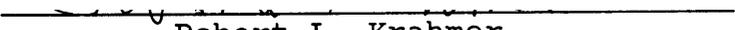


AN ABSTRACT OF THE THESIS OF

Abdelazim Yassin Abdel-Gadir for the degree of Doctor of
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From Provenance Plantations

Signature redacted for privacy.

Abstract Approved:


Robert L. Krahmer

The purpose of this study was to investigate variation in some intra-ring characteristics in juvenile and mature wood from two Douglas-fir genetic plantations established in 1912 by the U.S. Forest Service. The experimental material consisted of progeny from thirty families representing ten provenances (3 families per provenance) grown in two replications in each planting site. Each family was sampled by three trees, each tree by two increment cores. Using X-ray densitometry, the following characteristics were determined for juvenile and mature wood: earlywood density (EWD), latewood density (LWD), average ring density (RD), earlywood width (EWW), latewood width (LWW), ring width (RW), and latewood percent (LWP). Two models were used to analyze the variation patterns: 1) families pooled across provenances and 2) provenances and families-within-provenances. Heritabilities and correlations (phenotypic and genetic) were also determined. Differences between plantations were significant for

all traits except juvenile RD and mature RW and EWD. Genetic variation associated with provenances was evident for RD and EWD, but it was relatively unimportant for ring width parameters except LWP. There was significant variability among families-within-provenances for juvenile RW as well as for mature RD, LWW, and LWP, an indication that progress can be made for these traits by selection within populations. Heritabilities obtained from the analysis of the 30 families (pooled across provenances) were biased upwards due to the provenance variation. The RD components (EWD and LWD) had strong phenotypic and genetic correlations with their respective RW components (EWW and LWW). Contrariwise, phenotypic correlation between average RD and total RW was non-existent and genotypic correlation was weak. The potential exists for selection to improve juvenile and mature wood density, yet the impact of this on radial growth is low. Early selection is feasible for RD, EWD, LWW, and LWP. Selection to improve juvenile RW does not affect wood density during mature wood growth period.

Intra-Ring Variations in
Mature Douglas-fir Trees
From Provenance Plantations

by

Abdelazim Yassin Abdel-Gadir

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APPROVED :

Signature redacted for privacy.

Professor of Forest Products in charge of major

Signature redacted for privacy.

Head of Department of Forest Products

Signature redacted for privacy.

Dean of Graduate School

Date thesis is presented November 15, 1990

Typed by Abdelazim Yassin Abdel-Gadir

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INTRA-RING VARIATIONS IN MATURE
DOUGLAS-FIR TREES FROM PROVENANCE PLANTATIONS

INTRODUCTION

Among the many products from the forest, usually the most important one for which trees are managed and grown is wood. The primary North American tree species in terms of valuable timber and importance to the forest industry is Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco). The wood-based industry is becoming and will become increasingly dependent on young-growth timber of Douglas-fir for its raw material supply. This transition to young growth is accompanied by reduction in log size and increase in the volume of juvenile wood. The wood-based industry has to realize this and develop new technology to manufacture desirable or at least acceptable products from the new kinds of wood (Zobel, 1984). However, improvement in processing technology and manufactured products is usually done at the sacrifice of increased production inputs and costs, and/or reduced yield and quality of the products.

Although the primary emphasis of most tree-breeding programs is to obtain fast-growing, better-formed, well-adapted, and pest-resistant trees, improved wood properties could also be obtained from the same programs (Zobel and

Talbert, 1984). So foresters can contribute a great deal to solving the problem by means of tree improvement programs that allow growing of the best of the forest gene pool under optimal silvicultural regimes. A knowledge of genetic variation can help foresters realize the full potential of their forest trees so that they can utilize to the fullest the inherent good qualities of the plus trees. Essentially, the search for genetic knowledge is the study of variation in characters. An essential task is to determine what portion of the variation is genetically controlled and whether the performance of genotypes changes when grown in different environments. In this connection, it is imperative to have a basic understanding of the genetic structure of natural variation in the traits of interest. In order to breed effectively, it is also important to know what traits need be modified, how this modification affects the quality of the product made from wood, and how does the cost of this genetic modification compares to the cost of using other means and to the revenue obtainable from the change in the product value.

It is conceivable that the technical properties of wood are determined to a considerable extent by the basic chemistry and anatomy of the wood at either the cellular or ultracellular level. Due to the nature of improvement programs, it is desirable to confine the consideration in each program to improve a single or a few criteria that

well relate to the intended end use. To assure such simplification, wood density, a characteristic used to describe the mass of a material per unit volume, has been suggested by many researchers. Kellogg (1982) , for example, stated: "If one had to select the single most important clear wood characteristic affecting the quality of a softwood raw-material resource for pulp, lumber, and plywood, it would unquestionably be wood density". The development of X-radiographic methods added a new depth to this important wood quality index by allowing the measurement of various density and ring width parameters and complete intra-ring density profiles.

With the increasing emphasis toward forest-tree improvement, any information on the variation in wood traits has also become of increasing importance. Needed inferences are based on the pattern and magnitude of variation in wood traits among trees of known parentage. Because most genetic plantations are relatively young, usually tree breeders are not well placed to obtain estimates of genetic variability on mature trees. One of the few sources in the world of mature trees of known parentage is the 1912 Douglas-fir heredity study, which was established by the U.S. Forest Service using seed collected from 13 geographic seed sources (120 mother trees).

This thesis describes different levels of genetic variability for seven densitometric intra-ring variables

expressed in two of the 1912 Douglas-fir genetic plantations. The objectives of this study are:

- to analyze the influence of planting locations, provenances, families and individual trees on intra-ring characteristics in juvenile and mature wood,
- to investigate inheritance of intra-ring characteristics in juvenile and mature wood, and
- to examine the extent of phenotypic and genetic correlations among intra-ring characteristics within and between the two wood zones.

LITERATURE REVIEW

Generally speaking, no two individual organisms are exactly alike. What we observe or measure in the forest or in a piece of wood is the phenotype, which can be presented in the form of an equation:

$$\text{Phenotype} = \text{genotype} + \text{environment}$$

The genotype is the sum total of genes in the cell nuclei which carry the molecular code that governs an individual's development and the transformation of hereditary characteristics. The sum total of nongenetic factors that affect the growth of trees and wood formation is called the environment. Environmental factors may be divided into natural and artificial factors. Natural factors include features of the forest environment such as all terms applied to soil and all climatic means and extremes. Artificial factors include managerial and silvicultural practices.

ENVIRONMENTAL AND GENETIC VARIATION IN WOOD DENSITY

A major contribution by the early workers to the effect of environment and genetics on wood structure was the observation and categorization of variation patterns in wood characteristics of commercially important tree species. This variation can result from the genotype, the

environment, or a combination of both.

Since the 1930's publications on this respect have indicated that strains of trees with desired wood quality could be bred (Champion, 1933; Schreiner, 1935). Though some researchers were of the opinion that wood is the most 'conservative' part of the tree and therefore the least subject to genetic variations, they recognized the need for proper experimentation before deciding on the use of genetic improvements (Koehler, 1939).

Bisset et al. (1951), Fielding (1953), Zobel (1952), Echols (1955), and Zobel and co-workers (1956, 1958) referred to the wide variation in a full array of wood properties of various wood species. They discussed the potentiality of genetic control on wood characteristics and stressed the need for breeding strains with desirable wood attributes. Over the years a considerable amount of information has been published on the role that genetics and environment play in governing wood quality. In the following sections, the effect of geographic location, site condition and some of the immediate factors influencing tree growth and wood formation on wood density is discussed.

Geographic Location

Geographic variation results from large scale selection forces acting on a species gene pool to favor or

disfavor one genotype relative to another. This implies adaptation of a group of individuals to environmental conditions within a rather wide geographic range. Often a gradient of a characteristic is defined over a given range and usually correlated with an environmental gradient such as latitude and elevation.

Within the U.S. southern pine region, specific gravity tends to increase from north to south and from west to east (Larson 1957, Zobel et al. 1958, 1960). Zobel et al. (1972) noted that these geographic differences are small and might be accentuated at the edge of a species range. Similar trends have been reported for two northern pines (Gilmore 1968).

Cown (1974), working on radiata pine grown in New Zealand, also found an increase in wood density with decreasing latitude. Working on the same species growing in different localities in Greece, Matziris (1979) found density to be highest in the more southerly grown species.

The tendency of specific gravity to vary with latitude is probably related to length of growing season, with a longer season favoring formation of more latewood.

Singh (1986) examined the variation in wood density of 13 Canadian tree species including Jack pine, white spruce, black spruce, Tamarak and nine hardwoods growing in western Canada. The density means in his study varied from 5.4 to 18.2% from the mean densities of Canadian woods, and from

10.0 to 17.7% from the wood densities in the adjoining predominantly forest boreal region.

Markwardt and Wilson (1935) indicated that Douglas-fir grown in western Washington, Oregon, and California produced wood with remarkably greater density than that of the northern Rocky Mountains.

An investigation was conducted by Drow (1957) to comprehensively compare Coast and Inland Douglas-fir. He stated that in the moderate and slow growth-rate classes, the specific gravity and strength properties of Douglas-fir grown in the Rocky Mountain area are lower than for wood grown in coastal areas, the Cascades, and the Sierras. Material collected from the Southern Rocky Mountains was less dense than from the northern part.

McKimmy (1959) reported on factors related to variation in specific gravity on 36 trees of young-growth Douglas-fir grown at several locations in Oregon and Washington. He stated that variation of specific gravity within given groups of specimens, including three groups of geographic location, usually was sufficient to offset any effect these factors might have on this wood property.

A study which deserves special mention is the Western Wood Density Survey by the U.S. Forest Service (1965). This involved the collection of 30,000 increment cores (one per tree) on 4,067 plots located systematically in 11 states. The most significant influence on wood density was

exerted by the age of examined trees. The results showed that Douglas-fir does not show the clear-cut trends of geographic variation found in southern pines. When the increment cores were separated according to age, then there was a trend of decreasing specific gravity with increasing elevation and with decreasing latitude. These results, as stated in the report, could imply that a shorter, wetter, and cooler growing season or poorer soils at the higher elevation cause trees to produce slightly lower density wood than trees at the lower elevations.

It is noteworthy, at this point, that in most of the above mentioned studies the between tree variation in wood density in a stand or locality was very large.

However, the geographic location does not in itself affect wood density. It is important only to the extent that it reflects those factors that have a more direct influence on wood quality. Such influence has been explained to be either due to (external) environmental factors and/or (internal) genetic factors. The effect of such factors on wood density and related wood characteristics is the subject of the following sections.

Site Condition

Wood characteristics are the result of varying growth processes, and some effect of the environment on wood quality is to be expected. With this understanding, much

research has been conducted on the variation of wood density among stands and sites.

Jayne (1958) reviewed the literature on the effect of site qualities on specific gravity up to the early part of the 1950's. He showed that earlier writers were of the opinion that the poorer sites produce lighter wood than the better sites; the later workers, including himself, have noted exactly the contrary. Paul (1950) found average specific gravity of young-growth Douglas-fir wood from site II was lower, and from site IV was higher than the old growth values.

Working on similar material, Wellwood (1952) found that wood from good sites was significantly lower in specific gravity than that from average sites. This difference could be as much as twelve percent.

McKimmy (1959) gave for sites I, II and III average specific gravity values for young-growth Douglas-fir as 0.426, 0.434 and 0.448, respectively. However, he noted that specific gravity was not significantly related to site qualities due to large tree-to-tree variation.

Also Zobel and Rhodes (1957), investigating loblolly pine in east Texas, failed to correlate plot differences in specific gravity to site index.

In a rather extensive study, Zobel et al. (1965) found a very small negative effect of site index on specific gravity. They also noted considerable between tree

variation.

Recognizing that clonal population would be ideal for such type of studies, Harris (1962) examined the effect of two site qualities on specific clones of loblolly and slash pine. He reported that the wood of loblolly pine averaged slightly but significantly higher specific gravity on the poorer site, and slash pine showed no effect of site on specific gravity.

These contradictions may be partially understood in view of the fact that the effect of site is an effect of interacting environmental factors. And since the effects of site are complex, more intensive studies have been made to investigate the factors that might be involved. For example, the relationship between available soil moisture and density was examined in several wood species. The geographic variation in specific gravity for loblolly and shortleaf pine (Mitchell and Wheeler, 1959; Mitchell, 1964) as well as for white and red pine (Gilmore, 1968) has been related to summer rainfall and soil moisture. Similar results were reported for radiata pine by Nicholls and Wright (1976). They found that average density was less in the region with the highest summer rainfall due to lower proportion of latewood and low minimum density.

Zahner et al. (1964) stated that the volume of wood production was doubled and "... Latewood was greater in size of cells and in number at all stem positions in

irrigated trees" of red pine than in those subjected to artificial drought, "but percentage latewood was equal in both treatments."

On his wood density survey of cost-type Douglas-fir, Knigge (1962) found a decrease in average density with increasing rainfall and an increase with average temperature during the growing period. However, the effect of these environmental factors was insignificant compared to the stand and tree influences.

On approximately 50-year-old dominant trees grown on sites of average quality (III), Lassen and Okkonen (1969) analyzed the effects of five ranges of summer rainfall and three ranges of elevation on specific gravity of Coast Douglas-fir. The average specific gravity of wood and percentage of summerwood formed during a single growing season was significantly higher for dry summers (0.52) than for wet summers (0.45) and highest in trees from lowest elevations and lowest for trees from middle elevations.

Zahner (1963), based on previous work, discussed the effect of some environmental conditions on wood formation in terms of moisture stresses within the tree. He concluded that variations in dimensions and secondary wall thickening of tracheids may be related physiologically to moisture stress.

In contrast to the above findings, Paul (1959) found that drier sites produce lower density wood. Also, Larson

(1964) showed that drought favors the formation of low density and attributed this to the formation of narrow-diameter thin-walled tracheids. Paul and Martz (1931) reported that summerwood proportion in long leaf pine was increased by irrigation to more than 160%.

The work of Harris (1963) with 3,600 trees of radiata pine growing on 37 sites in New Zealand gave evidence of the temperature effect on wood quality. Of interest is the high correlation coefficient ($r = 0.939$) for specific gravity of outer wood over mean annual temperature. Further evidence can be seen in the work of Larson (1967) with red pine seedlings grown in four growth rooms maintained on different temperature regimes.

A recent work examined the specific gravity of 55-year-old, dominant red spruce growing on soils of three drainage classes in north central Maine (Shephard, 1987). It was concluded, that "Mean specific gravity on the poorly drained soil was significantly greater than mean specific gravity on the somewhat poorly drained soil, and than mean specific gravity on the moderately well and well drained soils combined." However, in an earlier study Schniewind (1961) found no differences in wood specific gravity for red fir growing in three topographic sites ranging from well drained to poorly drained. He observed that only the radial distribution of specific gravity differed among the three sites.

Some investigators worked on the effect of soil fertility on wood properties. For example, the effect of five types of sandy soils on the yield and quantity of jack pine pulp wood was studied by Wilde et al. (1951). The results indicated that the soil types, which varied in their state of fertility factors, had a marked influence on wood density.

On the other hand, the effects of fertilization on wood properties have been intensively studied in conifers (Elliott, 1970), including Douglas-fir (Erickson and Lambert, 1958; Parker et al., 1976; Brix and Mitchell, 1980). Slight to significant decreases in density have been reported.

Researchers have also given consideration to other wood attributes that are known to contribute to wood density. Of these, annual ring width and latewood percent received the greatest share of researchers' attention.

Working with Douglas-fir, Chalk (1930, 1951) reported that the production of summerwood was related to the amount of moisture available during the period of its production. On the other hand, the formation of springwood was induced by low average temperatures during May and June.

Zahner (1962) found that irrigation prolonged the formation of earlywood and drought induced early formation of latewood in loblolly pine. The dry treatment produced denser latewood than the wet (Zahner et al., 1964).

Smith and Wilsie (1961) studied the effect of June-October soil-water deficiencies on summerwood formation within annual increment sheaths of three loblolly pines. They concluded that annual increments produced during years of low water deficits are characterized by loss percentages of summerwood at the apex of the increments and high percentages of summerwood at the base of the increments. In years of greater water deficits, the trend became less pronounced and was reversed in years of severe drought. In an earlier study, Harris (1955) observed five latewood types in Scots pine in East Anglia and related these to weather conditions prevailing during their formation. He also noted that water deficits at the end of earlywood formation caused a sharp distinction between the early- and latewood. The work of Howe (1968) on Ponderosa pine substantiates such a view. He found that the major effect of irrigation was a more gradual transition from early to latewood with a significant increase in the number of large-diameter, thick-walled latewood cells.

Kennedy (1961) correlated the percentage of summerwood in Douglas-fir with total precipitation, minimum, maximum and average temperature and total hours of sunshine for each of the months April through July. Although he found high correlation coefficients (over 0.80) with several variables, only one (April sunshine hours) proved significant. He noted that this might be due to his small

sample size (the outermost four annual rings from 21 trees). His results also indicated that the weather in the month of April had the strongest effect on this wood trait. He further pointed out that the width of summerwood in the two extreme years in percentage of summerwood production was the same, but the width of springwood varied greatly between the two years.

In addition to the evidence presented by the studies referred to above, considerable understanding of the effect of environment on wood formation has been derived by studies employing controlled conditions. However, it is not the intention here to review work accomplished in this field. Examples can be seen in the works of Brazier (1977) and the proceedings of the Symposium on the Effect of Growth Acceleration on the Properties of Wood (1972).

Provenance

Tree species that have large natural habitat experience natural selection by the varying environmental conditions prevailing in that habitat. This produces populations that are more or less different with respect to their genetic make-up. The amount of such variation is dependent on the extent of gene exchange between these populations. Our present understanding of population variation has been mainly derived from provenance studies. Considerable evidence of genetic control of specific

gravity was expressed when trees from different geographical sources have been grown under similar environmental conditions. On the other hand, the effect of environment can be well studied if materials of common origin are grown in different sites.

Rees and Brown (1954) studied specific gravity variations of 19 geographic races in a sample of 190 17-year-old red pine trees. They concluded that wood specific gravity of one strain differed significantly from that of the remaining 18 seed sources. Latewood percentage did not differ significantly by seed sources. Similar results were reported for four provenances of Sitka spruce ranging from north California to British Columbia (Jeffers, 1959).

In a seed source test of density variation of longleaf pine from six provenances of the southeastern United States, Saucier and Taras (1966) examined stem segments of 8-year-old trees. They found that one seed source from Florida had significantly lower specific gravity than other sources tested. Similar results were obtained earlier for 5-year-old loblolly pine (Thor and Brown, 1962).

Haigh (1961) studied 7-year-old Douglas-fir trees representing five provenances and concluded that provenances had the major effect on wood density (cit. in Wellwood and Smith, 1962).

Working on Pinus pinaster in western Australia, Nicholls (1967) reported on wood characters of material

from four provenances and compared the effect of two plantations that were subject to the same climatic conditions, but differed with respect to soil types. His work showed that provenances significantly affected latewood percentage and basic density but not ring width. Significant site effect was evident only for ring width, latewood percentage in the mature wood, and for basic density in the core wood.

In his study of xylem characteristics in jack pine seedlings, Kennedy (1971) correlated paired mean values from two locations for each of 29 provenances. Together with other phenological and xylem attributes, the total ring, latewood, and earlywood width as well as specific gravity showed significant relationship with provenance, when geographic location of the provenance was expressed in terms of growing degree days (summation of mean daily temperatures exceeding 42° F). Latewood percentage showed considerable genotype-environment interaction.

It is interesting to note that Matziris (1979) found no significant effect of seed source on wood density of 10-year-old radiata pine grown at two sites in Greece. It was speculated that the seeds might have been brought from one origin to the countries from where the seed was introduced to Greece. On the other hand, the effect of site on wood density was found to be significant.

Several studies of the progeny of known parents grown in one or more sites have been reported.

Zobel and Rhodes (1957) examined the progeny of five loblolly pines (two open-pollinated and three supposedly selfed) and showed that the progeny of the higher density parent had significantly higher density than that of the low density parent.

Goddard and Cole (1965) investigated some growth and wood characteristics in six-year-old progenies of 13 select slash pines. Their results indicated substantial differences among the mean densities of the various geographic locations from which the parent trees were selected. There was a low, non-significant relationship between specific gravity of parents and that of progeny. However, when the parent values were adjusted to a common basis the above relationship became significant.

Echols and Conkle (1971) went into more detail and examined 29-year-old ponderosa pine progenies from 27 parent trees, grouped into seven elevation zones grown at three different elevations in the Sierra Nevada of California. They concluded, "High-elevation parents tended to produce offspring of lower average specific gravity, regardless of location, and all seed sources tended to produce less dense wood when grown at higher elevations." It is interesting to note that this conclusion has been shown to hold true for both the mature wood of the outer sections (rings 20-29) as well as for the inner sections (rings 12-19) which were considered to contain some

juvenile wood.

In a recent study, Byram and Lowe (1988) examined density variation in 28 planting locations of the Western Gulf loblolly pine seed source study. They sampled five open-pollinated families from each of four Western Gulf provenances. Significant differences were reported among provenances and among test locations. Families generally ranked the same in all locations.

The work of Yanchuk et al. (1984) with lodgepole pine, indicated only the importance of site and trees within provenances effects on specific gravity. Their study consisted of 14-year-old open-pollinated progenies from nine trees (families) in each of two provenances from each of five geographic sites.

As noted by many other workers, most provenance work has been reported on young trees. An exception is the work reported on mature trees of Douglas-fir at Oregon State University (McKimmy, 1966; McKimmy and co-workers, 1971, 1982). Their study material was obtained from the genetic plantations established in 1915-1916 by the U.S. Forest Service, These plantations were based on 120 half-sib families planted on four sites.

McKimmy (1966) took one 3-mm increment core from four 47-year-old trees from each of 13 seed sources planted in four different sites. He divided all increment cores into 5-year growth intervals from the cambium to the pith, for

which he determined the specific gravity and percentage summerwood. He concluded that both seed sources and plantations had a highly significant effect on specific gravity and summerwood percentage. However, it appeared that the environmental influences of the plantations have a greater effect on these traits than does the genetic influence of seed sources. The interaction between plantation and seed resource was also highly significant, indicating that the ranking of seed sources within plantations was not consistent. Progenies from Douglas-fir parents at low elevations near the Wind River plantation in southern Washington and from the Santiam valley in northwest Oregon were denser than the sources from higher elevations in the same areas. Other seed sources and other plantation locations provided no clear relationship.

McKimmy and Nicholas (1971) examined the effect of progeny from a single parent from each of five seed sources grown in three plantations on wood specific gravity and tracheid length of 47-year-old Douglas-fir. Their conclusion is similar to McKimmy's (1966).

A third paper reporting on material from this Douglas-fir provenance study is that by McKimmy and Campbell (1982). They sampled three 64-year-old trees for each of three families from ten sources grown in two plantations. Each tree was sampled with two 12-mm increment cores; the cores were further subdivided into juvenile sections and

mature sections. They found that specific gravity varied among sources and plantations. They also found that specific gravity appeared to be similar for sources at the two plantations, but not for families-within-sources. Among families there was a strong family X plantation interaction.

In his research with five provenances of 17-year-old Douglas-fir grown in four sites, Cown (1976) concluded insignificant provenance effect on core wood density. The relative contribution of the provenances to the variation in basic density was 1.2 % compared to 56.7 and 27.3 % contributed by the sites and the between-trees components respectively.

GENETIC AND ENVIRONMENTAL VARIATION IN INTRA-RING CHARACTERISTICS

The technique of x-ray densitometry has been developed by Polge (1963, 1965) to study intra-ring wood density variations. Subsequent studies led to an increasing awareness of the factors influencing this important wood trait.

Polge (1965) showed that total rainfall from August to October was negatively correlated to maximum density ($r = 0.89$) for Abies grandis in France. No conclusive relationship could be found for minimum density.

Similarly, Polge and Keller (1968) reported that

insufficient rains in the early part of the growing season increased the minimum density in Scots pine, and winter deficits occurring before the commencement of latewood increased maximum density. They further noted that irrigation increased ring width and reduced wood density by increasing the amount of earlywood but not latewood.

McKinnel and Shepherd (1971) worked on four radiata pine trees selected from the dendrometer records as having the best growth for the 1963 season. They related the density curves to weekly estimates of soil moisture. The results indicated very close correlation between the within-ring variation in wood density and available soil moisture during the growing season. Their results suggested that other environmental factors seem to have more influence on wood formation at the beginning and end of the growing season.

In contrast to these findings, Nicholls and associates (1976, 1977) were unsuccessful in attempts to relate maximum and minimum density to rainfall and temperature in better designed experiments for radiata pine. In the first study (Nicholls and Wright), clonal material was grown in five sites; highly significant variations between sites were reported for latewood ratio, minimum, maximum and average density. They further found that the number of potential growth days (based on limiting water deficits) within a growing season (defined by temperature thresholds)

correlated with ring width, and in autumn correlated with latewood ratio. In the later study, Nicholls and Waring investigated the effect of three treatments: partial drought, normal precipitation, and irrigation. They stated, "The partial droughting causes severe water stress throughout the growing season, increasing minimum density and latewood ratio and reducing ring width and maximum density." Irrigation, on the other hand, being most effective in summer and autumn, mainly resulted in an increase in ring width and maximum density. The expression of these components in the complex of average density was a slight increase for both treatments.

In contrast to the above findings, irrigation (Paul and Marts, 1931) and summer rainfall (Larson, 1957) have been found to favor latewood production in two southern pines. Paul (1959) found that drier sites produced lower density wood. Similarly, Larson (1964) showed that drought favors the formation of low density and attributed this to the formation of narrow-diameter thin-walled tracheids.

From the evidence presented for Douglas-fir, it is obvious that the weather factors play a role in governing intra-ring characteristics. An example is found in the work of Heger et al. (1972) based on 480 rings (20 trees x 3 cores x 8 annual rings). They reported significant differences in ring density components among the trees and among the annual rings. They explained the difference

among years in terms of the weather records for the entire effective growing season. Most high correlations were found for maximum density with temperature (positive), and for average latewood density with precipitation (negative).

A detailed investigation was made by Cown (1976) with five Douglas-fir provenances grown in five sites. It has been shown that earlywood and ring widths were increased by cool wet weather in June and by winter rainfall; latewood production was favored by wet cool summers. July rainfall was negatively related to both earlywood and latewood densities, and they were also negatively related to April and July temperatures, respectively. Only April temperatures were closely related to minimum and ring densities, higher values resulted from lower temperatures. Cown also found that maximum density was positively associated with minimum temperatures of July and August and negatively with that of September. However, this study had some limitations on the climatological data. On the other hand, it has been noted that weather fluctuations could be used to explain only a small proportion of the overall variation in the studied wood traits. The factors which contributed most to the total variation were site, plots (replications within sites), and individual trees within plots. No consistent provenance effect was found for any of the ring width and density components, except that the ring density range (MXD-MND) had a tendency to show significance in some

cases. Moreover, it was concluded that site caused more variation in the earlywood properties than in those of the latewood.

HERITABILITY

As pointed out previously, a number of investigators have reported very high tree-to-tree variability while studying the variation in wood density among geographic locations, sites, stands, and provenances grown in the same stand. It has been suggested that the between-tree differences in wood properties are the result of genotype control. Evidence has stemmed first from general observations made in many species during the fifties. For example, trees with high core density produced surrounding wood with high density (Turnbull, 1947); one clone consistently produced heavier wood than the other (Fielding, 1953); trees of the same age growing a few feet apart had considerable differences in densities (Zobel, 1956).

