hypothesized, for example, that earlywood and latewood densities are primarily related to rate of cambial growth during their respective formation periods, whereas latewood proportion is mostly determined by the length of the latewood formation period. Knowledge of the genetic interrelationships between wood density components and wood formation traits will increase our understanding of wood development in Douglas-fir, and might help us to better understand the genetic relationships between overall density and growth rhythm traits. This information will also enhance our ability to breed for wood density without inadvertently producing a negative impact on adaptation, which might result from extending or otherwise altering the growing period.

DENSITY PROFILE FOR  
SAMPLE S23669(2).

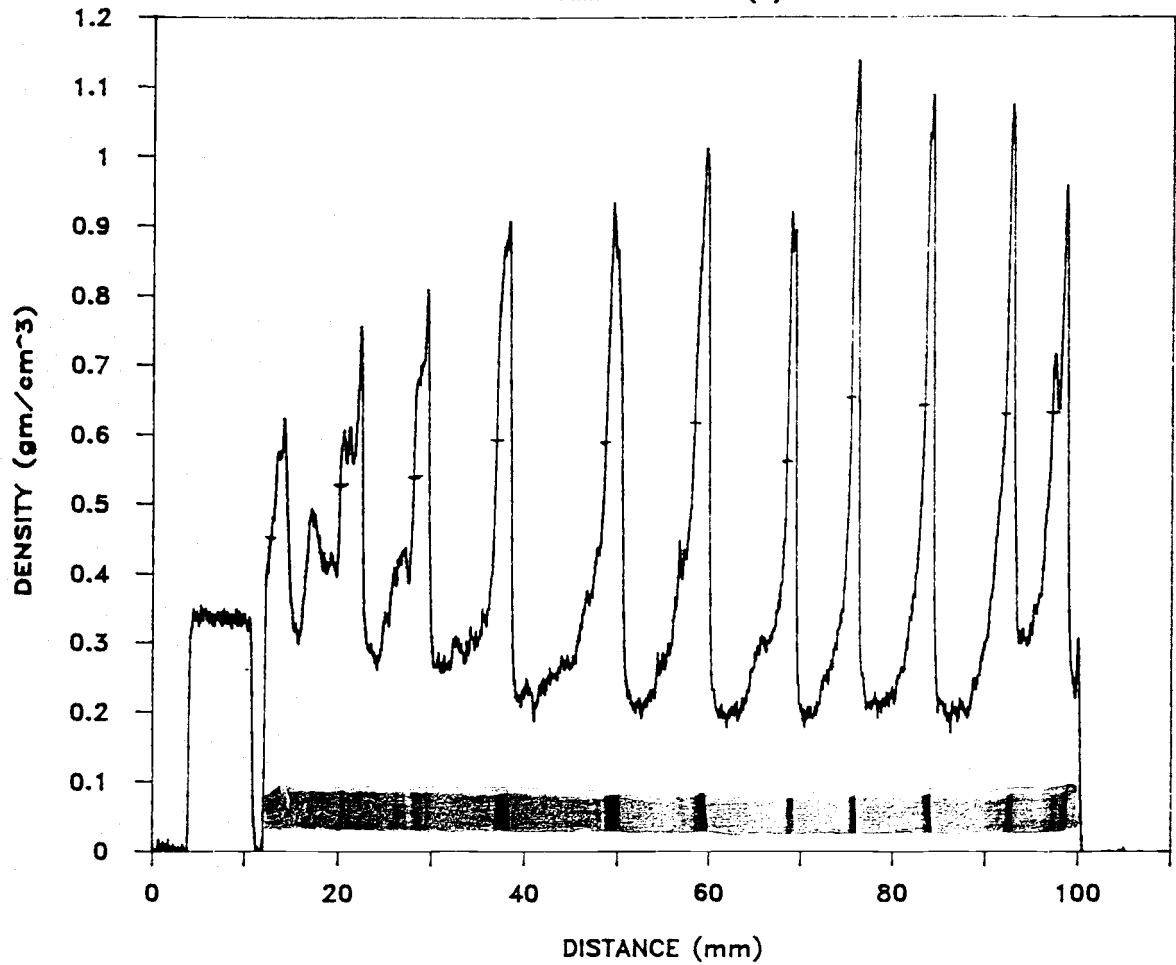


Figure I.1. Density profile of an increment core sample as obtained by X-ray densitometry analysis. The earlywood-latewood boundary in each ring is defined here as the point where density equals the average of the minimum and the maximum densities in the ring.

## CHAPTER II

GENETIC VARIATION OF WOOD DENSITY COMPONENTS IN YOUNG  
COASTAL DOUGLAS-FIR: IMPLICATIONS FOR TREE BREEDING

## ABSTRACT

The genetic control of wood density components (earlywood density, latewood density, and latewood proportion) and their relationships with overall density in coastal Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), were examined in order to assess the utility of this information in breeding for wood density. The genetic relationships of wood density with intra-ring density variation (IRV) and bole volume growth were also investigated. Increment core samples were taken at breast height from 15-year-old trees of 60 open-pollinated families. Averages across each core sample for overall wood density and its components and for IRV were determined by using X-ray densitometry. Bole volume at age 15 for the same trees was derived from data on tree height and diameter at breast height. Although wood density components varied significantly among families and were under moderate genetic control ( $h^2 > 0.24$ ), none had a higher heritability than overall density ( $h^2 = 0.59$ ). Density components had strong genetic correlations with overall density ( $r_A \geq 0.74$ ), but were also strongly related among themselves ( $0.57 \leq r_A \leq 0.92$ ). Thus, density components have limited value in improving the efficiency of selection for overall density. Confirming earlier reports, overall density was positively correlated



( $r_A=0.72$ ) with IRV and negatively correlated ( $r_A=-0.52$ ) with bole volume. Comparison of several selection indices containing wood density and one or more growth traits, however, showed that it is possible to obtain substantial gains in bole volume without loss in wood density, or even with modest wood density improvement. By restricting the response in wood density, the change in IRV can also be limited.

## INTRODUCTION

With the move in forest management to shorter rotations, wood quality has become a major concern, mainly because of the higher proportions of low-density juvenile wood found at harvest age in younger and faster grown trees (Bendtsen 1978, Pearson and Gilmore 1980). Wood density is probably the most important indicator of wood quality because of its important role in determining wood strength, pulp yield, and several other wood properties (Panshin and DeZeeuw 1980). One alternative for helping to offset some of the negative effects of short-rotation trees on wood quality would be to breed for increased density of juvenile wood. Increasing density of the juvenile core would improve the quality of this section of the tree, and might help to increase uniformity of wood density across the stem (Nicholls et al. 1980). In addition, earlier studies have shown a strong correlation between juvenile and mature wood (Cown 1976, Keller and Thoby 1977, McKimmy and Campbell 1982), so improvement in mature wood density should result as well.

Efficient application of breeding methods to increase density of juvenile wood in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), however, is hampered by lack of precise information on the genetic control of this trait. Although the presence of at least moderate levels of genetic variation for wood density is well documented in this species (McKimmy 1966, Kennedy 1970, Cown 1976, Bastien et al. 1985, King 1986), heritability estimates have been quite variable, with values ranging from 0.05 to 0.90 (McKimmy 1966, Cown 1976, Bastien et al. 1985,

King 1986).

Understanding the genetics of wood density is complicated by the composite nature of this trait. In temperate softwoods, where annual rings are easily identified, wood density (WD) can be considered the product of several interacting components, including the proportion of each ring that is earlywood or latewood and the relative densities of each (Nicholls et al. 1980); that is:

$$\begin{aligned} \text{WD} &= \text{ED} (1 - \text{LP}) + \text{LD} (\text{LP}) \\ &= \text{ED} + \text{LP} (\text{LD} - \text{ED}) \end{aligned} \quad (\text{II.1})$$

where:

ED = Earlywood density,

LD = Latewood density, and

LP = Latewood proportion (i.e., proportion of annual ring that is latewood).

A particular value of wood density can result from different combinations of its components. Therefore, knowledge of the genetic control of these components and their interrelationships would help in understanding the genetics of overall wood density. Moreover, information about the relative influence of individual components on overall wood density might prove useful for increasing the efficiency of selection for wood density, either by selecting directly for one or more components, as suggested by Nicholls et al. (1980), or by incorporating them as secondary traits in selection indices (Sales and Hill 1976). Selection indices employing secondary traits can improve the response in the trait of interest if one or more of the secondary traits has higher heritability than the trait of interest and has a high genetic

correlation with that trait (Baker 1986). In addition, if two or more secondary traits which are strongly correlated with the primary trait are included in the index, the index would be more efficient if the secondary traits were weakly interrelated among themselves (White and Hodge 1990).

In previous studies, undesirable genetic relationships between wood density and other economic traits in Douglas-fir have been observed. Particularly important is the negative genetic correlation between wood density and bole volume (Bastien et al. 1985, King 1986), and the strong positive correlation between wood density and intra-ring density variation (Vonnet et al. 1985, Bastien et al. 1985). Intra-ring density variation influences veneer quality, with high intra-ring density variation producing increased variation of veneer thickness and more veneer fissures (Keller and Perrin 1980, Birot et al. 1983, Aubert 1984, Thibaut 1987). Because gains from selection on wood density alone might be offset by a significant reduction in growth rate, or by a concomitant increase in intra-ring density variation, it is important to verify these relationships in other populations of Douglas-fir.

Knowledge of the genetic relationships between individual wood density components, bole volume, and intra-ring density variation might help minimize deleterious correlated responses when selecting for increased wood density. By emphasizing selection on components that show the least negative genetic correlations with growth, wood density could be improved while having the least negative impact on growth rate. In a similar fashion, individual density components might minimize the impact on intra-ring density variation when wood density is the target

of selection (Nicholls et al. 1980).

The objectives of this study were: (1) to determine the genetics of wood density components in Douglas-fir and their interrelationships with overall wood density, intra-ring density variation and bole volume; and, (2) to evaluate the implications of these relationships for tree breeding.

## MATERIALS AND METHODS

Plant material

Sixty open pollinated families of coastal Douglas-fir growing in the Coyote Creek progeny test plantation near Eugene, Oregon, were used in this study. These families correspond to sets 2 and 4 (30 families each) of the Noti Breeding Unit in the Umpqua Tree Improvement Cooperative (Silen and Wheat 1979). The parent trees were phenotypically selected in natural stands between elevations of 150 and 450 m in the central Coast Range of Oregon. Each set of families was planted in 1974 (1-0 plug seedlings) as a separate randomized complete block design experiment with four replications. Families in each block were represented by a four-tree non-contiguous plot, with trees assigned to planting spots at random. Up to the time when the measurements for this study were made, survival for these two sets was about 85%. Although mortality during the first two years after planting was replaced with trees from the original families, replacements were not included in the analyses.

Measurements

At the end of the 1987 growing season, when trees were 15 years-old from seed, total height and diameter at breast height were measured on all trees. With these data, individual-tree bole volume was estimated using an equation for young Douglas-fir trees (Adams and Joyce 1990).

To determine wood density traits, one 5-mm increment core sample

extending from pith to bark was taken at breast height (1.37 m) from the south side of each tree during the summer of 1988. Wood samples were dried to an equilibrium moisture content of about 9%, sawn to a uniform thickness of 1.5 mm in cross section, and then were chemically extracted with a solution of toluene:ethanol (2:1 vol) for 24 hours to reduce bias in the estimation of wood density (Taylor 1974). After extraction, samples were dried again to the initial equilibrium moisture content (9%) and kept in this condition throughout the remaining analyses.

Intra-ring density information for each core sample was obtained by using a direct scanning X-ray densitometry system (Hoag and McKimmy 1988). An X-ray beam is passed through the wood sample at equal step increments of 0.053 mm (i.e., 19 sampling points per mm). The amount of X-ray passing through the sample at a given point, which is inversely related to density of wood at that point, is registered by a sensor. A current output proportional to the amount of X-radiation detected is generated by the sensor and converted to voltage value which is stored in the computer. After the system is calibrated, voltage output is converted to wood density values. The first and last annual rings from the samples were discarded because they were incomplete. For each of the remaining rings, minimum, maximum, and average density values, and total ring width were obtained. Widths and average densities for earlywood and latewood, as well as latewood proportion, were also determined, using the average of the minimum and maximum ring densities as the criterion for defining the point of transition from earlywood to latewood (Green and Worrall 1964, Nicholls and Wright 1976).

Many criteria have been used to evaluate intra-ring density

variation (Olson and Arganbright 1977, Kanowski 1985). The criterion most recently used, however, is the standard deviation of density values (all X-ray data points) across the annual ring as described by Ferrand (1982) and Walker and Dodd (1988). In this study, intra-ring density variation for an individual ring (IRV) was estimated by the following equation:

$$\text{IRV} = [((\text{RD}-\text{ED})^2 * \text{EW} + (\text{RD}-\text{LD})^2 * \text{LW}) / \text{RW}]^{0.5} \quad (\text{II.2})$$

where:

RD = Average ring density,

ED = Earlywood density,

EW = Earlywood width,

LD = Latewood density,

LW = Latewood width, and

RW = Ring width.

This equation is a simplification of that used to obtain the standard deviation of density values in a given ring, which assumes this variation is primarily due to average differences in earlywood and latewood densities. Values obtained with this equation were closely correlated ( $r=0.96$ ) with the standard deviation of density values in a sample of 111 annual rings.

Weighted average values across the total core sample were calculated for individual ring variables, including overall density, earlywood density, latewood density, and intra-ring density variation, by weighting each individual ring value by its respective width. Core latewood proportion was obtained as the sum of latewood width of



individual rings divided by the length of the core sample. Although it might be preferred to weight individual ring values by ring area to obtain overall density values (Kanowski, 1985), weighting by ring width was chosen for several reasons. First, a preliminary correlation analysis (n=806 cores) showed that average core values based on the two types of weightings were strongly correlated ( $r=0.97$ ). In addition, width-weighted averages are equivalent to density values that would be obtained by determining wood density of the whole increment core using gravimetric methods. Since use of gravimetric methods on increment core samples is the cheapest non-destructive approach that still provides a good indication of whole-tree density (Cown 1976), it was of interest to simulate that approach.

#### Genetic parameter estimation

Variance and covariance analyses for all wood traits averaged across the core sample and for growth traits at age 15 (diameter, height, and bole volume) were performed using plot means. Missing values for two plots (from a total of 240) were estimated according to the method described by Steel and Torrie (1980, p. 209). Within-plot variances and covariances, as well as the harmonic mean of trees per plot, were estimated separately by pooling individual-plot values. Components of variance and covariance were estimated from the appropriate mean squares and cross products, using a random effects model (Table II.1). Standard errors of variance components were estimated following the procedures given by Namkoong (1979).

To determine the genetic control of wood density traits,

individual-tree and family heritabilities were estimated as in Falconer (1981). The additive genetic variance ( $\sigma_A^2$ ) was estimated as 3 times the family component of variance ( $\sigma_{f(s)}^2$ ), assuming that open-pollinated families are related to a greater extent than half-sibs (Campbell 1979, Sorensen and White 1988). The numerator used to estimate family heritability was  $\frac{1}{2}\sigma_A^2$ , which is appropriate for estimating gain from the progeny of a clonal seed orchard after roguing of clones based on performance of their open-pollinated families in progeny tests (Namkoong et al. 1966). The coefficient of  $\frac{1}{2}$  is used because gains are realized by planting the half-sib progeny obtained from the seed orchard. Standard errors for heritability estimates were calculated according to the procedures outlined by Osborne and Paterson (1952).

The relationships between traits were examined by estimating their respective genetic correlations, as well as their standard errors, following Becker (1984, p. 114). To evaluate the genetic interrelationships between wood density components and their direct and indirect effects on overall wood density, a path coefficient analysis, based on the estimates of genetic correlations, was done as described by Kempthorne (1957).

#### Construction of selection indices and response to selection

To evaluate the implications of the genetic relationships between wood density and its components, and between wood density, intra-ring density variation, and bole growth, expected genetic gains from parent-tree selection involving wood density, or wood density in combination with other traits were investigated. To evaluate gains in a single

trait (e.g. wood density) when selection is based on that trait, or indirectly on a single other trait, equations for direct and indirect response were used (Falconer 1981). When one or more density components were used as secondary traits to select for wood density, or multiple trait selection was of interest (e.g., selection for wood density and bole volume), index methods were employed (Lin 1978). In this case, selection was based on an index (I) which is defined as:

$$I = b_1X_1 + b_2X_2 + \dots + b_nX_n \quad (\text{II.3})$$

where the X's represent the traits used as criteria for selection and the b's are the coefficients associated with each trait in the index. The index coefficients are derived in such a way that the correlation between the index and the aggregate breeding value of the tree, which might be a function of one or more traits, is maximized (Lin, 1978).

To explore the effectiveness of wood density components as secondary traits to select for increased overall core density while reducing the correlated response in intra-ring density variation, several unrestricted selection indices (Smith and Hazel type; Lin 1978) were constructed. The breeding value of trees in this case was considered to be a function of overall core density alone.

To assess expected gains in wood density and bole volume when both traits are selected simultaneously, restricted and unrestricted indices were constructed. Selection indices with the Kempthorne-type restriction (Kempthorne and Nordskog 1959) were used to optimize the response in bole volume while limiting the change in overall core

density to zero. Unrestricted selection indices were employed when the method of desired gains was used to determine economic weights of the two traits (Cotterill and Jackson 1985). The RESI program described by Cotterill and Jackson (1981) was used to calculate the b coefficients and to compute expected genetic gains from applying the selection indices.

## RESULTS AND DISCUSSION

Genetic control of wood density components and intra-ring density variation

Analyses of variance showed significant differences ( $p < 0.01$ ) among families in average core sample values for all wood density traits considered. Population means for earlywood, latewood, and overall wood densities were 0.346, 0.824, and 0.455 g/cm<sup>3</sup>, respectively; while averages for latewood proportion and intra-ring density variation were 22.7% and 0.198 g/cm<sup>3</sup> (Table II.2). The mean for overall core density is slightly larger than values reported elsewhere for juvenile wood in Douglas-fir (0.409 g/cm<sup>3</sup> in Keller and Thoby (1977), 0.432 g/cm<sup>3</sup> in Cown and Parker (1979), 0.416 g/cm<sup>3</sup> in McKimby and Campbell (1982), and 0.363 g/cm<sup>3</sup> in King (1986)). It is difficult to determine, however, whether the greater overall density in these 60 families represents a real difference among populations, because juvenile wood density estimates are greatly influenced by the methods employed, particularly the moisture content used as a reference (e.g. a 9% moisture content was used in this study), as well as by the number of rings included and their distance from the pith (Cown and Parker 1979).

As reported previously in Douglas-fir (Bastien et al. 1985, King 1986), wood density traits have low coefficients of variation (in this case, only around one-third of those reported for growth traits (Li 1990)), but they are moderately to strongly inherited (Table II.2). Thus, even though phenotypic variation may be low, these traits are expected to respond well to selection in tree improvement programs.

None of the individual wood density components had estimates of heritability greater than that found for overall density. The same results were found in a provenance-progeny study of Douglas-fir in France (Bastien et al. 1985, Vonnet et al. 1985). Wood density components, however, appear to be under stronger genetic control than overall wood density in juvenile Pinus radiata (Nicholls et al. 1980).

#### Genetic relationships between wood density traits

All of the wood density components were strongly correlated genetically with overall density, and were also strongly interrelated among themselves, especially earlywood density and latewood proportion (Table II.3). This indicates that these traits are probably controlled to a large extent by the same set of genes. Similar conclusions have been reached in earlier studies with Douglas-fir (Keller and Thoby 1977, Birot et al. 1983), although the genetic relationships between traits were not as strong as reported here.

Intra-ring density variation is also strongly and positively correlated with overall density, but it seems to be much more strongly related to latewood density than to any other individual density component (Table II.3). The unfavorable genetic association between intra-ring density variation and overall density has also been observed in other populations of Douglas-fir (Keller and Thoby 1977, Bastien et al. 1985, Vonnet et al. 1985). These results are not surprising, however, since it can be seen from equation II.2 that intra-ring density variation will increase as average ring density increases. In addition, the difference between average latewood density and average ring density

is normally much larger than the difference between average ring density and average earlywood density, so variation in latewood density would be expected to have a larger impact on intra-ring density variation than any other wood density component. This would explain the stronger genetic correlation found between intra-ring density variation and latewood density, as compared to any other wood density component.