Supporting and conclusive proof of genetic influence on wood density has been put forward in the form of heritability values of several wood properties for various tree species. Heritability is a measure of the degree to which a given character is passed along from parents to offsprings by genetic code. Heritability values express the ratio of variation attributable to genetic differences to the total phenotypic variation.

$$H^2 = V_G / (V_G + V_E)$$

Over the years a considerable amount of information has been published on this relationship. The studies covered an array of wood quality criteria including chemical properties (Dadswell et al., 1961; Zobel et al., 1966; Van Buijtenen, 1968), cell dimensions (Goggans, 1962, 1964; Squillace, 1962; Kennedy, 1966; Smith, 1967), spiral grain (Nicholls et al., 1964; Zobel et al., 1968), heartwood proportion (Nicholls and Brown, 1974), longitudinal shrinkage (Nicholls et al., 1964), besides wood density. Most of these wood properties are from moderate to strongly inherited. Wood density is the most intensively studied wood property because of its economic importance and because of its relative ease of measurement. Appendix Table 9 lists some heritability estimates reported by various researchers for some intra-ring characteristics.

The total variation that is due to heredity refers to a numerical estimate including three values:

- Additive variance
- Dominance variance
- Variance due to epistatis.

Additive variance is due to the average or additive effect of a gene or genes. When a trait is controlled by a number of genes, each gene contributes a small addition to the overall effect. Dominance variance is due to the interaction between alleles (alternate forms of a gene).

Epistatic variance is due to the interaction between non-allelic genes.

Most of the early workers who studied the genetics of wood density made use of the total genetic variation and gave estimates of broad-sense heritability for vegetatively propagated material (Fielding and Brown, 1960; Dadswell et al., 1961; Goggans, 1962; Squillace et al., 1962; van Buijtenen, 1962). This was especially the case when researchers were looking for conclusive evidence on the possibility of genetic control of wood properties. As this evidence became well established, research work was oriented more towards heritability estimates that utilize only the additive portion of the genetic variance for material propagated by sexual means. Such an estimate is known as narrow-base heritability and is more relevant to the methods of forest regeneration prevailing nowadays because economical methods of vegetative propagation and of producing specific crosses are not yet available.

Two different ways of estimating heritability have been used: analysis of variance among progenies or clones (e.g. Dadswell et al., 1961; Squillace, 1962; McKimmy, 1966; Nicholls et al., 1964; Nicholls, 1967; Polge and Illy, 1968; Polge, 1971; Keller, 1973; Nicholls et al., 1980; Maziris and Zobel, 1973) and correlation between the mother-trees and the mean values of their progenies (van Buijtenen, 1962; Polge, 1971; Keller, 1973; Matziris and

Zobel, 1973).

It has been emphasized by many authors (e.g. Wright, 1976) that the term 'heritability' strictly applies to the character, species, population, and environment for which it is estimated. However, it can generally be said that wood density is under strong genetic control regardless of the species and has heritability values in the range of about 0.5 to 0.8 in conifers. Yet, the given heritability estimates will apply only to the populations for which and environmental conditions under which the experiments were carried out.

The vast majority of the published results for heritability of wood density, since the pioneering work of Fielding and Brown (1960), has been based on seedlings or very young trees. This fact is of special interest as the heritability estimates are more likely to change with age of material tested (Zobel, 1964; Nicholls, 1967; Cown, 1976). This change can be attributed to changes in the environment and/or in the genetic control of the trait as the tree matures. Nicholls (1967) observed a decrease in the heritability estimates for ring densities from pith until a minimum is reached at about the ninth growth ring followed by an increase with age in 25-year-old clonal plantation of radiata pine. He found no clear relationship for ring width heritability values with age. In contrast to the above findings, Cown (1976) found a pronounced

increasing trend of heritability values with age for all investigated ring width and density components in 10-year-old Douglas-fir clonal stock.

X-RAY DENSITOMETRY

Various techniques have been used to study the intra-ring density variations in wood samples. These include mechanical (Mayer-Wegelin, 1950), gravimetric (Ifju et al., 1965), photometric (Green and Worrall, 1964), and radiometric methods using beta rays (Phillips, 1960) and x-rays (Polge, 1963, 1966). The gravimetric and photometric methods are impractical for large-scale intra-ring density determinations because they require preparation of serial tangential microtome sections which is very time-consuming. The beta-ray and x-ray methods have been compared by Harris and Polge (1967) and Phillips (1968). It has been generally conceded that the x-ray method is superior. Its advantages are the production of more accurate and detailed data in a shorter time and the relative ease of ray penetration power adjustments.

The research in the field of x-radiography of wood arises from the publications of H. Polge and co-workers of the Centre National de la Recherche Forestiere, Nancy, France (Polge, 1963, 1965, 1966; Polge and Illy, 1968; Polge and Keller, 1968). This method makes use of the differential absorption of the soft x-rays by thin wood

specimens of uniform thickness and moisture content. The basic principles of the x-ray procedure were stated by Polge (1966) as "in an increment core the thickness is constant along a diametral plane and thus the x-rays are absorbed according to an exponential law, which depends mainly on wood density; now optical density of the radiograph (decimal logarithm of opacity) is, under definite conditions almost proportional to the logarithm of the x-ray intensity received; therefore, a linear relation may exist between optical density and wood density."

The basic technique of x-ray densitometry is to radiograph cross-sections of wood specimens and produce a negative image of the wood onto sheets of x-ray film. The film is then developed and the negative radiographs are scanned with a microdensitometer to give a shade intensity which is calibrated to indicate density. The densitometer converts the film density to graphical representation of ring width and intra-ring density data. The microdensitometer records may be calibrated directly into wood densities by radiographing control samples (of known densities) together with the specimen on the same film. Calibration is used to estimate the predicting coefficients that are used in the density calculations. The x-radiographic method facilitates continuous records of density from pith to bark, and permits the measurement of the complete intra-ring density profile. From such a

profile one can derive a whole list of intra-ring density characteristics including earlywood and latewood variables.

This technique has been adopted, modified and used for various purposes by several laboratories all over the world (Rudman et al., 1969; Fletcher and Hughes, 1970; Echols, 1970; 1973; Nicholls and Brown, 1971; Megraw and Nearn, 1972; Parker et al., 1973; Cown and Clement, 1983; Bonder, 1984). The main innovations include the use of:

- moving slit (in-motion) system allowing the x-beam to pass through a much shorter column of air and then parallel to the wood grain through the sample and hence reducing parallax
- direct scanning densitometry without using film as a medium
- stepping motor to traverse the specimen or the film to acquire data on an equidistant step basis
- computerized densitometer and automatic recording of data.

Some Considerations in Determining Earlywood-Latewood Boundary

It has been long recognized that growth rings in coniferous trees comprise two zones of different cell structures: earlywood (or springwood) and latewood (or summerwood). Compared to the latewood, the earlywood is characterized by having fibers with wider lumens and thinner walls.

One of the main problems encountered in the analysis of intra-ring density profile is the demarcation of the earlywood-latewood boundary. An adequate and universal definition of this boundary is yet lacking. Critical discussion of this problem has been presented by Harris (1967), Rudman (1968), and Brazier (1969). One of the alternatives used is to select a density that results in an earlywood-latewood boundary similar to that defined by Mork (1928) (Phillips, 1960). Mork defined latewood anatomically as the wood in which cell lumens have the maximum radial dimension equal to twice the thickness of the combined cell walls of two adjacent tracheids. Based on this definition, different values were obtained even within the same species. Using Mork's definition Heger et al. (1974) found a demarcation density value of 0.54 g/cm^3 for 33-year-old Douglas-fir. Microscopic examination of Douglas-fir samples and comparison with x-ray densitometry results showed that the earlywood-latewood boundary was about 0.65 g/cm^3 (Choi, 1987).

Another concept is to objectively fix a density level for each growth ring separately. Researchers advocating this principle have used the mid-point of the density range between the first-formed earlywood and last formed latewood (Green and Worrall, 1963), the mid-point of the maximum and minimum densities within a ring (Elliott and Brook, 1967), or used the minimum and maximum densities to derive a

latewood ratio (Harris, 1969; Nicholls and Brown, 1971). According to Rudman (1968), the mid-point principle is not suitable to compare between rings within the same tree since two rings could have the same percentage of latewood but different variations about the density figure. He suggested the use of a third alternative: the use of standard density levels (the percentage of the ring density that is greater than a specific standard density level) to describe the within-ring density, and proposed the phrase "relatively high wood density" where "latewood" is unsuitable. Polge (1966) showed that the proportion of wood density above certain levels (600 kg/cu m) is a more valuable criterion for mechanical strength of Abies grandis than the usual percentage of latewood (Keller, 1971).

MATERIALS AND METHODS

The purpose of this chapter is to describe the experimental and analytical procedures used to meet the objectives in this study. The wood material used in this study was obtained from trees established as a genetic experiment in 1912 by the Forest Service. This experiment is one of the few sources in the world that consist of maturing trees of known parentage.

THE 1912 DOUGLAS-FIR HEREDITY STUDY

The 1912 Douglas-fir heredity study is a half-sib progeny study established by the Forest Service in Oregon and Washington. This experiment has been described in detail by Munger and Morris (1936). The following description of the experimental conditions and procedure is taken from their article. The general purpose of that experiment was to test seed from the important commercial range of Douglas-fir in western Washington and western Oregon. The objectives were:

- to determine what class of tree will provide the best seed for artificial reforestation;
- to determine the influence of locality upon the seed collected for use in artificial reforestation;

- to determine what classes of Douglas-fir make suitable seed trees to leave in logging operations.

Selection of Parent Trees

The seed collection was made in the fall of 1912 from 120 different parent trees (also called families) growing in 13 different localities (also called seed geographic sources or provenances) in western Oregon and western Washington (Appendix Figure 9). The seed-source locations ranged from 100 to 3850 feet (30 to 1173 m) elevation. The trees varied in age from 15 to 600 years and they represented various site quality classes and stand densities. They differed in size, dominance, character of crown and health. Table 1 shows the age, elevation and location of individual trees from which seed was collected. Not all the classes of seed-source conditions covered by the study were represented in every one of the localities. Altogether, 26 seed collections were made. Seed was collected from 3 to 11 trees in each of these instances except three.

Sowing and Planting

The collected seeds of each parent tree were sown in the nursery in the springs of 1913 and 1914. The resultant seedlings were transplanted within the nursery when 1 year

Table 1. Location, age, and elevation of parent trees.

Locality	Provenance	Age (years)	Elevation (m)
Northwestern Oregon	Gates	15-40	273
	Gates	60->200	288
	Palmer	20- 100	606
	Palmer	>200	909
Wind River Valley in southwestern Washington	Carson	15-200	121
	Race Track	20-100	788
	Wind River	>200	424
Central western Washington	Lakeview	35-150	30
Stillaquamish Valley in north Washington	Darrington	15-70	152
	Granite Falls	60->200	121
	Fortson	60-100	152
	Hazel	>200	273

old and outplanted on deforested areas when 2 years old. They were spaced uniformly 7 by 7 feet (2 by 2 m).

The progeny of each tree was planted on a straight single row. The same diagram of planting was used on all plantation areas in 1915, so that the progeny of any given parent formed the same row, by number in every plantation. The areas planted in 1915 were each 700 feet (213 m) long by 238 feet (73 m) wide. In 1916, an area of 700 feet (213 m) long by 77 feet (23 m) wide was planted adjacent to each 1915 plantation. In 1916 the number of seedlings available was considerably smaller than in 1915 and the planting diagram used was different from that used in 1915. At the time of planting, identification stakes were placed at the end of each row and at the corner of each plot, and a numbered metal tag was loosely wired to each seedling. This tag showed the number of the parent tree and the number of the transplant in the row. Where pedigreed stock was insufficient to complete rows, fillers of nonpedigreed stock were used so as to equalize spacing and competition. Where pedigreed trees failed to become established, no trees were planted in the blanks.

Planting Areas

In order to test the planting stock in several contrasting conditions, four plantations were established in four widely separated localities:

- southern Washington Cascades (in the Columbia National Forest);
- northern Washington Cascades (in the Snoqualime National Forest);
- northern Oregon Coast Range (in the Siuslaw National Forest);
- northern Oregon Cascades (in the Mount Hood National Forest).

In the northern Oregon Cascades three planting areas were used, at different altitudes. In each of the other three localities a single area was used. All the planting areas had been burned and some had been cleared before being burned. None of them received any silvicultural treatment. Each area was selected to maximize uniformity in slope, aspect, soil, and drainage. The locations of the planting areas are shown in Appendix Figure 9. The samples for the current study were taken from two of those plantations, namely from the Columbia National Forest (Wind River area) and the Mount Hood National Forest. More description of these two areas is given in Table 2.

Damage to Plantations

Since the early years of the plantations, the small trees were exposed to a number of damaging agencies such as fire and animals. As a result a considerable number of trees were thus killed or deformed. In some cases damage

Table 2. Description of planting locations.

	Wind River	Mount Hood
Location	40 miles northeast of Portland, OR, and 7 miles north of Bonneville Dam on the Columbia River. It is on the mile-width floor of the valley drained by the Wind River.	40 miles northwest of Portland in the Still Creek drainage basin
Elevation	1,100 feet	2,800 feet
Soil	deep, sandy clay loam	sandy loam top soil mixed with much rock
Annual Precipitation	48 inches	50 inches
Temperature	Mean daily minimum temperature for the coldest month is 26°F; during growing season daily maximum temperatures are high; 6-7 months have mean daily temperature above 46°.	Min. temp. is 22°F; normal mean daily maximum temperature of the warmest month is 68°; only 4 months have normal mean daily temperature above 46°.
Bud Burst	May 15	June 15. Short growing season
Site Quality	III	IV
Stocking	49%	74%

was so severe that a whole plantation had to be abandoned. In other cases patches of trees or whole rows were killed. The test plantations have not experienced any extraordinary damage from environmental factors such as wind, snow, ice and soil erosion.

SAMPLE SELECTION AND PREPARATION

The sample materials that I used in the current study were collected in 1979 for another study (McKimmy and Campbell, 1982). Increment cores were collected from two plantations of the 1912 Douglas-fir heredity test. Mortality had eliminated many trees and several of the seed sources, so the study had to settle on a relatively small subsample of the original experiment. The sample cores were taken from three randomly selected trees representing each of thirty families (parent trees) grown in two replication blocks (1915, 1916) in each of two plantations. The 30 families represented ten geographic seed sources (three families per seed source). Thus 180 trees were sampled at each plantation, a total of 360. The two plantations are Wind River and Mount Hood. Wind River is in southwestern Washington (335 m elevation, 45.25° N latitude), and Mount Hood is in northwestern Oregon (850 m elevation, 45° N latitude). Four of the ten seed sources sampled were from the Stillaguamish River drainage in northwestern Washington (Darrington, Granite Falls, Hazel,

and Fortson, approximately 48° N latitude); three were from the Wind River drainage in southwestern Washington (Carson, Racetrack, and Wind River, approximately 45.5° N latitude); one was from central western Washington in the Puget Sound Trough (Lakeview, 47° N latitude); and two were from northwestern Oregon (Gates and Palmar, 45.2° and 45.8° N latitude, respectively). All except that from Lakeview were from the western slopes of the Cascade Mountains.

Tree density can be estimated to a reasonable degree of accuracy by using breast-height increment cores, a technique developed and used by the U.S. Forest Service (Mitchell, 1958; Western Wood Density Survey, 1965). This technique is non-destructive and facilitates a larger sample for given cost.

Each tree was sampled with two 12-mm increment cores at north and south cardinal directions 1.3 m from the ground. Care was taken to orient the increment borer to attain perpendicular orientation of the growth rings to the longitudinal axis of the increment cores. However, some of the original samples were missing and all but six (two from each of three trees) were replaced in 1987. The extraction of two cores per tree would enable a more accurate estimation of the tree mean values by catering for any circumferential variation in wood characteristics (Cown, 1976). Moreover, the two cores would give an idea about

the within-tree variation in the studied properties. As soon as collected, the samples were labeled and stored in plastic drinking straws.

The sample increment cores were allowed to dry in the plastic straws to prevent warping. After they reached the air-dry state, the cores were glued between two mounting supports and machined to a smooth and uniform thickness of 4.00 ± 0.05 mm with a table saw and then stored at the x-ray scanning site.

EQUIPMENT AND PROCEDURE

Equipment

The x-ray densitometer system available at O.S.U. has undergone several modifications, but in its present form it comprises the following:

- Kevex 50 kilovolt 2 milliamp water-cooled x-ray tube (producing polychromatic energy spectrum)
- Kevex high voltage power supply
- large lead-lined containment box
- Victoreen photodiode x-ray scintillation detector with 0.1 x 1.0 x 2.0 mm aperture
- Victoreen electrometer used as a picoammeter
- Stepper motor-driven translation table, designed and built in house (Hoag, 1988)

- Hewlett-Packard VectraR desktop computer
- Data translation DT 2801 A/D, D/A and digital I/O board used with the computer for both equipment control and data acquisition
- ASYSTR computer software for equipment control, data acquisition, and data analysis

X-Ray Scanning

Until 1984, the Forest Products Department at Oregon State University relied on the film exposure technique (Bonder, 1984). In 1985 a direct scanning technique was developed and used (Choi, 1987). Since then the facility has received certain modifications in technique, instrumentation, and processing program (Hoag, 1988) and was used to scan the sample cores for the present study. The following is a brief description of some aspects of the procedure used.

A prepared wood specimen is placed on the sample carriage which is linked to a stepper motor-driven translation table preceded by the calibration wedge. This specimen scanning tray travels at a rate of 1 mm/second and at increments of 0.1 mm between the x-ray tube and the scintillation detector. Density values are derived from the variations in the attenuated x-rays passing through the specimens. The detector generates a current proportional to the amount of x-radiation passing through the wood

specimen. The higher the density of the wood the larger will be the absorption of x-rays and thus smaller current will be generated by the detector. The picoammeter receives this current and converts it to a voltage which is then sampled by the A/D board under computer software control. The acquisition and control program utilizes ASYSTR (1986, 1988) software. This software facilitates development of a number of data acquisition and control programs that are menu-selected upon entering the ASYSTR operating environment. The operating program is an integrated series of seven programs that facilitate the entire sampling and control process. There are two basic forms of output data saved for each ring of the test specimen. The scan density data (Appendix Figure 10) are saved in an ASYSTR-modified binary data file which includes the density profile for each increment of the scan specimen, calibration coefficients, operator's comments and time/date information. The ring data files (Table 3) are ASCII files in table form including the intra-ring width and density variables. These variables are ring width (RW), average ring density (RD), earlywood width (EWW), earlywood average density (EWD), earlywood minimum density (EWMIN), latewood width (LWW), latewood percent (LWP), latewood average density (LWD), latewood maximum density (LWMAX).

The programs developed for data acquisition (Hoag,

Table 3. Example of a ring-data file.

Sample number DF300.VGR 12:37:00.19 02/17/89

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-----
ring  ewd  ewmin  eww   lwd  lwmax  lww  ew-lw  avgd  lwp
count (g/cm^3) (mm)  (g/cm^3) (mm)  (mm)  trig.(g/cm^3) (%)
-----
1   .459  .428  2.014 .633  .734  1.007 .500   .517  .333
2   .395  .347  2.215 .622  .701  .906  .500   .461  .290
3   .361  .315  2.920 .616  .676  .705  .500   .410  .194
4   .381  .349  1.813 .570  .614  .604  .500   .429  .250
5   .400  .340  2.417 .593  .660  .705  .500   .444  .226
.   .     .     .     .     .     .     .     .     .
.   .     .     .     .     .     .     .     .     .
.   .     .     .     .     .     .     .     .     .
27  .439  .407  .503  .681  .804  .604  .500   .571  .545
28  .440  .408  .503  .634  .742  .604  .500   .546  .545
29  .435  .416  .403  .647  .757  .604  .500   .562  .600
30  .410  .377  .604  .666  .783  .705  .500   .548  .538
31  .436  .402  .503  .632  .697  .604  .500   .543  .545
32  .466  .452  .302  .573  .628  .302  .500   .520  .500

```

Core Density = .472 g/cm³

Core Length = 6.989 cm

1988) facilitate automatic triggering of ring boundaries, changing ring angle of skewed ring boundaries, adjusting for unextracted samples, smoothing of density profiles, exclusion of aberrations such as cracks and pitch pockets, and immediate conversion of voltage values and radial steps for useful ring variables.

Density Calibration

In order to convert the relative density values detected by the system to absolute, accurate density values, it is necessary to calibrate the system. Calibration is used to determine and verify the attenuation coefficients that are used in the density calculation. The procedure is as follows:

- The densities of a number of wood specimens that span the entire, expected density range were determined by gravimetric methods.
- Then calibration wood specimens were prepared for scanning by cutting them to the same thickness as the test specimens.
- The calibration wood specimens were scanned at the same time as density calibration wedges made from cellulose acetate.
- The x-rays transmitted by the calibration wood specimens were compared with those of the stepped wedges; density equivalent values were assigned to

each of the steps of the step wedges.

- The step wedges were then scanned with each of the test wood specimens to provide the absorption coefficient necessary for calculating the test-specimen density.

Resolution, Precision, and Accuracy

Factors affecting the reliability of the x-ray density data obtained by the facility at O.S.U. were well discussed by Hoag (1988). The maximum system resolution, measured by the minimum specimen width that may be resolved, is 0.11 mm in the radial direction when scanning at two steps per second and 0.053 mm/step using an aperture of 0.1 mm x 1.0 mm. Increasing either of these values will be at the expense of resolution. The system resolution is a limiting factor when recording values of such points as the maximum density, the minimum density and the boundary between the successive rings. This is especially the case in the outer, narrow growth rings, in which zone the poor vertical alignment of the tracheids may add much to the expected blurring. Decreasing the specimen thickness will improve the resolution, but at the same time will sacrifice measurement accuracy.

Accuracy is the question of how well the predicted x-ray density values match the density values obtained by gravimetric methods for the same wood samples. Accuracy of

the system is affected by electronic noise in the system, variation in sample thickness, and the calibration accuracy.

Some of the electronic noise was portioned out by hardware filtering (the use of aluminum filters); much of the unfiltered noise was eliminated by multiple sampling and then averaging of the sampled data. Working with 1.5 mm thick specimens, averaging twenty readings taken at five millisecond intervals resulted in reducing the standard deviation of the calculated density from 0.01 g/cm³ to 0.004 g/cm³ (Hoag, 1988). Since the amount of x-ray attenuation is dependent on the thickness, any variation in this measure should be expected to result in some errors in the density calculations.

A good measure of the system accuracy is the correlation between the x-ray density obtained by using the cellulose acetate calibration and the density determined previously by gravimetric methods for a number of specimens. A high correlation ($R^2 = 0.94$) was found by Hoag (1988). The average x-ray density was 2.4 percent lower than the gravimetric density.

An important measure also is the precision of the system in producing density values from several scans of the same scan line. As a measure of the system precision, Hoag (1988) examined the consistency of the calculated absorption coefficient. Sixty-two values of the absorption

coefficient obtained during a three-week period of scanning using the cellulose acetate calibration wedge had a small coefficient of variation of only 0.4 percent.

JUVENILE AND MATURE WOOD SAMPLES

The goal of this study was to give information on both juvenile and mature wood zones. To successfully select samples from these zones, all variables that might introduce systematic variation in the data should be held constant or at least not significantly different.

Juvenile wood is classified as that portion of the tree stem surrounding the pith in a cylindrical column and characterized by progressive change in cell features and wood characteristics. Generally, wood density is low in the growth rings nearest the pith then it increases rapidly in each succeeding ring across the juvenile zone until it levels off in mature wood. Such radial pattern is true at any height along the stem and has been explained in terms of changes in tracheid dimensions and ultimately in terms of needle development and hormone production (Larson, 1973). Panshin and de Zeeuw (1980) stated "Juvenile wood forms...as the result of prolonged influence of the apical meristems in the region of active crown on wood formation by the cambium. As the tree crown moves farther upward in a growing tree, the influence of the apical meristems on a

given cambial region decreases and mature wood is formed."

The above mentioned cross-sectional pattern suggests that the effect of the age of the cambial cells at the point of wood formation (i.e. ring position from the pith) is more pronounced during juvenility than maturity. As juvenile wood merges into mature wood, variations in density can be better explained by fluctuations in the prevailing seasonal growing conditions.

Accordingly, I chose 10 rings from each core that have the same biological age (ring number from the pith) to represent the juvenile wood zone. In about 40% of the sample cores the pith was missing and the position of the first available annual ring had to be estimated. In instances where the pith was absent in one of the cores from the same tree, I used the ring counts in the other core to determine the exact number of missing rings. However, in several cases the pith was missing in both cores of a tree. In these cases I estimated the number of missing rings by matching growth patterns in trees growing in the same plot and/or by using different charts of concentric circles drawn on transparent sheets (Appelquist, 1958). Assuming uniform annual increments during the first years of growth, on each chart a series of concentric circles with constant radius increment were drawn. Various charts would be laid on the core and the one that most nearly match the given ring pattern would be selected.

Then the pith position and the number of missing rings could be approximated.

After comparing the cores and the density profiles produced from them, I decided to start with ring number 6 since it was available in almost all the samples. The juvenile wood sample consisting of rings 6 to 15, will still represent the juvenile wood which was found in other studies to extend to about the 15th to 20th year in Douglas-fir (Errickson and Harrison 1974; Senft et. al. 1985).

In order to eliminate any variation in the mature wood sample that might be caused by seasonal growth differences, I selected from each core 10 rings that have formed within the same calendar years. Because of the image-blurring effect of the narrow growth rings toward the ends of cores, I decided to work with the growth rings produced during the years 1956 to 1965 (rings 16 to 25 from the bark). The mature wood and the juvenile wood rings did not overlap and they were separated by 7 to 17 rings in the various cores.

METHODS OF ANALYSIS

Before creating the tables of identified intra-ring variables from the scan density data, I inspected each core density profile to match the scanned rings with the rings of the actual cores. Then I removed rings that included

cracks, compression wood, and pitch pocket from the profile. Due to this cleaning some of the juvenile and mature wood samples consisted of 8 to 9 rings. It was thought that sacrificing few rings per sample would be better than including rings from outside the previously selected zones.

Another decision that I had to make was the demarcation of the boundary between earlywood and latewood. In the previous chapter, I have discussed some of the alternatives for determining this boundary. Many of these proved unsuitable for the material used in this study. For example, relative boundaries, like the minimum and maximum density mid-point, have the advantage of being objective, but they result in growth rings that have variable earlywood-latewood boundaries even within the same core. The resultant earlywood and latewood characteristics will not have common bases for comparison and density values that are considered latewood in some rings may fall well below the ring mid-point density level in other rings. A fixed-level earlywood-latewood boundary is more appropriate to eliminate such sources of variation that may confound the interpretation of variations caused by the groups of interest. Considering the foregoing, I decided to use an earlywood-latewood boundary that gives a number of rings equal to that of the actual cores. It is a density level that would work both in the juvenile and mature wood zones.

I inspected the density profiles to estimate the number of rings that would be identified from the scan density data using each of four density levels, namely 0.50, 0.55, 0.60, and 0.65 g/cm³. I labeled a level satisfactory if using it would resolve all the rings at least up to a point beyond the mature wood sample. So adopting one of these levels does not mean that all the rings in all cores would be identified. The first figure was an arbitrary level suggested by Cown and Parker (1978), and was shown to be satisfactory in softwoods. The second and fourth figures were obtained respectively by Heger et. al. (1974) and Choi (1987) based on Mork's definition. Based on the results of the above comparison, I used an earlywood-latewood density level of 0.55 g/cm³ as it proved suitable in 99% of the cores. Then I compiled and filed all data relating to the intra-ring variables into the computer using the Symphony Spread Sheet where I added a new variable to label the sample rings of the two zones (juvenile and mature wood). For each zone and core, I calculated the arithmetic means of the intra-ring variables. All statistical analyses were carried out using the Statistical Analysis System computing package (SAS Institute, 1987) on IBM 4381 and an AST personal computer.

Analysis of variance provides a convenient means of partitioning the total variation into parts attributable to

the various effects under consideration. The analyses for each intra-ring characteristic employed two models. The first analysis of variance (PROC GLM, SAS Institute, 1987) utilized core averages (714 observations) to test for differences among the 30 half-sib families. The variation was partitioned into: plantation locations, replications within plantations, families (30 plots), family interactions with location and replication, and within plot. The ANOVA format and F-tests in terms of expected mean squares are given in Appendix Table 10. The second model included additional terms to separate the variance due to families into variance due to geographic seed sources (provenances) and that due to families within sources. This is the same as the model used by McKimmy and Campbell (1982). The format for this analysis is given in Appendix Table 11. These analyses were based on the assumptions of additivity, homogenous variance, zero correlations, and normally distributed variables.

The latewood percent (LWP) data, being proportional data, are constrained between two values (0.0 and 1.0) and thus will rarely produce normally distributed residuals and thereby violate one of the assumptions of variance analysis. Such data often need to be transformed prior to analysis; one transformation that will create unconstrained data and stabilize the variance if needed is the arcsine square root transformation. So, the analysis of variance

for LWP was conducted on both the actual LWP data and the arcsine square root transformed data. Since the F-test results of both the actual and transformed data were exactly the same and the back transformed variance components were very much the same as those for the actual data, only the results of the actual data will be given in the next chapter.

All effects, except the seed sources (provenances), were considered to be random. In order to determine which provenance means differ, Fisher protected LSD (Least Significant Difference) was used. Since some F-tests did not have appropriate denominators, approximate F-tests were conducted by synthesizing some of the denominators and degrees of freedom (Snedecor and Cochran, 1982). Beside these analyses, components of variance were calculated according to expectations of mean squares given in Appendix Tables 10 and 11. Studying the distribution of variance components as percentages of the total variance (sum of all variances) facilitates the determination of the relative importance of the sources of variation. Moreover, coefficients of variation (C.V. %) for each characteristic were calculated, as the square root of each variance component divided by the trait mean, to study changes in trends over time (from juvenile to mature period). The use of C.V. % would compensate for means of different sizes to make comparisons among intra-ring characteristics and

between the two zones. Here, all error deviations were grouped together to make one error term; thus the error term included replications within plantations ($\sigma_{r(l)}$), main plot error ($\sigma_{r(l)*s}$), subplot error ($\sigma_{r(l)*f}$), and sampling error (σ_c).

In addition, another set of analyses of variance was performed utilizing tree averages for each intra-ring characteristic in the juvenile and mature wood (Appendix Table 12). The purpose of this analysis was to facilitate heritability calculations and genetic correlations. To make biological interpretations of the variance components the following assumptions described by Stonecypher et.al. (1964) were accepted:

- inheritance is of a normal diploid type ,
- the parent trees are random members of non-inbred populations,
- there is no epistasis (inter-locus gene interaction),
- progenies are half-sibs (offsprings from one maternal parent have different paternal parents), and
- there are no maternal effects.

Narrow-sense heritability for an open-pollinated half-sib assumption is determined by dividing the additive genetic variance over the phenotypic variance. The additive

variance (denoted σ^2_a) was calculated as $4 \times \sigma^2_f$. With the seed sources confounded, phenotypic variance (σ^2_p) was calculated as :

$$\sigma^2_p = \sigma^2_w + \sigma^2_{f*l} + \sigma^2_{f*r(l)} + \sigma^2_f .$$

(with these and the following notations explained in Appendix Tables 10 and 11). Heritabilities were calculated on an individual tree (H^2_i) and family (H^2_f) basis using equations 1 and 2 (Wright, 1976).

$$H^2_i = \frac{4 * \sigma^2_f}{\sigma^2_w + \sigma^2_{f*r(l)} + \sigma^2_{f*l} + \sigma^2_f} \quad (1)$$

$$H^2_f = \frac{\sigma^2_f}{MS_f / 12} \quad (2)$$

MS_f is the mean square associated with the family

$$(MS_f = \sigma^2_w + 3 \sigma^2_{f*r(l)} + 6 \sigma^2_{f*l} + 12 \sigma^2_f).$$

In these traditional formulae, the variance components of the replication block and plantation site are invariably excluded from the denominator of single-tree heritability (H^2_i). The justification for this exclusion is that correction will be made for these effects before utilizing phenotypic measurements or gains in selection work (Cotterill, 1987). For the calculation of family heritability (H^2_f), these two variances are not included in the denominator because variation among families is usually free of the plantation and replication variance.

With the seed sources accounted in the analysis,

heritabilities were also obtained utilizing the variance of the families-within-sources. The following equations were used:

$$H^2_i = \frac{4 * \sigma_{f(s)}}{\sigma^2_w + \sigma^2_{f(s)*r(l)} + \sigma^2_{f(s)*l} + \sigma^2_{f(s)}} \quad (3)$$

$$H^2_{f(s)} = \frac{\sigma^2_{f(s)}}{MS_{f(s)} / 12} \quad (4)$$

$MS_{f(s)}$ is the mean square associated with the family within sources

$$(MS_{f(s)} = \sigma^2_w + 3 \sigma^2_{f(s)*r(l)} + 6 \sigma^2_{f(s)*l} + 12 \sigma^2_{f(s)}).$$

Namkoong et al. (1966) and Falconer (1989) discuss in details the theoretical bases of the above equations. The standard errors of heritabilities were estimated as shown by Wright (1976).

Pearson (simple) correlation coefficients (SAS Institute, 1987) between selected characteristics were calculated using tree averages (360 observations), family-plots means, and seed sources means. Estimates of genetic correlation coefficients between two characteristics (x,y) were computed as the family intra-class correlation coefficients (Falconer, 1989). Using the components of variance and covariance among families, additive genetic correlations were obtained as

$$r_a = \frac{COV_{f(x,y)}}{[\sigma^2_{f(x)} * \sigma^2_{f(y)}]^{1/2}} \quad (5)$$

The estimate of the covariance of two traits (x,y) was obtained using the variance of the sum of the two traits (Kempthorne, 1957).

Since

$$\sigma^2_{f(x+y)} = \sigma^2_{f(x)} + \sigma^2_{f(y)} + 2 \text{COV}_{f(x,y)}$$

then

$$\text{COV}_{f(x,y)} = \frac{\sigma^2_{f(x+y)} - \sigma^2_{f(x)} - \sigma^2_{f(y)}}{2} \quad (6)$$

$\sigma^2_{f(x+y)}$ was obtained from the analysis of variance of the compound observation x+y for each individual.

RESULTS AND DISCUSSION

Various characterizing data for both the juvenile and mature wood will be presented, together with the necessary explanatory information. This chapter is organized into the following sections, outlining the strategy for data analysis:

- general description of the data,
- analysis of variance and means,
- components of the phenotypic variance and heritabilities, and
- phenotypic and genetic correlations.