As a result of the strong interrelationships found between the wood density components, the relative influence (direct effect) of each component on overall core density, as estimated by path coefficient analysis (Figure II.1 and Table II.4), differs somewhat from the expectations based on their respective correlation coefficients alone (Table II.3). Earlywood density appears to have, by far, the largest direct effect on overall density, even though earlywood density and latewood proportion have similar genetic correlations with overall wood density. These results contrast with earlier studies in Douglas-fir and slash pine where the role of latewood proportion in explaining variation in overall wood density has been emphasized, with other components receiving less attention (Smith 1955, Kennedy 1961, Squillace et al. 1962). The larger direct effect of earlywood density found in our study, however, is probably due to the low proportion of latewood in these young trees. It can be seen from equation II.1, which relates the components to overall density, that if latewood proportion is small (or it shows limited variation), differences in overall density among trees will depend primarily on differences in earlywood density. In addition, a large proportion (on average, 57%) of the effects of individual components on overall wood density seems to be realized indirectly

through their relationships with the other components. Thus, even though latewood proportion was found to be strongly correlated with overall density ( $r_A=0.95$ ) almost half of its influence on overall density (0.46) is due to its strong correlation with earlywood density (Table II.4).

#### Implications of genetic interrelationships between wood density traits for breeding of overall density

Even though the components were strongly correlated with overall density, because of the lower heritabilities of the components and their strong interrelationships, expected response in overall density from direct selection for this trait (Table II.5, selection criterion 1) was always greater than indirect selection based on one or more components (Table II.5, selection criteria 2, 3, and 4). For similar reasons, adding the components as secondary traits in a selection index (Table II.5, selection criteria 5 and 6) did not increase the expected response to selection for overall density. Gjedrem (1967), and Sales and Hill (1976) found that inclusion of secondary traits in an index to select for a desired trait is more efficient than selection based on the desired trait alone only when the heritability of the desired trait is lower than the secondary traits, or when the secondary traits have low genetic but high phenotypic correlations with the desired trait. In the last situation, secondary traits are useful primarily to correct for environmental effects on the desired trait. White and Hodge (1990) also show that adding several secondary traits to an index is not appreciably better than direct selection if the secondary traits are strongly



correlated with each other. Moreover, adding secondary traits that are highly correlated into a selection index might reduce the precision of the index, since the sampling variance of the estimated covariance is higher for strongly correlated traits than for weakly correlated traits (Baker 1986).

Although direct selection for overall core density might be the most efficient selection criterion for improving wood density, selection for increased overall core density will lead to an estimated 3.5% increase in intra-ring density variation as a correlated response (Table II.5, selection criterion 1). Basing selection for wood density on earlywood density and latewood proportion (Table II.5, selection criterion 4), however, appears to produce nearly the same response in overall density, while reducing the negative effect in intra-ring density variation to 2.74%.

#### Genetic relationships between wood density and growth traits and implications for breeding

Moderately strong negative genetic correlations were found between bole volume and all density components (Table II.6). These unfavorable correlations appear to be primarily due to strong negative relationships between wood density traits and diameter growth (DBH), because the correlations between density traits and height were small. Similarly, strong negative genetic correlations between wood density and diameter growth in Douglas-fir were found by Keller and Thoby (1977), McKimmy and Campbell (1982), Nepveu (1984), Bastien et al. (1985), and King et al. (1988). Negative genetic correlations between these traits have also

been reported in other coniferous species (Chang and Kennedy 1967, Bendtsen 1978, McKinley et al. 1982, Dean et al. 1983, Loo et al. 1984, Fries 1986). In studies with southern pines, however, no correlation, or even a slightly positive correlation between wood density and growth rate have been found (Goddard and Cole 1966, Matziris and Zobel 1973, Rink and Thor 1973, Meier and Goggans 1977).

The emphasis in most coastal Douglas-fir tree improvement programs is in improving bole volume growth (Silen and Wheat 1979). Thus, potential implications of selection for this trait on wood density are of interest. The observed negative correlation between bole volume and intra-ring density variation (Table II.6) is presumably good because it means that selecting for increased growth rate would reduce intra-ring density variation. The negative correlation between bole volume and overall wood density, however, is a potential problem, since selection for bole volume alone will lead indirectly to trees with lower juvenile wood densities. Moreover, the use of individual wood density components either as indirect or auxiliary traits for selection of wood density would not alleviate this problem, since they have similarly strong negative correlations with volume growth.

Implications of the genetic relationships between wood density and growth traits on breeding for both volume growth and overall core density were explored by comparing various selection criteria, using selection index methods and the data in this study (Table II.7). Selection for volume alone without regard for wood density (selection criterion 1) will produce the maximum estimated increase in volume growth (13.37%), and the largest reduction in intra-ring density

variation, but at the expense of a reduction in overall core density (-2.41%), which in turn decreases wood strength. Although at first sight, a reduction of 2.41% in average wood density might appear unimportant, especially when compared with the gains obtained in bole volume, the impact of this reduction is substantial in terms of dry weight of fiber per hectare. For example, given a managed stand of coastal Douglas-fir producing 1000 m<sup>3</sup>/ha in a 60-year rotation (which seems reasonable for a site class II, Curtis et al. 1982), and assuming an average wood density of 0.455 g/cm<sup>3</sup>, a decrease of 2.41% in wood density would represent a reduction of about 11,000 kg of dry fiber per hectare.

Selection for core density alone (criterion 2), on the other hand, is expected to increase wood density by 5.66%, but this will lead to an increase in intra-ring density variation, a substantial reduction in volume growth (-8.47%), and, as a consequence, bole weight will be reduced by 3.29% with respect to the original population. Because of the large economic value placed on bole volume, this option is unlikely to ever receive serious consideration. Nevertheless, along with option 1 it is a useful point of reference for showing the results of assigning different economic weights to these traits.

From the results of these two extreme situations, it is obvious that multi-trait selection methods will be necessary to prevent undue loss in either trait. Restricted selection indices offer one of the best approaches for limiting the change in one trait while improving the other (Rehfeldt 1983 and 1985, Cotterill and Jackson 1981, Dean et al. 1986). A selection index imposing the restriction of no change in

overall core density (criterion 3) would produce 20% less volume than expected if selection were on volume alone, but total bole weight would remain about the same, with the additional advantage of no reduction in wood strength. Selection based on height growth alone (criterion 4) also seems to be a good option, giving slightly less volume gain and only about one-third the loss in wood density expected if selection were on volume alone. Total bole weight, however, was higher for this selection criterion than for any other explored. Fries (1986) obtained similar results when comparing selection methods to improve dry stem biomass in Pinus contorta. The better overall response from selection for height, as compared to selection for volume alone is due to the strong positive genetic correlation between height and volume, coupled with the weak negative correlation between wood density and height mentioned earlier (Table II.6).

Given the weak negative genetic correlation observed between height and overall core density, a selection index based on these two traits was constructed with the goal of optimizing gains in bole volume (by using a Binet-type restriction; Binet 1965), while limiting the response in overall core density (selection criterion 5). This selection criterion is expected to produce nearly as much response in bole weight as in selection for height alone, without decreasing overall core density and with only a small reduction in volume growth (compared to criterion 1). The overall response in bole volume is not modified substantially when volume is added to this index (criterion 6). The last alternative (criterion 7) illustrates that it is possible to obtain a slight increase in overall density (1.2%), with only a small reduction

in bole weight (less than 10% with respect to its maximum response), if less gain in bole volume is acceptable. More emphasis on increasing wood density, however, may not be desirable because it causes gain in volume to drop rapidly. Increasing the response in overall density would also have a negative correlated effect on intra-ring density variation.

Choosing the last option may have additional important implications. First of all, even a slight increase in juvenile wood density is helpful in offsetting reductions in overall wood density expected from shorter rotation ages. Kellogg (1982) estimated the move to shorter rotations in coastal Douglas-fir would result in a decrease of 2% to 5% in average wood density, due to a larger proportion of juvenile wood found in younger trees. Thus, an increase of 1.2% in overall density of juvenile wood would be important in reducing that deficit. In addition, it has been argued by King et al. (1988) that selecting for a positive response in two traits that are negatively correlated may help to break the negative genetic correlation between those traits caused by the pleiotropic action of genes.

Final decisions regarding the weighting given to wood density and volume growth in selection indexes will require more information about their relative contributions to product value in this species (i.e., their contribution to the value of lumber, plywood, pulp, etc.). It should be kept in mind, however, that an increase in the emphasis on selection for one trait will always be accompanied by a smaller response on the other. Maximum gains cannot be obtained on both traits at the same time.

If simultaneous improvement in both traits is desired, it might be worthwhile considering other breeding strategies. Dean et al. (1983) suggested that one possible solution for improving two negatively correlated traits, such as volume growth and wood density, is to select for those traits in separate "lines" or populations, using the multiple population concept of Burdon and Namkoong (1983). It is argued that the hybrid progeny of such lines might have better growth and wood density than can be achieved through the simultaneous selection in one line. This alternative, however, might not be appealing because of the long time required to achieve desired results.

## CONCLUSIONS

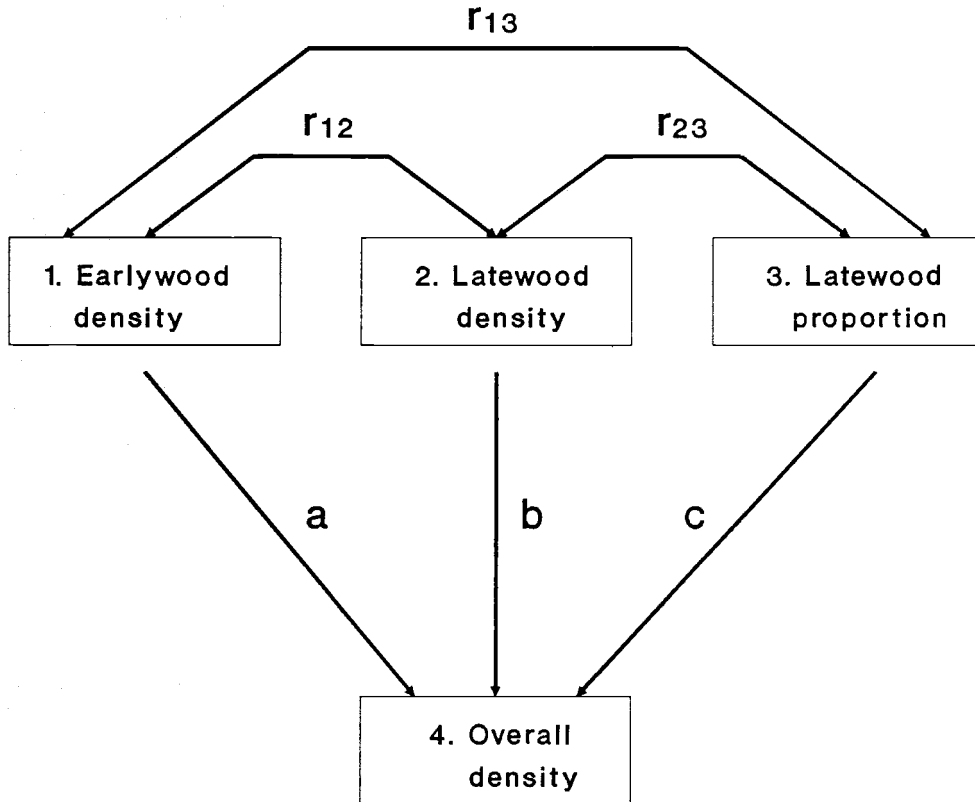
The results of this study are in agreement with earlier reports in coastal Douglas-fir that juvenile wood density is strongly inherited and can readily be manipulated by selection and breeding. Also supporting earlier work, moderate unfavorable correlations between wood density and bole volume and intra-ring density variation were observed.

Separation of wood density into components indicated that overall density in young trees is primarily influenced by earlywood density. All individual components, however, had strong genetic correlations with overall wood density, but lower heritabilities than the composite trait. Furthermore, because of the strong genetic interrelationships between the density components and overall density, the components were similarly unfavorably correlated with bole volume growth and intra-ring density variation. Therefore, information on individual density components appear to have little or no value for improving the efficiency of selection for overall wood density in this species, or for reducing the potential negative effects that selection for wood density might have on those other traits. Under these circumstances, breeding programs would not benefit from the additional effort and expense required to measure individual density components.

Despite the moderate negative genetic correlation between wood density and bole volume, comparisons of alternative selection indices including both traits showed that substantial gains in bole volume can be achieved without loss in wood density, or even while wood density is slightly increased, when the appropriate indices are employed. Given the value of wood quality, it is important to measure both traits in

Douglas-fir tree improvement programs. If selection is based on bole volume alone, lower wood quality can be expected. Comparisons of selection indices also indicated that significant, unwanted, increases in intra-ring density variation would occur only if wood density is given precedence over bole volume in selection programs. This is unlikely given the strong emphasis placed on improving volume growth in Douglas-fir tree improvement programs.





$$r_{14} = a + br_{12} + cr_{13}$$

$$r_{24} = ar_{12} + b + cr_{23}$$

$$r_{34} = ar_{13} + br_{23} + c$$

Figure II.1. Model of path coefficient analysis of the genetic relationships between wood density components and overall core density. Where:  $a$ ,  $b$ , and  $c$  are the direct effects to be estimated, and  $r_{ij}$  are the genetic correlations between traits.

Table II.1. Form of the variance and covariance analyses for wood density and growth traits at age 15.

Source of variation	Degrees of freedom	Expected mean squares <sup>a</sup>
Sets	s-1	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2 + f\sigma_{b(s)}^2 + bf\sigma_s^2$
Blocks/set	(b-1)s	$\sigma_w^2/k + \sigma_e^2 + f\sigma_{b(s)}^2$
Families/set	(f-1)s	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2$
Block*Fam./set (plot error)	(f-1)(b-1)s	$\sigma_w^2/k + \sigma_e^2$
-----		
Within-plot	$\sum_{i=1}^t (n_i - 1)$	$\sigma_w^2$

<sup>a</sup>/ For covariance analyses, cross products are used instead of mean squares.

s = number of sets.

b = number of blocks/set.

f = number of families/set.

k = harmonic mean of trees per plot for all sets.

$n_i$  = number of trees in plot i.

t = total number of plots in the experiment.

$\sigma_w^2$  = within-plot variance.

$\sigma_e^2$  = plot-to-plot variance.

$\sigma_{f(s)}^2$  = variance among families in sets.

$\sigma_{b(s)}^2$  = variance among blocks in sets.

$\sigma_s^2$  = variance among sets.

Table II.2. Estimates of population means ( $\bar{X}$ ), phenotypic (P) and genetic (A) coefficients of variation, and narrow sense heritabilities ( $h_i^2$ ) for overall core density and its components, and intra-ring density variation at age 15.

Trait	$\bar{X}^{a,b}$	Coefficients of variation (%)		
		P	A	$h_i^2 \pm \text{s.e.}$
Earlywood density	0.346 g/cm <sup>3</sup> (0.324-0.375)	7.33	5.02	0.47 $\pm$ 0.11
Latewood density	0.824 g/cm <sup>3</sup> (0.763-0.875)	5.54	3.31	0.36 $\pm$ 0.10
Latewood proportion	0.227 (0.202-0.260)	15.78	7.79	0.24 $\pm$ 0.08
Overall density	0.455 g/cm <sup>3</sup> (0.419-0.499)	7.29	5.62	0.59 $\pm$ 0.12
Intra-ring density variation	0.198 g/cm <sup>3</sup> (0.175-0.217)	9.64	4.80	0.25 $\pm$ 0.09

<sup>a/</sup> Range over 60 family means shown in parentheses. Differences among families for all traits were significant ( $p < 0.01$ ).

<sup>b/</sup> Density values are based on a moisture content of 9% in the samples. Approximate basic density values (based on oven-dry weight) can be calculated by dividing  $\bar{X}$  by 1.095.

Table II.3. Estimates of genetic correlations between wood density components and intra-ring density variation at age 15<sup>a</sup>.

Trait	Latewood density	Latewood proportion	Overall density	Intra-ring density variation
Earlywood density	0.61 (0.14)	0.92 (0.12)	0.97 (0.02)	0.56 (0.19)
Latewood density		0.57 (0.20)	0.74 (0.10)	0.99 (0.05)
Latewood proportion			0.95 (0.06)	0.58 (0.18)
Overall density				0.72 (0.12)

<sup>a</sup>/ Standard errors of genetic correlation estimates are given in parentheses.

Table II.4. Path-coefficient analysis of direct and indirect genetic effects of wood density components on overall density at age 15<sup>a</sup>.

	Wood density components		
	Earlywood density	Latewood density	Latewood proportion
Direct effect on Overall density:	0.50	0.23	0.36
-----			
Indirect effects on Overall density:	(0.47)	(0.51)	(0.59)
via Earlywood density	—	0.30	0.46
via Latewood density	0.14	—	0.13
via Latewood proportion	0.33	0.21	—
-----			
Totals (Genetic correlations)	0.97	0.74	0.95

<sup>a</sup>/ Model of path coefficient analysis is shown in Figure II.1.

Table II.5. Expected response in overall core density and correlated response in intra-ring density variation at age 15 when different wood density components are used as selection criteria.

Selection criteria	Response (%) <sup>a</sup>	
	Overall core density	Intra-ring density variation
1. Overall core density (CD)	5.66	3.47
2. Earlywood density (ED)	5.29	2.60
3. Latewood proportion (LP)	4.53	2.35
4. ED and LP	5.48	2.74
5. CD and ED	5.66	3.46
6. CD, ED, and LP	5.66	3.55

<sup>a</sup>/ Response expected in seed orchard offspring when the top 20% of parental clones ( $i=1.354$ ) are selected.

Table II.6. Estimates of genetic correlations between core density components and growth traits at age 15<sup>a</sup>.

Trait	DBH	Height	Volume
Earlywood density	-0.66 (0.18)	-0.24 (0.21)	-0.55 (0.18)
Latewood density	-0.44 (0.24)	-0.08 (0.24)	-0.30 (0.23)
Latewood proportion	-0.54 (0.25)	-0.10 (0.26)	-0.46 (0.18)
Overall density	-0.63 (0.18)	-0.19 (0.21)	-0.52 (0.18)
Intra-ring density variation	-0.51 (0.27)	-0.07 (0.26)	-0.38 (0.26)
DBH	—	0.77 (0.13)	0.96 (0.02)
Height		—	0.90 (0.06)

<sup>a</sup>/ Standard errors of genetic correlation estimates are given in parentheses.

Table II.7. Expected response in intra-ring density variation, overall core density, bole volume, and bole weight at age 15 when different selection criteria are used.

Selection criteria	Response (%) <sup>a</sup>			
	Intra-ring density variation	Overall core density	Volume	Bole weight <sup>b</sup>
1. Volume (VOL)	-1.50	-2.41	13.37	10.64
2. Overall core density (CD)	3.47	5.66	- 8.47	- 3.29
3. VOL and CD (0% change) <sup>c</sup>	0.00	0.00	10.53	10.53
4. Height (HT)	-0.28	-0.89	12.19	11.19
5. HT and CD (0% change) <sup>c</sup>	0.27	0.00	10.97	10.97
6. VOL, HT, and CD (0% change) <sup>c</sup>	0.14	0.00	11.11	11.11
7. VOL, HT, and CD (+1.2% change) <sup>c</sup>	0.55	1.13	8.95	10.18

<sup>a</sup>/ Response expected in seed orchard offspring when the top 20% of parental clones ( $i=1.354$ ) are selected on the basis of the various selection criteria given in the left-hand column.

<sup>b</sup>/ Bole weight = [Average bole volume]\*[Average core density].

<sup>c</sup>/ Selection index in which the response in overall core density was restricted to the percentage indicated.



## CHAPTER III

AGE-AGE CORRELATIONS AND EARLY SELECTION FOR WOOD DENSITY  
IN YOUNG COASTAL DOUGLAS-FIR

## ABSTRACT

To assess the potential for early selection of wood density in coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), age-age correlations and age-associated changes in the genetic control of wood density and its components (earlywood density, latewood density, and latewood proportion) were investigated. The possibility of using wood density components as secondary traits to increase the efficiency of early selection for overall wood density was also explored. Increment core samples were taken at breast height from 15-year-old trees of 60 open-pollinated families. Average values of wood density and its components at the different ages represented in the core samples (ages 7 to 15) were estimated by using X-ray densitometry. Heritability estimates for overall density and its components increased with age, mainly because of a decrease in the error variance as the number of rings in the core sample increased. Overall density and its components at age 15 were strongly genetically correlated with their respective traits at all younger ages analyzed. Moreover, with only a few exceptions, age-age genetic correlations were always greater than phenotypic correlations. Therefore, using phenotypic instead of genetic correlations will underestimate the efficiency of early selection,

especially at very young ages (i.e., ages 7 to 11). Early selection to improve overall density at age 15 was quite efficient (relative efficiency above 79%), even when early selection was based on core density at the youngest age (age 7). Using wood density components as secondary traits, however, produced only a slight increase in the efficiency of early selection at the youngest ages, presumably because age-age correlations for overall core density were already strong, so there was little room for additional improvement.

## INTRODUCTION

Determining the age at which trees or families in genetic tests can be reliably selected for relative performance at a later age (often, rotation age) is critical to the efficiency of tree improvement programs, because age of selection determines, to a large extent, the length of the breeding cycle and the amount of genetic gain that can be achieved per unit of time (Lambeth 1980, McKeand 1988). Selection at an early age, with the goal of improving a trait expressed at a later age, is a particular case of indirect selection, in which the response in the later trait relies on the correlated response from selection on the early trait (Nanson 1969).