An interpretation of the results for each section follows the data presented.

The study included the following intra-ring variables: early-wood density (EWD), earlywood width (EWW), latewood density (LWD), latewood width (LWW), average ring density (RD), ring width (RW), and latewood percent (LWP). The abbreviations shown between parentheses will be used in subsequent presentation of the results and discussion. The terms 'rate of growth' and 'growth rate parameters or components' are used occasionally when referring to ring width and/or its components; however, I am aware of the fact that these radial characteristics are not ideal measures of the rate of growth, which should be assessed as

a three-dimensional property. These radial parameters are part of volume growth and might have direct correlation with height, and they are included in most lumber grading systems because of their indirect relation to some wood quality parameters.

GENERAL DESCRIPTION OF THE DATA

To give a general view of the study material, simple statistics are listed in Table 4. The means were calculated using data for tree averages (360 observations). Mean ring density (RD) in juvenile wood varied from 0.376 to 0.599 around an average of 0.484 g/cm³. The values in mature wood were respectively 0.436, 0.754, and 0.570 g/cm³. It is of special interest to compare our averages with those of McKimmy and Campbell (1982) who used the same core sample to study wood density and ring width. The ring widths obtained in the current study were almost the same as those obtained by McKimmy and Campbell, but the densities were higher. The difference in the technique used in the density determination and in sampling within cores may account for part of this. For example, the density values were based on 9% moisture content and for an estimate of a value based on oven-dry weight the density values in Table 4 may be multiplied by 0.91. It is also possible that the presence of some extractives contributed to the high density values in this study by causing a

Table 4. Simple descriptive statistics for the intra-ring characteristics in (a) juvenile and (b) mature wood.

a) JUVENILE WOOD SAMPLE

Variable ¹⁾	Minimum	Maximum	Mean	CV %
EWD	0.2923	0.4869	0.3800	6.84
EWW	1.4601	5.6628	2.8963	26.04
LWD	0.5890	0.8666	0.7289	7.09
LWW	0.4329	2.5275	1.1972	34.03
RD	0.3763	0.5989	0.4836	7.48
RW	2.3009	7.6523	4.0932	25.96
LWP	0.1463	0.4742	0.2932	18.67

b) MATURE WOOD SAMPLE

Variable	Minimum	Maximum	Mean	CV %
EWD	0.3244	0.5258	0.4231	7.11
EWW	0.3684	1.7522	0.9533	28.61
LWD	0.6030	0.9528	0.7415	7.99
LWW	0.3753	1.6686	0.8020	29.34
RD	0.4362	0.7538	0.5703	9.68
RW	0.9420	2.9603	1.7553	22.07
LWP	0.2638	0.6896	0.4637	19.42

¹⁾ densities are in g/cm³ and widths are in mm.

differential absorption of the X-rays. Current research work at the Department of Forest Products, O.S.U. (Krahmer, 1990) supports this proposition and shows that a difference of 0.05 g/cm^3 between extracted and unextracted core density can be expected. Considering the above, the juvenile and mature wood average densities can be adjusted to 0.39 and 0.47 g/cm^3 , respectively. Average values published for coastal Douglas-fir were 0.43 g/cm^3 by Drow (1957) and 0.45 g/cm^3 by the U.S. Forest Service (1965). In this connection, it is of interest to note that the study by the Forest Service (1965) shows that whole-tree density seems to be lower than the core density at breast height.

Within a juvenile growth ring, wood density increased from earlywood to latewood (Table 4) by an average of 350 kilogram per cubic meter (92 % of the EWD). Within a mature growth ring the average difference between earlywood and latewood density was 75 % of the EWD value. In the juvenile zone, the average earlywood width was 2.5 times the latewood width; when the trees reached maturity, the widths of earlywood and latewood were, in average, almost equal (Table 4).

As would be expected, the values of the density parameters and the latewood percent were greater in the mature wood than in the juvenile wood sample, and the

values of the other growth rate parameters were lower (Table 4). Based on the juvenile wood values, there was an average increase of about 18 % (87 kg/m^3) in ring density (RD), 11 % (43 kg/m^3) in earlywood density (EWD), and 58 % in latewood percent (LWP) from juvenile to mature wood. In comparison, latewood density (LWD) showed, in average, a very small change (1.7 %). From these results it seems that the variation in wood density between the juvenile and mature wood were caused mainly by differences in the width of latewood relative to that of earlywood and by differences in earlywood density (EWD). The difference between the two zones in wood density is comparable to that known for conifers (Bendtsen 1978), but appears mild if compared to the findings of Senft et al. (1985) in a study of 60-year-old Douglas-fir. They reported a difference of 32 % between the average wood density of the first 15 rings and that of the rings formed after. The above results also clearly demonstrates that, in terms of wood density, the variation within growth rings is much larger than that between an average ring in juvenile wood and an average ring in mature wood.

Figure 1 illustrates the variation of the studied characteristics along the radius; each point, at least from ring number six onward, is the average of 360 trees. The plots confirm the trends already shown by other workers for

ring density and its components in small samples of Douglas-fir (Kennedy and Warren, 1969, Senft et al., 1985, and Megraw, 1986,). Average ring density (RD), earlywood density (EWD), and latewood percent (LWP) decreased in the first few rings and thereafter increased linearly across the radius up to ring 35; the higher density of rings 1 to 5 in comparison to rings 6 to 10 is attributable to the higher earlywood density and higher percentage of latewood within the first five years. The rest of the growth rate parameters increased within the first six to eight years of growth and then dropped gradually to a minimum around age thirty. These trends of the average data (Fig. 1) seem to be typical for Douglas-fir. The trends suggest that, at least at breast height, biological maturity (stability) begins sometime after 30 years of growth depending upon the property under consideration. The gradual change observed in the individual-tree data for most of these variables (not shown here) makes it unclear as to where a demarcation line between juvenile and mature wood can be drawn. Only latewood density (LWD) showed a more or less sharp boundary between the two zones as they exhibited a rapid increase during the first twelve years followed by a constant or a mild decreasing trend. For the other traits, it seems reasonable to use some optimum values to set a boundary between the two zones; good candidates should be searched for among optimum values that have meaning to the

Figure 1. Intra-ring characteristics at breast height as a function of ring position (age) from the pith.

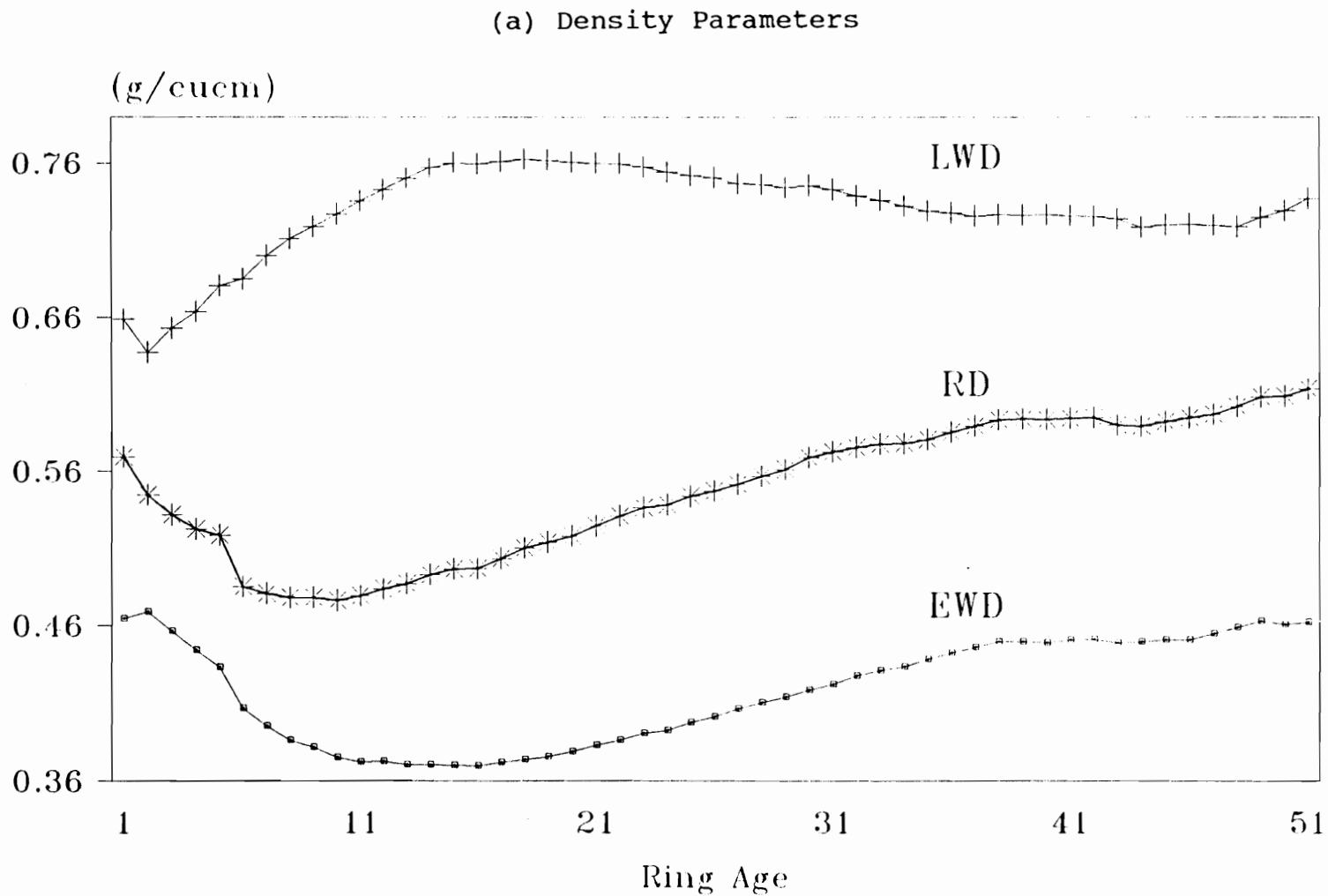
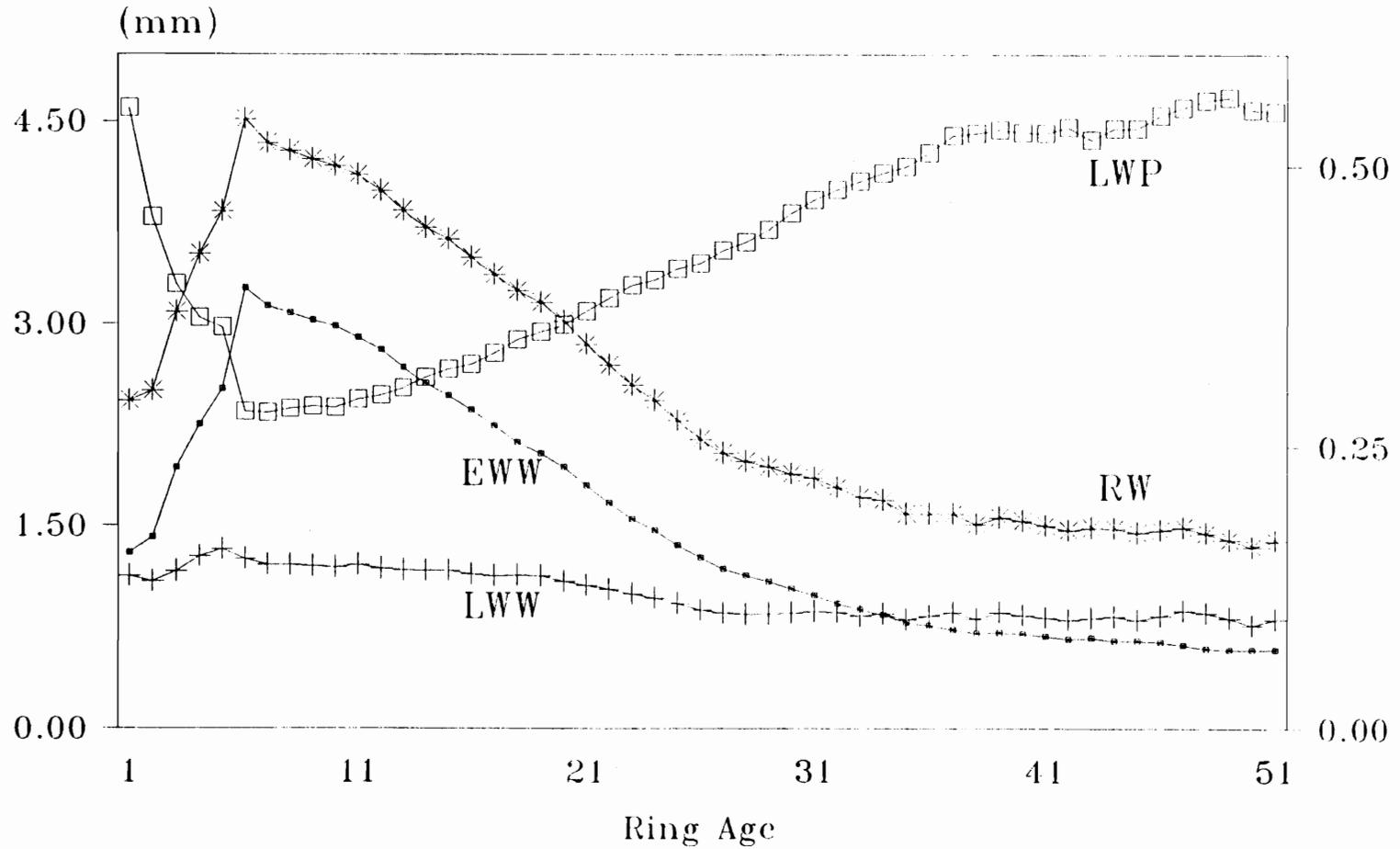


Figure 1. (continued)

(b) Width Parameters



intended end uses. Unfortunately, such values are not available in the scarce literature of intra-ring variables or even of the more thoroughly investigated wood density. Judging by an optimum density such as the average listed for Coast Douglas-fir in the Wood Handbook (0.45), it seems that juvenile wood does not extend beyond ring 20 from the pith (Fig. 1).

Based on the coefficient of variation (Table 4), the ring width components (EWW, LWW, RW, and LWP) exhibited considerably more variation than the ring density components (EWD, LWD, and RD). This was true in both the juvenile and mature wood samples. Partitioning of the variation around the above discussed averages is the subject of the following sections.

ANALYSIS OF VARIANCE

Analysis of variance was performed on core averages (714 observations) to test for differences between the two plantations as well as among and within the 30 half-sib families (Appendix Table 10). Another analysis of variance was conducted using core averages to separate the variation among the 30 families into that due to provenances (geographic seed sources) and families within provenances (Appendix Table 11). All effects, except seed sources, were assumed to be random. Tables 5 gives the mean squares

and the results of the F-tests obtained from both analyses of variance for the juvenile wood data and Table 6 for the mature wood data. Significant differences were determined at the probability level $\alpha = 0.05$ and 0.01 . Components of variance were calculated to facilitate determination of the major sources of variation for each trait; Table 7 lists the variance components together with their relative magnitudes for juvenile and mature wood. Figure 2 shows graphical presentation of the coefficients of variation (which were calculated as the percentage the square roots of the variance components to the trait mean) to compare variation around means of variable sizes.

Before proceeding in discussion of the results, I draw attention to two features of the current data:

The mature wood sample was selected in a way to avoid systematic variations attributable to seasonal growth conditions; therefore it exhibited large variations in ring age. The sample that had the youngest wood consisted of rings 23 to 32 and that with the oldest wood consisted of rings 33 to 42 from the pith. Thus, it was of interest to see if ring age was important enough to be included as a covariate in the analysis of the mature wood data. Whether or not an increase in precision would result from the covariance analysis would depend on how closely the intra-

ring variables and ring age were linearly related after removal of the treatments effects. So, the appropriateness of the previous analysis was checked by recalculating the analysis of variance for RD and RW using ring age (ring number from the pith) as a covariate. This preliminary analysis (Appendix Table 20) revealed that adjustment of the mature wood data for differences in ring age did not change the map of significance of the sources of variation and generally had little or no effect in the relative magnitudes of the variance components. One exception was the relative contribution of plantations to the total variation in ring density, which decreased considerably as a result of adjusting the data for differences in ring age. This reduction in the relative importance of plantation effect was compensated for by increased contributions of the other sources proportional to their relative importance before adding the covariate to the model. The results also indicate that variation in ring age, which reflects differences among the trees in the rate of early height growth, were caused mainly by differences between the two plantation sites.

The earlywood-latewood boundary was objectively selected as the fixed value (0.55 g/cm^3) that divide the density profile across the radius into a number of units (each comprising a minimum and a maximum) comparable to the

actual number of rings in the corresponding core (see relevant section in chapter 3). The terms earlywood and latewood, in the present study, simply refer to the two zones within the growth ring with wood densities less and greater than 0.55 g/cm^3 , respectively. So these terms do not necessarily bear relationship to Mork's definition. In this context, it is noteworthy that Heger et al. (1974), based on Mork's definition, suggested a similar demarcation density value (0.54 g/cm^3) for 33-year-old Douglas-fir.

Planting Locations

The analysis of variance indicated significant differences between the two plantations for most of the studied characteristics (Tables 5 and 6). In juvenile wood, plantation variance accounted for more than 55 percent of the total variation in ring width and its components (EWW and LWW), and for about 6 (RD) to 45 (LWD) percent of the total variation in ring density parameters (Table 7). In the mature wood sample, the relative contribution of plantations showed an average of 28 percent and ranged from about 2 (RW) to above 52 (LWP) percent.

The warmer environment at Wind River produced the wider juvenile ring width (RW) and the higher mature ring density (RD) ($p \leq 0.01$). This result is in accordance with the findings of McKimmy and Campbell (1982). Wind River also produced the wider latewood width (LWW) and higher

Table 5. Summary of variance analysis (F-test) in juvenile wood.

SOURCE	EWD		EWW		LWD		LWW		RD		RW		LWP	
PLANTATION	13.52	*	132.75	**	36.19	**	252.86	**	4.94	NS	298.77	**	19.32	**
REP in PLANT	7.70	**	0.54	NS	3.61	*	0.62	NS	6.08	**	0.08	NS	2.79	NS
FAMILY	2.57	**	1.84	NS	1.53	NS	2.35	**	3.61	**	1.16	NS	2.97	**
PLANT x FAM	1.29	NS	1.34	NS	0.88	NS	1.25	NS	1.19	NS	1.20	NS	1.30	NS
REP(PL) x FAM	1.03	NS	0.94	NS	1.33	NS	0.91	NS	0.84	NS	0.98	NS	0.97	NS
PROVENANCE	5.75	**	1.50	NS	1.18	NS	2.49	*	4.98	**	1.34	NS	3.34	**
PLANT x PROV	0.73	NS	1.33	NS	1.35	NS	1.34	NS	1.07	NS	1.22	NS	1.63	NS
REP(PLANT) x PROV	1.18	NS	1.19	NS	1.25	NS	1.22	NS	0.59	NS	1.53	NS	0.51	NS
FAMILY (PROV)	0.65	NS	1.42	NS	1.89	NS	1.60	NS	1.14	NS	1.61	NS	1.31	NS
PLANT x FAM (PROV)	1.45	NS	1.08	NS	0.57	NS	0.89	NS	1.10	NS	0.96	NS	0.94	NS
REP(PL) x FAM (PROV)	0.98	NS	0.89	NS	1.24	NS	0.85	NS	0.97	NS	0.84	NS	1.15	NS
WITHIN PLOT	1.62	**	3.99	**	2.02	**	3.50	**	3.77	**	3.54	**	3.50	**

** significant at the 0.01 level; * significant at the 0.05 level;
 NS not significant at the 0.05 level.

Table 6. Summary of variance analysis (F-test) in mature wood.

SOURCE	EWD	EWV	LWD	LWV	RD	RW	LWP
PLANTATION	2.18 NS	11.47 *	24.02 *	23.03 *	178.67 **	1.81 NS	157.54 **
REP in PLANT	2.23 NS	1.47 NS	3.13 NS	7.26 **	1.63 NS	3.36 NS	1.29 NS
FAMILY	2.75 **	1.61 NS	1.26 NS	2.36 NS	4.49 NS	1.33 NS	4.82 NS
PLANT x FAM	0.79 NS	0.92 NS	0.8 NS	1.21 NS	0.83 NS	1.09 NS	0.71 NS
REP(PL) x FAM	1.46 *	1.09 NS	1.32 NS	1.11 NS	0.88 NS	1.09 NS	1.02 NS
PROVENANCE	3.67 **	1.97 NS	1.26 NS	0.93 NS	2.76 *	1.12 NS	2.44 *
PLANT x PROV	0.43 NS	0.69 NS	0.70 NS	1.19 NS	0.82 NS	0.79 NS	0.93 NS
REP(PL) x PROV	3.03 **	1.62 NS	1.69 NS	1.03 NS	0.86 NS	1.57 NS	1.15 NS
FAMILY (PROV)	1.09 NS	1.03 NS	1.24 NS	2.70 **	2.54 *	1.26 NS	3.23 **
PL x FAM (PROV)	1.44 NS	1.16 NS	0.93 NS	0.97 NS	0.88 NS	1.28 NS	0.69 NS
REP(PL) x FAM (PROV)	0.90 NS	0.91 NS	1.08 NS	1.10 NS	0.92 NS	0.92 NS	0.98 NS
WITHIN PLOT	2.65 **	5.22 **	1.76 **	2.77 **	3.50 **	4.47 **	3.23 **

** significant at the 0.01 level; * significant at the 0.05 level;
 NS not significant at the 0.05 level.

latewood percent (LWP) and latewood density (LWD) during both juvenility and maturity (Tables 5 and 6). The results of mature RD and LWD support the findings of Lassen and Okkonen (1969) that wood density and latewood percent in trees from low elevations were greater than in trees from high elevations.

The lack of significance of plantation differences in mature ring width (RW) and juvenile ring density (RD) was caused by an outweighing effect of their components. Ring width was obtained as the sum of EWW and LWW and in mature wood, the plantation that had the wider EWW (Mt. Hood) produced the narrower LWW. This result is not in keeping with the dates of bud bursting in the two plantations, which suggest that radial growth resumes in Mt. Hood several weeks later than in Wind River (Table 2). The most plausible suggestion may be that the growth conditions in Mt. Hood allowed the trees to produce earlywood for a longer period than in Wind River where latewood formation commenced much earlier. To give similar reasoning for ring density is not as direct as it is for ring width. This is because RD was obtained as the weighted average of EWD and LWD, the weighing factors being EWW and LWW. However, juvenile EWD was significantly lower in Wind River than in Mt. Hood and LWD was higher. This trend, coupled with a higher LWP in Wind River (and hence a higher contribution

of LWD to RD), resulted in a non-significant plantation effect for juvenile ring density.

The effect of replication blocks probably reflects micro-environmental variations (e.g. soil nutrients, competition) within plantation locations. Variation between replications was significant only for density parameters (EWD, LWD, and RD) in the juvenile wood zone and for LWW and RW in the mature wood zone (Tables 5 and 6).

The relative contribution of the plantation variance component to the total variance during maturity was smaller than during the early years of growth for most of the traits (Table 7); exceptions were RD, LWD, and LWP. The results of the coefficients of variation (Fig. 2), shows that even after accounting for the decline in the mean values of RW, EWW, and LWW from juvenile to mature wood, a decrease in the plantation variance was still evident. The decline in the plantation variance component was, in all instances, accompanied with a comparable rise in the sum of error deviations (the term error in Fig. 2).

Expressing the square root of plantation variance as a ratio of the RD and LWP means (Fig. 2), gave the evidence that the increase in the absolute size of the plantation variance with advanced stand development (Table 7) was real

and not just the result of increasing means. This increasing importance of the plantation effect from the juvenile to mature period was accompanied by a decrease in the cumulative error in LWP but not in RD. For LWD, the magnitudes of the plantation variance in juvenile and mature wood were not different (Table 7) and so were the coefficients of variation (Fig. 2) because LWD means in the two zones were only slightly different (Table 4).

Genetic Parameters

The distinctiveness of the family and provenance groupings reflect the strength of genetic effect. The analysis of variance showed significant variability among the 30 half-sib families for all traits ($p \leq 0.05$) in the juvenile wood zone except for EWW and RW ($p \approx 0.07$) and LWD ($p \approx 0.10$). When families were grouped by their geographic origins (provenances), none of the traits in the juvenile wood exhibited significant differences ($p \leq 0.05$) among families-within-provenances; only LWD and RW showed a slight tendency to differ among families-within-provenances (significance at $p \approx 0.08$ and 0.10). At the same time, differences among provenances were statistically significant ($p \leq 0.05$) for EWD, RD, LWW, and LWP. The above results, taken together, might be construed to mean that when the effect of provenances was removed, the remaining variation in juvenile wood traits due to families-within-

Table 7. Variance components and their relative contribution to the total variance of intra-ring characteristics in juvenile and mature wood.

SOURCE OF VARIATION	JUVENILE WOOD		MATURE WOOD	
	VARIANCE COMPONENT	% OF TOTAL	VARIANCE COMPONENT	% OF TOTAL
Earlywood density (EWD)				
PLANTATION	0.000285	28.71	0.000030	2.39
REP in PLANT	0.000036	3.62	0.000025	1.96
FAMILY	0.000076	7.98	0.000114	9.39
PLANT x FAM	0.000017	1.76	0.000000	0.00
REP(PL) x FAM	0.000006	0.60	0.000105	8.65
PROVENANCES	0.000101	10.18	0.000114	8.80
PLANT x PROV	0.000000	0.00	0.000000	0.00
REP(PL) x PROV	0.000008	0.82	0.000138	10.71
FAMILY(PROV)	0.000000	0.00	0.000006	0.53
PLANT x FAM(PROV)	0.000030	3.06	0.000045	3.51
R(PL) x FAM(PROV)	0.000000	0.00	0.000000	0.00
WITHIN PLOT	0.000292	29.40	0.000422	32.61
CORES in TREES	0.000241	24.21	0.000511	39.48
Earlywood width (EWW)				
PLANTATION	0.504305	55.46	0.011326	11.61
REP in PLANT	0.000000	0.00	0.000502	0.51
FAMILY	0.021146	2.35	0.003509	3.73
PLANT x FAM	0.015084	1.67	0.000000	0.00
REP(PL) x FAM	0.000000	0.00	0.002044	2.17
PROVENANCES	0.012720	1.40	0.003360	3.45
PLANT x PROV	0.010741	1.18	0.000000	0.00
REP(PL) x PROV	0.005555	0.61	0.004073	4.18
FAMILY(PROV)	0.009906	1.09	0.000199	0.20
PLANT x FAM(PROV)	0.003552	0.39	0.001612	1.65
R(PL) x FAM(PROV)	0.000000	0.00	0.000000	0.00
WITHIN PLOT	0.214169	23.55	0.051864	53.17
CORES in TREES	0.148377	16.32	0.024603	25.22

Table 7. (Continued)

SOURCE OF VARIATION	JUVENILE WOOD		MATURE WOOD	
	VARIANCE COMPONENT	% OF TOTAL	VARIANCE COMPONENT	% OF TOTAL
Latewood density (LWD)				
PLANTATION	0.002068	45.31	0.001955	32.83
REP in PLANT	0.000064	1.41	0.000099	1.67
FAMILY	0.000097	2.17	0.000074	1.25
PLANT x FAM	0.000000	0.00	0.000000	0.00
REP(PL) x FAM	0.000159	3.54	0.000241	4.07
PROVENANCES	0.000022	0.48	0.000035	0.60
PLANT x PROV	0.000062	1.37	0.000000	0.00
REP(PL) x PROV	0.000049	1.09	0.000191	3.21
FAMILY(PROV)	0.000075	1.65	0.000045	0.77
PLANT x FAM(PROV)	0.000000	0.00	0.000000	0.00
R(PL) x FAM(PROV)	0.000114	2.50	0.000064	1.08
WITHIN PLOT	0.000712	15.60	0.000979	16.46
CORES in TREES	0.001396	30.59	0.002583	43.38
Latewood width (LWW)				
PLANTATION	0.193715	67.20	0.035957	42.12
REP in PLANT	0.000000	0.00	0.002378	2.79
FAMILY	0.009338	3.29	0.004328	5.08
PLANT x FAM	0.000804	0.28	0.000477	0.56
REP(PL) x FAM	0.000000	0.00	0.001173	1.38
PROVENANCES	0.007206	2.50	0.000000	0.00
PLANT x PROV	0.002147	0.74	0.000691	0.81
REP(PL) x PROV	0.001295	0.45	0.000106	0.13
FAMILY(PROV)	0.002372	0.82	0.004546	5.33
PLANT x FAM(PROV)	0.000000	0.00	0.000000	0.00
R(PL) x FAM(PROV)	0.000000	0.00	0.000992	1.16
WITHIN PLOT	0.042222	14.65	0.019112	22.39
CORES in TREES	0.039315	13.64	0.021573	25.27

Table 7. (Continued)

SOURCE OF VARIATION	JUVENILE WOOD		MATURE WOOD	
	VARIANCE COMPONENT	% OF TOTAL	VARIANCE COMPONENT	% OF TOTAL
Ring density (RD)				
PLANTATION	0.000098	5.66	0.002606	52.79
REP in PLANT	0.000034	1.96	0.000008	0.18
FAMILY	0.000231	13.55	0.000341	6.91
PLANT x FAM	0.000023	1.36	0.000000	0.00
REP(PL) x FAM	0.000000	0.00	0.000000	0.00
PROVENANCES	0.000232	13.35	0.000186	3.78
PLANT x PROV	0.000006	0.38	0.000000	0.00
REP(PL) x PROV	0.000000	0.00	0.000000	0.00
FAMILY(PROV)	0.000013	0.75	0.000162	3.28
PLANT x FAM(PROV)	0.000016	0.94	0.000000	0.00
R(PL) x FAM(PROV)	0.000000	0.00	0.000000	0.00
WITHIN PLOT	0.000785	45.15	0.001096	22.20
CORES in TREES	0.000552	31.80	0.000877	17.77
Ring width (RW)				
PLANTATION	1.326484	67.99	0.003674	1.92
REP in PLANT	0.000000	0.00	0.005151	2.69
FAMILY	0.029465	1.53	0.004565	2.48
PLANT x FAM	0.009693	0.50	0.001845	1.00
REP(PL) x FAM	0.000000	0.00	0.004415	2.40
PROVENANCES	0.012593	0.65	0.001217	0.64
PLANT x PROV	0.011300	0.58	0.000000	0.00
REP(PL) x PROV	0.021782	1.12	0.007951	4.16
FAMILY(PROV)	0.018098	0.93	0.003403	1.78
PLANT x FAM(PROV)	0.000000	0.00	0.005738	3.00
R(PL) x FAM(PROV)	0.000000	0.00	0.000000	0.00
WITHIN PLOT	0.313695	16.08	0.104070	54.43
CORES in TREES	0.247032	12.66	0.059991	31.38

Table 7. (Continued)

SOURCE OF VARIATION	JUVENILE WOOD		MATURE WOOD	
	VARIANCE COMPONENT	% OF TOTAL	VARIANCE COMPONENT	% OF TOTAL
	Latewood percent (LWP)			
PLANTATION	0.000697	16.82	0.007195	54.57
REP in PLANT	0.000024	0.60	0.000014	0.11
FAMILY	0.000453	11.36	0.000920	6.97
PLANT x FAM	0.000089	2.23	0.000000	0.00
REP(PL) x FAM	0.000000	0.00	0.000028	0.21
PROVENANCES	0.000414	9.99	0.000440	3.34
PLANT x PROV	0.000124	3.00	0.000000	0.00
REP(PL) x PROV	0.000000	0.00	0.000063	0.48
FAMILY(PROV)	0.000059	1.42	0.000484	3.67
PLANT x FAM(PROV)	0.000000	0.00	0.000000	0.00
R(PL) x FAM(PROV)	0.000106	2.58	0.000000	0.00
WITHIN PLOT	0.001513	36.51	0.002631	19.96
CORES in TREES	0.001205	29.08	0.002356	17.87

Figure 2. Coefficients of variation based on variance components for intra-ring variables in juvenile and mature wood.

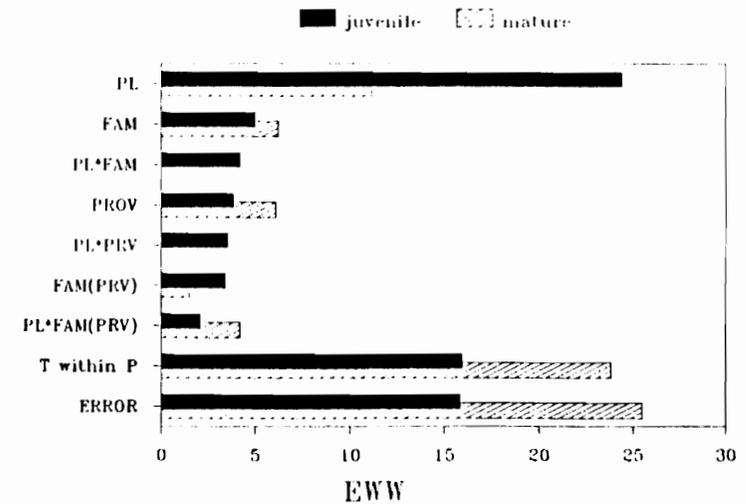
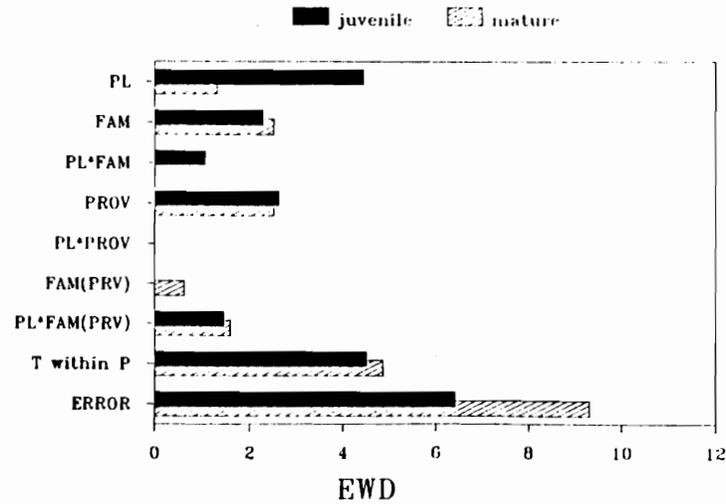
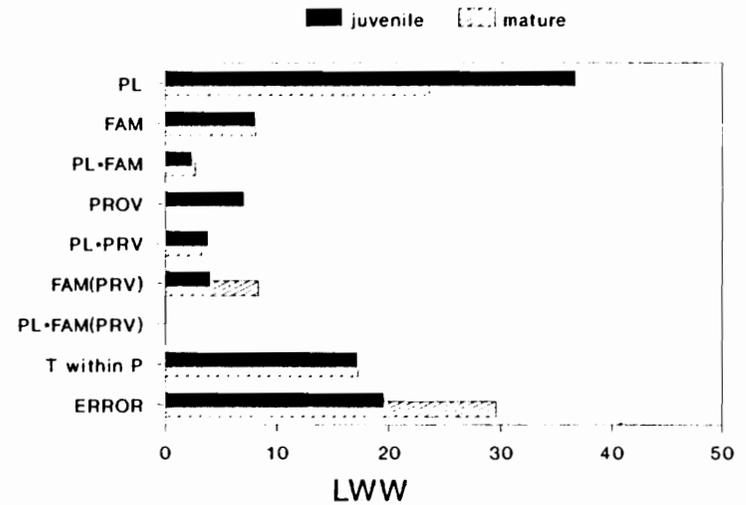
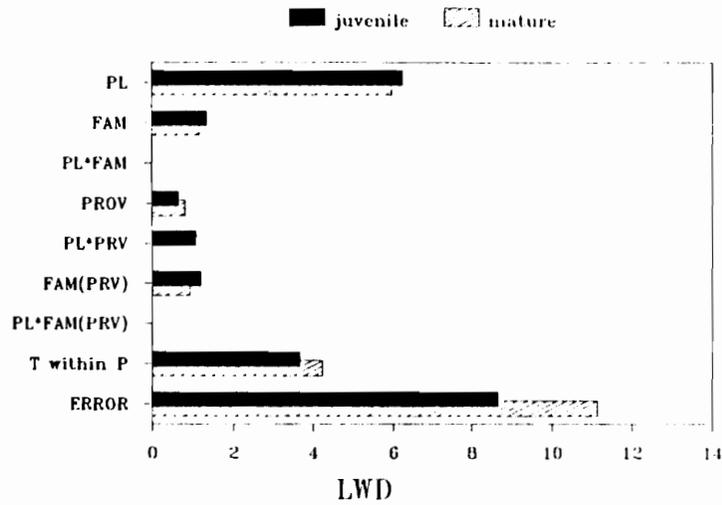
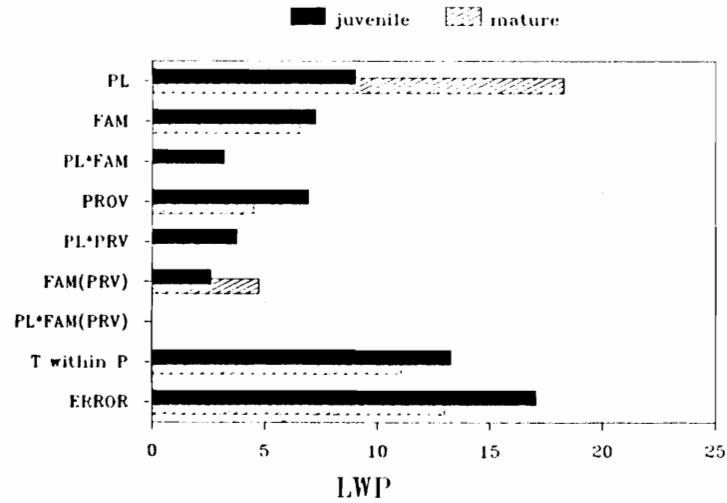
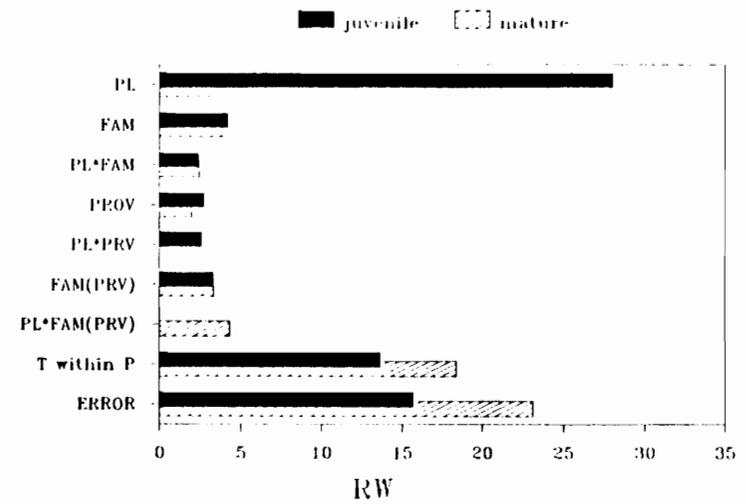
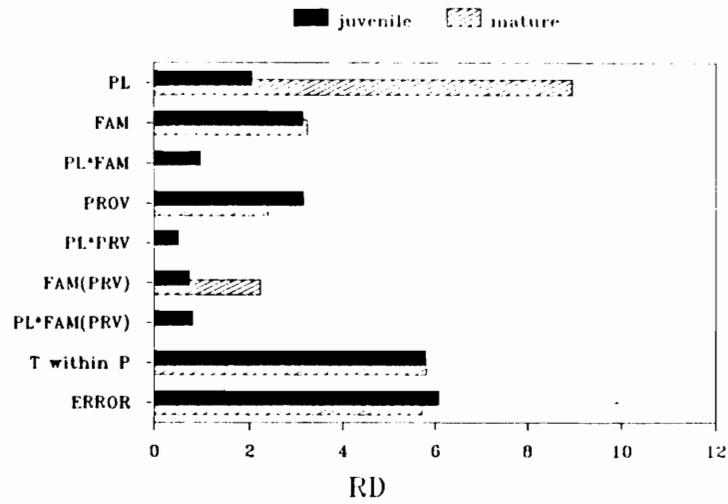


Figure 2. (Continued)



provenances failed to reach an acceptable level of significance. In other words, the significant difference established among the 30 families for these traits was caused by differences among families belonging to different provenances rather than by families within the same provenances.

In the mature wood zone, variation among the 30 families was significant for EWD, RD, LWW, and LWP. When families were grouped into provenances, the following results were obtained: provenances had significantly influenced EWD, RD, and LWP but not LWW, and families within provenances had significantly influenced RD, LWW, and LWP but not EWD. These results suggest that, in mature wood, the significant variability among the 30 families for

- EWD was caused by variation among families belonging to different provenances, for
- LWW was caused by variation among families belonging to the same provenances, and for
- RD and LWP was caused by differences among families representing different provenances as well as families within provenances.

The previous conclusions about the family effect can be substantiated by a closer look at the relative magnitudes of the variance components of the 30 families, provenances, and families-within-provenances (Table 7). For example, the family components of variance for juvenile

EWD (significant at $p=0.006$) and for mature EWD (significant at $p=0.004$) accounted for about 8.0 and 9.4 percent of the total variation, respectively. When the provenance effect was accounted in the analysis, it appeared that almost all the variation in EWD among the 30 families was due to provenances; the families within provenances contributed nothing to the total variation in juvenile EWD and only about 0.5 percent to that of the mature EWD. Similar results were established for juvenile RD where the variance component due to families-within-provenances was less than 6 percent of that due to provenances. This means that for the above traits, estimates of the variance components associated with the 30 families were biased upward when provenances were confounded into families.

In contrast, partitioning of the family component of variance for mature LWV (Table 7) revealed that provenances contributed nothing to the variation in this trait; the genetic variation was entirely due to families-within-provenances. The performance of other variables was between these extremes. For example, the variance component due to families-within-provenances for juvenile RW was about 1.4 times that due to provenances. Mature RD and LWP, showed the case where variation among the 30 families was divided almost equally between the provenances and-families-within provenances. In contrast to the RD

results in juvenile and mature wood, Bastien et al. (1985), working in 14-year-old provenance trials in France, reported that genetic variability was much higher at the family than the provenance level (cit. in King et al., 1988). Such discrepancies can be attributed to differences in both the populations and environments under study. It is also possible, although not necessary, that the non-significance of the family-within-provenance effect, which was evident for some traits in the current study, was due to the small number of families-within-provenances involved, leading to limited variation and small degrees of freedom. A significant family-within-provenance effect was detected only where the signals were extremely strong with reference to the plantation X family-within-provenance interaction, which was used as the error term for the F-test. Although a larger sample of families-within-provenances is needed before final conclusions can be made, the results at hand indicate different architectures of genetic variation for the various intra-ring components. It seems that forest trees within provenances may differentiate genotypes in response to the micro-environments surrounding individual trees as well as to the means and extremes of the macro-environments in which they are found (Campbell, 1979).

Subsequent discussion of the genetic parameters will focus on trends between the juvenile to mature period using

the coefficients of variations (square roots of variance components divided by the trait mean) shown in Figure 2. Ignoring the geographic sources, the genetic variance due to the 30 families relative to its mean remained almost the same between juvenile and mature wood for all seven traits. When the families were grouped by their provenances, the structure of genetic variation in juvenile and mature zones was the same in some traits and different in other traits.

There was no general trend among the ring-width components. While in earlywood width (EWW) the coefficient of variation for provenance increased and that for family-within-provenance decrease from juvenile to mature wood, the opposite was true in latewood width (LWW) and percent (LWP). Consequently, the genetic structure in ring width (RW) remained more or less unchanged with advancing stand development (Fig 2). Although the effect of families-within-provenances on RW didn't change with age, as demonstrated by the equal coefficients of variation, the importance of this source in mature sample seems to be overshadowed by the relatively large variance associated with the plantation-by-family interaction.

The ring density components, earlywood and latewood densities behaved similarly; the coefficients of variation of both the provenance and family-within-provenance remained remarkably the same during the juvenile and mature periods. The genetic structure in average ring density

followed the trend of LWW and LWP rather than that of its components (EWD and LWD); from juvenile to mature period, differences among families-within-provenances increased and that among provenances slightly decreased (Fig. 2).

McKimmy and Campbell (1982), whose mature sample consisted of the 10 rings just to the outside of our mature wood sample, concluded that the genetic structure for wood density and ring width did not vary appreciably between the juvenile and mature wood.

Provenance Means

The provenances included in the study were all from the Pacific Coast region, a population known to consist of one variety of Douglas-fir. The analysis of variance revealed that, in the juvenile wood sample, differences among provenance means were significant for earlywood density (EWD), average ring density (RD), latewood width (LWW), and latewood percent (LWP) (Table 5); for these traits the provenance component of variance accounted for an average of 9 percent of the total variance with a range of 2.5 to 13.3 percent (Table 7). Differences among provenances were also significant for EWD, RD, and LWP in the mature wood sample (Table 6) and they were responsible for about 3.4 to 8.8 percent of the total variation in these traits. Interest now lies in identifying which provenance means differ for the above intra-ring variables.

Appendix Table 14 lists the provenance means and the results of the multiple comparison test.

The results clearly demonstrate the excellent performance of the Lakeview provenance during the juvenile period. This provenance not only ranked the best for RD, LWV, and LWP, but also was separated by a major gap from the other provenances. During early years of growth, provenance means for ring density ranged from 0.467 to 0.517 g/cm³. The difference in RD between the lowest and highest was 10 percent (50 kg/m³) and between the overall mean and the highest was about 7 percent (34 kg/m³). Such differences are not as small as they might seem if we consider the large area over which selection efforts are applied and the volume of wood produced during the whole rotation. Greater mean differences were evident for LWV and LWP. For these two traits the difference between the last- and first-ranked provenances was 27 percent. These results indicate that some improvement in the quality of juvenile wood can be achieved by provenance selection. Kellogg (1982) pointed to the huge change in product value associated with a 2 % change in raw-material density. His estimates indicate that the change in gross value for several pulp and paper mills (producing about 9000 tons/day) might amount to over \$28 million/year.

During the mature period, there was significant variation in RD among provenance means such that the means

for Lakeview and Race Track were significantly higher and that for Darrington was significantly lower than the other provenances. Differences between the lowest and highest and between the mean and highest were of the same magnitudes as was in the juvenile wood. Similar results were obtained for LWP. Moreover, for mean density and latewood percent, the top four provenances in juvenile wood showed exactly the same ranking in mature wood. Similarly the ranking of the top five provenances according to their EWD differed slightly between the juvenile and mature wood. Within these sampling zones, provenance means for RD and LWP showed exactly the same ranking.

The above results and results from other studies (Haig, 1961; McKimmy 1966; Wilcox, 1974 (cit. in Cown, 1976); McKimmy and Campbell, 1982) give strong evidence of provenance genetic variation in coastal Douglas-fir wood density. If radial growth is highly correlated with volume growth, then any improvement in wood density that can be obtained by provenance selection would be a bonus over normal production since there is no significant difference among provenances in radial rate of growth.

There was no definite relationship of any of the above traits (EWD, RD, LWW, and LWP) to altitudinal distribution of the provenances. For example, Race Track, Wind River, and Palmer, which are high-elevation provenances, ranked

respectively second, fifth, and eighth for juvenile wood density and latewood percent. In juvenile and mature wood, Race Track had the highest EWD and Palmer had the second lowest EWD. There was also no definite relationship between intra-ring characteristics and latitudinal distribution of the provenances. For juvenile RD and LWP, the southernmost provenance, Carson, ranked sixth and the most northerly provenance ranked fourth. The same two provenances ranked fifth and fourth for mature RD and LWP. The best provenance, Lakeview, is mid-way between the high- and low-latitude provenances. Similar results were found for EWD. However, there is some indication that provenances from similar geographic origins behaved similarly during the juvenile period. For example, the three progenies originating from the Wind River Valley ranked second, third, and fifth for juvenile RD and LWP; the four provenances from the Stillaguamish Valley were tailing the lists of RD, LWW, and LWP. It seems that the environments within which the sampled seed sources evolved did not have a strong environmental gradient. The result was an ecotypic pattern of genetic variation rather than a cline. Of interest is the fact that all provenances were from the western slopes of the Cascade Mountains except Lakeview, which outperformed the rest of provenances in most of the studied traits.

Although elucidation of the effect of genetic variation upon the age of maturity awaits further study, it was of interest to see if the age of transition from juvenile to mature wood was influenced by provenances or plantations. Plotting of average ring density (RD) versus ring age by provenances revealed that each of the provenances had the same trend of the average data (Fig. 1). From ring number ten outward, RD increased linearly with ring number until a maximum was reached and thereafter it stayed constant. The age at which RD starts to level off was assumed to be the age of biological maturity. Based on visual examination of 40 scatter plots, the age of biological maturity was estimated for the ten provenances in each of two replications within the two plantations. Also, estimated was the age at which RD started to increase above 0.52 g/cm^3 (an optimum density level equivalent to the species average after adjustment of the present data for the effect of extractives). An analysis of variance was conducted to determine the significance of the above effects on these two points and the results are listed in Appendix Table 15.

The results of this analysis indicate that the age at which biological maturity begins did not differ among provenances. It showed some response to the variation within plantations ($p=0.07$) but great response to environmental differences between plantations ($p\leq 0.01$);

there is also some indication that this sensitivity to environmental differences varied among genetic groups (interaction significant at $p=0.07$).

The analysis of variance revealed significant differences among provenances ($p\leq 0.01$) for the age at which RD exceeded the optimum density. This result was not unexpected since RD in the juvenile and mature wood samples had also been significantly different among provenances. The variance analysis also detected significant differences ($p\leq 0.01$) between the two plantations; the plantation that produced the higher mature RD (Wind River) had the shorter juvenile period. Neither the replication effect nor plantation-by-provenance interaction was significant. The results of the multiple comparison test (LSD) shows that the top three provenances for juvenile and mature RD had the shortest periods of time to reach maturity. The two provenances that had the lowest-gravity trees appeared to have the longest juvenile period. However, not all provenances behaved in a manner predictable by their juvenile RD. The best example is the performance of the Hazel and Palmer provenances, which based on their juvenile RD, ranked fourth and eighth, but based on the age of exceeding the density value of 0.52 g/cm^3 , had the eighth and fourth shortest juvenility period. This observation indicates the importance of another parameter in this connection, that is the rate of the linear increase in RD

during the transition period, which seemed to vary among provenances.

Provenance and Family Stability

In spite of the fact that the magnitudes of the variance components of the interactions were in some instances greater than or as great as the main effects, all the F-tests of the family-by-location effect were non-significant at both zones. Also, in no instance was the provenance-by-location effect significant (Tables 5 and 6). These results indicate that there was no tendency for provenance or family ranking to differ between plantations. Moreover, differences between the two environments in the degree of expression of genetic variation was not large enough to result in significantly diverging family or provenance means. These results disagree with the findings of McKimmy (1966) for wood density and latewood percent. McKimmy and Campbell (1982) reported significant plantation-by-provenance interaction for juvenile ring width and plantation-by-family interaction for juvenile wood density. In the present study, these interactions, although not statistically significant, were as large as the corresponding genetic main effect. Calculation of the provenance and family means in each of the two plantations revealed that the above interactions had a slight effect on ranking of the means and on the scale of mean differences.