The ratio of genetic gain on an older trait expected from indirect selection based on an early trait, relative to the gain expected when the older trait is selected directly, is called the relative efficiency (RE) of indirect (early) selection. Assuming equal intensity of selection at both ages, RE is expressed by the following equation (Falconer 1981):

$$RE = r_{Aeo} * (h_e/h_o) * 100 \quad (\text{III.1})$$

where  $r_{Aeo}$  = Genetic correlation between the trait selected at the early age and the trait of interest at an older age. When the trait at both ages is the same, the correlation is called an age-age genetic correlation,

$h_e$  = Square-root of heritability of the selected (early) trait, and

$h_o$  = Square-root of heritability of the trait of interest  
(older trait).

Thus, the degree to which heritability of the selected trait and its genetic correlation with the older trait (e.g., age-age correlation) changes with age is important in evaluating the feasibility of early selection.

Previous studies on efficiency of early selection have primarily focused on growth traits (Lambeth et al. 1983, Foster 1986, Gill 1987, Cotterill and Dean 1988, Magnussen 1988, Riemenschneider 1988), and only limited information on age trends of heritability of wood density or age-age correlations for this trait is available (McKimmy, 1966, Nicholls 1967). There is some evidence, though, that much genetic variation for wood density exists in young progeny tests (Stonecypher et al. 1964, Stonecypher and Zobel 1966, Talbert et al. 1983, Loo et al. 1984, Cown 1976), and that early selection for wood density is feasible (Nebgen and Lowe 1985, Gonzalez and Richards 1988). In general, previous studies have emphasized early selection based on an individual trait, usually the same trait as the trait of interest at the older age. Information on multiple early traits, however, may improve the efficiency of early selection (Foster 1986, Cotterill and Dean 1988, Burdon 1989).

In this study, overall wood density of 60 open-pollinated families of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at age 15 was obtained by X-ray densitometry of increment core samples (Chapter II). At this age, all wood is considered to be juvenile wood (Megraw 1985). From X-ray densitometry data, mean wood density of each annual

ring outward from the pith can be determined and used to calculate average core densities at various ages (for example, average core density at age 10 can be obtained by calculating the average density of the rings present in the core sample at that age). In addition, mean wood density of each ring, or average core density at a given age, can be partitioned into three components: mean earlywood density, mean latewood density, and latewood proportion. Information on genetic parameters of wood density components over time might be useful for helping to understand the genetic control of overall wood density at different ages. Particularly important in this context is the degree to which genetic relationships between individual components and overall density change with age. Although information on wood density components is not useful for selection of overall wood density at age 15 (Chapter II), it still is important to determine whether wood density components have value for early selection purposes.

At present, most tree improvement programs in coastal Douglas-fir plan to make final selections between 15-20 years of age (Silen and Wheat 1979). Can overall wood density at this age be reliably predicted at much younger ages? In addition to addressing this general question, the following objectives were of interest in this study: (1) to describe age trends in variance components and heritabilities for wood density and its components, (2) to describe age-age correlations for wood density and its components, (3) to examine the relative influence of wood density components on overall density at different ages, and (4) to assess the utility of information on wood density components for the purposes of early selection.

## MATERIALS AND METHODS

Measurements

During the summer of 1988, one pith-to-bark (5-mm) increment core sample was taken at breast height (1.37 m) from each tree of 60 open-pollinated families in a 15-year-old progeny test of coastal Douglas-fir, established at Coyote Creek, near Eugene, Oregon. These families corresponded to sets 2 and 4 (30 families each) of the Noti Breeding Unit in the Umpqua Tree Improvement Cooperative (Silen and Wheat 1979). The original parent trees were selected in natural stands located between 150 and 450 m elevation in the central Coast Range of Oregon. Each set of families was planted in 1974 as a separate randomized complete block design experiment with four replications. Four-tree non-contiguous family plots were established in each block, with trees in each plot assigned to planting spots at random. Up to the time when the increment core samples were taken, survival for these two sets was about 85%.

Intra-ring density information for each sample was obtained by using the direct scanning X-ray densitometry system described by Hoag and McKimmy (1988). The first and the last rings from every sample were discarded from further analysis because they were usually incomplete. For each of the remaining annual rings in the samples, earlywood density, latewood density, latewood proportion, and whole ring density were obtained directly from the X-ray density profiles. The average of the minimum and maximum density in the ring was used as criterion to separate earlywood from latewood (Nicholls and Wright 1976).

The number of growth rings in each sample varied slightly as trees reached the breast-age sampling position at different ages. Annual rings were identified and numbered starting from the bark inward, so they represent the age of the tree at which they were formed (Dodd and Power 1986). Average values of core density and its components were obtained cumulatively from age 7 (first annual ring from the pith in most samples) through age 15 (i.e., core ages 7 to 15). To obtain the averages for each core age, the mean values of annual growth rings present in the sample up to that age were weighted by their respective width. These averages, therefore, represent those values that would be obtained if increment core samples had been taken every year, beginning at age 7. Weighting individual ring density values by ring width, rather than by ring area (Kanowski 1985), was chosen because the average core values obtained this way would be similar to those obtained using gravimetric methods to estimate wood density from increment cores, which is the most commonly employed non-destructive method of estimating wood density in standing trees. Overall core density obtained in this manner has been shown to be strongly correlated to whole-tree wood density in young Douglas-fir (Cown 1976).

#### Statistical analyses

Analyses of variance for all ages were performed according to the random effects model for individual-tree data (Table III.1) using the SAS GLM procedure (SAS 1987), and the type III sums of squares. Type III sums of squares are least squares estimates that take into account the imbalance in number of observations per plot. Analyses of

covariance between all pairs of traits at the same age, and between traits at different ages were also computed as in Table III.1, using expected cross-products instead of expected mean squares. Due to the differences in the number of growth rings in each core sample, early ages (age 7 and age 8) were not represented in all core samples. Covariance analyses for age 7 (n=521 cores and 19 missing plots) and age 8 (n=737 cores and 5 missing plots) with all other ages included only the individuals having these particular growth rings, so they were performed separately from the age-age covariance analyses at ages 9 to 15 (n=806 cores and 3 missing plots).

To describe the age trends in variance components and heritabilities for wood density traits (Objective 1), family/sets, error, and within-plot variances were estimated by equating the Mean Squares for family/sets, error, and within-plot to their respective expectations from the model (Table III.1), using the estimates of the  $k_j$  coefficients given by the SAS GLM procedure. Age trends in variance components were expressed in terms of coefficients of variation to avoid potentially confounding scale effects. Individual-tree and family heritabilities were estimated as in Falconer (1981), assuming that the variance among open-pollinated families ( $\sigma_{f(s)}^2$ ) estimates 1/3 of the additive genetic variance ( $\sigma_A^2$ ) (Campbell 1979, Sorensen and White 1988). The numerator used to estimate family heritability was  $\frac{1}{4}$  of the additive genetic variance ( $\sigma_A^2$ ), which is appropriate for estimating gain from the progeny of a clonal seed orchard after roguing of clones based on the performance of their open-pollinated families in progeny tests (Namkoong et al. 1966). Standard errors for heritability estimates were



calculated following the procedures given by Osborne and Paterson (1952).

To describe age-age correlations for wood density and its components (objective 2), genetic and phenotypic correlations for all pairwise combinations of core ages, 7 through 15, were calculated for each wood density trait. Genetic correlations were estimated using the appropriate variance and covariance components according to Becker (1984), while the phenotypic correlations were estimated as simple correlation coefficients (Falconer 1981). Standard errors for genetic correlations were calculated as outlined by Becker (1984). Because the annual rings in a younger core make up part of the same core at an older age (i.e., they have rings in common), age-age correlations for average core values can exist even when the wood properties of different aged rings are uncorrelated (Lambeth et al. 1983). To determine the degree to which individual rings of increasingly different ages are correlated for each wood trait, genetic and phenotypic correlations were calculated between individual ring values for all pairwise combinations of ring ages.

To examine the relative influence of wood density components on overall core density at different ages (objective 3), genetic correlations between overall core density and its components at each particular core age were calculated. The direct genetic effects of individual components on overall density at a given age were estimated by path-coefficient analysis, using the model described in Chapter II.

The relative efficiency (RE) of parent tree selection for overall core density at age 15 (older trait) based on early measurements of

overall core density (early trait) was calculated using equation III.1, assuming the same selection intensities at both ages. The efficiency of wood density components as additional traits in early selection for overall core density (objective 4) was assessed by using index selection methods. Selection indices which incorporated information on particular wood density components, in addition to overall core density at age of selection, were employed to maximize gains in overall core density at age 15 by imposing a Binet-type restriction (Cotterill and Jackson 1981, Burdon 1989). The Binet restriction is intended to maximize indirect genetic response in traits which are of economic value but for some reason are not actually measured (Cotterill and Dean 1988), as in this case overall density at age 15, which is not measured in the interest of reducing the length of the selection cycle. To calculate the relative efficiency of early selection based on the selection indices, expected gains in overall core density at age 15 from index selection based on early traits, were estimated with the RESI program (Cotterill and Jackson 1981) and divided by the gain expected from direct selection at age 15.

## RESULTS AND DISCUSSION

Age trends in population means, variance components, and heritability

Population means for earlywood density and overall core density both decreased slowly with increasing core age, but levelled off in the last two years (Figure III.1). Latewood proportion decreased sharply during the first four years, from 0.384 at age 7 to 0.214 at age 11, and then also levelled off. Latewood density, unlike the other wood density traits, increased steadily from 0.659 g/cm<sup>3</sup> at age 7 up to 0.824 g/cm<sup>3</sup> at age 15. These age trends resemble those reported previously for average ring density and its components in young Douglas-fir (Cown and Parker 1979, Megraw 1985).

The analyses of variance showed significant differences ( $p \leq 0.05$ ) among families for all wood density traits, at all core ages. A strong decrease in the magnitude of the coefficient of environmental variance, and consequently in the coefficient of phenotypic variance, was observed for all traits during the first 5 years (Figure III.2). The reduction in environmental variance with increasing age can be attributed to the higher precision in estimating the average values of wood density traits as the number of growth rings included in the sample increased. The coefficient of additive genetic variance, on the other hand, followed different age trends among traits, slightly increasing for earlywood density and overall core density, but decreasing for the two other traits (Figure III.2). The absolute changes in additive variance, however, were small compared to the overall reduction observed in environmental and phenotypic variance for all traits.

The age trends in variance components for latewood density and latewood proportion resemble those normally observed for growth traits in young conifer plantations (Lambeth et al. 1983, Foster 1986, Gill 1987, Cotterill and Dean 1988), in which all the coefficients of variation decrease with age, and there is a larger decline in the coefficient of environmental variance, than in the coefficient of additive variance.

The strong decrease in the coefficient of environmental variance, observed for all traits, resulted in a steady increase in heritability estimates for overall core density and its components, especially during the first 5 years (Figure III.2). Age trends in heritability were quite similar for all traits, with overall core density always showing the strongest genetic control and maintaining its relative advantage over all the other traits (Figure III.3). Standard errors of heritability estimates for all traits were very similar, normally lower than 0.10 (the largest error (0.13) was obtained at age 15 for overall core density). Earlywood density and latewood proportion always showed the highest and lowest heritabilities, respectively, among the components, except at age 7, when all the components had similar estimates. This suggests that latewood proportion is more strongly affected by environment variation than any other wood density component. Based on average values of individual rings, Nicholls (1967), and Nicholls and Brown (1971) also found much lower heritabilities for latewood proportion than for average ring density at different ages in Pinus radiata.

Previous studies in Douglas-fir found similar increases in the

heritability of wood density (McKimmy 1966) and its components (Cown 1976) with age, at least for the first 10-15 growth rings from the pith. A strict comparison between different studies, however, is difficult because in some cases heritability estimates are based on individual growth rings (Cown 1976) or core sections (McKimmy 1966), rather than on the whole core, as in this study. Nevertheless, it seems that the degree of genetic control for wood density traits in Douglas-fir changes with age. The similarity of heritability trends found in Douglas-fir is in contrast with differences among studies found in other species. In Pinus radiata, for example, based on individual growth rings, Nicholls (1967) reported that heritability of average ring density remains relatively constant with age, whereas Nicholls and Brown (1971) found it increased with age. In P. taeda, Zobel (1964) found that heritability of wood density increased for at least the first 15 years, whereas Loo et al. (1984) reported similar heritability values up to age 10.

Knowledge of age trends in heritability is important for early selection. Most studies on the efficiency of early selection have assumed that heritability remains constant with age (Squillace and Gansel 1974, Lambeth 1980, Gonzalez and Richards 1988). If heritability really increases with age, as in this case for juvenile wood density in Douglas-fir, assuming the same heritability at younger ages as that for age 15 would overestimate the relative efficiency of early selection.

#### Age-age correlations

With the exception of latewood proportion, genetic correlations for overall core density and its components at younger ages, with their

respective values at age 15, were normally stronger and more stable than the corresponding phenotypic correlations (Figure III.4). This indicates that as the age interval increases, genetic correlations decline more slowly than phenotypic correlations. Similar results have been observed for growth traits (Lambeth et al. 1983, Cotterill and Dean 1988, Riemenschneider 1988). Thus, using age-age phenotypic correlations rather than genetic correlations to evaluate efficiency of early selection as was done by Lambeth (1980) and Gonzalez and Richards (1988), will underestimate potential gains from early selection, especially if selection is applied at very young ages. Standard errors of genetic correlations were normally lower than 0.05 when the difference in core age was 6 years or less, but increased to about 0.15 when the difference in age was 8 years. Thus, a larger error might be expected in estimates of potential gains from early selection at younger ages.

There seems to be no clear explanation for the different results found for latewood proportion, in which age-age genetic correlations at early core ages were weaker than the respective phenotypic correlations. One possibility could be a larger influence of environmental effects on the phenotypic correlations for this trait. Lambeth et al. (1983) argued that the magnitude of the age-age genetic correlation for a particular trait normally corresponds to its degree of genetic control, since genetic correlations are estimated on the basis of genetic effects; and trends of decreasing age-age genetic correlations with decreasing genetic control of traits have been reported (Squillace and Gansel 1974, Steinhoff 1974). Apparently, when the genetic control of a

trait is weak, as is the case of latewood proportion in our study, environmental correlations might cause phenotypic correlations to be stronger than genetic correlations.

Genetic correlations estimated between individual growth rings at different ages were almost as strong as the age-age genetic correlations for all overall core density traits (Figure III.5a). Rings separated in age by as much as 5-7 years had mean estimates of genetic correlations between 0.7 and 0.8 for most traits. Standard errors of genetic correlations between individual rings, however, were larger (between 0.10 and 0.30 in most cases) than those for overall core density values. Thus, averaging wood density traits over several rings resulted in more precise estimates of genetic correlations. These results indicate that the strong age-age genetic correlations observed in overall core density traits were not due to autocorrelation. Phenotypic correlations between individual ring values at different ages, however, were considerably lower than those observed for age-age correlations of overall core density and its components involving similar age differences (Figure III.5b). Therefore, it seems that autocorrelation has a greater influence on phenotypic correlations, probably because of a stronger effect of shared environment on phenotypic than on genetic correlations.

#### Relative influence of wood density components on overall density at different ages

The relative influence of individual density components on overall density, as measured by path-coefficient analysis, appears to be relatively stable in juvenile cores of different ages. Earlywood

density had the largest direct effect of all the components, except at age 7 when latewood proportion was slightly more important (Figure III.6). With increasing core age beyond 13 years, however, the relative influence of earlywood density seems to decrease slightly, being replaced by an increasing influence of latewood proportion on overall density. This trend resembles the age trend normally followed by latewood proportion in annual growth rings, in which this trait steadily increases as trees get older (Megraw 1985). If this trend actually continues with increasing core age, then latewood proportion eventually would become the most important component of wood density in mature trees, as has been previously observed (Kennedy 1961, Worrall 1970).

#### Efficiency of early selection for overall core density

The relative efficiencies of different selection criteria for early selection of overall core density are presented in Table III.2. As expected from the strong age-age genetic correlations for overall core density, early selection for core density at age 15 was quite efficient, even at age 7 when selection was based on information from one growth ring only. Early selection at age 7, based on overall density alone, is expected to produce about 79% of the gain in overall density at age 15 that would be obtained if selection were delayed until age 15. The efficiency of early selection based on overall density alone steadily improves with increasing core age, and by age 11 early selection is nearly as effective as direct selection at age 15.

Using information on density components, as well as overall density in selection indexes, seems to produce only a slight improvement



in the relative efficiency of early selection (Table III.2). At the earliest ages, in particular, relative efficiencies of early selection were improved by only 4 to 8 percent when all three density components were included along with overall core density in the selection index. The limited usefulness of wood density components for increasing the efficiency of early selection for overall core density can be partially attributed to the strong genetic correlations found between overall core density at younger ages and overall core density at age 15, which were always greater than 0.9. White and Hodge (1990) have shown that if the genetic correlation between a single selected trait and a target trait is high, very little additional improvement in the target trait can be expected when additional traits are incorporated into the selection index. Thus, wood density components might become more important for early selection of overall core density as the difference between the age of selection and the target age increases beyond the ages considered in this study, because age-age genetic correlations for overall core density would be expected to decrease.

The ability to utilize density components in indexes for early selection, however, requires a priori information on the genetic and phenotypic covariances between the core density components at the age of selection and overall wood density at age 15. These data would not be available unless they were generated in a previous generation of the same breeding population or in another breeding population. The accuracy of such estimates for the population of concern may, therefore, be questioned. Although this problem is common to any criterion used for early selection, it becomes more serious as the number of traits

included in the selection index increases, because the weights assigned to the traits in the index are sensitive to changes in the correlations between traits (Burdon, 1989). In addition, the extra cost associated with obtaining information on the individual density components must be compared against the additional gains expected from the increase in selection efficiency.

## CONCLUSIONS

This study shows that heritability estimates for overall core density and its components steadily increase with core age. Because the coefficients of additive genetic variance changed little with core age, the increase in heritability was primarily due to a decrease in environmental and phenotypic variance components with time, presumably because of the higher precision in estimating average core density values as the number of rings in the core sample increased.

Strong genetic correlations between core density values at younger ages and their respective values at age 15 were observed for all wood density traits. With the exception of latewood proportion at very young ages, phenotypic correlations were always smaller than genetic correlations, and approached the values of genetic correlations only at the oldest core ages. Therefore, if age-age phenotypic correlations are used to estimate age-age genetic correlations, the relative efficiency of early selection for overall core density will be underestimated.

Because of strong age-age genetic correlations and a moderate to strong heritability of overall core density, even at the youngest ages, early selection with the goal of improving overall core density at age 15 would be very efficient. Using information on wood density components as secondary traits in selection indices, however, would produce only a slight increase in the efficiency of early selection at the youngest ages. The strong age-age correlation in overall core density, which already explains most of the variation in overall core density at age 15, appears to be the reason why information on density

components adds little to the efficiency of early selection.

This study investigated age-age genetic correlations in juvenile wood density only (i.e., in 15-year-old trees). Although selection at age 15 may be appropriate for improving density of juvenile wood, the degree to which selection at this age would be adequate for improving density of mature wood is uncertain. If early selection for mature wood is to be considered, it is necessary to know the genetic relationship between mature wood density and wood density at the age of selection. Two earlier studies in Douglas-fir suggest the correlation between wood density at age 15 and mature wood density may be quite strong (McKimmy and Campbell 1982, Gonzalez and Richards 1988). Given that heritability for wood density remains relatively stable between ages 10 to 15, and that genetic correlations between these ages are high, selection for mature wood density at age 10 should be nearly as effective as early selection at age 15. Although it may prove necessary to wait until age 15 or later before making final selections on other traits (e.g., stem form or growth rate) in Douglas-fir, it is useful to know that wood density can be selected with fairly reasonable precision at early ages. For example, wood density may be given heavy weight when early selections are used to rogue seed orchards, or for the purposes of culling breeding populations prior to controlled crossing programs.