In the early reproductive years, the variance component due to the plantation-by-provenance interaction for the growth-rate parameters was greater than for the wood-density parameters. When the trees reached maturity, this interaction term diminished to zero (small negative values) in all traits except LWW (Fig. 2). However, judging by McKimmy and Campbell's results (1982), it seems that the relative importance of this interaction for RW increases again with further development of the stand.

Trees Within Plots

The analysis of variance showed significant heterogeneity among trees-within-families for all traits. As all trees within a family had a mother tree in common, it can be concluded that these differences were due to the different genotypes of the male parents and to variations in the micro-habitat within plots. The estimated variance components associated with trees-within-plots accounted for an average of 29 percent and ranged from 14.6 (juvenile LWW) to 54.4 (mature RW) percent of the total variation (Table 7). Variability among trees-within-plots was generally more pronounced in ring width than in ring density components (Fig.2). The within-plot variance for wood density parameters and for LWW and LWP did not differ between the juvenile and mature period (Fig. 2) indicating that differences among trees remained unchanged with

advanced age. In contrast, the importance of this source of variation for RW and its major component, EWW, increased from juvenile to mature period.

The variation among cores-within-trees accounted for an average of 25.6 percent with a range from 12.6 (juvenile RW) to 43.4 (mature LWD) percent of the total variation. The magnitudes of these sub-sampling variances reflect circumferential variation plus errors of measurements and they were by far the largest component of the cumulative error deviation shown in Figure 2. The variation among trees-within-plot was for most of the variables greater than within trees; LWD was an exception.

COMPONENTS OF PHENOTYPIC VARIANCE AND HERITABILITIES

For purposes of this and the following sections, the analysis of variance utilized tree averages of the intra-ring variables (Appendix Table 12). The main objective of this analysis was to obtain estimates of the degree of variation associated with the factors that contribute to the variance of individual-tree phenotypic values. The non-significant family-by-plantation interaction from the previous section suggested that there was no need to analyze the data of each plantation separately. Since the analysis partitioned the variation among trees and not that among cores as in the previous chapter, there were some

differences in the relative magnitudes of variance components. Nevertheless, the results of the two analyses were quite similar in terms of the significance of all studied sources; exceptions were family differences for earlywood width, ring width, and latewood density; the first two turned to be significant at about the 0.05 (instead of 0.07) and the later at about 0.08 probability levels (instead of 0.10).

Components of Phenotypic Variance

Phenotypic variance (σ^2_p) for the purpose of calculation of individual-tree heritability is, in practice, estimated as the sum of the variance among families (σ^2_f) plus the variance within families ($\sigma^2_w + \sigma^2_{f*l} + \sigma^2_{f*r(l)}$) and not as the sum of all variances involved in the study. Interpretation of these components is as follows. For an open-pollinated half-sib assumption (progenies from one mother tree have different parents), the family component (σ^2_f) is a quarter of the additive genetic variance (σ^2_a). The validity of the half-sib assumption is uncertain because, in reality, a proportion of within family relationship might be full-sibs (Squillance et al., 1962 and van Buijtenen, 1962); this results in overestimation of the additive genetic variance. The family interaction components, σ^2_{f*l} and $\sigma^2_{f*r(l)}$, result from the failure of families to behave the same way

relative to each other in different plantations and replications, respectively. The within-plot variance (σ^2_w) is composed of the remainder of additive ($3/4 \sigma^2_a$) and all the nonadditive (σ^2_{na}) genetic variation as well as tree-to-tree environmental variation within plots (Zobel and Talbert, 1984). Figure 3 illustrates the percent contribution by families, family interactions, and trees-within-families to the phenotypic variation.

The within-plot (among-trees within family plots) variation was by far the largest component of phenotypic variance. In juvenile wood, σ^2_w accounted for about 80 % (EWD, RD, and LWP) to 92 % (RW) and in the mature wood sample, for 74 % (EWD) to 93 % (EWW and RW) of the phenotypic variance.

Despite the large tree-to-tree variation, there was a tendency for families to maintain similar ranking within plantations. The interaction of family by location (σ^2_{f*l}) contributed less than 5% to phenotypic variance in the juvenile wood and less than 1.3% in the mature wood zone. In several cases the variance component of this interaction was negative and hence considered to be zero. These results indicate that there is no necessity for family selection to be based on individual plantation ranking. The contribution of the plot-error component of variance ($\sigma^2_{f*r(l)}$) during juvenility was negligible except

Figure 3. Relative contribution of family, family interactions, and trees-within-plot to the phenotypic variance (a) in juvenile and (b) in mature wood.

Figure 3.

(a) Juvenile Wood

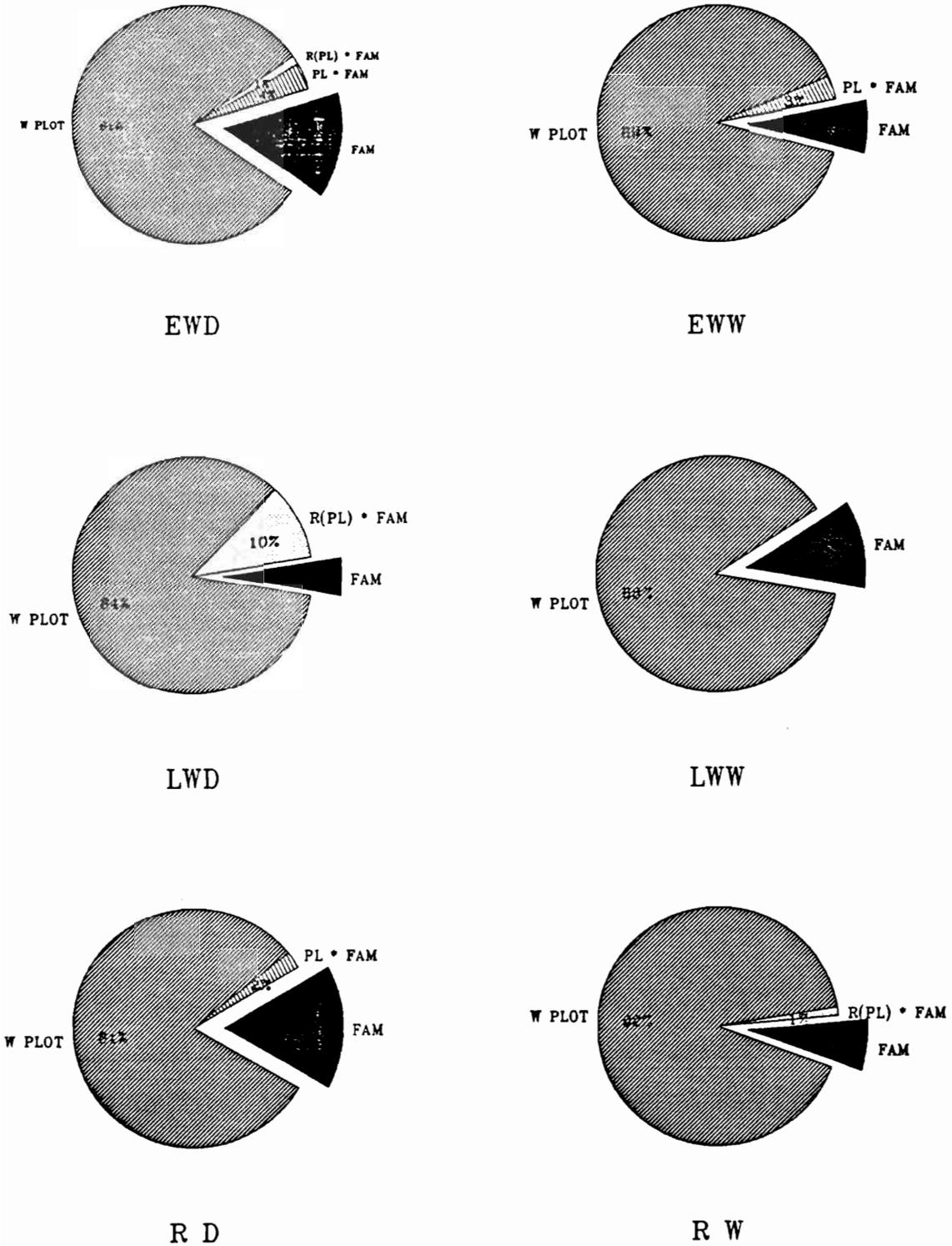
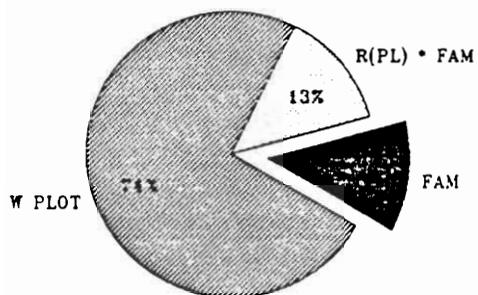
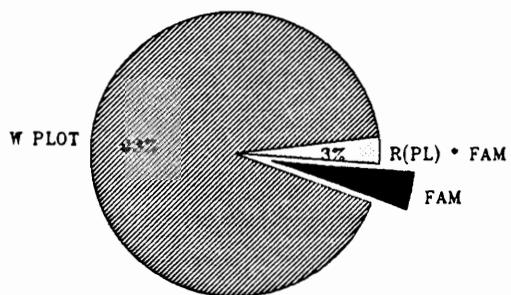


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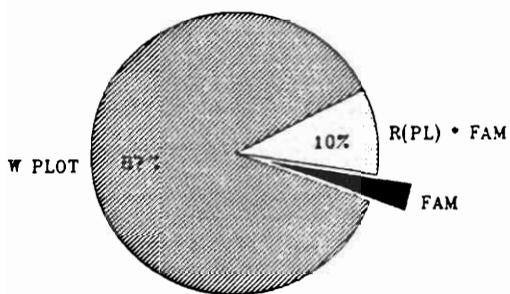
(b) Mature Wood



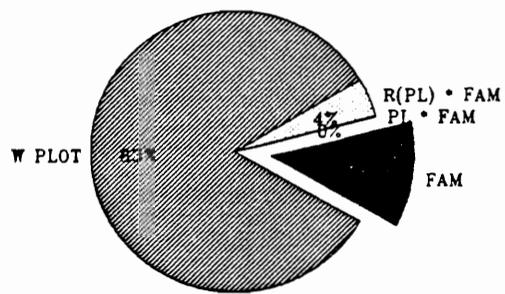
E W D



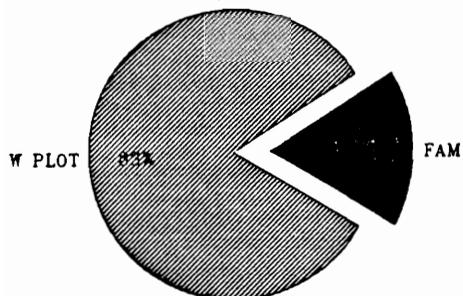
E W W



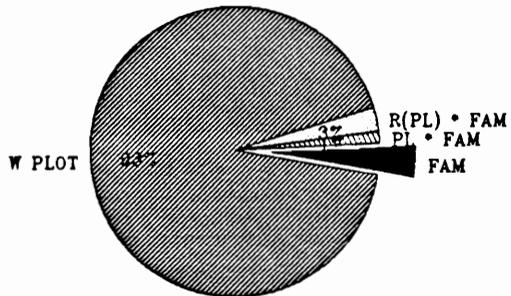
L W D



L W W



R D



R W

for LWD where it furnished double the contribution of families. In the mature wood, $\sigma^2_{f*r(l)}$ explained less than 4.3 % of the phenotypic variation except for EWD and LWD where its contribution was as much as and thrice that of the families, respectively.

Variation due to family effect was for all traits greater than that due to the genotype by plantation interaction. The estimated family components of variance (σ^2_f) suggested that the effect of families accounted for approximately 17 % of the phenotypic variation in RD, 14 % in EWD, and 5 % in LWD during juvenile period. In the mature wood sample, σ^2_f accounted for 17 %, 12 %, and 3 %, respectively. In comparison, proportional variation as a result of family effects for the growth rate parameters (RW, EWW, LWW, and LWP) was 4, 7, 12, and 15 % in juvenile wood and 4, 4, 12, and 18 % in mature wood, respectively. It seems from these results that for most of the traits, the relative importance of additive genetic variance remained slightly changed between juvenile and mature wood (i.e. the effect of families is of the same order in both growth zones).

It is important to note that the above discussed family variation comprises both provenance and family-within-provenance variation (see previous section). In practice, tree breeders traditionally select their superior

entries from a population (e.g. a provenance) of presumably general adaptability over a wide range of environments (they do so to avoid future risk of failure that might materialize from the utility of unadapted races). More appropriate for purposes related to such breeding programs are family variations and additive variances within populations. Unfortunately, the material available for this study included a limited number (three) of families per provenance, which does not allow much to be learned about the heritability within populations. Even the total number of families (30) is considered small (Campbell, 1990). In the remainder of this section and in the next section, genetic estimates were calculated using variances derived from the analysis of the 30 families (without regard to their provenances). The heritability results were compared with those determined from the analysis of families-within-provenances. These estimates may be considered as general guide lines.

Heritabilities

Estimates of narrow-sense heritability derived from analysis of the 30 half-sib families together with their standard errors are set out in Appendix Table 16. These estimates were also presented graphically in Figure 4. While family mean heritability is an estimate of the portion of phenotypic variance that is due to differences

among family groups, single tree heritability is an estimate of that portion due to genetic differences among individuals (Wright, 1976). Falconer (1989) noted that standard errors of heritability estimates are usually very large unless the study comprises a very large number of observations. Although the present study was based on only 30 families and 12 trees per family over all replications, the standard errors of the heritabilities were fairly small, an indication that the heritabilities were estimated with a reasonable degree of precision. However, due to the inability of the design to detect significant family differences for some traits, the reliability of some of the H^2 estimates should still be questioned. Namkoong et al. (1966) states that for an effective selection for general combining ability, family differences must be significantly different from zero. The significance levels (p-values) of the family source of variation were also included in Appendix Table 16 to indicate the weakly-based family inferences.

Heritability of the magnitude of 0.50 to 0.70 for wood density in conifers has been reported (Zobel and Talbert, 1984). For Douglas-fir, McKimmy (1966) estimated wood density heritabilities for different tree ages; the estimates in the different plantations ranged from 0.00 to 0.66. In the current study family narrow-sense heritabilities for ring density were 0.70 and 0.78 in

juvenile and mature wood, respectively. The values of heritability for ring width were 0.48 and 0.27 (Fig. 4). These results are in general agreement with those reported in the literature in showing that wood density is more genetically controlled than rate of growth (Appendix Table 17). In comparison to the juvenile wood values, King et al. (1988), working on 12 years old Douglas-fir progenies in a full-sib trial (from crossing of 22 females and 4 males), reported family heritability values of 0.93 for wood density and 0.66 for diameter.

The current study allows extending the conclusions to other intra-ring variables. The heritability among the 30 families (H^2_f) for EWD, LWW, and LWP ranged between 0.62 and 0.66 in juvenile wood, and 0.60 and 0.78 in mature wood, which indicate that genetic control for these traits as well as for RD is strongly additive. For the rest of the traits the family heritabilities were low to moderate. Each of these estimates is strictly applicable to the sampled genotypes and to environments analogous to those of the experimental plantations.

Heritability estimates (H^2_f) for EWD and EWW (Fig. 4) suggest that the density component in earlywood was more heritable than the growth-rate component. Contrariwise, in the latewood zone growth rate was more heritable than wood density (Fig. 4). Among the ring density parameters, RD

Figure 4. Family and single-tree heritability for intra-ring characteristics (a) in juvenile and (b) in mature wood.

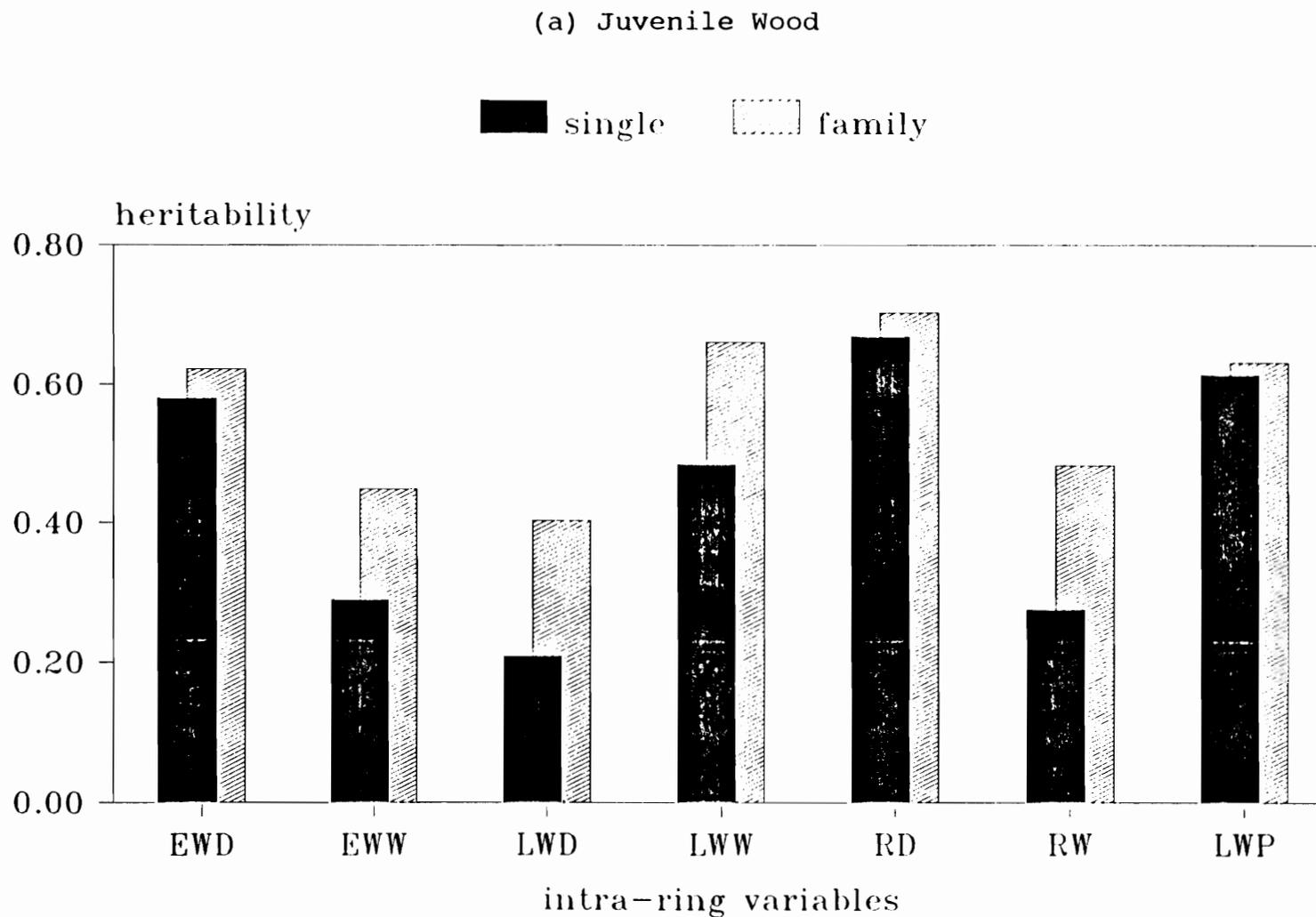
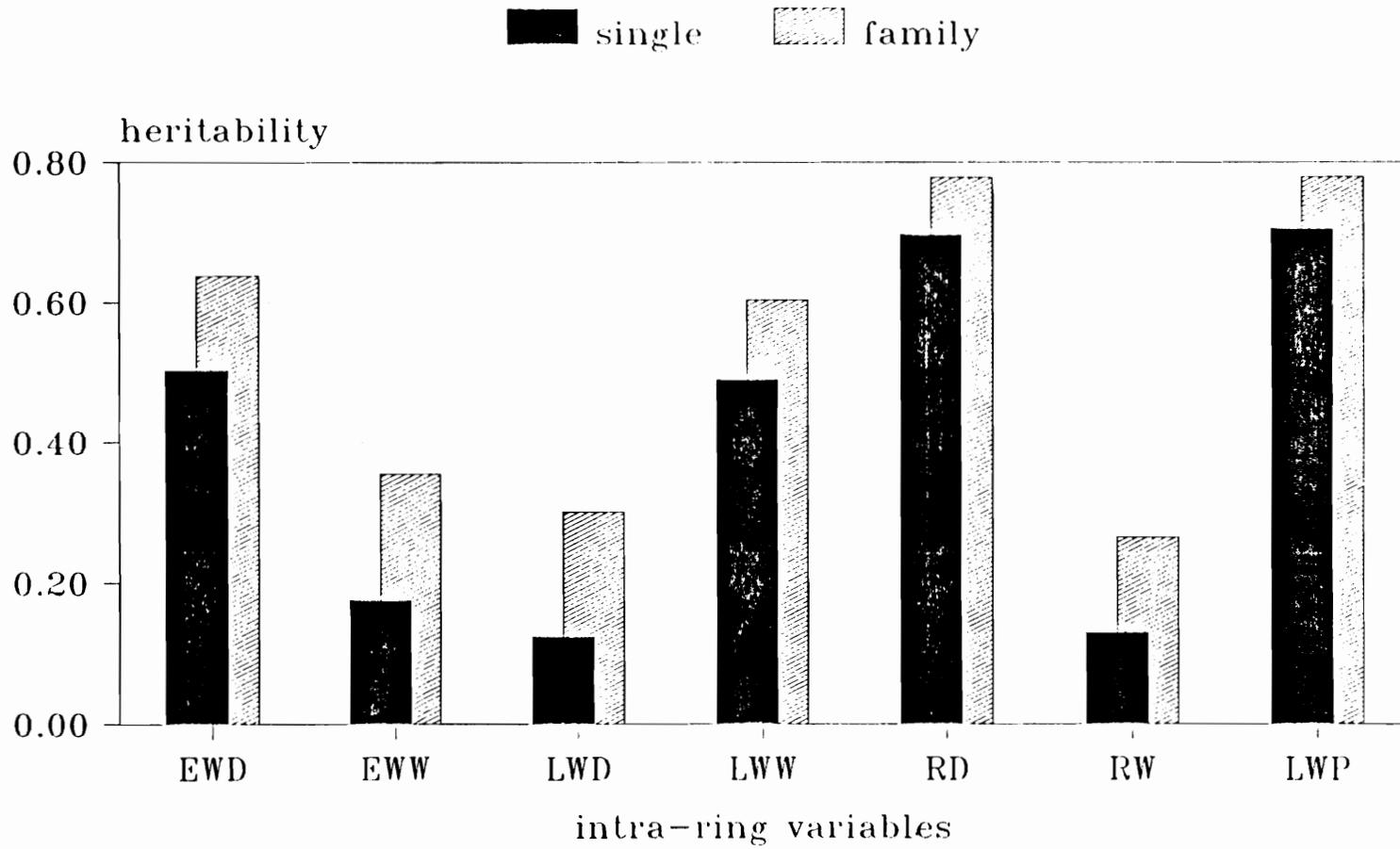


Figure 4. (continued)

(b) Mature Wood



had the greatest heritability estimate and LWD had the lowest. Among the ring width parameters, LWW and LWP were more heritable than EWW and RW. These conclusions apply for both the juvenile and mature wood. While the estimates of H^2_f for EWW, LWD, LWW, and RW showed a slight decrease from juvenile to mature wood, EWD, RD, and LWP had a slight increase.

Single-tree heritabilities (H^2_i) for all traits (Appendix Table 16, Figure 4) followed similar trends to family heritabilities (H^2_f). The calculated standard errors indicate that the estimates of single-tree heritability were more precise than those of family heritability. H^2_i for EWD, RD, LWW, and LWP were equal to or slightly less than the corresponding H^2_f , and for EWW, LWD, and RW were about half of the corresponding H^2_f . Although the heritability estimates indicate that for most of these traits gain may be obtained by both single-tree and family selection, the former would be more effective in obtaining immediate gain. The reason for this is the greater variability among trees than among families, which results in a higher selection differential ($i * \sigma_p$) for the calculations of gain from single-tree heritability (gain = $H^2 * i * \sigma_p$). Let us for example compare the gain for RD and RW per one unit of selection intensity ($i=1$) (i.e. when selecting a group that have a mean value one standard

deviation above the mean of the whole population). The expected gain for juvenile RD and RW was, respectively, 5 and 4.5 % from individual selection and 2.6 and 3.1 % from family selection. The calculated gains in the previous example also demonstrate how the greater variation in RW had offset its smaller heritability compared to RD. Using the same reasoning, it can also be said that ring width parameters will have greater gain than ring density parameters of comparable heritabilities (LWW versus EWD and EWW versus LWD). This conclusion holds for both individual and family selection. For example, the expected gain from individual selection per one unit selection intensity would be 14.2 % for mature LWW and 4.5 % for mature EWD. Bendtsen (1978) estimated a decrease in wood density of 2 to 5 % due to the increasing proportions of juvenile wood from fast-grown plantations. The above estimates of gain suggest that individual selection for juvenile RD will readily compensate for the expected reduction in this trait.

It is important to note at this point that the data represent only two plantations; this might have resulted in underestimation of the value of the environmental variance and, in turn, inflated the additive variance and heritability estimates (Namkoong et al., 1969). Moreover, the heritability values obtained from the analysis of the 30 families were biased upward due to provenance variation

(because provenances were confounded with families). When the effect of provenances was removed (by including them in the model), most heritability estimates among the families-within-provenances ($H^2_{f(s)}$) were lower than those among the 30 families (Appendix Table 17). This difference was remarkable in instances where the magnitude of the variation due to provenances was considerably larger than that due to families-within-provenances; examples are EWD, LWW, RD, and LWP in the juvenile wood as well as EWD and EWW in the mature wood. On the other hand, where the variance components due to provenances were comparable to or less than that due to families-within-provenances, $H^2_{f(s)}$ were only slightly lower than or equal to H^2_f ; examples are EWW, LWD, and RW in juvenile wood and LWW, RD, and LWP in mature wood. For the results of the density-components there are published values for comparison only in the case of juvenile wood. H^2_f estimates for juvenile EWD, LWD, and RD (from the analysis of families-within provenances) are generally smaller than the estimates of Vargas-Hernandez (1990) even before adjusting for differences in estimation of the additive variance.

Some of the studied traits exhibited significant provenance differences and had high family heritabilities. This coupled with the provenance and family stability over locations could lead to rapid loss of genetic diversity in long-term tree improvement programs. In such cases even a

light family selection would reduce the number of geographic sources (provenances) represented in the study. For example, selecting the best one in two out of 30 families for higher juvenile EWD will reduce the original geographic sources from ten to five. This might be of concern because, for a successful long-term breeding program, it is essential to begin with a broad genetic base to achieve continued progress over many generations (Zobel and Talbart, 1984).

PHENOTYPIC AND GENETIC CORRELATIONS

A phenotypic correlation coefficient is a measure of the closeness of relationship between two phenotypic (observed) values. The genetic correlation between two traits expresses whether or not they are inherited as a unit. The genetic cause of this correlation is mainly the control of two or more traits by a single gene or a group of genes (pleiotropy) (Falconer, 1989). With this understanding, genetic correlations are used to show the relative size and direction of the change brought about in one trait by selecting for another one.

Correlations Among Various Traits

Appendix Table 18 lists the phenotypic correlation coefficients between all pairs of the seven characteristics in the juvenile and mature wood using tree averages. Figure

5 illustrates some of these correlations for selected pairs. In no instance was there a curva-linear relationship. Almost all the correlation coefficients were statistically significant. In the following, the trends rather than the magnitudes of the individual correlations will be discussed.

During juvenile period, ring density (RD) was positively, moderately, and equally correlated with earlywood and latewood density (EWD and LWD). Each of these components, taken alone, explained about 30 % of the variation in the average ring density of the trees. There was a slight trend indicating that the higher EWD trees had slightly low LWD. Ring density had a very strong correlation with latewood percent (LWP); about 87 % of the phenotypic variation in RD among trees could be explained by variation in LWP. Such result suggests that the variation in RD and that in LWP depend on almost the same set of factors. Most of the above relationships remained slightly changed during maturity.

Being negatively correlated with earlywood width (EWW) and positively with latewood width (LWW), RD appeared to have a very weak, non-significant correlation with total ring width (RW) in both zones. Contrariwise, the ring density components had strong, significant correlations with their respective ring width components, but the signs