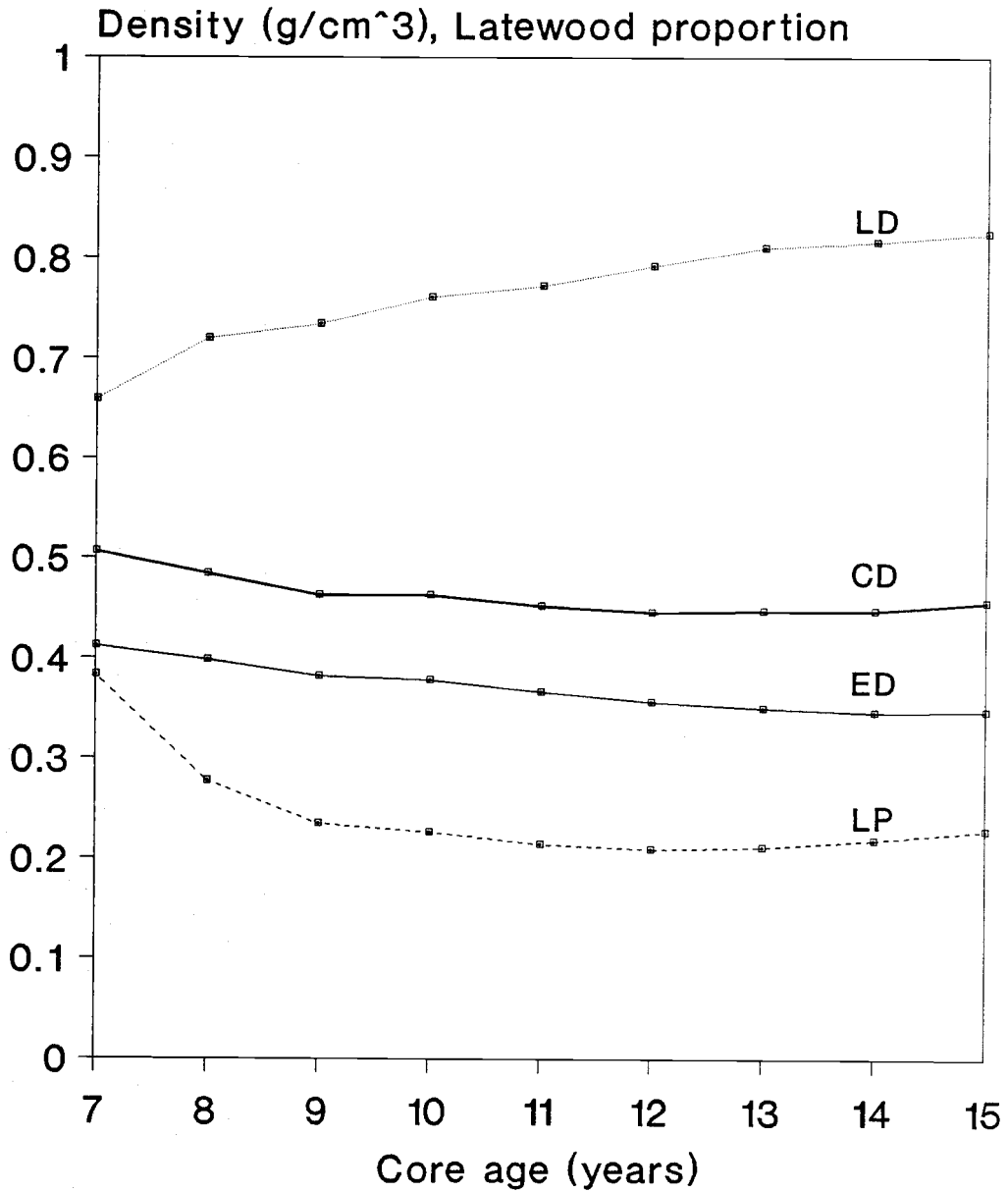


Figure III.1. Age-associated changes in population means for overall density (CD) and its components. ED=Earlywood density; LD=Latewood density; and, LP=latewood proportion.

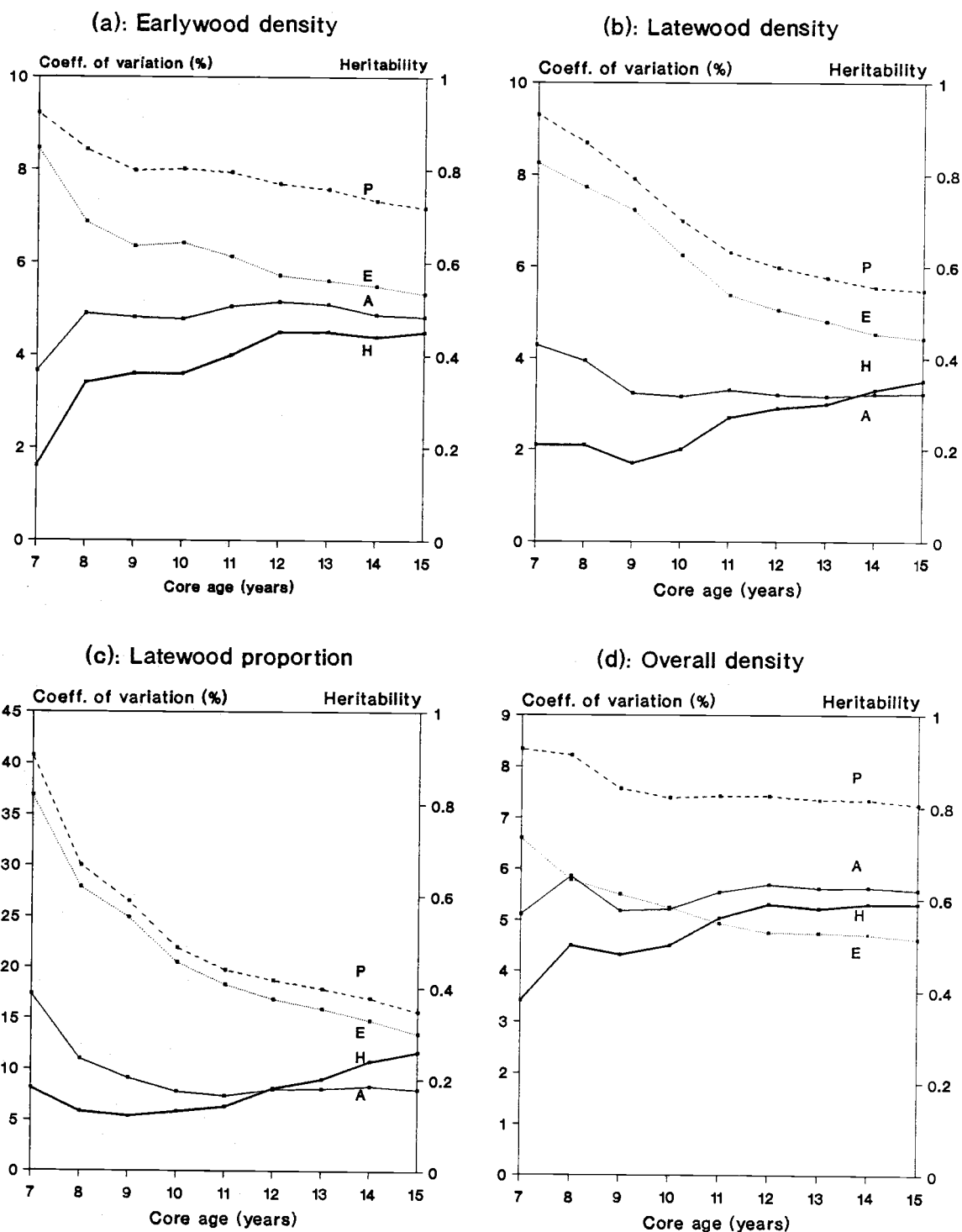


Figure III.2. Age trends in phenotypic (P), environmental (E), and additive (A) variance components (expressed as coefficients of variation), and individual-tree heritability (H), for overall core density and its components.

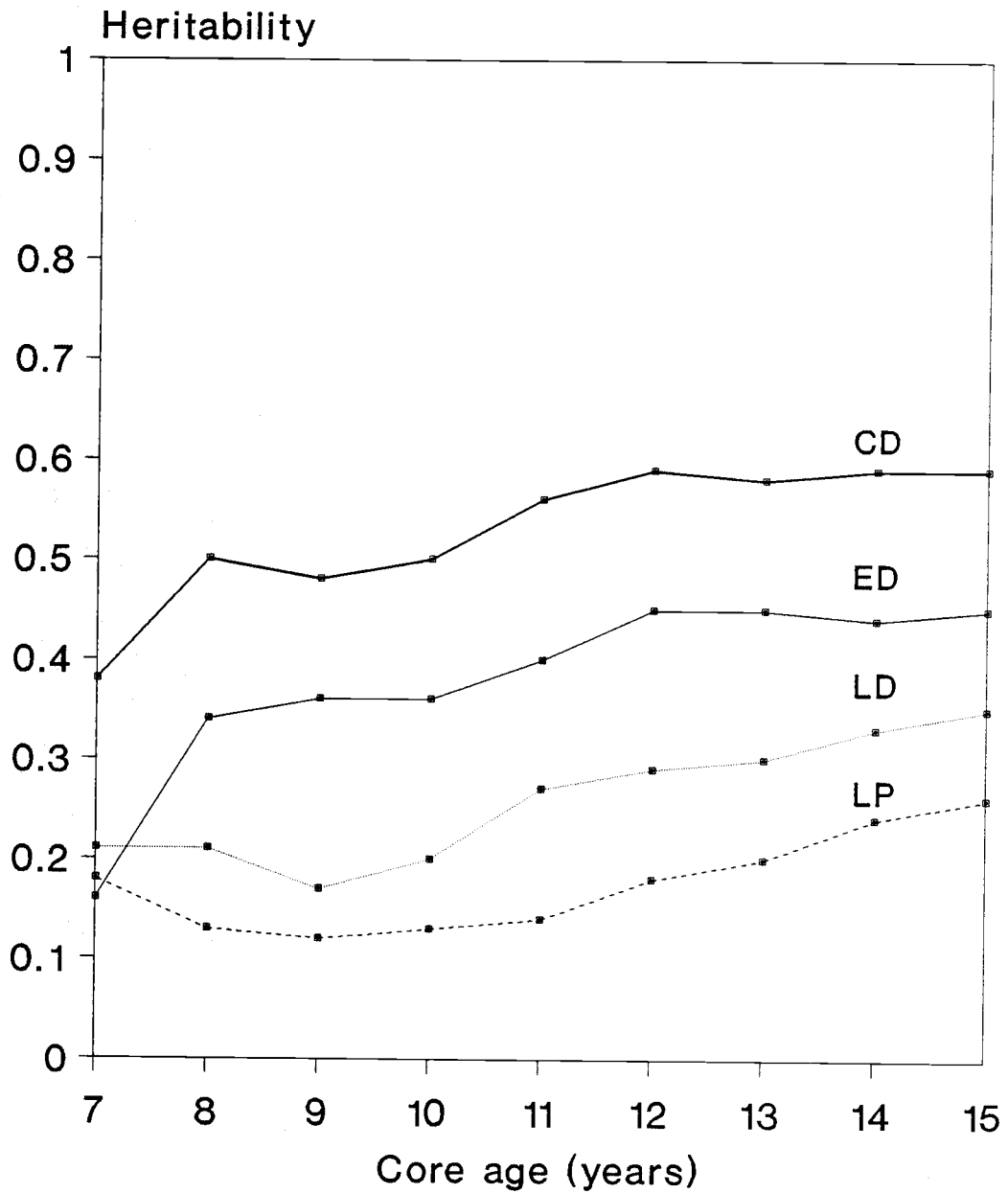
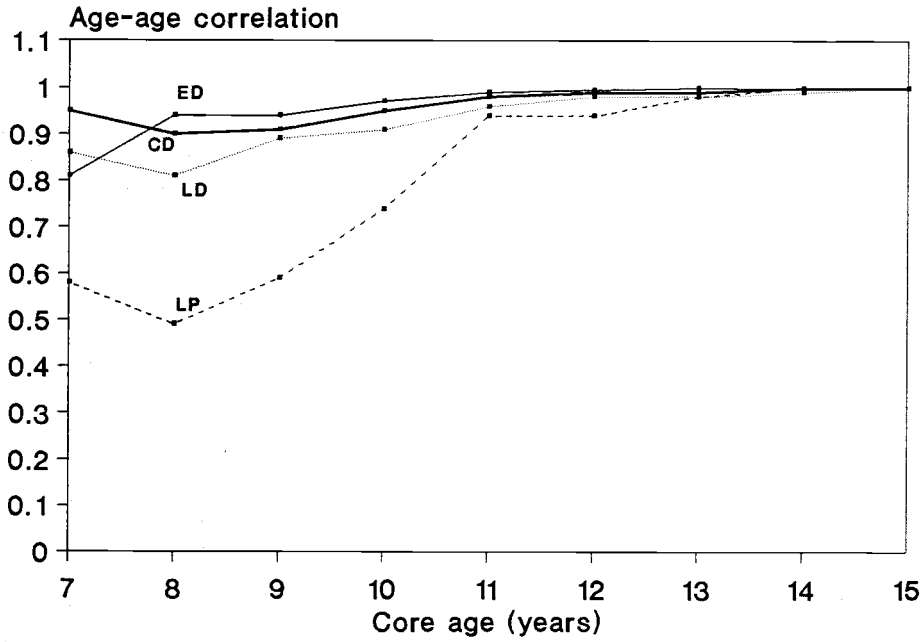


Figure III.3. Age-associated changes in individual-tree heritability for overall core density (CD) and its components. ED=Earlywood density; LD=Latewood density; and, LP=Latewood proportion.

(a): Genetic correlations



(b): Phenotypic correlations

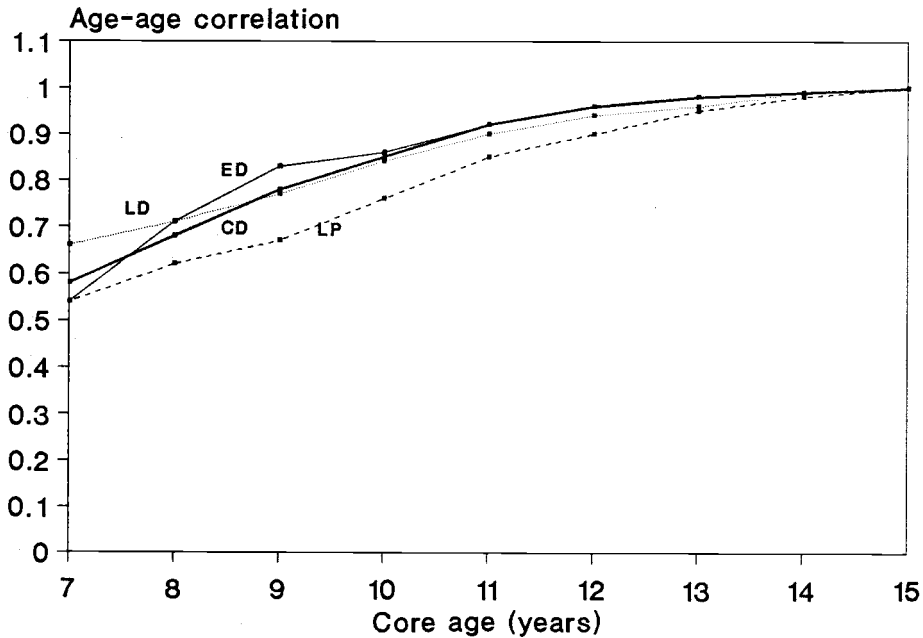


Figure III.4. Genetic (a) and phenotypic (b) correlations for overall core density (CD) and its components at different ages, with their respective values at age 15. ED=Earlywood density; LD=Latewood density; and, LP=Latewood proportion.



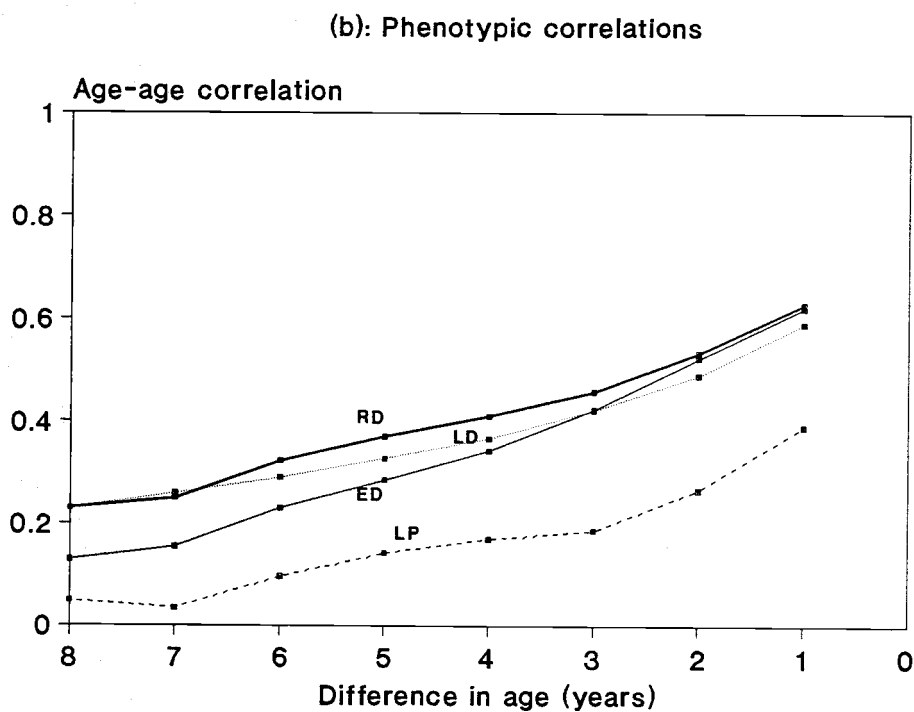
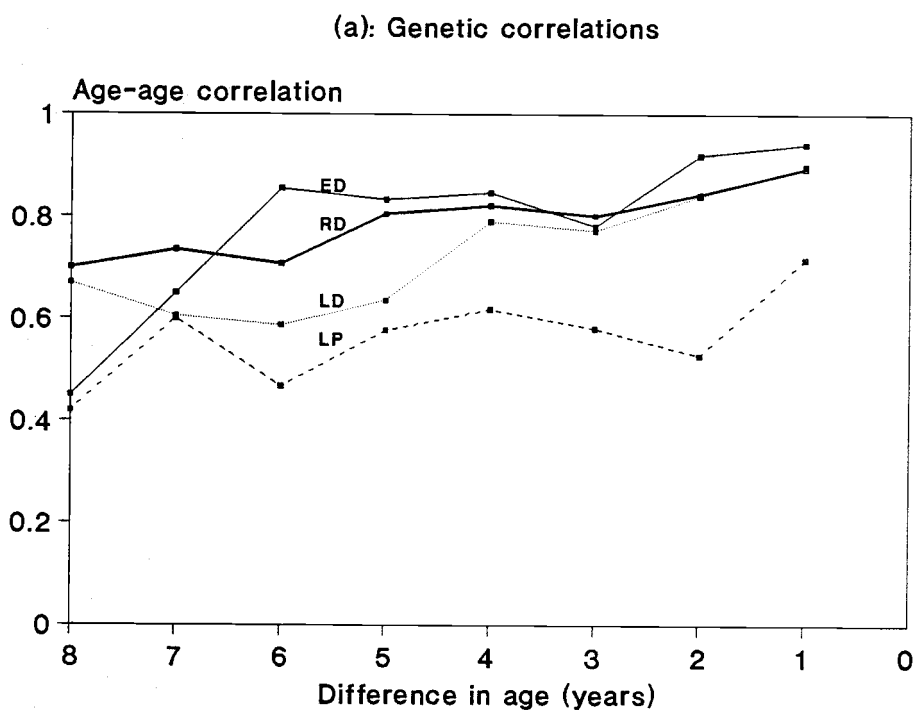


Figure III.5. Mean genetic (a) and phenotypic (b) correlations between annual rings of different ages for ring density (RD) and its components, plotted over the difference in years of the two ring ages involved. ED=Earlywood density; LD=Latewood density; and, LP=Latewood proportion.

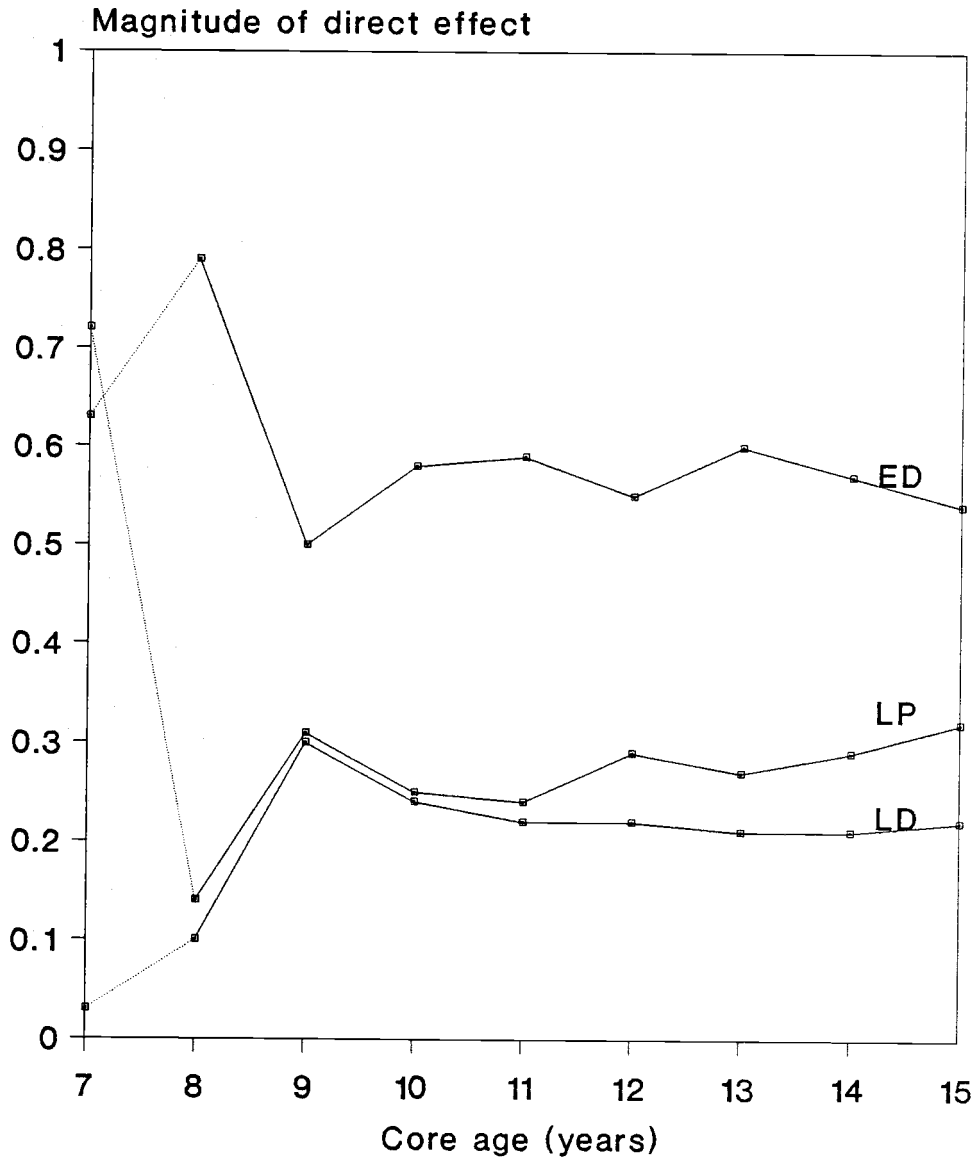


Figure III.6. Age-associated changes in the direct effect of individual density components on overall core density, as estimated by path coefficient analysis. ED=Earlywood density; LD=Latewood density; and, LP=Latewood proportion.

Table III.1. Form of the variance and covariance analyses for overall core density and its components measured at different ages.

Source of variation	Degrees of freedom	Expected mean squares <sup>a</sup>
Sets (S)	s-1	$\sigma_w^2 + k_6\sigma_e^2 + k_7\sigma_{f(s)}^2 + k_8\sigma_{b(s)}^2 + k_9\sigma_s^2$
Blocks/Set	s(b-1)	$\sigma_w^2 + k_4\sigma_e^2 + k_5\sigma_{b(s)}^2$
Families/Set	s(f-1)	$\sigma_w^2 + k_2\sigma_e^2 + k_3\sigma_{f(s)}^2$
Plot error	s(b-1)(f-1) <sup>b</sup>	$\sigma_w^2 + k_1\sigma_e^2$
Within-plot	$\sum_{i=1}^t (n_i - 1)$	$\sigma_w^2$

<sup>a</sup>/ For covariance analyses, cross products are used instead of mean squares.

<sup>b</sup>/ Actual degrees of freedom varied depending on the total number of missing plots (see text).

s = number of sets.

b = number of blocks/set.

f = number of families/set.

$k_j$  = Coefficient associated with the  $j^{\text{th}}$  variance component.

$n_i$  = number of trees in plot i.

$\sigma_w^2$  = within-plot variance.

$\sigma_e^2$  = plot-to-plot variance.

$\sigma_{f(s)}^2$  = variance among families in sets.

$\sigma_{b(s)}^2$  = variance among blocks in sets.

$\sigma_s^2$  = variance among sets.

Table III.2. Relative efficiencies (%) of early selection for overall core density when different selection criteria are used.<sup>a</sup>

Age of selection	Selection criteria <sup>b</sup>				
	Overall core density	(CD and ED)	(CD and LD)	(CD and LP)	(CD, ED, LD, and LP)
15	100.0	100.0	100.0	100.0	_____
7	79.5	82.8	82.2	82.3	86.2
8	87.6	89.7	88.5	90.0	90.3
9	89.0	91.0	89.3	91.0	91.5
10	92.0	93.1	93.0	93.4	93.4
11	97.7	97.8	97.9	97.8	98.5
12	99.0	99.1	99.3	99.1	99.3
13	99.4	99.4	99.5	99.5	99.6
14	99.9	99.9	99.9	99.9	100.0

<sup>a</sup>/ Relative efficiency is genetic gain in overall core density at age 15 from early selection, relative to gain expected when selection is applied to overall core density directly at age 15.

<sup>b</sup>/ CD = Overall core density at age of selection,  
 ED = Earlywood density at age of selection,  
 LD = Latewood density at age of selection, and  
 LP = Latewood proportion at age of selection.

## CHAPTER IV

FAMILY VARIATION IN AGE TRENDS OF WOOD DENSITY TRAITS  
IN YOUNG COASTAL DOUGLAS-FIR

## ABSTRACT

In order to examine the extent of genetic differences in ring-to-ring density variation and to explore the possibility of selection for a shorter juvenile wood formation phase, the age trends of ring density and its components were examined in 15-year-old trees from 60 open-pollinated families of coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco). A single increment core was extracted from each tree at breast height and ring density information was obtained by scanning X-ray densitometry. The youngest annual ring in most cores was produced when the tree was 7 years old, so age trends from age 7 to 15 years were evaluated. Prior to analysis, earlywood density, latewood density, and overall density for each ring in a core sample were weighted by the ring area occupied by each trait to produce relative ring density (RRD) values. Age trends differed for the different traits. Overall RRD and latewood RRD steadily increased with age over the entire core, while latewood proportion showed a decreasing but irregular trend during the early years of growth, followed by a steady increase after age 11. Age trends in these traits were relatively consistent over all trees sampled. Age trends for earlywood RRD varied among trees, with a steady increase in this trait across all rings in

some trees, while in others, a steady increase continued until around age 12, when a plateau occurred. With the exception of earlywood RRD, age trends did not appear to vary among families. Thus, selection for less ring-to-ring variation in wood density does not seem possible. Significant family differences were found in the proportion of trees which reached a plateau in earlywood RRD by age 12. This proportion was under moderate genetic control (family  $h^2=0.30$ ) and was not genetically correlated with overall core density or growth traits at age 15. Although the practical implications of these results are uncertain, there are reasons to hypothesize that the plateau in earlywood RRD is an indication of transition from juvenile to mature wood formation. Thus, selecting for families having higher proportions of individuals with a plateau in earlywood RRD might lead to a reduction in the period of juvenile wood formation. This hypothesis needs to be verified in older trees.

## INTRODUCTION

Wood density normally follows a predictable pattern of ring-to-ring variation in the radial direction across the stem (i.e., a predictable "age trend"). Most coniferous species that have been examined show a tendency towards increasing ring density outward from the pith, at least for the first 10 to 20 years, before levelling off (Harris and Birt 1972, Cown and Parker 1978). Young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), on the other hand, normally begins with a radial trend of decreasing average density in the first 3 to 5 annual rings from the pith, followed by a gradual increase as the distance from the pith increases (Cown and Parker 1979, Megraw 1985, Jozsa and Brix 1989).

Average (overall) ring density (ORD) is determined by three interacting components, average earlywood density, average latewood density, and the proportion of latewood in the ring (Nicholls et al. 1980). In Chapter III, it was shown that the relative influence of different components on the average density of increment core samples begins to change after 6 to 7 rings from the pith, suggesting that density components follow different age trends. Although Megraw (1985) made a similar observation, there have not been further attempts to analyze the implications of age trends of individual density components. Age trends in the individual components influence the age trend in ORD, affecting the levels of ring-to-ring density variation across the stem.

Substantial genetic variation in the slope of the age trend (i.e., the rate of change per year) for ORD has been observed in loblolly pine

(Loo et al. 1985). Similarly, significant genetic variation might also be present for the slope of the age trends of ORD and its components in Douglas-fir. Steeper slopes in the age trends of these traits imply larger ring-to-ring density variation. Thus, if genetic differences in the slope of age trends are large enough, it may be possible to increase the uniformity of wood density across the stem by selecting for trees or families with smaller slopes.

Probably more important, however, is the possibility of using genetic differences in age trends of ORD and its components to breed for an earlier transition from juvenile to mature wood formation (Loo et al. 1985). Juvenile wood, formed during the early years of growth, normally has relatively wide annual growth rings, low density, and several other undesirable characteristics (i.e., shorter cell lengths, thinner cell walls, lower wood strength, higher longitudinal shrinkage, etc.; Paul 1957, Yang et al. 1986). Therefore, reducing the proportion of juvenile wood, by selecting for a shorter juvenile wood formation phase, is an attractive option for improving wood quality (Loo et al. 1985).

An approach proposed to estimate the age of transition to mature wood formation in loblolly pine employs the age trend of ORD values (Loo et al. 1985). The age of transition is considered to be the age at which the slope of the trend levels off (Loo et al. 1985, Bendtsen and Senft 1986). This approach, however, is not useful in Douglas-fir where ORD normally continues to gradually increase up to at least age 40 (Megraw, 1985), while the juvenile period is assumed to end around age 15 (Erickson and Harrison 1974, Cown 1976, Hoag 1988). In addition, ORD in young Douglas-fir is strongly affected by ring size (McKimmy and



Campbell 1982, Ferrand 1982), making it difficult to identify and quantify the age trend for ORD. To adjust for the effects of ring size on ORD, it has been suggested to weight ORD by ring area (Olson and Arganbright 1977, Kanowski 1985), to obtain overall relative ring density (RRD) values. The age trend of overall RRD in Douglas-fir has been observed to steadily increase up to around ring 15 from the pith and then level off, suggesting that this trend might be a useful indicator of the age of transition to mature wood in this species (M. Hoag, personal communication).

In this study, age trends in RRD traits are analyzed in 15-year-old trees of 60 open-pollinated families of Douglas-fir. Although trees at this early age would normally be expected to produce only juvenile wood, the age trends may reveal some trees approaching the transition from juvenile to mature wood formation sooner (at younger ages) than others. In addition, because changes in the age trends of overall RRD must be associated with changes in one or more of the individual components, the age trends of the components may be more sensitive to changes occurring early in the transition phase. The objectives of the study were: (1) to determine the extent of genetic variation in age trends of RRD traits and their relationships with overall density of increment cores, and (2) to explore the possibility of selection for a shorter juvenile wood formation phase in coastal Douglas-fir.

## MATERIALS AND METHODS

Measurements

Pith to bark (5-mm diam.) increment core samples were collected at breast height (1.37 m) during the summer of 1988 from 15-year-old trees in the Coyote Creek progeny test plantation, located near Eugene, Oregon. The open-pollinated families included in this study correspond to sets 2 and 4 (30 families each) of the Noti Breeding Unit, in the Umpqua Tree Improvement Cooperative (Silen and Wheat 1979). Parent trees are located in natural stands in the central Coast Range of Oregon, between 150 and 450 m elevation. Each set of families was planted as a separate randomized complete block design experiment with four replications. Families in each block were represented at planting by a four-tree non-contiguous plot, with trees assigned to planting spots at random. At the time increment core samples were taken, survival for these two sets was about 85%.

Information on wood density and its components for each core sample was obtained by using a direct scanning X-ray densitometry system (Hoag and McKimmy 1988). After discarding the first and last annual rings from all the samples (because they were usually incomplete), widths and average density values for earlywood, latewood and the overall ring were obtained for each of the remaining rings. The transition from earlywood to latewood was defined as the point where density was midway between the minimum and maximum densities of the ring (Green and Worrall 1964, Nicholls and Wright 1976). The number of growth rings measured in each core sample varied because trees reached

the breast-height sampling position at different ages. Annual rings were numbered in descending order from the farthest (age 15) to the closest to the pith, so they represented the age of the tree at the time each ring was formed. Only core samples having the first annual ring at age 7 or age 8 (n=737, 91% of total trees sampled) were included in the analyses.

For each ring in an increment core sample, RRD values for overall, earlywood, and latewood densities were calculated using the following equation:

$$\text{RRD} = D * (A/\Sigma A), \quad (\text{IV.1})$$

where D = Average density of the portion of the ring represented by particular variable of interest (i.e., overall, earlywood, or latewood density),

A = Cross-sectional area of the ring corresponding to the variable of interest, and

$\Sigma A$  = Total cross-sectional area of the increment core occupied by the variable of interest.

Latewood proportion (LP) is defined as the proportion of the cross sectional area of the ring occupied by latewood. Since LP is already expressed as a proportion, no adjustment for ring area was needed for this trait.

### Statistical analysis

Inspection of age-trend plots for individual trees showed that age trends differed among traits (Figure IV.1). Overall RRD and latewood

RRD appeared to steadily increase across the whole core. LP showed a decreasing but irregular trend in early years, then steadily increased after age 11. The general form of the age trends for these traits was consistent over all trees. The age trend in earlywood RRD, on the other hand, differed among trees. In some trees, earlywood RRD appeared to steadily increase over all rings, whereas in others, earlywood RRD plateaued at age 11 or later.

For each core sample, a linear regression model was fitted to the portion of each age trend that steadily increased with increasing age (i.e., all rings for overall and latewood RRD, the first 5 rings for earlywood RRD, and the last 5 rings for LP). Thus, the slope of these regressions gave a measure of ring-to-ring variation over the portion of the juvenile core where the greatest changes in those traits were taking place. In addition, because latewood proportion normally increases as trees approach the age of transition to mature wood formation (Bendtsen and Senft 1986), the slope of the age trend for LP during the last 5 years might estimate the rate of increase in LP during this transition phase. Coefficients of determination ( $R^2$ ) for the linear regressions were normally high for all traits (in most cases  $R^2 > 0.90$ ).

To examine family differences in the slopes of these age trends, analyses of variance of the slopes for all traits were performed according to a random-effects model (Table IV.1), using the SAS GLM procedure (SAS 1987). Type III sums of squares, which are least squares estimates that take into account the imbalance in number of observations per plot, were used to estimate the mean squares for each source of variation. F-tests were used to determine significance of family

differences in the slope of the age trends.

Because the plateau observed in the age trend for earlywood RRD might be related to an earlier transition from juvenile to mature wood formation, it was of interest to determine whether families differed in the age at which this plateau is reached. The age at which earlywood RRD reached the plateau was identified by fitting a two-segment regression line, using piece-wise regression techniques (Neter et al. 1983). With this method, two regression lines were fitted simultaneously, one to the rapid increase in earlywood RRD that occurred in early rings, and the second to the relatively stable values for this trait that occurred later. Regression models in which the age of intersection of the two regression segments was varied from age 9 to age 15, were fitted to each sample. The point (age) of intersection of the two regression segments in the best fitting model (i.e., the model with the lowest error sum of squares) estimated the age at which the plateau was reached. The regression models, however, could not precisely estimate changes in slope that might have occurred after age 13, because there were not enough data points to fit the regression line after that age, making it impossible to get an unbiased estimate of the mean age at which the plateau in earlywood RRD was reached. Instead, the proportion of trees per plot that reached the plateau in earlywood RRD by age 12 was estimated. Age 12 was chosen because most trees estimated to have a plateau by the two-segment regression, did so by age 12. Presumably, families with higher proportions of individuals reaching this plateau by age 12 would, on average, reach the plateau at earlier ages.

To test for family differences in the proportion of trees per plot

with earlywood RRD plateau by age 12, an analysis of variance of this proportion was done using a similar random-effects model as used for the other traits (Table IV.1), except that the within-plot source of variation was not included. Analysis of residuals showed a slightly non-uniform variance among families in the error term for the proportion of trees with earlywood RRD plateau. Although a Logit transformation (Weisberg 1985) corrected this problem, the results of the analysis of variance were basically the same, so the results using the non-transformed variable (proportion of trees per plot) are presented.

To determine the degree of genetic control of the age trends, family heritability estimates were calculated for those traits that showed significant family differences ( $p \leq 0.05$ ), following Falconer (1981). Variance components were estimated by equating the mean squares in the analyses of variance to their respective expectations from the model in Table IV.1, using the estimates of the  $k_j$  coefficients given by the SAS GLM procedure. Family heritability ( $h_f^2$ ) was estimated as:

$$h_f^2 = \frac{(1/4)\sigma_A^2}{\sigma_{pf}^2} \quad (\text{IV.2})$$

where  $\sigma_A^2$  = Additive genetic variance,  
 $\sigma_{pf}^2$  =  $\text{MSF}/k_3$  = Phenotypic variance of family means,  
 MSF = Expected mean square of families/set, and  
 $k_3$  = Coefficient associated with the family component of variance.

The additive genetic variance ( $\sigma_A^2$ ) was estimated as 3 times the family component of variance ( $\sigma_{f(s)}^2$ ), assuming that open-pollinated families are

related to a greater extent than half-sibs (Campbell 1979). Standard errors for heritability estimates were calculated according to Osborne and Paterson (1952).

The genetic relationships of age trends with overall density of the core sample, and with growth traits [diameter at breast height (DBH), height, and volume] at age 15, were investigated by calculating their respective genetic correlations, and their standard errors, according to Becker (1984). Only those traits that showed significant family differences were included.

## RESULTS AND DISCUSSION

Genetic variation in age trends of ring density and its components

Overall RRD increased, on average, 0.011 g/cm<sup>3</sup> per year across increment core samples (Figure IV.1). Latewood RRD increased over twice as fast (0.026 g/cm<sup>3</sup> per year) over the same period of time. LP, though irregular during the early growth rings, increased on average 3.5% per year in the later growth rings (portion of the core that showed a steady increase). Earlywood RRD increased at about the same rate in the first five years (0.013 g/cm<sup>3</sup>) as overall density did over the entire period. Analyses of variance, however, showed no significant family differences ( $p \leq 0.05$ ) in the slopes of the age trends for any RRD trait, indicating little or no genetic variation for these traits in the sample population. Thus, there appears to be little opportunity for increasing uniformity of wood density in the juvenile section of the tree by selecting for flatter slopes in the age trends.

On average, the proportion of trees per plot with an earlywood RRD plateau was 0.82, but this proportion varied significantly ( $p < 0.01$ ) among families, with a range of 0.30 to 1.00. Even though the plateau in the earlywood RRD trend was estimated to occur as early as ring 6 from the pith, there are reasons to believe that the plateau may be related to the transition from juvenile to mature wood. As indicated earlier, in a previous study of Douglas-fir (M. Hoag, personal communication) overall RRD was found to plateau at around 15 rings from the pith, which coincides with the age normally assumed as the transition from juvenile to mature wood in this species (Erickson and



Harrison 1974, Cown 1976, Senft et al. 1985, Hoag 1988). It seems reasonable to expect genetic variation in the timing of this transition and in the age at which the plateau occurs. In the present study, trees were apparently too young to observe a plateau in overall RRD (i.e., the number of rings from the pith were  $<10$ ), but a plateau in earlywood RRD was observed in many trees. Perhaps earlywood is more sensitive to changes in cell morphology accompanying the transition from juvenile to mature wood formation, and the plateau in overall RRD is not observed until later because latewood RRD and latewood proportion are still increasing at these early ages, more than compensating for the plateau in earlywood RRD.

If these assumptions are correct, then the differences among families in the proportion of trees reaching the plateau in earlywood RRD by age 12, might be used as an early indicator of genetic differences in the age of transition to mature wood formation, which could be important for reducing the age of selection for this trait (i.e., the age of transition). The estimated family heritability for this proportion was 0.30 ( $\pm 0.10$ ), so at least a moderate response to selection would be expected in this characteristic. This estimate of family heritability is similar to that obtained for the age of transition to mature wood in *P. taeda* (Loo et al. 1985).

#### Genetic relationships between the age trends and overall core density and growth traits

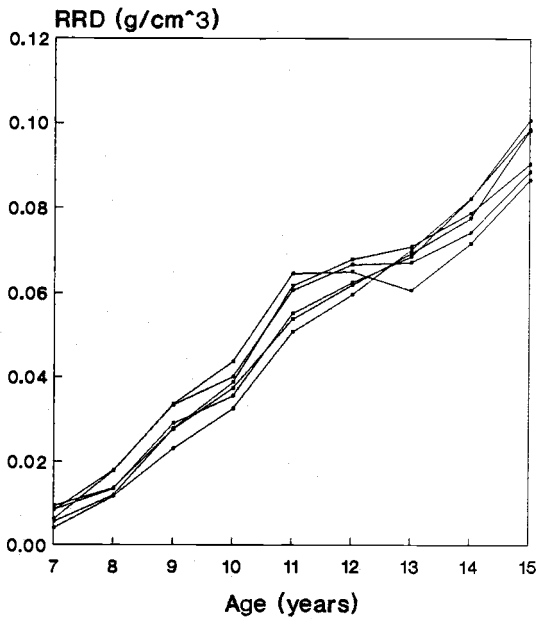
Because family differences in the slopes of the age trends were not significant, genetic correlations involving these traits could not

be estimated. The proportion of trees with an earlywood RRD plateau by age 12 was not genetically correlated with overall core density, nor with growth traits (Table IV.2). These results might be contrasted to those in one study of *P. taeda* (Loo et al. 1985), where the age of transition to mature wood (as estimated from age trends in average ring density) was negatively correlated with both diameter growth ( $r_A = -0.61$ ) and overall core density ( $r_A = -0.68$ ), i.e., an earlier age of transition was associated with both faster growth and higher wood density. However, in another study in *P. taeda*, Bendtsen and Senft (1986) suggested that the age of transition from juvenile to mature wood was not related to growth rate or overall density, but correlation estimates were not given.