Figure 5. Relationship between intra-ring characteristics (a) in juvenile and (b) in mature wood.

(a) Juvenile Wood

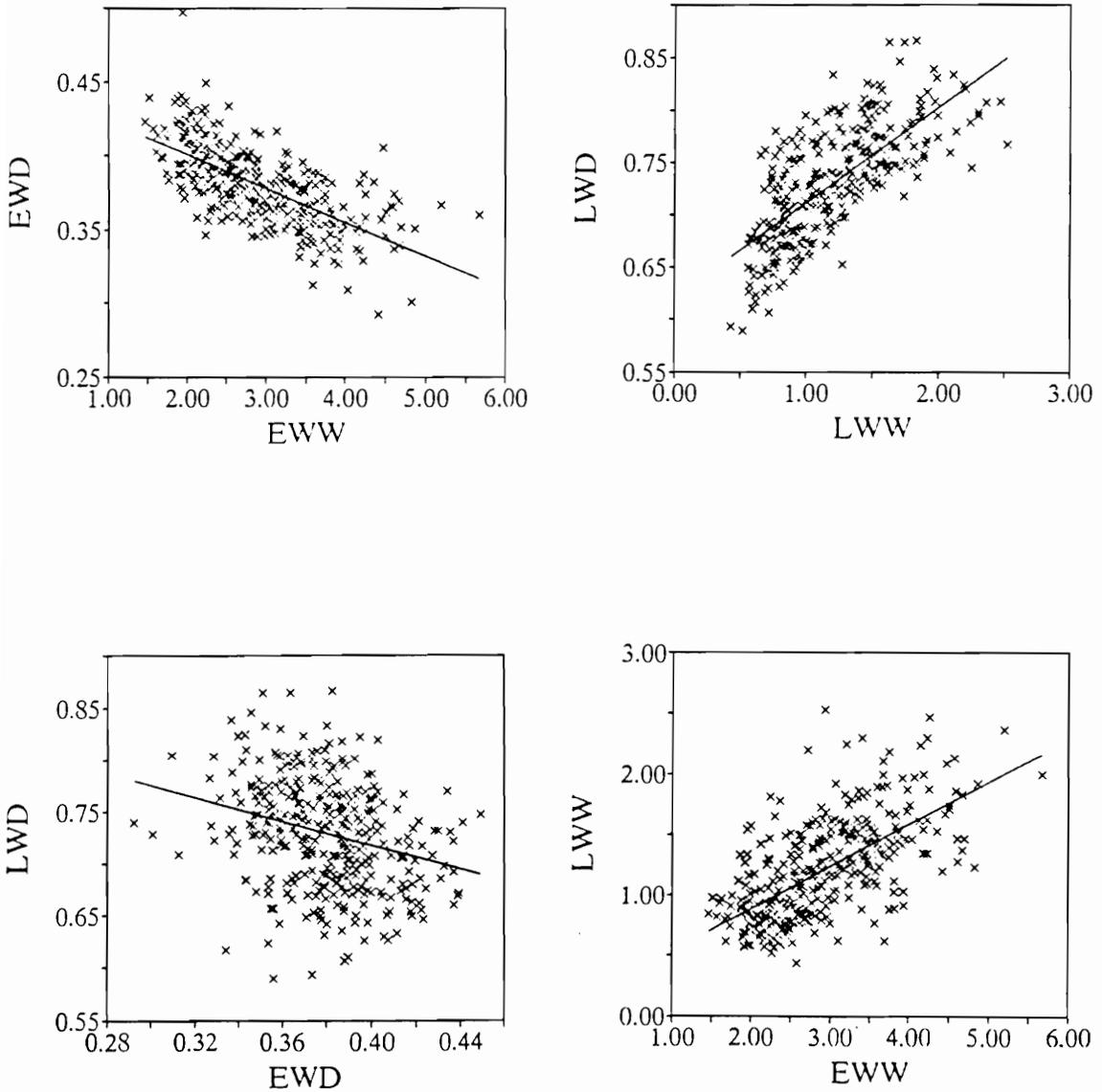


Figure 5 (a). (continued)

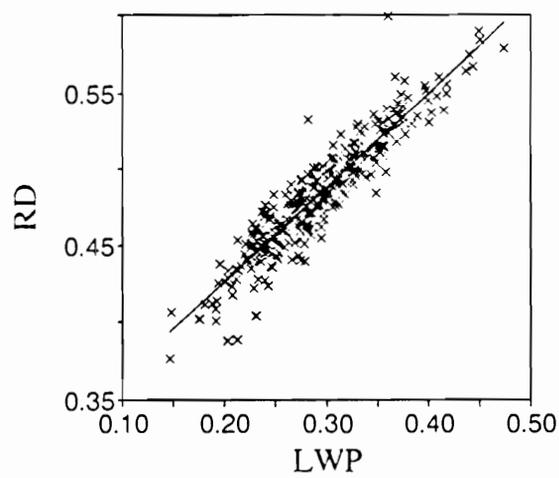
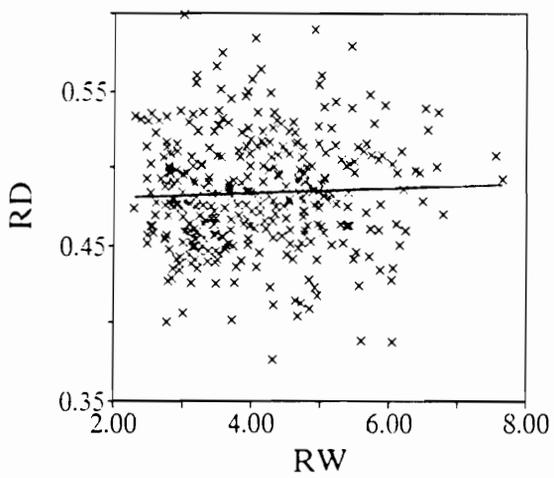
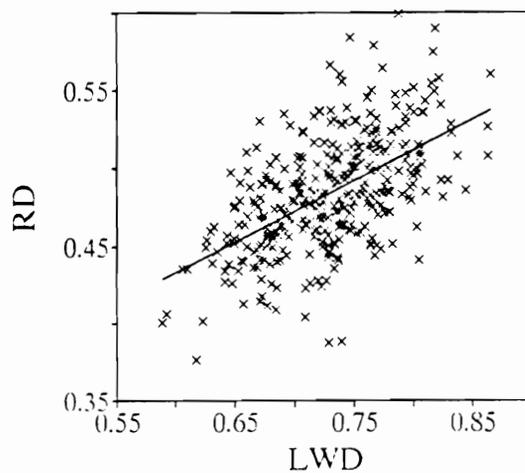
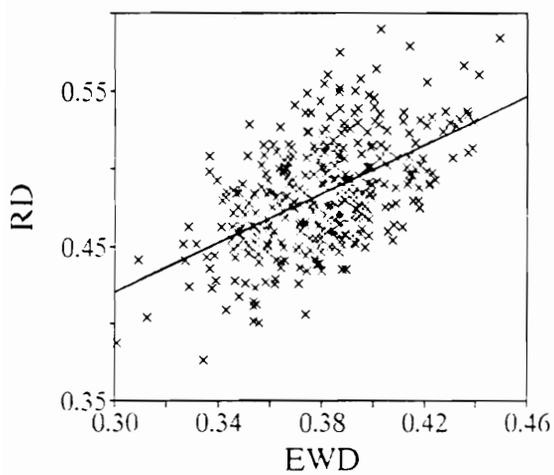


Figure 5. (continued)

(b) Mature wood

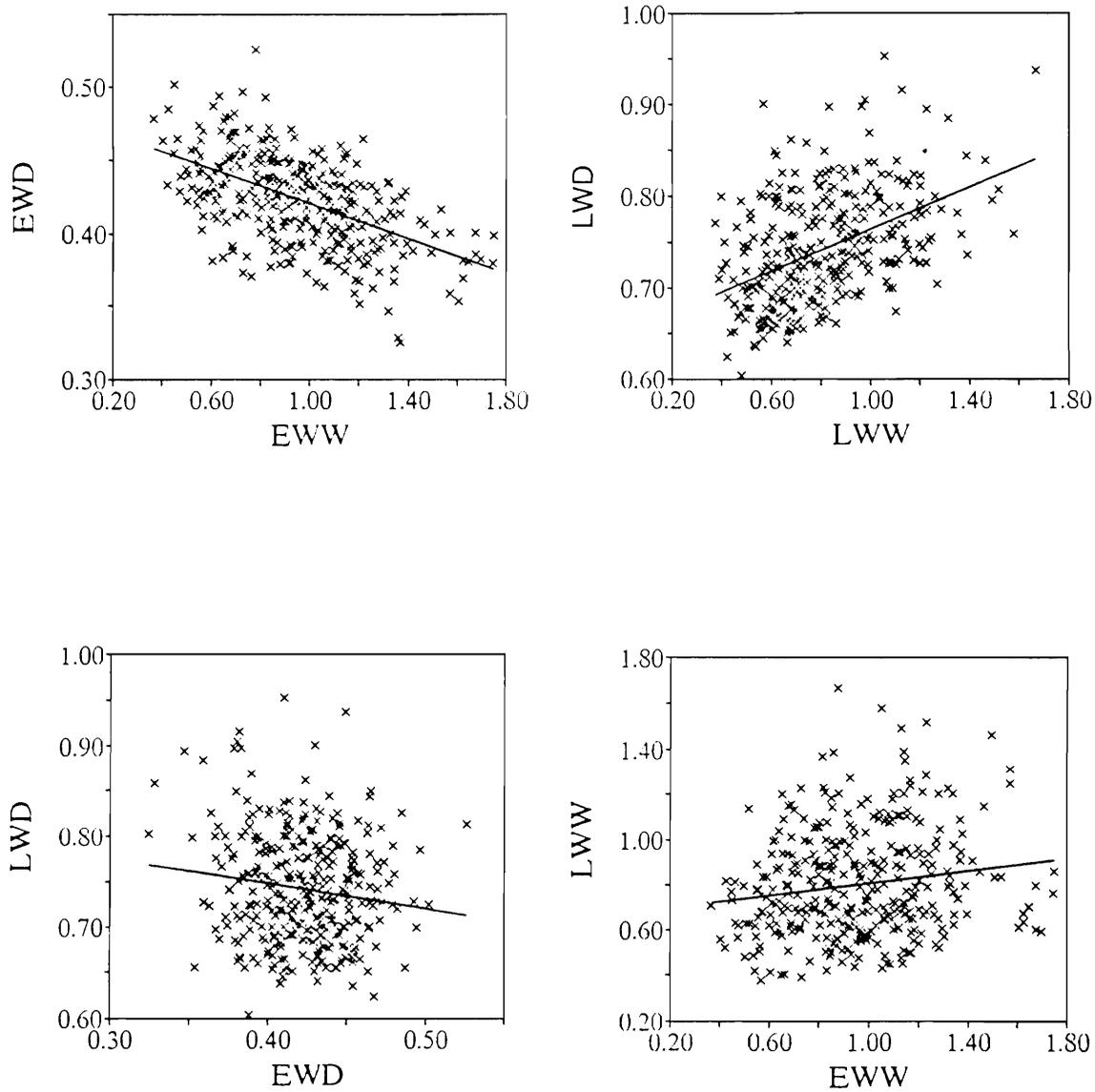
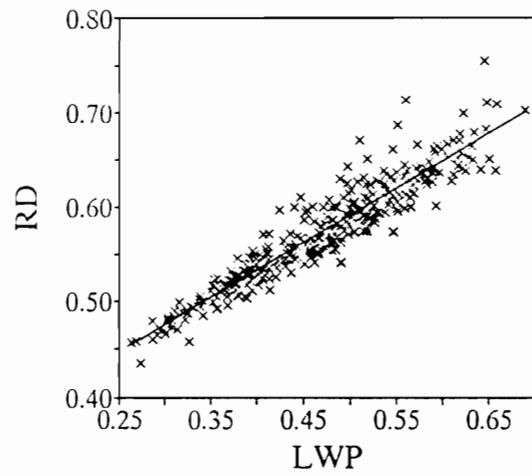
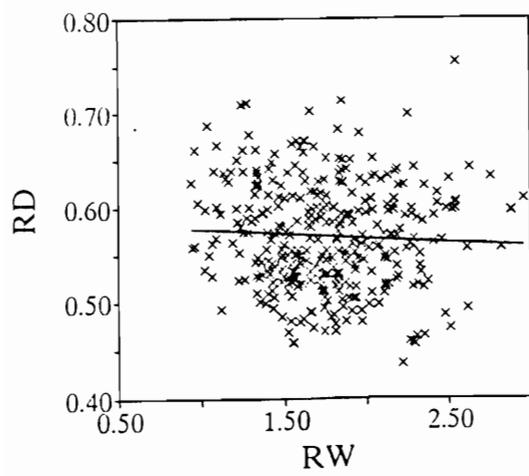
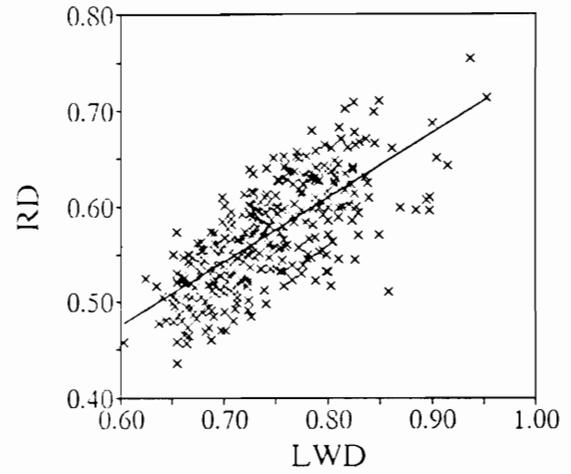
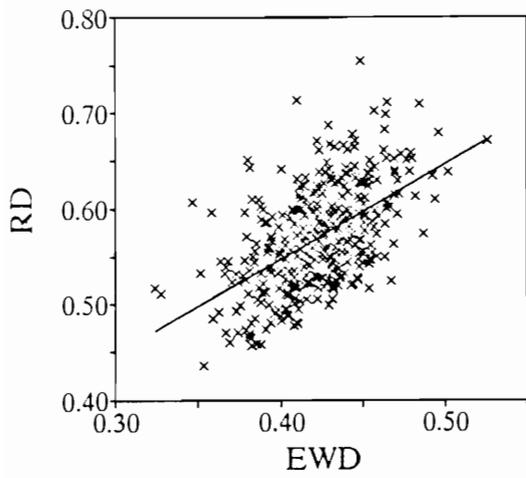


Figure 5 (b). (continued)



were different. While growth rate and density were negatively related in earlywood (EWD with EWW), they were positively related in latewood (LWD with LWW). These results demonstrate the tendency for faster growth to be associated with thin-walled tracheids in earlywood, but with thick-walled tracheids in latewood. These trends might be inherent, a response to the environmental conditions prevailing during the period of wood formation, or a combination of both.

The relatively high, positive correlation between EWW and LWW during juvenility suggests that trees with early fast growth had the tendency to maintain that during the whole season. However, this high EWW-LWW correlation dropped dramatically when the trees approached maturity, and this drop was accompanied by a comparable increase in the size of the negative correlation between LWP and EWW.

Judging by the low magnitudes of the phenotypic correlation coefficients between some traits, it can be postulated that one can have trees that are highly valued for one trait and are either highly or not so highly valued for another. For instance, trees that have high EWD may or may not have high LWD. Fast growing trees may be high- or low-gravity trees and they may have low or high proportions of thick-walled tracheids. These observations, coupled with the high positive RW-LWW relationship, is not in support of the general understanding that fast rate of

growth results in low-gravity trees due to the lack of latewood.

The interesting question remaining to be answered is how much improvement in one characteristic can be obtained by selecting for another. The results of the additive genetic correlations (r_g) are presented in Figure 6(a,b). Because genetic correlation coefficients usually have high standard errors, Goggans (1964) suggested that only the sign and relative size of genetic correlation need to be considered. In the current study, genetic correlations were only obtained for pairs where the family components of variance were significantly different from zero.

In all cases, genetic correlations were greater than the corresponding phenotypic correlations. Genetic correlations and the moderate to strong heritabilities, in juvenile wood, indicate that the inverse phenotypic relationship between EWD and EWW and the positive one between LWD and LWW (Fig. 5) had substantial genetic bases (Fig. 6-a). These trends, were probably a direct response of the genotypes to the relative availability of photothynthates and growth regulators at different times in the growth season. In contrast to the above relationships, there was a weak, negative genetic correlation between average ring density and ring width. The lack of sizable correlation between average ring

density and ring width suggests that selection for juvenile wood density may be carried out without or with little prejudice against growth rate. Because of this independent inheritance, there is also possibility to combine fast growth with either dense or light wood in a breeding program. In contrast to the above results, King et al. (1988), Bastien et al. (1985; cit. in King et al., 1988), and Vargas-Hernandas (1990) reported significant correlations for wood density with diameter and volume growth in other populations of Douglas-fir.

The moderately strong genetic correlation between juvenile EWD and LWD ($r_a=0.56$) indicate that these traits were not inherited independently. Each of these density components (EWD LWD) had a very strong, positive genetic correlation with the average ring density (Fig. 5-a). A selection program aiming only at high EWD to indirectly increase RD or to reduce density variation within growth rings, may bring about a decrease in radial growth because of the close, negative EWD-EWW genetic relationship (r_a). Highest genetic correlations with RD were obtained for LWW and LWP. These results suggests that RD and LWP are controlled by almost the same genes and selection for LWP will inherently cause a sizable increase in wood density.

Due to the inability of the analysis to detect family differences, few genetic correlations could be calculated

Figure 6. Comparison of genetic and phenotypic correlations for intra-ring characteristics (a) in juvenile and (b) in mature wood.

(a) Juvenile Wood

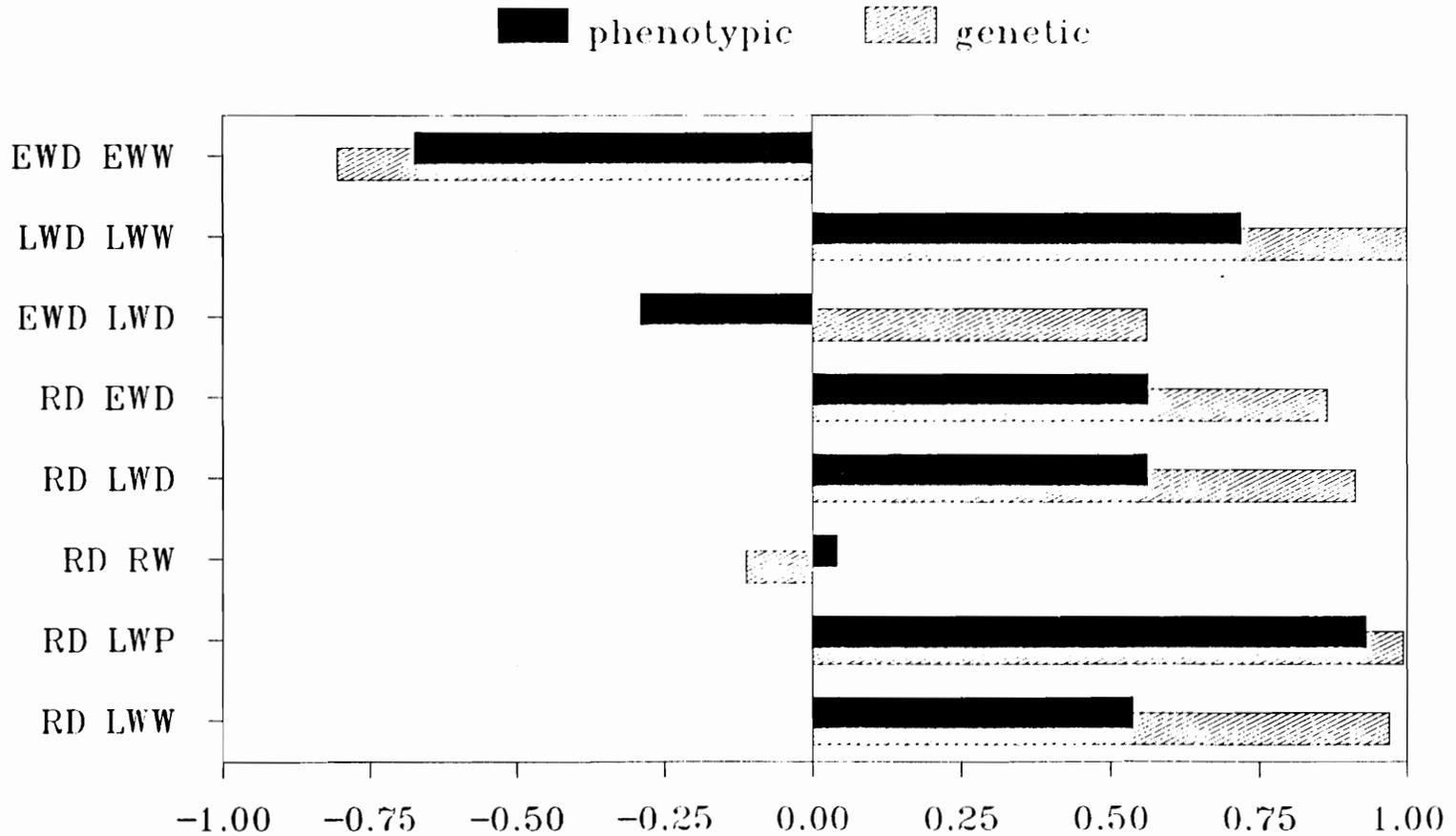
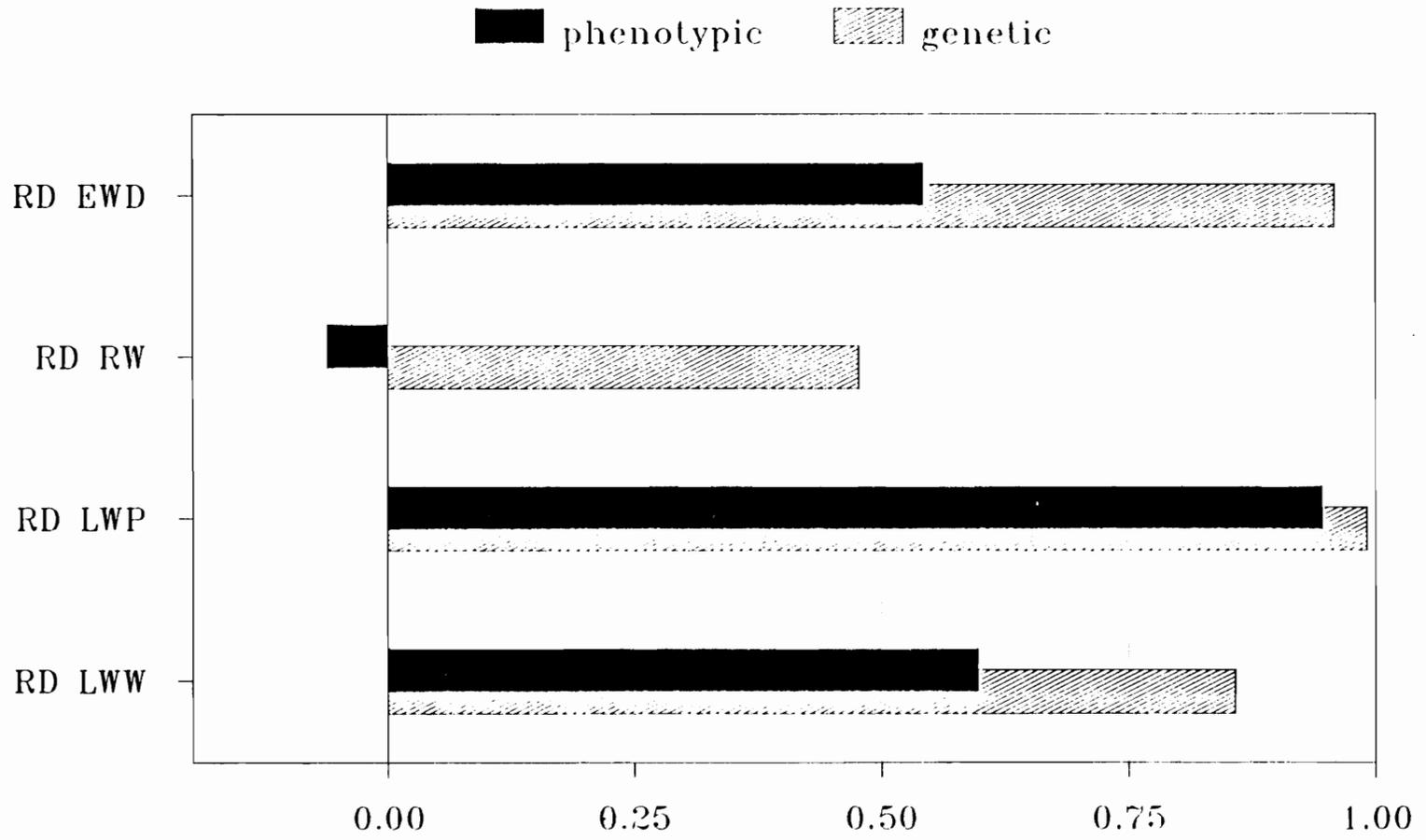


Figure 6. (continued)

(b) Mature Wood



in the mature wood zone. The results are shown in Figure 6-b. In this zone, ring density genetic relationships with EWD, LWW, and LWP remained as high as in the juvenile wood zone. These results give the impression that the genes controlling RD and each of these traits have pleiotropic effect; such dependent inheritance was clear in the juvenile as well as mature wood. Falconer (1989) stated that genetic correlation expresses the net effects of all genes that affect the two traits; therefore, pleiotropy does not necessarily cause a detectable correlation as in the case where the effect of some genes is positive on one trait and negative on the other.

Although differences among families for RW were not significant in mature wood, genetic correlation of this trait with mature RD was also estimated (Fig. 6-b) to give at least an idea about the direction of this relationship, which is lacking in the literature. While phenotypic correlation was negligible, there seems to be a favorable genetic relationship between the two traits in mature wood.

Juvenile-Mature Correlations

The objective in this section is to report on how the tree values observed in the mature wood sample correlate with those in the juvenile wood sample. Appendix Table 19 lists the correlation coefficients for all possible

combinations and Figure 7 illustrates the relationship of a wood characteristic in juvenile wood to the same characteristic in mature wood. All these phenotypic correlations (Fig. 7) were positive and highly significant ($p \leq 0.001$), and they ranged from 0.16 to 0.84.

Highest juvenile-mature phenotypic correlations were evident for latewood density (LWD) and width (LWW) indicating that for these traits the values of juvenile wood were consistently indicative of those of the mature wood. Ring density (RD) of the juvenile wood showed moderately strong correlations with ring density of the outer wood. Similar results were found for latewood percent (LWP). For each unit change in RD or LWP of the juvenile wood, there was about 0.64 unit change in RD or LWP of the mature wood. The above relationships suggest that a tree that produces high gravity wood and LWP during the early years of growth (rings 6 to 15) would continue to do so during mature period. McKimmy (1966) found that the density of wood at the pith (first 5 rings) was not reliable for estimating the density of mature wood, but the density of the wood just to the outside of the first 15 rings was highly reliable. Juvenile-mature correlations for earlywood density (EWD) and ring width (RW) were moderate; variation in each of these traits during juvenility explained around 20 % of the variation in the respective trait during maturity. The weakest phenotypic

Figure 7. Correlations for intra-ring characteristics between juvenile and mature wood.

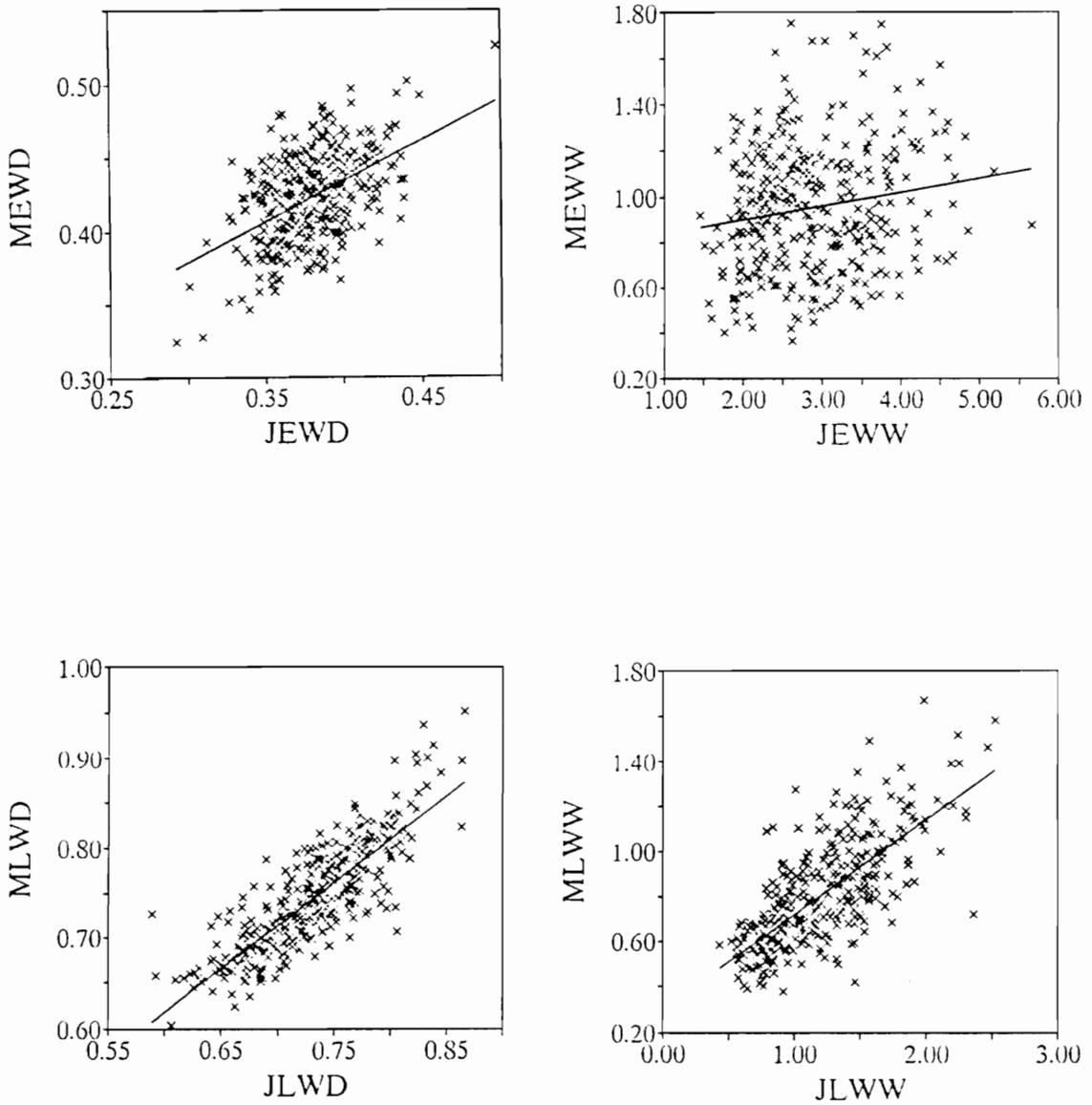
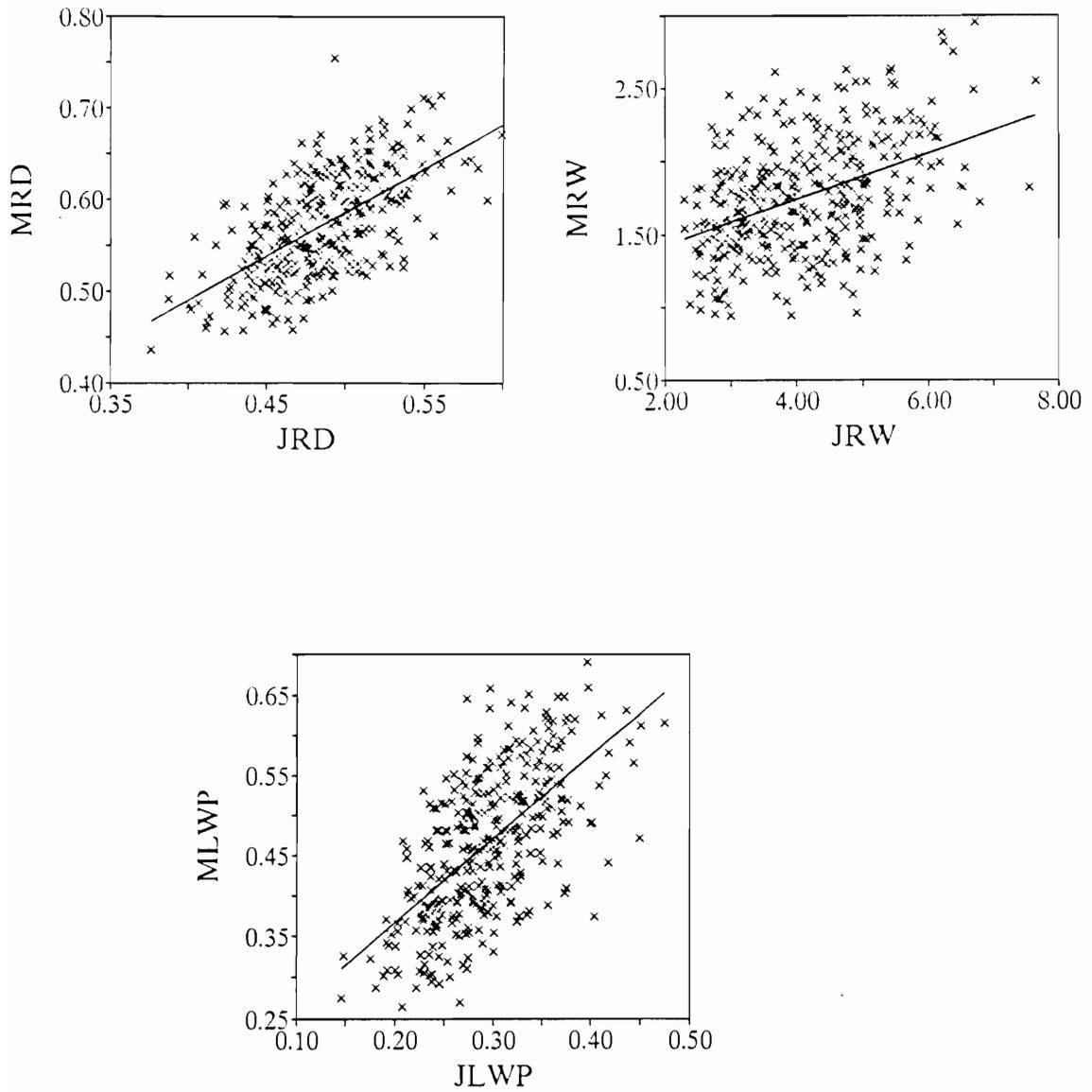


Figure 7. (continued)

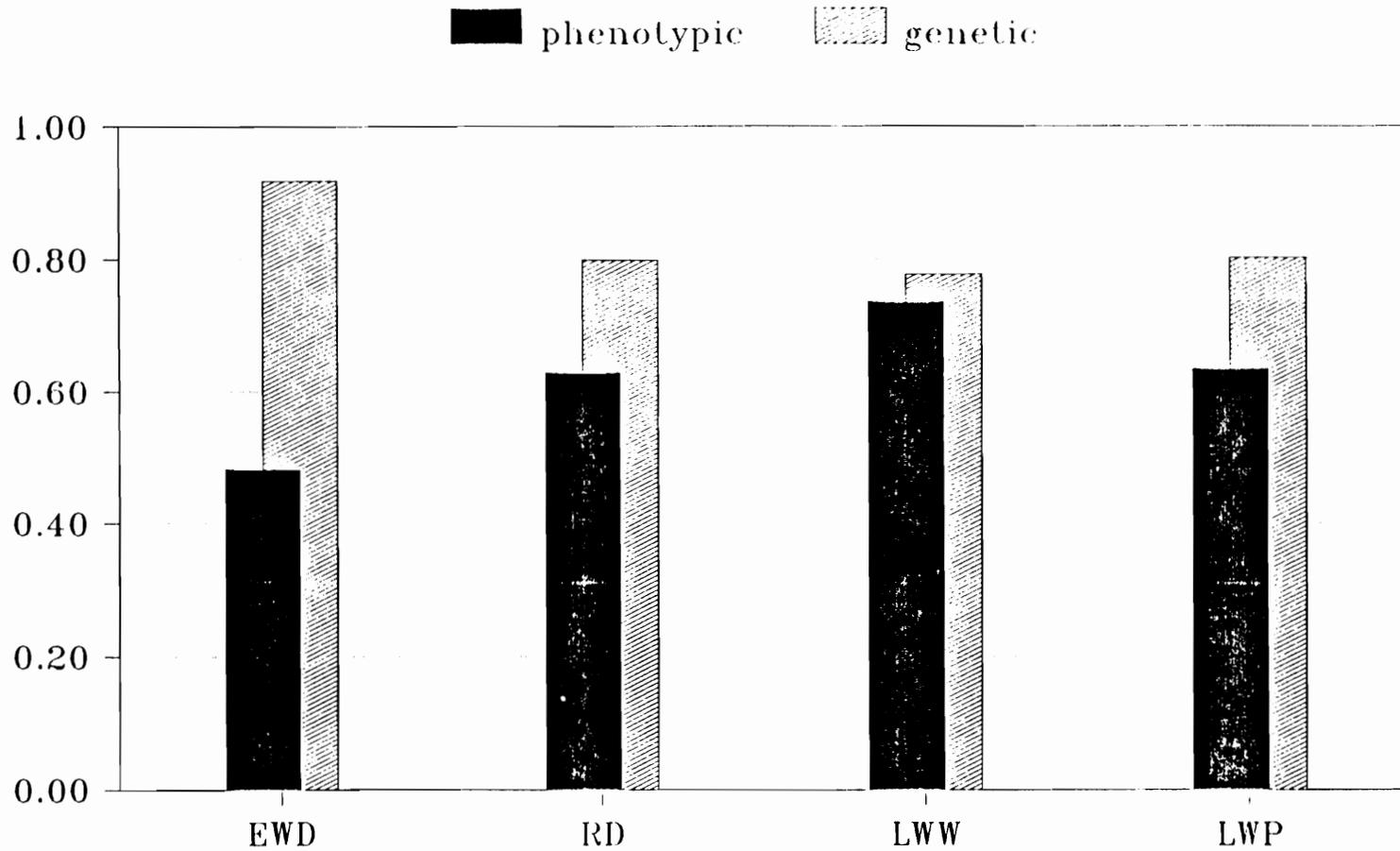


juvenile-mature relationship was that for earlywood width (EWW).

Genetic correlations were obtained for the traits that exhibited significant differences among families during both juvenile and mature periods. Figure 8 illustrates juvenile-mature genetic correlations for four traits in comparison with the corresponding phenotypic correlations.

In all cases, the genotypic correlation coefficients were more or less greater than the phenotypic coefficients. It appears that the positive phenotypic relationships for these traits had strong genetic bases. Nepveu (1976) noted that, assuming independent environmental effects at the juvenile and mature stages, the phenotypic covariance becomes a genetic covariance. He further suggested that the phenotypic correlation becomes a lower limit for the corresponding genetic correlation because the denominator in the former ratio is greater than that of the later. At least for RD, LWW, and LWP, the phenotypic juvenile-mature correlations can be used to throw light on the corresponding genetic correlations. The magnitudes of the genetic correlations indicate that trees with high-gravity wood during the early years of growth would inherently produce high-gravity wood when they reach maturity. Consequently, early selection for RD seems to be quite feasible. Likewise, selection for EWD, LWW, or LWP of the

Figure 8. Comparison of genetic and phenotypic correlations for intra-ring characteristics between juvenile and mature wood.



mature wood can be achieved to a great extent by selecting for these traits in young trees.

Beside the above single-trait correlations it was of interest to know how RD in one zone relates to RW in the other zone. The moderate, positive, phenotypic correlation between mature RD and juvenile RW indicates that trees which grew fast during the juvenile period had tendency to produce denser wood during mature period (Appendix Table 19). Mature RW had a non-significant phenotypic relationship with juvenile RD. The juvenile-mature genetic correlation for juvenile RW and mature RD was $r_g = 0.16$ indicating that early selection to improve radial growth does not affect wood density during maturity; in fact, this might bring about a slight increase in wood density. However, the genetic correlation between juvenile RD and mature RW was $r_g = - 0.24$. Since the family effect on mature RW was statistically non-significant, this estimate is to give a rough indication about a relationship that is not available in the literature for Douglas-fir.

Relationship Between Wood Density and Growth Rate Within Groups

The relationship between wood density and growth is of special interest due to the economic importance of both traits. Also, this relationship appears in timber grading where minimum standards of structural-grade timber quality

has been established on the basis of number of rings per unit length; the width of annual ring is employed by inspectors into various grades. Many foresters believe that faster growing trees will have lower wood density. While this appears to be the case for some tree species such as spruce (Keith, 1961), most hard pines show a lack of correlations between growth rate and wood density (Goggans, 1961, Goddard and Cole, 1966; Matzaris and Zobel, 1973; and Megraw, 1985). Early studies reporting in Douglas-fir have shown ring width as one of the important factors that explain the variation in wood density (Janka, 1921; Drow, 1957; and Mozina, 1960). Knigge (1962) observed that wood near the pith is lighter than outer wood of similar growth rate. He further suggested that the influence of growth rate on wood density is more obvious during early years of growth. McKimmy (1959) noted that "a constant rate of growth with differing percentage of summer wood caused more variation in specific gravity than did a constant percentage of summer wood under differing rate of growth". In a later study, he confirmed the non-significance effect of growth rate on wood density. The data at hand allow further investigation of this relationship by sorting the tree data into various groups and by using means of different combinations. Table 8 gives the results.

The correlations shown in a previous part of this

section, using tree averages, indicate that the relationship between wood density and rate of radial growth is non-existent in both juvenile and mature wood samples. Performing correlation analysis using all the ring data (10 rings/zone in each tree) resulted in significant negative correlations, but nonetheless of no practical importance; RW explained less than 1 % of the variation in RD in juvenile wood and less than 2 % in mature wood. When the tree averages in juvenile wood were sorted by plantation, the relationship was significant in the slow-growing trees at Mt. Hood but non-significant in the fast-growing trees at Wind River. During the mature period, RD and RW were inversely correlated in both plantations; however, the correlation seems to be stronger in the plantation with low-gravity trees (Mt. Hood).

The results of family mean correlations over plantations between RD and RW suggest that, in juvenile wood, fast growing families tend to produce high-density wood; with advanced stand development this relationship turned to be insignificant in mature wood. Family mean correlation by plantation indicate that RD-RW correlation was non-significant at the plantation that produced faster growth (Wind River); the less favorable growth conditions at Mt. Hood allowed expression of a negative correlation between the two traits. Similar results were obtained in another study involving 34 open-pollinated families of

Table 8. Correlation coefficients between ring density (RD) and ring width (RW) based on various groupings.¹⁾

	Juvenile wood			Mature wood		
	Mt. Hood	pooled data	Wind River	Mt. Hood	pooled data	Wind River
All rings		-0.09 (0.0001)			-0.13 (0.0001)	
Tree averages	-0.25 (0.0007)	0.04 (0.43)	0.16 (0.03)	-0.30 (0.0001)	-0.06 (0.23)	-0.15 (0.05)
Family averages	-0.25 (0.05)	0.20 (0.02)	-0.12 (0.33)	-0.23 (0.08)	0.12 (0.17)	-0.01 (0.95)
Provenance averages	-0.25 (0.29)	0.35 (0.03)	0.02 (0.94)	-0.28 (0.23)	0.24 (0.14)	-0.04 (0.87)
	pooled data					
trees in provenances	0.14 (0.22)	-0.08 (0.50)	0.11 (0.37)	-0.01 (0.91)	-0.07 (0.57)	0.19 (0.11)
	0.32 (0.006)	0.04 (0.73)	-0.04 (0.71)	0.05 (0.65)	0.15 (0.20)	-0.09 (0.47)
	-0.27 (0.02)	0.02 (0.89)	0.09 (0.45)	-0.33 (0.005)	-0.08 (0.50)	-0.08 (0.62)
		0.04 (0.71)			-0.22 (0.06)	

¹⁾ Coefficients are significantly different from zero at the probability levels given between parenthesis.

7-year-old Douglas-fir (Megraw, 1985). Considering provenance means for RD and RW, the only significant correlation was the positive correlation in juvenile wood using averages over plantations. To summarize, the relationship between wood density and ring width was either non-existent or positive and weak when taking averages of the entire replications. That was generally the case regardless of the group being averaged. When correlations were performed under uniform environments wood density related negatively to radial growth in the less favorable plantation. These results give more depth to the significant effect of plantations that was established for these traits in the previous section.

Before concluding this section, it is of interest to see if the relationship between RD and RW was the same in the different provenances. The results (Table 8) indicate a non-significant relationship in eight of the ten provenances during the juvenile period. In the other two provenances a distinct positive correlation was evident in the Darrington provenance and distinct negative correlation in the Hazel provenance; both seed sources were from the Stillaguamish River drainage in northwest Washington and relative to the others they ranked, respectively, ninth and fourth for RD. Similarly, during the mature period RD related significantly to RW in only two provenances, Hazel and Palmer. In both cases the relationships were negative.

SUMMARY AND CONCLUSIONS

The study material contained 360 mature trees representing 30 families (parent trees) selected from 10 provenances (geographic seed sources). The trees were growing in two replications in each of two plantations; each tree was sampled by two increment cores. The use of X-ray densitometry facilitated the determination of seven intra-ring characteristics: earlywood density (EWD), latewood density (LWD), average ring density (RD), earlywood width (EWW), latewood width (LWW), ring width (RW), and latewood percent (LWP).

The progenies included in this study displayed great variation in the properties analyzed within and among trees. Evidently, this variation is controlled to a great extent by the varying environmental conditions, but the genotypes also have a strong influence on the development of the trees.

Differences in wood density between the juvenile and mature wood zones are governed mainly by variations in the structure of wood produced during the early months of growth season (EWD) and by the rate of growth towards the end of the season (LWW and LWP).

Planting site influences all intra-ring characteristics except juvenile ring density (RD), mature earlywood density (EWD) and ring width (RW). The lack of

significance of the plantation effect on juvenile RD and mature RW is caused by an outweighing effect of their components.

During early years of growth, ring density components (EWD, LWD, and RD) are the only traits to be influenced by replications within plantations. During maturity, latewood width (LWW) and ring width (RW) are the most likely characteristics to reveal non-uniformity within plantation sites.

There is considerable genetic variation among families (when confounded into their geographic origins) for almost all the juvenile wood traits as well as for RD, EWD, LWW, and LWP in the mature-wood zone.

The results further show two genetic components to the variation in most of the studied intra-ring variables. One component is related to provenances; the other is related to families-within-provenances.

Provenance influences ring density in both juvenile and mature wood but not ring width, and family-within-provenance influences ring width only during juvenility and ring density (RD) only during maturity.

No definite trend is present for either the wood density or growth rate parameters. The dominant feature of genetic variation for EWD, LWW and LWP during the juvenile period, and for EWD during the mature period is the provenance variation. For juvenile LWD and mature LWW, the

dominant feature of genetic variation is the family-within-provenance variation. In other traits the two components of genetic variability are almost equal; they are either both significant as in mature LWP or both insignificant as in juvenile EWW and mature LWD.

The plantation-genotype interaction is of little importance if at all; both provenances and families were stable over locations and showed more or less the same ranking in Wind River and Mount Hood.