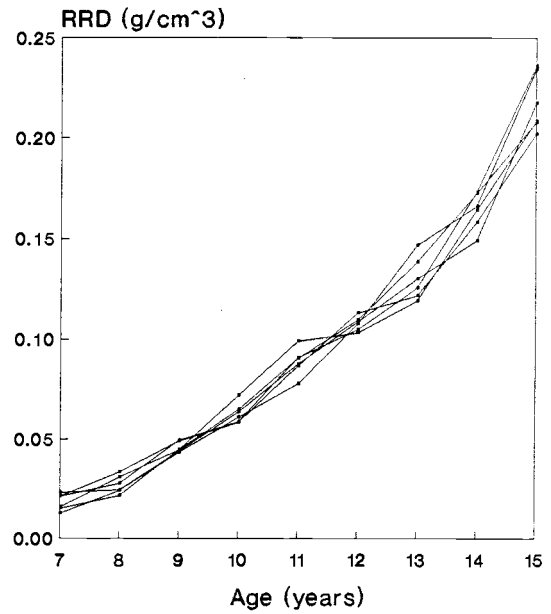
The lack of genetic relationships between the proportion of trees with an earlywood RRD plateau and overall core density and growth rate suggests that selecting for families with a higher proportion of individuals with earlywood RRD plateau by age 12 would result in a shorter juvenile wood formation phase without negatively influencing wood density or growth rate. Before proceeding, though, it will be necessary to confirm that the plateau observed in the earlywood RRD trend is, indeed, strongly related to the age of transition from juvenile to mature wood formation. This could be done by examining the age trends of RRD traits in trees that are already producing mature wood, and determining the genetic relationship between the plateau in earlywood RRD and the plateau in overall RRD. Obviously, this assumes that the plateau in overall RRD is an acceptable indicator of the age of transition to mature wood formation in this species. This assumption

can be tested by comparing the age trend in overall RRD to changes in other characteristics (e.g. latewood proportion, tracheid length, fibril angle, or mechanical properties) normally associated with the transition to mature wood.

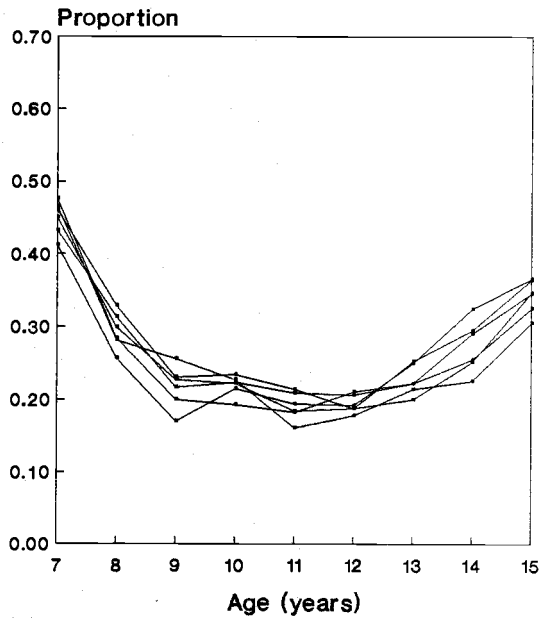
(a): Overall RRD



(b): Latewood RRD



(c): LP



(d): Earlywood RRD

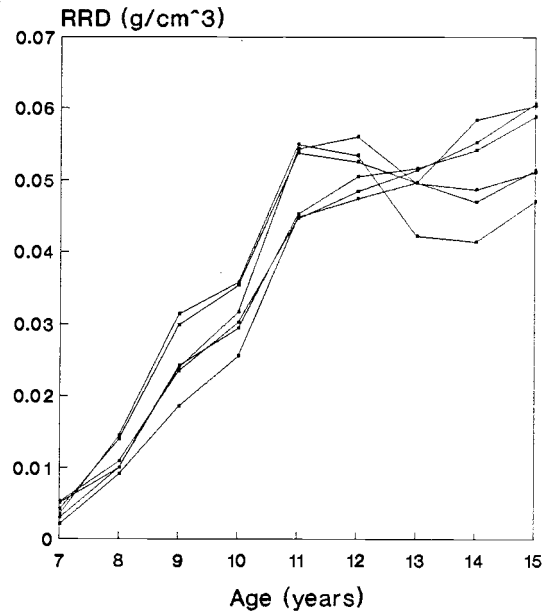


Figure IV.1. Age trends of relative ring density (RRD) traits and latewood proportion (LP) in a representative sample of six open-pollinated families of coastal Douglas-fir. Each point represents the average family value at that age.

Table IV.1. Form of the variance and covariance analyses for age trends of wood density traits.

Source of variation	Degrees of freedom	Expected mean squares <sup>a</sup>
Sets	s-1	$\sigma_w^2 + k_6\sigma_e^2 + k_7\sigma_{f(s)}^2 + k_8\sigma_{b(s)}^2 + k_9\sigma_s^2$
blocks/set	(b-1)s	$\sigma_w^2 + k_4\sigma_e^2 + k_5\sigma_{b(s)}^2$
Families/set	(f-1)s	$\sigma_w^2 + k_2\sigma_e^2 + k_3\sigma_{f(s)}^2$
Block*Fam./set	(f-1)(b-1)s	$\sigma_w^2 + k_1\sigma_e^2$
Within-plot <sup>b</sup>	$\sum_{i=1}^t (n_i - 1)$	$\sigma_w^2$

<sup>a</sup>/ For covariance analyses, cross products are used instead of mean squares.

<sup>b</sup>/ This source of variation was not included in the analysis of variance for the proportion of trees with earlywood RRD plateau.

s = number of sets.

b = number of blocks/set.

f = number of families/set.

$k_j$  = Coefficient associated with the  $j^{\text{th}}$  variance component.

$n_i$  = number of trees in plot i.

t = total number of plots in the experiment.

$\sigma_w^2$  = within-plot variance.

$\sigma_e^2$  = plot-to-plot variance.

$\sigma_{f(s)}^2$  = variance among families in sets.

$\sigma_{b(s)}^2$  = variance among blocks in sets.

$\sigma_s^2$  = variance among sets.

Table IV.2. Estimates of genetic correlations between the proportion of trees with an earlywood RRD (relative ring density) plateau by age 12 and overall core density and growth traits at age 15.<sup>a</sup>

Trait	Overall core density	Growth traits		
		DBH	Height	Bole volume
Proportion of trees with earlywood RRD plateau by age 12	0.09 (0.24)	-0.04 (0.32)	-0.12 (0.30)	-0.11 (0.30)

<sup>a</sup>/ Standard errors of genetic correlation estimates are given in parentheses.

## CHAPTER V

GENETIC RELATIONSHIPS BETWEEN WOOD DENSITY COMPONENTS  
AND GROWTH RHYTHM TRAITS IN YOUNG COASTAL DOUGLAS-FIR

## ABSTRACT

To obtain a better understanding of the genetic control of wood formation in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and to assess the potential impact of selecting for increased wood density on adaptation of trees, genetic relationships between wood density and its components (earlywood density, latewood density, and latewood proportion) and growth rhythm traits were examined in a 15-year-old progeny test (60 open-pollinated families). Wood density traits were estimated by X-ray densitometry of increment core samples. Timing of budburst and diameter growth during the 1987 growing season were available from an earlier study. By comparing the wood density profile of the annual ring formed in 1987 with the diameter growth curve for the same year, several wood formation traits (date of latewood transition, lengths and rates of earlywood and latewood formation) were also estimated for each tree.

Wood formation traits were found to be under weak genetic control ( $h^2 < 0.20$ ), and lengths of the earlywood and latewood formation periods mostly determined by the timing of latewood transition, rather than by timing of initiation and cessation of cambial growth. Overall density of the entire core was negatively correlated with the dates of cambial

growth initiation ( $r_A=-0.41$ ) and latewood transition ( $r_A=-0.62$ ), and positively correlated with the date of cambial growth cessation ( $r_A=0.40$ ). As a result of these relationships, higher wood density was associated with a longer duration of cambial growth ( $r_A=0.67$ ) and a slower rate of wood formation ( $r_A=-0.37$ ). All density components showed similar relationships with cambial phenology and wood formation traits. No significant genetic relationships were observed between wood density traits and date of budburst. Although selection for increased wood density is expected to cause only a slight extension of the cambial growth period, it would also cause an earlier transition to latewood formation, negatively affecting growth rate.



## INTRODUCTION

Physiological studies have shown that wood formation in conifers is regulated by seasonal changes in the physiological activity of the tree crown (Larson 1960, Gordon and Larson 1968, Brown 1970, Nix and Wodzicki 1974). Therefore, strong genetic relationships between wood density and growth rhythm traits (i.e., phenology of shoot and cambium growth) are expected in conifer species (Mergen et al. 1964, Smith 1977, Dodd and Power 1986).

Knowledge of genetic relationships between wood density and growth rhythm traits is important for understanding the physiological mechanisms of wood formation, and the degree to which the phenotypic relationships between these traits are under genetic control. Understanding the genetic relationships between wood density and growth rhythm traits is also important for tree breeding purposes. Shoot phenology traits are normally under very strong genetic control, and they are often more readily measured than wood density (Kennedy 1970). Thus, if a strong genetic correlation exists between these traits, selection for phenological traits might be effective for indirectly improving wood quality (Mergen et al. 1964, Kennedy 1970). On the other hand, undesirable genetic correlations between wood density and growth rhythm could cause serious problems for tree breeders, because growth rhythm traits are important for adaptation (Dietrichson 1961, 1964). If, for example, wood density is negatively correlated with the dates of budburst and cambial growth initiation (i.e., trees with earlier flushing or cambial growth initiation have higher wood density),

selection for increased wood density would result in increased susceptibility to shoot and cambial damage from spring frosts.

Despite the importance of genetic relationships between wood density and growth rhythm traits, very limited information is available on these relationships in any conifer species. In fact, previous studies, which primarily focused on phenotypic correlations between wood density and shoot phenology, give contradictory results. In Norway spruce (*Picea abies* (L.) Karst.), for instance, Mergen et al. (1964) found a positive phenotypic correlation between wood density and date of budburst (i.e., trees with an earlier flushing date had lower wood density), whereas Worrall (1970) found these traits to be unrelated. Similarly, in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), McKimmy (1966) and Kennedy (1970) reported a negative correlation between wood density and date of budburst, while Cown (1976) concluded these traits were uncorrelated.

Because of the difficulty of measuring cambial phenology, relationships between wood density and cambial phenology traits have been studied in only a few cases (Worrall 1970, Cown 1976). From those studies, it appears that the relationships between wood density and cambial phenology are quite complex. Average (overall) wood density results from three interacting components, earlywood density, latewood density, and latewood proportion, and it has been hypothesized that these components are affected by different factors during the process of wood formation (Worrall 1970, Nicholls and Wright 1976). Presumably, cambial division is reactivated by shoot growth in the spring, and earlywood is formed until shoot elongation stops, at which point

latewood formation commences and continues until cambial growth ceases in late summer (Wareing 1958, Wodzicki and Wodzicki 1980, Savidge and Wareing 1984). Since cell diameter and cell wall thickness are affected by the rate of cambial division, it might be expected that earlywood and latewood densities are primarily related to the rate of cambial growth during their respective formation periods. Similarly, latewood proportion might be expected to be mostly determined by the length of the latewood formation period. Knowledge of the genetic interrelationships between wood density components and wood formation traits (i.e., date of latewood transition, lengths and rates of early and latewood formation) may help in understanding the relationships between overall density and cambial phenology.

In 1987, shoot and cambial phenology data were collected from 60 open-pollinated Douglas-fir families growing on a single test site in western Oregon (Li 1990). X-ray densitometry of increment cores collected from the same trees in summer, 1988, provided wood density profiles for the 1987 annual ring, as well as the entire core (Chapter II). In this chapter, growth phenology and wood density traits in these trees are compared, in order to: (1) estimate the extent of genetic control of wood formation traits and their relationships with wood density components; (2) determine genetic relationships between overall core density and individual growth phenology traits; and, (3) examine the potential effects of selection for increased wood density on individual growth phenology traits.

## MATERIALS AND METHODS

Plant materials

Families included in this study are growing in a progeny test at Coyote Creek, near Eugene, Oregon. They correspond to sets 2 and 4 (30 families each) of the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979). Parent trees were phenotypically selected in natural stands located between 150 and 450 m elevation in the central Coast Range of Oregon. Each set of families comprised a separate randomized complete block experiment with four replications. Families in each block were originally represented by a four-tree non-contiguous plot, with trees assigned to planting spots at random. Trees were 15-years-old from seed in 1987, when the measurements were made. At that time, survival of trees in these two sets was about 85%. Most mortality, however, occurred during the first two years after planting, and dead seedlings were replaced with seedlings from the same families. The replacements were not measured in this study.

Measurements and derivation of traits

Details on the methods of shoot and cambium phenology measurements of the 60 families in 1987 are presented by Li (1990); only an outline is given here. With the aid of binoculars, the date of budburst in the terminal shoot of each tree was estimated from observations made every 3 days. The date of budburst was defined as the date when new shoots were visible for the first time outside the bud scales. Li, however, was not

able to determine the date of budset in these trees because needles at the top of the leader made it impossible to see the setting terminal bud from the ground. Thus, date of budburst is the only shoot phenology trait considered in this study.

Diameter growth at breast height (1.37 m) was monitored on a weekly basis with a high precision caliper, by measuring the distance (approximated to the nearest 0.01 mm) between two thumbtacks located on opposite sides of the stem. Trees were measured from the week of March 26 until the week of September 27, when no further diameter change could be detected. Cumulative diameter growth curves were generated for each tree from the weekly diameter measurements. The dates at which 5% and 95% of the diameter growth was completed estimated dates of initiation and cessation of diameter growth, respectively. The length of the cambial growth period was estimated as the difference in the number of days between the dates of cessation and initiation of diameter growth.

To estimate wood density traits, a 5-mm diameter increment core sample, extending from pith to bark, was taken from the same spot where diameter growth was measured one growing season earlier (Chapter II). Intra-ring density information across each core sample was obtained by using a direct scanning X-ray densitometry system (Hoag and McKimby 1988). Ring density and its components (i.e., earlywood density, latewood density, and latewood proportion) for the annual ring formed in the 1987 growing season, as well as average values of these components for the whole core, were calculated from the X-ray density profiles. The point in the ring where density equals the average of the minimum and maximum density values for that ring was used as the criterion to

separate earlywood from latewood (Green and Worrall 1964, Nicholls and Wright 1976).

Wood formation traits were estimated by comparing, for each tree, the cumulative diameter growth curve in 1987 with the densitometric profile for the ring formed in the same year. The approximate date of latewood transition was assumed to occur at the time when the percentage of cumulative diameter growth was identical to the percentage of earlywood in the annual growth ring (Figure V.1). This method assumes that total ring width obtained from the core sample is closely correlated to total diameter growth obtained from the growth curves. A plot of ring width against total diameter growth showed that these traits were linearly related, but the correlation between them was only 0.76. Several factors could have contributed to this imperfect correlation, including asymmetric diameter growth around the stem, differences among trees in the amount of phloem production, and differences in shrinkage of the core samples. Non-uniform diameter growth around the stem is the most likely cause of the correlation being lower than expected. Diameter growth was estimated from measurements that included cambial growth on two sides of the tree, whereas ring width was estimated using only one side. Phloem growth, on the other hand, is normally less than 10% of the total annual xylem growth, and it is not expected to differ much among trees (Bannan 1957, Grillos and Smith 1959). Similarly, radial shrinkage of the core samples at 10% moisture content has been estimated to be only around 3% (Erickson 1955, Kennedy 1961). Because of the imperfect relationship between ring width and diameter growth, the error in estimating the date of latewood

transition on an individual tree basis may be large. Nevertheless, residuals of the regression of ring width on total diameter growth were randomly distributed among families, so the estimates of family means for the date of latewood transition are likely to be unbiased.

The length of the earlywood formation period in 1987 was estimated as the number of days from initiation of diameter growth to the date of latewood transition, and the length of the latewood formation period was estimated as the number of days from the date of latewood transition to cessation of diameter growth. In addition, the rates of earlywood and latewood formation in the 1987 annual ring were calculated by dividing earlywood width and latewood width by the lengths of their respective formation periods.

#### Data analysis

All variance and covariance analyses were performed on a plot-mean basis using a random-effects model (Table V.1). Missing values for three plots (out of a total of 240) were estimated according to the method described by Steel and Torrie (1980). Within-plot variances and covariances, as well as the harmonic mean for number of trees per plot were estimated separately by pooling individual-plot values. Components of variance and covariance were estimated from the appropriate mean squares and cross products (Namkoong 1979).

To determine the genetic control of wood formation traits, individual-tree heritabilities for those traits were estimated as in Falconer (1981), assuming a coefficient of genetic relationship of  $1/3$  among progeny within open-pollinated families (Campbell 1979). Standard

errors for heritability estimates were calculated following Osborne and Paterson (1952). The genetic interrelationships of wood density and its components with growth phenology and wood formation traits were analyzed by estimating their respective genetic correlations (and their standard errors) as in Becker (1984). Expected changes in growth rhythm traits resulting from selection on overall wood density were explored by estimating and comparing the correlated responses of individual growth rhythm traits (Falconer 1981).



## RESULTS AND DISCUSSION

Genetic control of wood formation traits

Analysis of variance showed significant differences ( $p \leq 0.05$ ) among families in the date of latewood transition and the lengths and rates of earlywood and latewood formation (Table V.2). These results are important; despite the error in estimating the date of latewood transition, it still was possible to detect family differences in this trait and all the traits derived from it. All the wood formation traits, however, had low coefficients of genetic variation. In addition, they had low estimates of individual-tree heritability ( $h^2 < 0.20$ ), indicating they are under weak genetic control. The levels of genetic variation and magnitudes of genetic control observed for these traits are similar to those presented by Li (1990) for cambial phenology traits (initiation, cessation and duration of cambial growth) in the same families.

The average date of latewood transition during the 1987 growing season was June 27 (i.e., 177 days after January 1, Table V.2); this date is about one month earlier than the earliest average date of transition (measured in 1971) estimated by Emmingham (1977) for several provenances of young Douglas-fir growing in different sites in Oregon. Differences between these two studies in the age of latewood transition may be due to differences in seed source, year-to-year variation, or tree age. Emmingham (1977) reported differences of 10 to 20 days in the average date of latewood transition among provenances growing on the same plantation site, with seed sources from drier areas having an

earlier date of latewood transition. As to differences between years, Kennedy (1961) reported a large variation in date of latewood initiation from one growing season to the next, even in the same population of Douglas-fir. In addition, Cregg et al. (1988) found that latewood initiation in Pinus taeda occurred 3-4 weeks earlier in a growing season with a relatively dry summer, than in a growing season with average precipitation. According to the precipitation records for the area where the progeny test in the current study is located, rainfall in 1987 was below average. Total rainfall during the first 6 months of 1987 was 83% of the average precipitation in that period for the last 15 years, and total rainfall in the period April-June was only 56% of the average in that period for the last 15 years. The possibility that low rainfall caused the early date of latewood transition is supported by the fact that diameter growth in these families ceased about one month earlier than in the populations studied by Emmingham (1977). Differences in age might also contribute to differences in the date of latewood transition. Trees in the populations studied by Emmingham (1977) were 2-4 years younger than trees in this study and, since the proportion of latewood normally increases with age, it might be expected that our older trees had earlier dates of latewood transition.

Of the four months of cambial growth in 1987 (Li 1990), approximately 2½ months (71 days), on average, corresponded to earlywood formation, and 1½ months (48 days) to latewood formation (Table V.2). Families varied, however, 17 days in the mean date of latewood initiation, 16 days in the length of the earlywood formation period, and 20 days in the length of the latewood formation period. These family

differences are about twice as large as the range in family means reported by Li (1990) for the total length of cambial growth (9 days). Cregg et al. (1988) suggested that a large amount of variation in the timing of latewood initiation, and thus in the lengths of earlywood and latewood formation periods, should normally be expected in young trees that are in the transition phase from juvenile to mature wood formation. Although the transition from juvenile to mature wood in Douglas-fir occurs at around 15 rings from the pith (Cown 1976, Senft et al. 1985), and in this study trees had only 8-9 rings at breast height, there appears to be some evidence that changes related to this transition are occurring in these trees (Chapter IV).

The estimated average rate of earlywood formation (0.059 mm/day) was greater (by about 40%) than the average rate of latewood formation (0.042 mm/day) (Table V.2). In contrast, Emmingham (1977) found a nearly constant rate of cambial growth over the entire growing season.

#### Genetic interrelationships between wood density components, wood formation traits, and growth rhythm

Estimated genetic correlations of wood density and its components with wood formation and growth rhythm traits were similar, regardless of whether wood density traits were based on the 1987 annual ring alone, or on the entire core sample. This is not surprising, however, since it was shown earlier (Chapter III) that genetic correlations between wood density traits at different ages were strong; in this case, genetic correlations between wood density traits in the 1987 annual ring and their respective values for the entire core varied from 0.73 to 0.94.

Because one goal of this study was to examine the potential impact of selection for increased wood density (based on information from the entire core) on individual growth phenology traits, only the genetic correlations of overall core density and its components with wood formation and growth rhythm traits are discussed.

Estimated genetic correlations of overall core density and all its components with dates of diameter growth initiation and latewood transition were negative (Table V.3). This indicates that families with higher wood density tend to have earlier dates of diameter growth initiation and latewood transition. Wood density traits had stronger genetic correlations with the date of latewood transition than with the date of diameter growth initiation, suggesting that despite the positive genetic association ( $r_A=0.52 \pm 0.28$ ) between initiation of cambial growth and latewood transition, the timing of latewood transition is more important in determining wood density. This seems logical, because an earlier date of latewood transition would increase the length of latewood formation at the expense of reducing the length of earlywood formation, which would result in a higher proportion of latewood in the ring. This is especially so in these data, where Li (1990) found little family variation for date of cambial cessation or for total length of cambial growth. As might be expected, the strongest genetic correlations involving the date of latewood transition were found with latewood density ( $r_A=-0.75$ ) and latewood proportion ( $r_A=-0.66$ ).

Although overall core density and its components were positively correlated with date of cambial growth cessation, the standard errors of these estimates were large. Nevertheless, the combined tendency for

wood density to increase with both earlier diameter growth initiation and later cessation, resulted in moderately strong positive genetic correlations between wood density traits and the length of their respective formation periods (e.g., genetic correlation between overall core density and length of the growing season was 0.67). The only exception was the estimated correlation between earlywood density and length of the earlywood formation period, which was weakly negative. The positive genetic correlation between overall core density and length of the growing season, therefore, was due to the positive correlations of latewood density and latewood proportion with length of the latewood formation period. Similar relationships were reported by Kennedy (1961), and Nicholls and Wright (1976). Moreover, as in those earlier studies, the length of the latewood formation period was negatively correlated with the length of the earlywood formation period ( $r_A = -0.77 \pm 0.23$ ), indicating again that the longer period of latewood formation was primarily due to an earlier latewood transition date, rather than to a later cessation of cambial growth.

Estimated genetic correlations of overall core density and its components with their respective rates of formation were all weak (and of similar magnitude to their standard errors), but negative. Negative correlations between these traits were not unexpected, because overall core density was shown in Chapter II to have a negative genetic correlation with bole diameter at age 15. The stronger genetic correlations found between wood density traits and the length of their respective formation periods, as compared to their rates of formation, suggests that the length of the formation periods is more important in

affecting wood density and its components. This interpretation, however, should be made with caution, because of the interrelationships between length of the formation periods and rates of formation ( i.e., rates of formation were estimated using length of the formation period in the denominator, so these traits are not independent). Besides, the magnitude of the standard errors associated with the correlation estimates are large enough to indicate that differences between the magnitudes of these estimates could be due entirely to sampling error.

The negative relationship observed between wood density and growth rate may be primarily due to differences among families in the time of latewood initiation, since a moderately positive genetic correlation ( $r_A=0.67 \pm 0.21$ ) was found between the overall rate of wood formation and date of earlywood-latewood transition, indicating slow-growing trees tended to switch earlier to latewood production. This earlier latewood initiation may be associated with greater internal water stress developed early in the growing season in small trees, due to their inability to compete against bigger individuals. Brix (1972) and Cregg et al. (1988) have suggested that an increase in water stress can promote the initiation of latewood production.

Unlike cambial growth phenology, budburst of the terminal shoot does not appear to be correlated with any of the wood density traits (Table V.4). Lack of genetic correlations between date of budburst and wood density traits in these families is not surprising, because Li (1990) found weak genetic correlations between date of budburst and cambial phenology in the same materials. In earlier studies based on phenotypic correlations, moderately negative correlations between wood

density and date of budburst were found in Douglas-fir (Kennedy 1970, McKimmy 1966). In our study, however, phenotypic correlations between budburst and wood density traits were as weak as the genetic correlations mentioned above. Discrepancies between our study and previous studies may be partially due to the fact that earlier studies either compared populations from a broader geographic range, having large differences in both shoot and cambium phenology (McKimmy 1966), or included only individuals with extreme dates of budburst (Kennedy 1970). Correlations between traits may also differ among populations. In a recent study, Bastien et al. (1985) found that estimated genetic correlations between date of budburst and wood density varied from -0.7 to 0.4 in different populations of Douglas-fir.

#### Implications of selection for wood density on growth rhythm traits

The lack of genetic correlation between wood density and date of budburst indicates that selection for wood density is unlikely to have much of an influence on budburst phenology, and that budburst phenology would not be useful as an indirect measure of wood density. In addition, despite the moderate genetic correlations observed between overall density and cambial phenology traits in this study, only weak correlated responses in cambial phenology are expected from selection to increase wood density. This is primarily due to the low heritability and limited amount of variation observed in cambial phenology traits.

Based on the data presented in this study, mating of the top 20% of parents selected for greater overall density would result in progeny with an average cambial growth period 2 days longer than in progeny

resulting from crosses among all parents prior to selection. Both an earlier initiation and a later cessation would contribute to the extended period of cambial growth. The extent to which this small increase in the length of the cambial growth period may influence adaptability, however, is unclear. Dietrichson (1961 and 1964) found an increased cambial frost damage and snowbreak frequency in southern provenances of Pinus sylvestris growing in Norway associated with an extended cambial growth period, presumably because of an incomplete lignification of the outer latewood zone. In those provenances, however, the cambial growth period was over two weeks longer than the average growth period for local sources. In addition, Dietrichson's study was conducted in a harsher climate than normally experienced in the Oregon Coast Range.

Selecting for increased overall wood density would accelerate the transition from earlywood to latewood formation. Using the same selection intensity indicated above, date of latewood transition in the progeny of the selected parents would occur 2 days earlier than in the population prior to selection. This would increase the length of the latewood formation period at the expense of the earlywood formation period, affecting negatively the rate of diameter growth.

Given the time and cost of measuring cambial phenology traits, it is not likely that these traits will be included in tree improvement programs for Douglas-fir in the Pacific Northwest. Nevertheless, genetic correlations between wood density and cambial phenology do not appear to be very strong, so even if the intensity of selection for increased wood density were relatively high, the impact on cambial



phenology is not expected to be great. The intensity of selection applied for increasing wood density, however, is not likely to be large, otherwise gains in volume growth would have to be sacrificed (Chapter II). In addition, selection for increased volume growth is not expected to have much effect on cambial phenology, because genetic correlations between volume growth and cambial phenology traits also appear to be weak in this species (Li 1990).

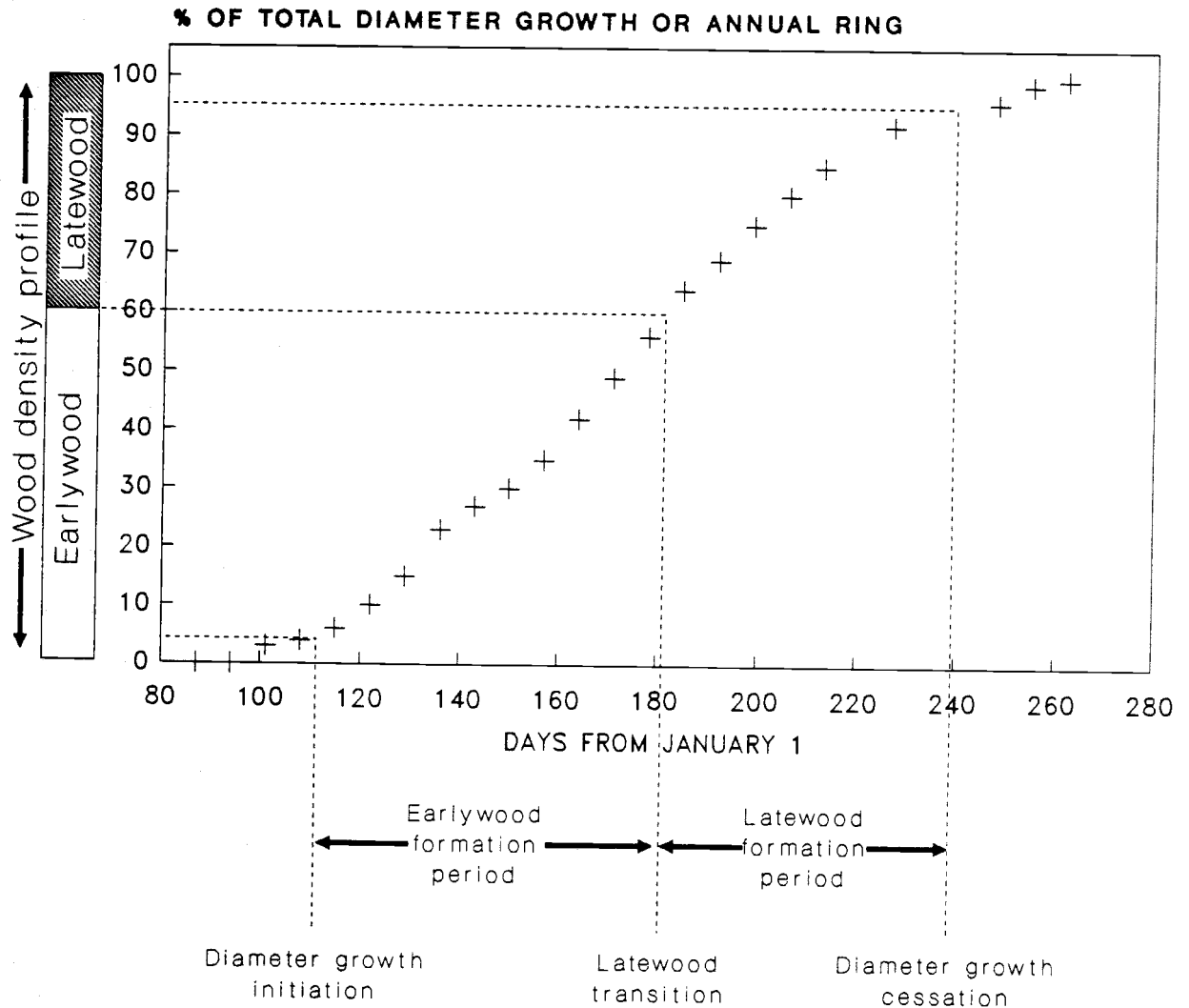


Figure V.1. Comparison of a diameter growth curve and wood density profile for an individual tree in the 1987 growing season, illustrating the method of estimating the date of earlywood-latewood transition and duration of the earlywood and latewood formation periods.

Table V.1. Form of the variance and covariance analyses for wood density, growth phenology, and wood formation traits.

Source of variation	Degrees of freedom	Expected mean squares <sup>a</sup>
Sets	s-1	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2 + f\sigma_{b(s)}^2 + bf\sigma_s^2$
blocks/set	(b-1)s	$\sigma_w^2/k + \sigma_e^2 + f\sigma_{b(s)}^2$
Families/set	(f-1)s	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2$
Block*Fam./set (plot error)	(f-1)(b-1)s	$\sigma_w^2/k + \sigma_e^2$
-----		
Within-plot	$\sum_{i=1}^t (n_i - 1)$	$\sigma_w^2$

<sup>a</sup>/ For covariance analyses, cross products are used instead of mean squares.

s = number of sets.

b = number of blocks/set.

f = number of families/set.

k = harmonic mean of number of trees per plot for all sets.

$n_i$  = number of trees in plot i.

t = total number of plots in the experiment.

$\sigma_w^2$  = within-plot variance.

$\sigma_e^2$  = plot-to-plot variance.

$\sigma_{f(s)}^2$  = variance among families in sets.

$\sigma_{b(s)}^2$  = variance among blocks in sets.

$\sigma_s^2$  = variance among sets.

Table V.2. Estimates of population means ( $\bar{X}$ ), phenotypic (P) and genetic (A) coefficients of variation, and individual-tree heritabilities ( $h_i^2$ ) for wood formation traits in the 1987 annual ring.

Trait	$\bar{X}^a$	p-value <sup>b</sup>	Coefficients of variation (%)		$h_i^2 \pm \text{s.e.}$
			P	A	
Date of latewood transition <sup>c</sup>	177 days (170-187)	(<0.01)	5.67	1.81	0.10 $\pm$ 0.05
Length of the earlywood formation period	71 days (65-81)	(0.05)	13.61	3.83	0.08 $\pm$ 0.06
Length of the latewood formation period	48 days (38-58)	(<0.01)	21.28	9.17	0.19 $\pm$ 0.06
Earlywood formation rate	0.059 mm/day (0.049-0.068)	(0.02)	22.03	7.57	0.12 $\pm$ 0.07
Latewood formation rate	0.042 mm/day (0.033-0.049)	(0.01)	22.65	8.27	0.13 $\pm$ 0.07

<sup>a</sup>/ Range over 60 family means shown in parentheses.

<sup>b</sup>/ p-value for testing differences among family means.

<sup>c</sup>/ Number of days after January 1<sup>st</sup>.

Table V.3. Estimates of genetic correlations between overall wood density traits at age 15 and cambial (diameter) growth phenology and wood formation traits in the 1987 growing season.<sup>a</sup>

Wood density trait	<u>Date of diameter growth</u>		Date of earlywood/latewood transition	Length of formation period <sup>b</sup>	Formation rate <sup>c</sup>
	initiation	cessation			
Earlywood density	-0.24 (0.22)	0.51 (0.31)	-0.43 (0.24)	-0.32 (0.28)	-0.22 (0.27)
Latewood density	-0.48 (0.22)	0.15 (0.35)	-0.75 (0.22)	0.63 (0.18)	-0.37 (0.28)
Latewood proportion	-0.46 (0.26)	0.28 (0.35)	-0.66 (0.25)	0.65 (0.20)	-0.42 (0.28)
Overall core density	-0.41 (0.20)	0.40 (0.30)	-0.62 (0.20)	0.67 (0.28)	-0.37 (0.23)

<sup>a</sup>/ Standard errors of genetic correlation estimates are given in parentheses.

<sup>b</sup>/ Refers to the length (days) of the formation period for the corresponding wood density trait. In the case of latewood proportion (LP), the correlation is between LP and the length of the latewood formation period.

<sup>c</sup>/ Refers to the formation rate (mm/day) for the corresponding wood density trait. In the case of LP, the correlation is between LP and rate of latewood formation.

Table V.4. Estimates of genetic correlations between overall wood density traits at age 15 and date of budburst in the terminal shoot in the 1987 growing season.<sup>a</sup>

	Earlywood density	Latewood density	Latewood proportion	Overall density
Budburst (terminal)	-0.08 (0.17)	0.03 (0.18)	-0.20 (0.19)	-0.10 (0.17)

<sup>a</sup>/ Standard errors of genetic correlation estimates are given in parentheses.

## CHAPTER VI

## GENERAL CONCLUSIONS

This study examined the genetic control of wood density and its components, the extent to which information on individual components improve the efficiency of selection for overall density, and the genetic relationships between wood density components and annual growth rhythm traits in young coastal Douglas-fir. Wood density components, on a ring-by-ring basis, were obtained by X-ray densitometry of increment core samples taken from 15-year-old trees of 60 open-pollinated families. In addition to providing information on wood density traits averaged over the entire core, X-ray densitometry made it possible to examine genetic parameters of wood density and its components at younger core ages, and to follow age trends in each of the wood density traits at the individual ring level.

Wood density had moderate amounts of genetic variation and was under strong genetic control, confirming previous reports in Douglas-fir. The study also confirmed the presence of a moderately negative genetic correlation between wood density and volume growth, indicating that selection to improve one trait alone would produce a negative correlated response in the other trait. The individual density components were strongly correlated with overall density, but were highly interrelated among themselves and were under less genetic control than overall density. Thus, information on the density components does not appear useful for improving the efficiency of selection for wood

density or for reducing negative impacts on growth. For the purposes of improving overall wood density, less expensive methods of estimating density from increment cores would be adequate.

The negative genetic relationship between wood density and bole volume has important implications for tree improvement programs of Douglas-fir in the Northwest, where bole volume growth is currently the main criterion for selection. In order to avoid reductions in wood density, it is necessary to include this trait in selection programs. Although it will not be possible to achieve maximal gains in bole volume without negatively affecting wood density, substantial gains in bole volume can be achieved without loss in wood density or even while wood density is slightly increased, if appropriate selection indices are used. Comparison of selection criteria in this study illustrated some of the possibilities in terms of simultaneous selection for wood density and bole volume. Further research, however, is required to determine the relative importance of these two traits on the final value of different wood products. Incorporating economic weights for each trait into selection indices would lead to index coefficients appropriate to maximizing economic gains for a particular situation. The strength of the genetic correlation between these two traits may vary among populations, especially when extreme environments are considered, so indices would need to be developed separately for each breeding population. Further research is necessary to examine the stability of genetic parameters for these traits in different test environments.

The genetic control of overall density and its components increased with increasing core age. The observed increase in



heritability, however, was primarily due to a reduction in the error of estimating average density values as the number of rings in the sample increased, rather than to an increase in additive genetic variance. Thus, it is uncertain whether heritability will continue increasing at older ages. Wood density and its components at age 15 showed strong genetic correlations with their respective traits at all younger ages evaluated in this study (i.e., ages 7-14). Due to the strong age-age genetic correlations, early selection for overall density in juvenile Douglas-fir appears to be very efficient; selecting at age 10, for example, would result in nearly the same gains in wood density at age 15, as would selections made 5 years later.

Knowledge that wood density can be efficiently evaluated at early ages could be very useful for roguing seed orchards or culling breeding populations prior to a controlled mating program. This study, however, was only focused on juvenile wood density. Although previous studies have shown that density of juvenile wood is genetically correlated with overall density at mature ages, further research is required to confirm the strength of these juvenile-mature relationships, and to examine the degree of genetic control for wood density in mature trees. This would make it possible to determine whether early evaluations of wood density (as those made in this study) can be used as a reliable estimate of mature wood density.

Due to the limited number of annual rings present in the sample, the analysis of age trends of relative ring density (RRD) traits did not provide a conclusive answer with respect to the possibility of selection for a shorter juvenile wood formation phase. Although RRD traits

followed different age trends, the study failed to detect significant family differences in the slope of these age trends. In addition, even though the earlywood RRD trend was observed to plateau at around age 12 in some trees, and there were significant family differences in this characteristic, the practical implications of those differences are uncertain. There are reasons to hypothesize that the plateau in earlywood RRD might be an early indicator of the age of transition from juvenile to mature wood formation in these trees, but further research using older trees is required to confirm or reject this hypothesis. In order to test this hypothesis it will be necessary not only to determine the genetic correlation between the ages at which the plateaus in earlywood and overall RRD are reached, but also to confirm that the plateau in overall RRD is a reliable indicator of the juvenile-mature transition age. If the hypothesis is correct, results from the present study would be important for improving wood quality, because it might be possible to reduce the amount of juvenile wood in trees by selecting at age 15 families having greater proportions of individuals with the earlywood RRD plateau.

Analysis of the genetic interrelationships between wood density components and growth rhythm traits provided information about the process of wood formation in Douglas-fir and the possible implications of selection for increased wood density on adaptation of trees. The negative genetic relationship between wood density and growth rate observed in this population seems to be associated primarily with differences among families in the date of latewood transition. Families with higher wood density normally had an earlier date of latewood

transition, increasing the length of latewood formation at the expense of the length of earlywood formation. Wood density was also positively correlated with the duration of the cambial growth period, due both to an earlier initiation and a later cessation of cambial growth. Unlike cambial phenology traits, date of budburst was not correlated with wood density traits.

Despite the unfavorable genetic relationships between wood density and cambial phenology traits, the risk of extending the annual growth cycle by selecting for increased wood density seems to be low, because of the limited variation and weak genetic control observed in cambial phenology. In this study, however, cambial phenology traits were measured only during one growing season and it seems that rainfall during that particular year was below average. Thus, the genetic parameters estimated for cambial phenology and wood formation traits may have been affected by this 'unusual' growing season. It is necessary to follow-up this study by examining other populations and growing seasons, in order to determine the stability of cambial phenology and wood formation traits.