Heritability estimates, obtained from the analysis of the 30 families, are moderate-to-high for EWD, RD, LWW, and LWP, and low-to-moderate for LWD, EWW, and RW. For most of the studied traits, those estimates are biased upward due to the provenance variation and due to the limited number of environments included in the study.

The magnitude of the difference between the family heritabilities (provenances confounded) and family-within-provenances heritabilities (provenances accounted) depends on the relative importance of the provenance effect for the respective trait. It must be stressed, however, that these heritability estimates strictly apply to the sampled populations in the studied plantations. Generalization, hindered in part by the limited sample involved in this study, depends on the distribution of variances of the original total population.

Individual-tree heritabilities are lower than or equal

to the corresponding family heritabilities; however, in gain calculations, the variation among trees is greater enough than that among families to offset the low individual-tree heritabilities.

Being negatively correlated with EWW and positively with LWW, RD (tree averages) appears to have a weak, non-significant phenotypic correlation with RW, but a very strong correlation with LWP in both juvenile and mature wood.

In the various provenances, the relationship between RD and RW can be positive, negative, or non-existent. When sorting by plantations, RD relates negatively to RW in the less favorable site, but there is weak relationship in the fast-growing trees at the more favorable site.

Genetic correlation coefficients are consistently greater than the corresponding phenotypic coefficients.

In juvenile wood, fast growth is genetically associated with low density in earlywood but with high density in latewood. The weak, negative genetic correlation between RD and RW indicates that it is feasible to develop a strain of Douglas-fir with high juvenile wood density yet the impact of this on juvenile radial growth is low.

Although there is a slight trend suggesting that higher-EWD trees have low LWD, the two traits exhibit a genetically positive correlation.

For each of the traits, the observed mature wood values relate significantly and positively to the juvenile wood values. Juvenile-mature phenotypic correlations are highest for LWD, RD, LWW, and LWP and lowest for EWW.

Juvenile-mature genetic correlations indicate that selection to improve juvenile wood density will bring about favorable changes in mature wood density. Early selection to improve traits at rotation age is also feasible for EWD, LWW, and LWP.

Trees with wide rings during the early years of growth produce high-gravity wood when they reach maturity; however, the genetic correlation (positive) was weak.

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APPENDIX

Figure 9. Location of seed sources and plantation sites.

-  Principal range of Pacific coast form of Douglas fir in Oregon and Washington
-  Plantations
-  Seed sources

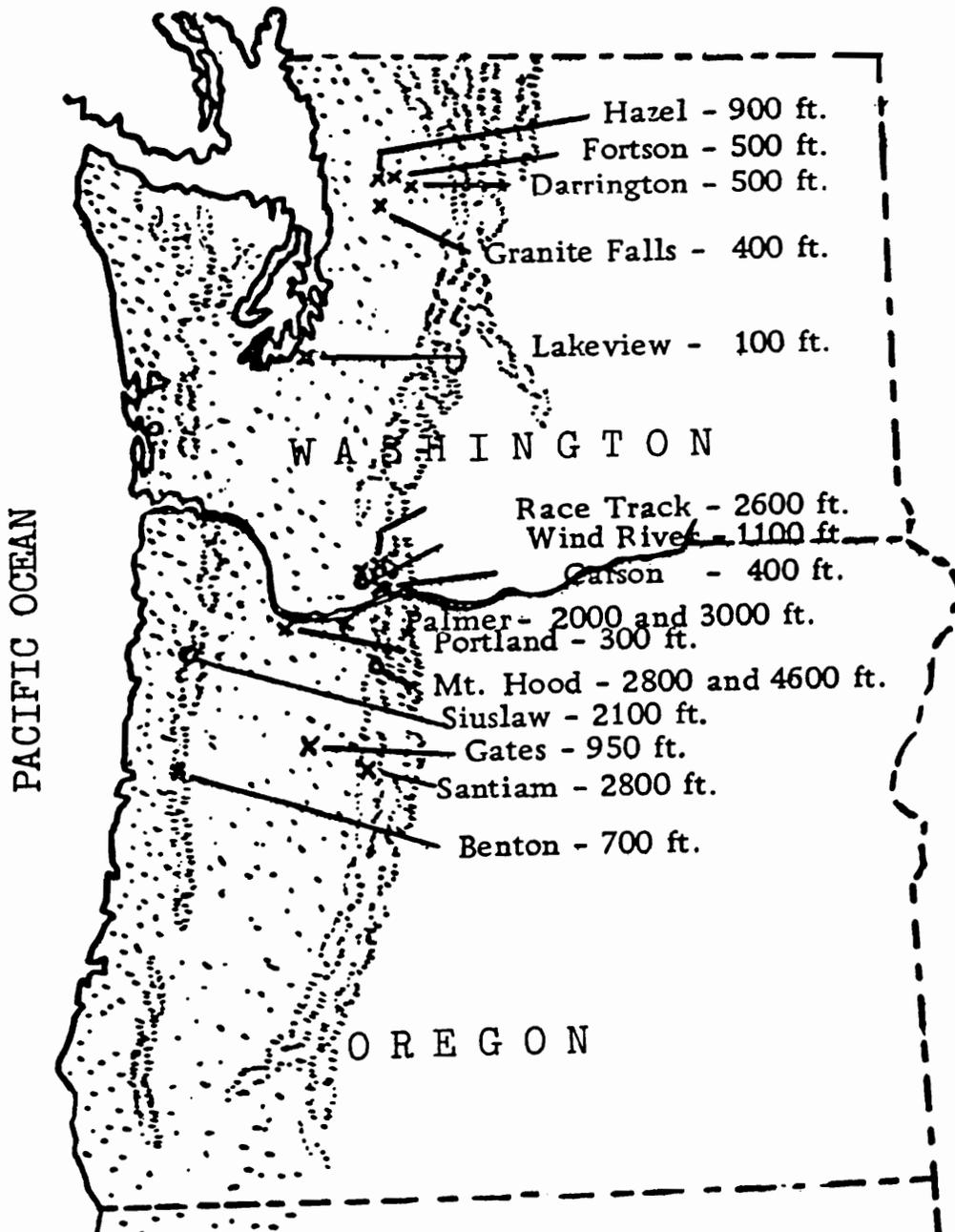


Figure 10. Example of a scan data file.

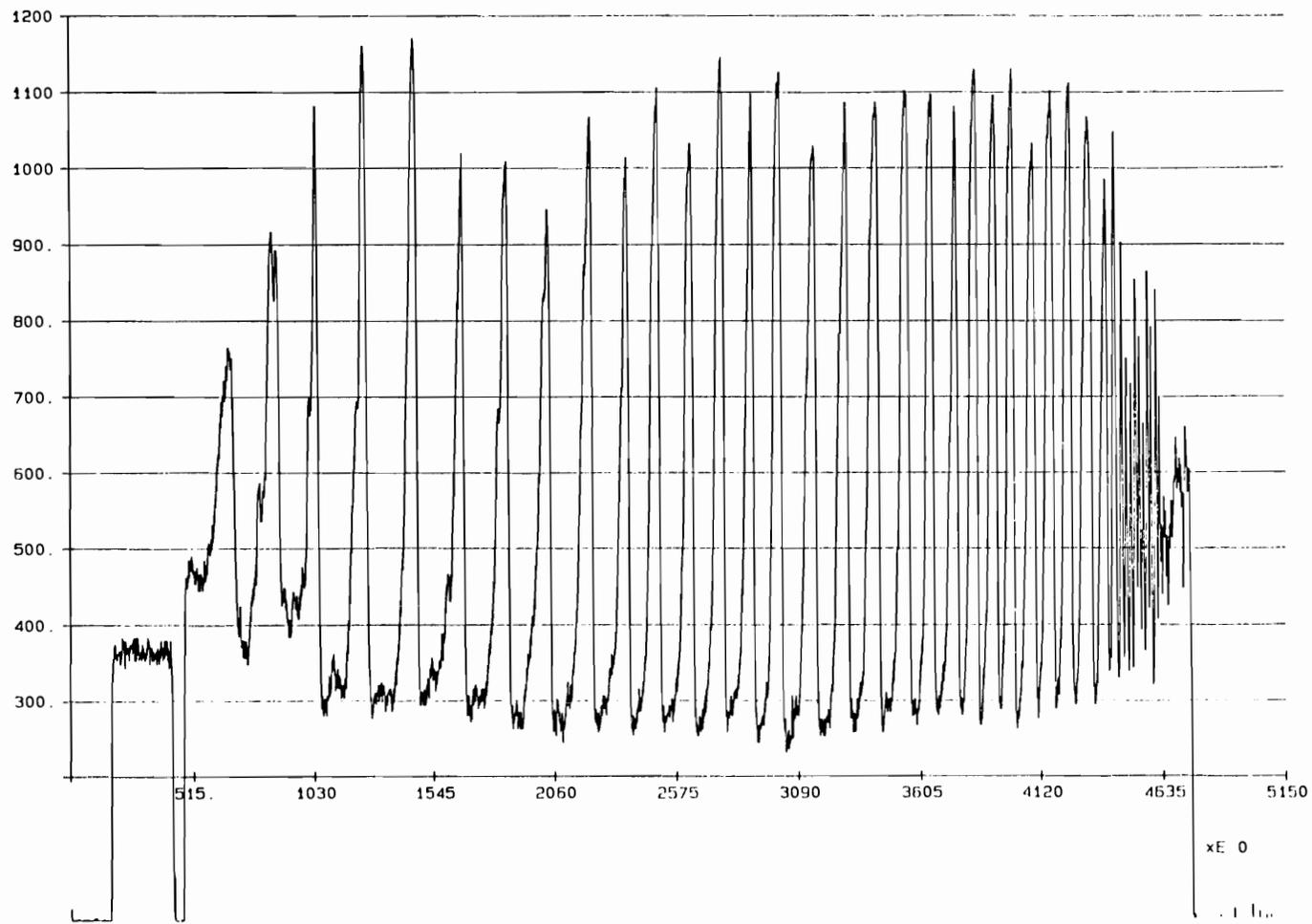


Table 9. Heritability estimates reported for intra-ring variables.

SPECIES	AGE	HERITABILITY		REFERENCE
		NARROW SENSE	BROAD SENSE	
Wood Density				
Abies alba	4	.22 - .33		Poge (1971)
Picea abies	18		.84	Kennedy (1966)
"	24-29	.61	.51 - .70	Worrall (1975)
Pinus				
elliottii	12-14	.21 - .56	.73	Squillace et al. (1962)
"	3	.43	.46 - .62	Zobel et al. (1962)
"	5		.44 - .49	Einspahr et al. (1964)
"	6	.43		Goddard and Cole (1966)
"	3	.43		Franklin and Squillace (1973)
P. pinaster	3	.65 - .75		Polge and Illy (1968)
"	6	.30 - .50		Killer (1973)
P. radiata	13-19		.50 - .70	Fielding and Brown (1960)
"	12		.74 - .75	Dadswell et al. (1961)
"	10		.53 - .75	Nichollas et al. (1964)
"	12		.57 - .90	Burdon and Harris (1973)
P. taeda	2-6	.37 - 1.00	.74 - .84	Van Buijtenen (1962)
"	7-8	.76 - .87		Goggans (1964)
"	2-3	.56 - .72		Stonecypher et al. (1964)
"	5	.47		Matziris and Zobel (1973)
Pseudotsuga				
menziesii	64	.00 - .66		McKimmy (1966)
"	14		.90	King et al. (1988)
"	15	.59		Vargas-Hernandez (1990)
Earlywood Density				
Picea abies	18		.86	Kennedy (1966)
"	24-29	.80	.63 - .86	Worrall (1975)
Pinus taeda	7-8	.04 - .35		Goggans (1964)
Pseudotsuga				
menziesii	15	.47		Vargas-Hernandez (1990)
Latewood Density				
Picea abies			.56	Kennedy (1966)
Pinus radiata	12		.45	Dadswell et al. (1961)
P. tadea	7-8	.63 - .67		Goggans (1964)
Pseudotsuga				
menziesii	15	.36		Vargas-Hernandez (1990)

Table 9. (continued).

SPECIES	AGE	HERITABILITY		REFERENCE
		NARROW SENSE	BROAD SENSE	
Ring Width				
<i>Picea abies</i>	24-29	.50	.69	Worrall (1975)
<i>Pinus pinaster</i>	3	.53		Polge and Illy (1968)
"	6	.02 - .09		Keller (1973)
<i>P. radiata</i>	12		.50 - .63	Dadswell et al. (1961)
"	10	.00 - .05		Nichollas et al. (1964)
"	10		.20	Nichollas and Brown (1971)
<i>P. taeda</i>	2-3	.14 - .35		Stonecypger et al. (1964)
"	5	.20		Natzirisand Zobel (1973)
Earlywood Width				
<i>P. taeda</i>	7-8	.25 - .26		Goggans (1964)
Latewood Width				
<i>Picea abies</i>	24-29	.51	.65	Worrall (1975)
<i>Pinus taeda</i>	7-8	.28 - .88		Goggans (1964)
Latewood Percent				
<i>Picea abies</i>	18		.85	Kennedy (1966)
<i>Pinus radiata</i>	12		.45 - .72	Dadswell et al. (1961)
"	10	.14		Nichollas et al. (1964)
<i>P. taeda</i>	7-8	.25 - .81		Goggans (1964)
<i>Pseudotsuga menziesii</i>	15	.24		Vargas-Hernandez (1990)

Table 10. Analysis of variance format and F-tests for families pooled across provenances using averages of the increment cores.

SOURCE	D.F.	M.S.	EXPECTED MEAN SQUARE
PLANTATION	1	A	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f} + 12\sigma_{l*f} + 180\sigma_{r(l)} + 360\sigma_l$
REPLICATIONS in PLANTATIONS	2	B	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f} + 180\sigma_{r(l)}$
FAMILY	29	C	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f} + 12\sigma_{l*f} + 24\sigma_f$
PL * FAM	29	D	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f} + 12\sigma_{l*f}$
REP(PL) * FAM	58	E	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f}$
WITHIN PLOT	240	F	$\sigma_e + 2\sigma_w$
ERROR	360	G	σ_e

Note: Numerals are coefficients of the variance components of the mean squares. The following notations are the variance components of the respective effect: σ_e = cores within trees; σ_w = within plot; $\sigma_{r(l)*f}$ = plot error; σ_{l*f} = plantaion x family; σ_f = family; $\sigma_{r(l)}$ = replication-within-plantation; σ_l =plantation.

F-Tests:

$$F_{\text{plantation}} = (A+E)/(B+D), \text{ with } [A+E]^2/[(A^2)+(E^2/58)] \text{ and } (B+D)^2/[(B^2/2)+(D^2/29)] \text{ degrees of freedom;}$$

$$F_{\text{replication (plant)}} = (B/E), \text{ with 2 and 58 degrees of freedom;}$$

$$F_{\text{family}} = (C/D), \text{ with 29 and 29 degrees of freedom;}$$

$$F_{\text{plant * family}} = (D/E), \text{ with 29 and 58 degrees of freedom;}$$

$$F_{\text{rep(plant) * family}} = (E/F), \text{ with 29 and 58 degrees of freedom;}$$

Table 11. Analysis of variance format and F-tests for families-within-provenances (provenances accounted) using averages of the increment cores.

SOURCE	D.F.	M.S.	EXPECTED MEAN SQUARE
PLANTATION	1	A	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 12\sigma_{l*f(s)} + 18\sigma_{r(l)*s} + 36\sigma_{l*s} + 180\sigma_{r(l)}$
REPLICATION in PLANT	2	B	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 18\sigma_{r(l)*s} + 180\sigma_{r(l)}$
PROVENANCES	9	C	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 12\sigma_{l*f(s)} + 24\sigma_{f(s)} + 18\sigma_{r(l)*s} + 36\sigma_{l*s} + Q\sigma_s$
PLANT * PROV	9	D	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 12\sigma_{l*f(s)} + 18\sigma_{(r)l*s} + 36\sigma_{l*s}$
REP(PLANT) * PROV	18	E	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 18\sigma_{(r)l*s}$
FAMILY (PROV)	20	F	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 12\sigma_{l*f(s)} + 24\sigma_{f(s)}$
PL * FAM (PROV)	20	G	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)} + 12\sigma_{l*f(s)}$
REP(PL) * FAM(PROV)	40	H	$\sigma_e + 2\sigma_w + 6\sigma_{r(l)*f(s)}$
WITHIN PLOT	240	I	$\sigma_e + 2\sigma_w$
ERROR	360	J	σ_e

Note: Numerals are coefficients of the variance components of the mean squares. The following notations are the variance components of the respective effect: σ_e = cores in trees; σ_w = within plots; $\sigma_{r(l)*f(s)}$ = subplot error; $\sigma_{l*f(s)}$ = plantations x families-within provenances; $\sigma_{f(s)}$ = family-within-provenance; $\sigma_{r(l)*s}$ = main plot error; σ_{l*s} = plantation x provenance; σ_s = provenance; $\sigma_{r(l)}$ = replication-within-plantation; σ_l = plantation.

Table 11. (continued)

F-Tests:

$F_{\text{plantation}} = (A+E)/(B+D)$, with $[A+E]^2/[(A^2/1)+(E^2/18)]$ and $[B+D]^2/[(B^2/2)+(D^2/9)]$ degrees of freedom;

$F_{\text{replication in plant.}} = (B/E)$, with 2 and 18 degrees of freedom;

$F_{\text{plant} * \text{prov}} = (D+H)/(E+G)$, with $[D+H]^2/[(D^2/9)+(H^2/40)]$ and $[E+G]^2/[(E^2/18)+(G^2/20)]$ degrees of freedom;

$F_{\text{provenance}} = (C+G)/(D+F)$, with $[C+G]^2/[(C^2/9)+(G^2/20)]$ and $[D+F]^2/[(D^2/9)+(F^2/20)]$ degrees of freedom;

$F_{\text{rep(plant)} * \text{prov}} = (E/H)$, with 18 and 40 degrees of freedom;

$F_{\text{family(prov)}} = (F/G)$, with 20 and 20 degrees of freedom;

$F_{\text{plant} * \text{fam(prov)}} = (G/H)$, with 20 and 40 degrees of freedom;

$F_{\text{rep(plant)} * \text{fam(prov)}} = (H/I)$, with 40 and 240 degrees of freedom;

$F_{\text{within plot}} = (I/J)$, with 240 and 360 degrees of freedom;

Table 12. Analysis of variance format for families pooled across provenances using tree averages.

SOURCE	DF	EXPECTED MEAN SQUARE
PLANTATION	1	$\sigma_w + 3\sigma_{r(l)*f} + 6\sigma_{l*f} + 90\sigma_{r(l)} + 180\sigma_l$
REPLICATIONS in PLANT	2	$\sigma_w + 3\sigma_{r(l)*f} + 90\sigma_{r(l)}$
FAMILY	29	$\sigma_w + 3\sigma_{r(l)*f} + 6\sigma_{l*f} + 12\sigma_f$
PLANT * FAM	29	$\sigma_w + 3\sigma_{r(l)*f} + 6\sigma_{l*f}$
REP(PL) * FAM	58	$\sigma_w + 3\sigma_{r(l)*f}$
WITHIN PLOT	240	σ_w

Table 13. Analysis of variance format and F-tests for families-within-provenances (provenances accounted) using tree averages.

SOURCE	D.F.	M.S.	EXPECTED MEAN SQUARE		
PLANTATION	1	A	$\sigma_w + 3\sigma_{r(l)*f(s)} + 6\sigma_{l*f(s)}$	$+9\sigma_{r(l)*s} + 18\sigma_{l*s}$	$+90\sigma_{r(l)} + 180\sigma_l$
REPLICATION in PLANT	2	B	$\sigma_w + 3\sigma_{r(l)*f(s)}$	$+9\sigma_{r(l)*s}$	$+90\sigma_{r(l)}$
PROVENANCES	9	C	$\sigma_w + 3\sigma_{r(l)*f(s)} + 6\sigma_{l*f(s)} + 12\sigma_{f(s)}$	$+9\sigma_{r(l)*s} + 18\sigma_{l*s} + Q\sigma_s$	
PLANT * PROV	9	D	$\sigma_w + 3\sigma_{r(l)*f(s)} + 6\sigma_{l*f(s)}$	$+9\sigma_{r(l)*s} + 1836\sigma_{l*s}$	
REP(PLANT) * PROV	18	E	$\sigma_w + 3\sigma_{r(l)*f(s)}$	$+9\sigma_{r(l)*s}$	
FAMILY (PROV)	20	F	$\sigma_w + 3\sigma_{r(l)*f(s)} + 6\sigma_{l*f(s)} + 12\sigma_{f(s)}$		
PL * FAM (PROV)	20	G	$\sigma_w + 3\sigma_{r(l)*f(s)} + 6\sigma_{l*f(s)}$		
REP(PL) * FAM(PROV)	40	H	$\sigma_w + 3\sigma_{r(l)*f(s)}$		
WITHIN PLOT	240	I	σ_w		

Table 14. Multiple comparison tests (LSD) for provenance means (a) in juvenile and (b) in mature wood.¹⁾

(a) Juvenile Wood

PROV	EWD	T-GROUPING	PROV	LWW	T-GROUPING
2	0.39629	A	5	1.3952	A
1	0.39065	B	2	1.2839	B
5	0.38909	C B	10	1.2677	C B
7	0.38512	C D	1	1.2277	C B
3	0.38130	E D	9	1.2072	C D
8	0.37807	E	3	1.1498	E D
9	0.37266	F	4	1.1363	E
6	0.37166	G F	8	1.1064	E
10	0.36823	G F	7	1.1010	E
4	0.36657	G	6	1.0964	E

PROV	RD	T-GROUPING	PROV	LWP	T-GROUPING
5	0.51670	A	5	0.34293	A
2	0.50263	B	2	0.31302	B
1	0.49482	C	1	0.30838	B
7	0.48276	D	7	0.29078	C
3	0.47971	D	3	0.28917	C
9	0.47814	D	9	0.28586	D C
8	0.47731	E D	8	0.27989	D C E
10	0.47032	E F	10	0.27692	D E
4	0.46870	F	6	0.27302	E
6	0.46667	F	4	0.27208	E

PROV	EWW	PROV	LWD	PROV	RW	
10	3.3180	5	0.75317	10	4.5857	
9	2.9860	9	0.73430	9	4.1929	
4	2.9719	2	0.73193	2	4.1258	
6	2.9185	4	0.73169	4	4.1082	
8	2.8725	8	0.72938	5	4.0973	N.S.
2	2.8420	10	0.72922	6	4.0149	
3	2.8273	1	0.72502	8	3.9792	
7	2.7942	7	0.72180	3	3.9776	
1	2.7309	3	0.71920	1	3.9586	
5	2.7021	6	0.71362	7	3.8952	

¹⁾ Means with the same letter are not significantly different.

Table 14. (continued)

(b) Mature Wood

PROV	EWD	T-GROUPING	PROV	RD	T-GROUPING
2	0.44042	A	5	0.60245	A
5	0.43588	A	2	0.59293	A
1	0.43377	B A	1	0.57422	A
7	0.42790	B C	7	0.56896	C B
3	0.42098	D C	9	0.56831	C B
6	0.42072	D C	10	0.56768	C B
8	0.41859	D	6	0.56120	C
9	0.41593	D	3	0.56057	C
10	0.41381	D	8	0.56026	C
4	0.40307	E	4	0.54817	D

PROV	LWP	T-GROUPING	PROV	EWW
5	0.51827	A	10	1.0716
2	0.49443	B	4	1.0377
1	0.47673	C	9	0.9931
7	0.45821	D	6	0.9705
9	0.45769	D	3	0.9498
10	0.45756	D	8	0.9461 N.S.
6	0.45500	E D	7	0.9282
3	0.45318	E D	2	0.9061
8	0.44088	E F	1	0.8923
4	0.42786	F	5	0.8375

PROV	LWD	PROV	LWW	PROV	RW
5	0.75871	10	0.8628	10	1.9344
10	0.75107	2	0.8625	9	1.8105
2	0.75049	5	0.8605	4	1.7979
9	0.74873	9	0.8174	6	1.7755
4	0.74164	6	0.8050	2	1.7686 N.S.
8	0.74023	1	0.7934	3	1.7265
7	0.73568	3	0.7767	5	1.6980
6	0.73023	4	0.7602	1	1.6856
3	0.72930	7	0.7574	7	1.6855
1	0.72905	8	0.7241	8	1.6702

Table 15. Analysis of variance for the the influence of plantations and provenances on age of (a) biological maturity and (b) optimal wood density.

(a) Age of biological maturity

Source	DF	Anova SS	F Value	Pr > F
PLANTATION	1	291.60	26.20	< 0.01
REPLICATIONS in PLANT	2	13.00	3.00	0.0751
PROVENANCE	9	90.40	2.13	0.137
PLANT*PROV	9	42.40	2.17	0.0768
Error	18	39.00		
		R-Square	C.V.	Mean
		0.92	4.78	30.8

(b) Age of optimal density

Source	DF	Anova SS	F Value	Pr > F
PLANTATION	1	705.60	41.17	< 0.01
REPLICATIONS in PLANT	2	14.80	0.72	0.5024
PROVENANCE	9	439.90	4.89	0.0135
PLANT*PROV	9	89.90	0.97	0.4978
Error	18	186.20		
		R-Square	C.V.	Mean
		0.87	16.66	19.3

T-tests (LSD) for variable: Age of optimal wood density.
Means with the same letter are not significantly different.

T	Grouping	Mean	PROV
	A	24.0	4
B	A	22.8	6
B	A	20.8	7
B	A	20.5	3
B	A	20.5	8
B	A C	19.7	9
B	A C	19.2	0
B	C	18.2	1
	D C	15.2	2
	D	12.0	5

Table 16. Narrow-sense heritabilities and associated standard errors for intra-ring characteristics based on analyses of families pooled across provenances.¹⁾

	FAMILY		INDIVIDUAL		P-VALUE
	HER.	S.E.	HER.	S.E.	

Juvenile wood					
EWD	0.62	0.18	0.58	0.05	0.005
EWW	0.45	0.13	0.29	0.04	0.057
LWD	0.40	0.12	0.21	0.03	0.081
LWW	0.66	0.16	0.48	0.05	0.002
RD	0.70	0.19	0.67	0.05	0.001
RW	0.48	0.13	0.28	0.04	0.046
LWP	0.63	0.18	0.61	0.05	0.004

Mature wood					
EWD	0.64	0.17	0.50	0.05	0.004
EWW	0.36	0.11	0.18	0.03	0.127
LWD	0.30	0.10	0.12	0.03	0.171
LWW	0.60	0.16	0.49	0.05	0.008
RD	0.78	0.19	0.70	0.06	0.0001
RW	0.27	0.10	0.13	0.03	0.205
LWP	0.78	0.19	0.71	0.06	0.0001

¹⁾ Differences among families are significant at the indicated probability levels.

Table 17. Narrow-sense heritabilities and associated standard errors for intra-ring characteristics based on analyses of families-within-provenances.¹⁾

	FAMILY		INDIVIDUAL		P-VALUE
	HER.	S.E.	HER.	S.E.	
----- Juvenile wood -----					
EWD	0.0	0.0	0.0	0.0	0.836
EWV	0.33	0.11	0.15	0.03	0.191
LWD	0.43	0.11	0.17	0.03	0.102
LWV	0.41	0.11	0.16	0.03	0.125
RD	0.09	0.08	0.04	0.02	0.415
RW	0.43	0.11	0.18	0.03	0.102
LWP	0.20	0.09	0.09	0.03	0.309
----- Mature wood -----					
EWD	0.16	0.09	0.08	0.03	0.346
EWV	0.02	0.08	0.01	0.02	0.491
LWD	0.20	0.09	0.08	0.03	0.315
LWV	0.60	0.26	1.62	0.07	0.011
RD	0.59	0.15	0.38	0.04	0.027
RW	0.24	0.10	0.11	0.03	0.286
LWP	0.67	0.16	0.44	0.04	0.009

¹⁾ Differences among families-within-provenances are significant at the indicated probability levels.

Table 18. Correlation coefficients between all possible pairs of intra-ring characteristics in juvenile and mature wood.¹⁾

	EWD	EWW	LWD	LWW	RD	RW	LWP
EWD		-0.67 0.0001	-0.29 0.0001	-0.22 0.0001	0.56 0.0001	-0.56 0.0001	0.38 0.0001
EWW	-0.54 0.0001		0.40 0.0001	0.64 0.0001	-0.23 0.0001	0.96 0.0001	-0.14 0.009
LWD	-0.14 0.007	-0.23 0.0001		0.72 0.0001	0.56 0.0001	0.56 0.0001	0.55 0.0001
LWW	0.24 0.0001	0.16 0.003	0.45 0.0001		0.54 0.0001	0.84 0.0001	0.65 0.0001
RD	0.54 0.0001	-0.61 0.0001	0.72 0.0001	0.60 0.0001		0.04 0.45	0.93 0.0001
RW	-0.23 0.0001	0.80 0.0001	0.11 0.04	0.72 0.0001	-0.06 0.23		0.15 0.004
LWP	0.63 0.0001	-0.67 0.0001	0.53 0.0001	0.59 0.0001	0.94 0.0001	-0.11 0.04	

¹⁾ Juvenile wood above and mature wood below diagonal.

Table 19. Correlation coefficients among all possible pairs of intra-ring characteristics between juvenile and mature wood.

	MEWD	MEWW	MLWD	MLWW	MRD	MRW	MLWP
JEWD	0.48 0.0001	-0.12 0.02	-0.31 0.0001	-0.14 0.006	-0.03 0.61	-0.17 0.001	-0.02 0.66
JEWW	-0.05 0.31	0.16 0.002	0.33 0.0001	0.51 0.0001	0.29 0.0001	0.43 0.0001	0.26 0.0001
JLWD	0.02 0.75	-0.32 0.0001	0.84 0.0001	0.43 0.0001	0.72 0.0001	0.04 0.42	0.60 0.0001
JLWW	0.24 0.0001	-0.14 0.006	0.57 0.0001	0.74 0.0001	0.70 0.0001	0.34 0.0001	0.66 0.0001
JRD	0.45 0.0001	-0.39 0.0001	0.42 0.0001	0.34 0.0001	0.63 0.0001	-0.07 0.20	0.57 0.0001
JRW	0.05 0.30	0.06 0.25	0.45 0.0001	0.65 0.0001	0.47 0.0001	0.44 0.0001	0.44 0.0001
JLWP	0.40 0.0001	-0.39 0.0001	0.42 0.0001	0.43 0.0001	0.64 0.0001	-0.01 0.82	0.63 0.0001

Table 20. The effect of using ring age as a covariate on the ANOVA results for (a) ring density and (b) ring width.

(a) RING DENSITY

SOURCE	DF	MEAN SQ	F-VALUE	VAR.COMP.	%

WITHOUT COVARIATE					
PLANTATION	1	0.9304	178.7	0.0025767	53.74
REPLICAT. in PLANT	2	0.004	1.633	8.614E-06	0.18
PROVENANCES	9	0.01836	2.757	0.0001864	3.887
PLANT * PROV	9	0.00122	0.82	-2.47E-05	-0.51
REP(PLANT) * PROV	18	0.00245	0.865	-2.13E-05	-0.44
FAMILY (PROV)	20	0.00634	2.544	0.0001635	3.409
PL * FAM (PROV)	20	0.00249	0.88	-2.82E-05	-0.59
REP(PL) * FAM(PROV)	40	0.00283	0.923	-3.96E-05	-0.83
TREE within PLOT	237	0.00307	3.5	0.0010963	22.86
CORES in TREES	357	0.00088		0.000877	18.29
WITH RING AGE AS A COVARIATE					
PLANTATION	1	0.44361	70.76	0.0012226	35.83
REPLICAT. in PLANT	2	0.00502	1.776	1.219E-05	0.357
PROVENANCES	9	0.01513	2.415	0.0001461	4.283
PLANT * PROV	9	0.00129	0.778	-3.39E-05	-0.99
REP(PLANT) * PROV	18	0.00283	0.949	-8.64E-06	-0.25
FAMILY (PROV)	20	0.00608	2.287	0.0001454	4.26
PL * FAM (PROV)	20	0.00266	0.893	-2.67E-05	-0.78
REP(PL) * FAM(PROV)	40	0.00298	0.971	-1.48E-05	-0.43
TREE within PLOT	237	0.00307	0.001	0.0010979	32.18
CORES in TREES	356	0.00087		0.0008717	25.55
RING AGE	1	0.00034	0.39		

Table 20. (continued)

(b) RING WIDTH

SOURCE	DF	MEAN SQ	F-VALUE	VAR.COMP.	%
WITHOUT COVARIATE					
PLANTATION	1	2.53603	1.809	0.0036329	1.982
REPLICAT. in PLANT	2	1.30461	3.364	0.0050933	2.778
PROVENANCES	9	0.47905	1.123	0.0012176	0.664
PLANT * PROV	9	0.31141	0.794	-0.004015	-2.19
REP(PLANT) * PROV	18	0.38783	1.575	0.0078634	4.289
FAMILY (PROV)	20	0.39521	1.257	0.0034328	1.873
PL * FAM (PROV)	20	0.3144	1.277	0.0056761	3.096
REP(PL) * FAM(PROV)	40	0.24629	0.919	-0.003641	-1.99
TREE within PLOT	237	0.26813	4.47	0.1040705	56.77
CORES in TREES	357	0.05999		0.059991	32.72
WITH RING AGE AS A COVARIATE					
PLANTATION	1	0.7088	1.288	0.0006777	0.399
REPLICAT. in PLANT	2	0.532	1.397	0.0008392	0.495
PROVENANCES	9	0.39401	0.988	0.0001216	0.072
PLANT * PROV	9	0.31378	0.755	-0.004585	-2.71
REP(PLANT) * PROV	18	0.38094	1.946	0.0102867	6.072
FAMILY (PROV)	20	0.38258	1.303	0.0037764	2.229
PL * FAM (PROV)	20	0.29368	1.5	0.008158	4.816
REP(PL) * FAM(PROV)	40	0.19578	0.747	-0.011076	-6.54
TREE within PLOT	237	0.26224	4.322	0.1007815	59.49
CORES in TREES	356	0.06068		0.060675	35.82
RING AGE	1	0.12835	2.115		