## LITERATURE CITED

- Adams, W.T. and D.G. Joyce. 1990. Comparison of selection methods for improving volume growth in young coastal Douglas-fir. *Silvae Genet.* (In Press).
- Aubert, M. 1984. Relations entre l'hétérogénéité d'épaisseur des placages de cinq essences résineuses (*Pinus sylvestris*, *P. strobus*, *Pseudotsuga menziesii*, *Pinus pinaster*, *Picea excelsa*) déroulé en conditions pré-industrielles et les composantes densitométriques de leur bois. D.E.A. Sciences du Bois, I.N.P.L., University de Nancy I. 67 p.
- Baker, R.J. 1986. Selection indices in plant breeding. CRC Press, Boca Raton, FL. 218 p.
- Bannan, M.W. 1957. The structure and growth of the cambium. *Tappi* 40: 220-225.
- Bastien, J.Ch., B. Roman-Amat, and G. Vonnet. 1985. Natural variability of some wood quality traits of coastal Douglas-fir in a French progeny test: implications on breeding strategy. In: W. Ruetz and J. Nather (eds.) Proc. IUFRO working party on breeding strategies for Douglas-fir as an introduced species. June 1985, Vienna, Austria. pp. 169-186.
- Becker, W.A. 1984. Manual of quantitative genetics. 4th edition. Academic Enterprises, Pullman, WA. 186 p.
- Bendtsen, B.A. 1978. Properties of wood from improved and intensively managed trees. *For. Prod. Jour.* 28: 61-72.
- Bendtsen, B.A. and J. Senft. 1986. Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. *Wood Fiber Sci.* 18: 23-38.
- Binet, F.E. 1965. On the construction of an index for indirect selection. *Biometrics* 21: 291-299.
- Biot, Y., G. Nepeu, J.R. Perrin, F. Mothe, P. Triboulot, J.C. Ferrand, J.C. Bastien, G. Vonnet, B. Thibaut, and L. Mathon. 1983. Caractéristiques physiques du bois de Douglas et d'Épicéa: hérédité et effets du milieu. Liaison avec la qualité des placages obtenus en déroulage. Compte-rendu final. Action de Recherches D.G.R.S.T. I.N.R.A. No. 81-Q-1157. 33 p.
- Brix, H. 1972. Nitrogen fertilization and water effects on photosynthesis and earlywood-latewood production in Douglas-fir. *Can. J. For. Res.* 2: 467-478.

- Brown, C.L. 1970. Physiology of wood formation in conifers. *Wood Sci.* 3: 8-22.
- Burdon, R.D. 1989. Early selection in tree breeding: principles for applying index selection and inferring input parameters. *Can. J. For. Res.* 19: 499-504.
- Burdon, R.D. and G. Namkoong. 1983. Short note: multiple populations and sublines. *Silvae Genet.* 32: 221-222.
- Campbell, R.K. 1979. Genecology of Douglas-fir in a watershed in the Oregon cascades. *Ecology* 60: 1036-1050.
- Chang, C.I. and R.W. Kennedy. 1967. Influence of specific gravity and growth rate on dry wood production in plantation-grown white spruce. *For. Chron.* 43: 165-173.
- Cotterill, P.P. and C.A. Dean. 1988. Changes in the genetic control of radiata pine to 16 years and efficiencies of early selection. *Silvae Genet.* 37: 138-146.
- Cotterill, P.P. and N. Jackson. 1981. Short note: Index selection with restrictions in tree breeding. *Silvae Genet.* 30: 106-108.
- Cotterill, P.P. and N. Jackson. 1985. On index selection I. Methods of determining economic weight. *Silvae Genet.* 34: 56-63.
- Cown, D.J. 1976. Densitometric studies on the wood of young coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Ph.D. Thesis, University of British Columbia. Vancouver, B.C. 241 p.
- Cown, D.J. and M.L. Parker. 1978. Comparison of annual ring density profiles in hardwoods and softwoods by X-ray densitometry. *Can. J. For. Res.* 8: 442-449.
- Cown, D.J. and M.L. Parker. 1979. Densitometric analysis of wood from five Douglas-fir provenances. *Silvae Genet.* 28: 48-53.
- Cregg, B.M., P.M. Dougherty, and T.C. Hennessey. 1988. Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. *Can. J. For. Res.* 18: 851-858.
- Curtis, R.O., G.W. Clendenen, D.L. Reukema, and D.J. DeMars. 1982. Yield tables for managed stands of coast Douglas-fir. USDA For. Serv. Pacific Northwest For. and Range Exp. Sta., Portland OR. Gen. Tech. Rep. PNW-135. 182 p.
- Dean, C.A., P.P. Cotterill, and J.N. Cameron. 1983. Genetic parameters and gain expected from multiple trait selection of radiata pine in Eastern Victoria. *Aust. For. Res.* 13: 271-278.

- Dean, C.A., P.P. Cotterill, and R.L. Eisemann. 1986. Genetic parameters and gains expected from selection in Pinus caribaea var. hondurensis in Northern Queensland, Australia. *Silvae Genet.* 35: 229-236.
- Dietrichson, J. 1961. Breeding for frost resistance. *Silvae Genet.* 10: 172-179.
- Dietrichson, J. 1964. The selection problem and growth rhythm. *Silvae Genet.* 13: 178-184.
- Dodd, R.S. and A.B. Power. 1986. Variation in wood structure of white fir along an elevational transect. *Can. J. For. Res.* 16: 303-310.
- Emmingham, W.H. 1977. Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. *Can. J. For. Res.* 7: 154-164.
- Erickson, H.D. 1955. Tangential shrinkage of serial sections within annual rings of Douglas-fir and Western red cedar. *For. Prod. J.* 5: 241-250.
- Erickson H.D. and A.Th. Harrison. 1974. Douglas-fir wood quality studies Part I: Effects of age and stimulated growth on wood density and anatomy. *Wood Sci. Tech.* 8: 207-226.
- Falconer, D.S. 1981. Introduction to quantitative genetics. Second Edition. Longham Inc. New York. 340 p.
- Ferrand, J.C. 1982. Réflexion sur la densité du bois. II: Calcul de la densité et de son hétérogénéité. *Holzforschung* 36: 153-157.
- Foster, G.S. 1986. Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *For. Sci.* 32: 944-959.
- Fries, A. 1986. Volume growth and wood density of plus tree progenies of Pinus contorta in two Swedish field trails. *Scand. J. For. Res.* 1: 403-419.
- Gill, J.G.S. 1987. Juvenile-mature correlations and trends in genetic variances in Sitka spruce in Britain. *Silvae Genet.* 36: 189-194.
- Gjedrem, T. 1967. Selection indexes compared with single trait selection I. The efficiency of including correlated traits. *Acta Agric. Scand.* 17: 263-268.
- Goddard, R.E. and D.E. Cole. 1966. Variation in wood production of six-year-old progenies of selected slash pines. *Tappi* 49: 359-362.

- Gonzalez, J.S. and J. Richards. 1988. Early selection for wood density in young coastal Douglas-fir trees. *Can. J. For. Res.* 18: 1182-1185.
- Gordon, J.C. and P.R. Larson. 1968. Seasonal course of photosynthesis, respiration, and distribution of  $^{14}\text{C}$  in young *Pinus resinosa* trees as related to wood formation. *Plant Physiol.* 43: 1617-1624.
- Green, H.V. and J. Worrall. 1964. Wood quality studies I. A scanning microphotometer for automatically measuring and recording certain wood characteristics. *Tappi* 47: 419-427.
- Grillos, S.J. and F.H. Smith. 1959. The secondary phloem of Douglas-fir. *For. Sci.* 5: 377-388.
- Harris, J.M. and D.V. Birt. 1972. Use of beta rays for early assessment of wood density development in provenance trials. *Silvae Genet.* 21: 21-25.
- Hoag, M.L. 1988. Measurement of within-tree density variations in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) using direct scanning X-ray techniques. M.Sc. Thesis. Oregon State University. Corvallis, OR. 96 p.
- Hoag, M. and M.D. McKimmy. 1988. Direct scanning X-ray densitometry of thin wood sections. *For. Prod. Jour.* 38: 23-26.
- Jozsa, L.A., and H. Brix. 1989. The effects of fertilization and thinning on wood quality of a 24-year-old Douglas-fir stand. *Can. J. For. Res.* 19: 1137-1145.
- Kanowski, P. 1985. Densitometric analysis of a large number of wood samples. *J. Inst. Wood Sci.* 10: 145-151.
- Keller, R. and J.R. Perrin. 1980. Relations entre les résultats de l'analyse densitométrique du bois de quelques résineux et la qualité des placages qu'il sont susceptibles de produire. Station de Recherches sur la Qualité du Bois, C.N.R.F., doc. No. 1980/4. 28 p.
- Keller, R. and M. Thoby. 1977. Liaisons entre l'état juvénile et l'état adulte pour quelques caractères technologiques et auxométriques chez le Douglas (*Pseudotsuga menziesii*). *Ann. Sci. For.* 34: 175-203.
- Kellogg, R.M. 1982. Coming to grips with wood quality. *Forestry Chronicle* 58: 254-257.
- Kempthorne, O. 1957. An introduction to genetic statistics. John Wiley & Sons. New York. 545 p.

- Kempthorne, O. and A.W. Nordskog. 1959. Restricted selection indices. *Biometrics* 15: 10-19.
- Kennedy, R.W. 1961. Variation and periodicity of summerwood in some second growth Douglas-fir. *Tappi* 44: 161-166.
- Kennedy, R.W. 1970. Specific gravity of early- and late-flushing Douglas-fir trees. *Tappi* 53: 1479-1481.
- King, J.N. 1986. Selection of traits for growth, form, and wood quality in a population of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), from British Columbia. Ph.D. Thesis, University of Alberta. Edmonton, Alberta. 165 p.
- King, J.N., F.C. Yeh, J.Ch. Heaman, and B.P. Dancik. 1988. Selection of wood density and diameter in controlled crosses of coastal Douglas-fir. *Silvae Genet.* 37: 152-157.
- Lambeth, C.C. 1980. Juvenile-mature correlations in *Pinaceae* and implications for early selection. *For. Sci.* 26: 571-580.
- Lambeth, C.C., J.P. Van Buijtenen, and S.D. Duke. 1983. Early selection is effective in 20-year-old genetic tests of loblolly pine. *Silvae Genet.* 32: 210-215.
- Larson, P.R. 1960. A physiological consideration of the springwood-summerwood transition in red pine. *For. Sci.* 6: 110-112.
- Li, P. 1990. Genetic variation in phenology of bud and cambial activity in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Ph.D. Thesis. Oregon State University. Corvallis, OR.
- Lin, C.Y. 1978. Index selection for genetic improvement of quantitative characters. *Theor. Appl. Genet.* 52: 49-56.
- Loo, J.A., C.G. Tauer, and J.P. Van Buijtenen. 1984. Juvenile-mature relationships and heritability estimates of several traits in loblolly pine (*Pinus taeda*). *Can. J. For. Res.* 14: 822-825.
- Loo, J.A., C.G. Tauer, and R.W. Mcnew. 1985. Genetic variation in the time of transition from juvenile to mature wood in loblolly pine (*Pinus taeda* L.). *Silvae Genet.* 34: 14-19.
- Magnussen, S. 1988. Minimum age-to-age correlations in early selections. *For. Sci.* 34: 928-938.
- Matziris, D.I., and B.J. Zobel. 1973. Inheritance and correlations of juvenile characteristics in loblolly pine (*Pinus taeda* L.). *Silvae Genet.* 22: 38-45.
- McKeand, S.E. 1988. Optimum age for family selection for growth in genetic tests of loblolly pine. *For. Sci.* 34: 400-411.



- McKimmy, M.D. 1966. A variation and heritability study of wood specific gravity in 46-year-old Douglas-fir from known seed sources. *Tappi* 49: 542-549
- McKimmy, M.D. and R.K. Campbell. 1982. Genetic variation in the wood density and ring width trends in coastal Douglas-fir. *Silvae Genet.* 31: 43-55.
- McKinley, C.R., W.J. Lowe, and J.P. Van Buijtenen. 1982. Genetic improvement of wood specific gravity in loblolly pine (*Pinus taeda* L.) and its relation to other traits. In: Proc. Tappi Research and Development Conference. August 1982, Ashville, N.C. pp. 153-158.
- Megraw, R.A. 1985. Douglas-fir wood properties. In: C.D. Oliver, D.P. Hanley, and J.A. Johnson (eds.) Proc. of the symposium, Douglas-fir: Stand management for the future. June 1985, University of Washington, Seattle WA. pp. 81-96.
- Meier, R.J. and J.F. Goggans. 1977. Heritabilities of height, diameter, and specific gravity of young Virginia pine. *For. Sci.* 23: 450-456.
- Mergen F., J. Burley, and C.W. Yeatman. 1964. Variation in growth characteristics and wood properties of Norway spruce. *Tappi* 47: 499-503
- Namkoong, G. 1979. Introduction to quantitative genetics in forestry. U.S.D.A. For. Serv. Tech. Bull. 1588. 342 p.
- Namkoong, G., E.B. Snyder, and R.W. Stonecypher. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards. *Silvae Genet.* 15: 76-84.
- Nanson, A. 1969. Juvenile and correlated trait selection and its effect on selection programs. In: Proc. IUFRO second meeting of the working group on quantitative genetics. August 1969, Raleigh N.C. pp. 17-26.
- Nebgen, R.J. and W.J. Lowe. 1985. The efficiency of early and indirect selection in three sycamore genetic tests. *Silvae Genet.* 34: 72-75.
- Nepveu, G. 1984. Variabilité génétique de la qualité du bois chez l'Épicéa et le Douglas. *Rev. For. Franc.* 36: 303-312.
- Neter, J., W. Wasserman, and M.H. Kutner. 1983. Applied linear regression models. Irwin Inc. Homewood, Illinois. 547 p.
- Nicholls, J.W.P. 1967. Preliminary observations on the change with age of the heritability of certain wood characteristics in *Pinus radiata* clones. *Silvae Genet.* 16: 18-20.

- Nicholls, J.W.P. and A.G. Brown. 1971. The ortet-ramet relationship in wood characteristics of Pinus radiata. *Appita* 25: 200-209.
- Nicholls, J.W.P., J.D. Morris, and L.A. Pederick. 1980. Heritability estimates of density characteristics in juvenile Pinus radiata wood. *Silvae Genet.* 29: 54-61.
- Nicholls, J.W.P. and J.P. Wright. 1976. The effect of environmental factors on wood characteristics 3. The influence of climate and site on young Pinus radiata material. *Can. J. For. Res.* 6: 113-121.
- Nix, L.E. and T.J. Wodzicki. 1974. The radial distribution and metabolism of IAA-<sup>14</sup>C in Pinus echinata stems in relation to wood formation. *Can J. Bot.* 52: 1349-1355.
- Olson, J.R. and D.G. Arganbright. 1977. The uniformity factor. -a proposed method for expressing variations in specific gravity. *Wood Fiber Sci.* 9: 202-210.
- Osborne, R. and W.S.B. Paterson. 1952. On the sampling variance of heritability estimates derived from variance analyses. *Proc. Roy. Soc. Edinburgh. B.* 64: 456-461.
- Panshin, A.J. and C. DeZeeuw. 1980. Textbook of wood technology. McGraw-Hill Book Co. New York. 722 p.
- Paul, B.H. 1957. Juvenile wood in conifers. U.S. For. Prod. Lab. Rep. No. 2094. 8 p.
- Pearson, R.G. and R.C. Gilmore. 1980. Effect of fast growth rate on the mechanical properties of loblolly pine. *For. Prod. Jour.* 30: 47-54.
- Rehfeldt, G.E. 1983. Genetic variability within Douglas-fir populations: implications for tree improvement. *Silvae Genet.* 32: 9-14.
- Rehfeldt, G.E. 1985. Genetic variances and covariances in Pinus contorta: estimates of genetic gains from index selection. *Silvae Genet.* 34: 26-33.
- Riemenschneider, D.E. 1988. Heritability, age-age correlations, and inferences regarding juvenile selection in jack pine. *For. Sci.* 34: 1076-1082.
- Rink G. and E. Thor. 1973. Inheritance and gains of three wood properties in Virginia pine. In: Proc. 12th Southern Forest Tree Improvement Conference. Baton Rouge, Louisiana. pp: 24-30.

- Sales, J. and W.G. Hill. 1976. Effect of sampling errors on efficiency of selection indices. 2. Use of information on associated traits for improvement of a single important trait. *Anim. Prod.* 23: 1-14.
- SAS Inst. 1987. SAS/STAT Guide for personal computers. Version 6 Edition. SAS Institute Inc. Cary, N.C. 1028 p.
- Savidge, R.A. and P.F. Wareing. 1984. Seasonal cambial activity and xylem development in Pinus contorta in relation to endogenous indol-3-yl-acetic and (S)-abscisic acid levels. *Can. J. For. Res.* 14: 676-682.
- Senft, J., M.J. Quanci, and B.A. Bendtsen. 1985. Property profile of 60-year-old Douglas-fir. In: D. Robertson (ed.) *Proc. Technical Workshop: Juvenile wood - what does it mean to forest management and forest products?* October 1985, Portland, OR. Forest Products Research Society, Proceedings 47309: 17-28.
- Silen, R.R. and J.G. Wheat. 1979. Progressive tree improvement program in coastal Douglas-fir. *J. For.* 77: 78-83.
- Smith, D.M. 1955. Relationships between specific gravity and percentage of summerwood in wide-ringed, second-growth Douglas-fir. U.S. For. Prod. Lab. Rept. No. 2045.
- Smith, W.J. 1977. The phenology of growth and wood formation in three Queensland-grown exotic conifers. In: D.J. Nikles, J. Burley, and R.D. Barnes (eds.). *IUFRO Workshop on progress and problems of genetic improvement of tropical forest trees.* April 1977, Brisbane, Australia. pp. 100-120.
- Sorensen, F.C. and T.L. White. 1988. Effect of natural inbreeding on variance structure in tests of wind-pollinated Douglas-fir progenies. *For. Sci.* 34: 102-118.
- Squillace, A.E., R.M. Echols, and K.W. Dorman. 1962. Heritability of specific gravity and summerwood per cent and relation to other factors in slash pine. *Tappi* 45: 599-601.
- Squillace, A.E. and C.R. Gansel. 1974. Juvenile:mature correlations in slash pine. *Forest Sci.* 20: 225-229.
- Steel, R.G. and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill Book Co. New York. 633 p.
- Steinhoff, R.J. 1974. Juvenile-mature correlations in ponderosa and western white pines. In: *Proc. IUFRO joint meeting of working parties on population and ecological genetics, breeding theory and progeny testing.* August 1974, Stockholm, Sweden. Published by Department of Forest genetics, Royal Coll. For. pp. 243-250.

- Stonecypher, R.W., F.C. Cech, and B.J. Zobel. 1964. Inheritance of specific gravity in two and three-year-old seedlings of loblolly pine. *Tappi* 47: 405-407.
- Stonecypher, R.W. and B.J. Zobel. 1966. Inheritance of specific gravity in five-year-old seedlings of loblolly pine. *Tappi* 49: 303-305.
- Talbert, J.T., J.B. Jett, and R.L. Bryant. 1983. Inheritance of wood specific gravity in an unimproved loblolly pine population: 20 years of results. *Silvae Genet.* 32: 33-37.
- Taylor, F.W. 1974. Effect of extraction on the volume dimensions and specific gravity of solid wood blocks. *Wood Sci.* 6: 396-404.
- Thibaut, B. 1987. Variation d'épaisseur du placage dans le déroulage des bois hétérogènes. Actes du 2ème colloque Sciences et Industrie du Bois, Nancy, France 1987. pp. 25-33.
- Vonnet, G., J.R. Perrin, and J.C. Ferrand. 1985. Réflexions sur la densité du bois. IV: Densité et hétérogénéité du bois de Douglas. *Holzforschung* 39: 273-279.
- Walker, N.K. and R.S. Dodd. 1988. Calculations of wood density variation from X-ray densitometer data. *Wood Fiber Sci.* 20: 35-43.
- Wareing, P.F. 1958. The physiology of cambial activity. *J. Inst. Wood Sci.* 1: 34-42.
- Weisberg, S. 1985. *Applied linear regression*. Second edition. Wiley & Sons, New York. 324 p.
- White, T.L. and G.R. Hodge. 1990. Indirect prediction of genetic values. *Silvae Genet.* (In Press).
- Wodzicki, T.J. and A.B. Wodzicki. 1980. Seasonal abscisic acid accumulation in stem cambial region of *Pinus sylvestris*, and its contribution to the hypothesis of a late-wood control system in conifers. *Physiol. Plant.* 48: 443-447.
- Worrall, J.W. 1970. Interrelationships among some phenological and wood property variables in Norway spruce. *Tappi* 53: 58-63.
- Yang, K.C., C.A. Benson, and J.K. Wong. 1986. Distribution of juvenile wood in two stems of *Larix laricina*. *Can. J. For. Res.* 16: 1041-1049.
- Zobel, B.J. 1964. Breeding for wood properties in forest trees. *Unasylva* 18: 89-103.