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Dr. M. D. McKimmy

The relationships of several wood quality traits with seed origin and phenological characteristics, measured at a young age, were tested from six seed sources in a young Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) provenance plantation. The wood quality traits measured were wood density, uniformity of wood density, percentage latewood, fiber length, Runkel ratio, and holocellulose content. Data for each seed source concerning the phenological characteristics of bud bursting time, bud set time, and needle length during the second growing season, were obtained from an earlier study. Seed origin data concerning the latitude and elevation of each seed source were also obtained from an earlier study. As an estimate of mature wood properties the outer three annual rings (most samples contained ten rings) away from the pith were used. It was hoped that these relationships would show possible predictors of mature wood properties from young seedlings. Such predictors could be used as

selection criteria for out planting seedlings with desired properties or as early indicators of the genetic influence on wood properties in genetic experiments.

The overall average wood density, uniformity of wood density, percentage latewood, and annual ring width were measured for each of the six seed sources. These measurements were used to test the influence of seed origin or phenological characteristics (measured at age two) on juvenile wood formation. These same traits were measured ring by ring, from pith to bark, in each of the seed sources in an attempt to explain some of the results encountered.

The latitude of seed source origin showed a significant relationship with mature wood fiber length indicating strong genetic control. Time of bud set appeared to have an influence on holocellulose content in mature wood. Needle length showed a significant negative correlation with average wood density but not mature wood density, indicating it may have some influence on wood formation but may not be used as a predictor of future wood properties. From the variation patterns in wood density, uniformity of wood density, percentage latewood, and ring width from pith to bark it appeared that a possible relationship between wood formation and crown development may exist.

The Influence of Seed Source Origin and Phenological Characteristics on Wood Quality in a Young Douglas-Fir Provenance Plantation

by

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THE INFLUENCE OF SEED SOURCE ORIGIN AND PHENOLOGICAL CHARACTERISTICS ON WOOD QUALITY IN A YOUNG DOUGLAS-FIR PROVENANCE PLANTATION

I. INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the principal forest species in the Pacific Northwest in terms of importance to the forest products industry. Further, Douglas-fir is the largest tree in the Northwest, and in the United States is second only to the giant sequoias (*Sequoia gigantea* (Lindl.) Decne.) of California (Harlow and Harrar, 1968). Trees in virgin forests average 180 to 250 feet in height and four to six feet in diameter, although heights of 325 feet and diameters of eight to ten feet are not uncommon. Conditions for optimum growth of Douglas-fir occur west of the cascade mountains in Washington and Oregon. This area contains over 50% of the standing volume of Douglas-fir. The overall range of this species is one of the largest of all gymnosperms. The north-south distribution extends from the central British Columbia coast (latitude 55^{o}N.) to central Mexico (latitude 19^{o}N.) and from the Pacific coast to western Alberta in the north and inland through Arizona, New Mexico and Texas in the south. Site altitude varies from sea level to 10,000 feet, and rainfall varies from 18 inches to over 100 inches per year.

Because of the large variation in geographic and climatic conditions, morphological and physiological differences have been observed in Douglas-fir. These observations have resulted in the subdivision of the species into two more or less distinct types. The two varieties recognized are the coast type or green Douglas-fir, Pseudosuga menziesii, var. menziesii, and the interior or Rocky Mountain type Douglas-fir, Pseudotsuga menziesii, var. glauca.

The wood of Douglas-fir is moderately light (wood density approximately 0.43 g/cm^3 green, 0.48 g/cm^3 ovendry- Rocky Mountain type) to moderately heavy (wood density approximately 0.45 g/cm^3 green, 0.51 g/cm^3 ovendry - Pacific coast type), and moderately hard (Panshin and de Zeeuw, 1970). The principal use for Douglas-fir wood is in building and construction. Lumber is used largely in light frame construction and in the manufacture of large laminated beams and arches for churches, schools, and commercial buildings. Other uses of Douglas-fir lumber include planing-mill products (sash, doors, flooring, and general mill work), crates and pallets, boatbuilding and furniture. Veneer peeled from Douglas-fir logs is used in the production of structural plywood used extensively in building and construction. Douglas-fir is also used in pulp and paper production and is the leading pulpwood species in the west for sulfate pulp. Also, Douglas-fir wood is used extensively in the production of various composition boards (fiberboard, particleboard, and hardboard). Other uses of Douglas-fir are for utility poles, piling, mine timbers, and railroad ties.

Douglas-fir grown in the Rocky Mountain region, especially in southern parts of the range, tends to contain smaller percentages of latewood at a given rate of growth, and to be lower in average wood density and strength than Douglas-fir grown in the coastal areas, the Cascades, and the Sierras. Likewise, wide-ringed, second-growth Douglas-fir grown in the coastal areas is frequently lighter in weight and lower in strength properties than virgin growth wood from the same region.

Wood density, as well as many other wood properties have been shown to be quite highly genetically inheritable (Silen, 1962). As a result, wood scientists and tree breeders believe it is possible, through genetic manipulation, to maintain or improve present levels of wood properties. In genetic studies with Douglas-fir it is difficult to evaluate the influence of genetics on wood properties since the tree forms juvenile or core wood during its early years of growth. There is some evidence suggesting that properties of juvenile wood are not correlated to properties of mature wood (McKimmy, 1966). Thus it is necessary to wait the number of years required for a tree to start forming mature wood before evaluating wood properties. This problem is further complicated by the fact that the time span for juvenile wood formation (number of annual rings) is not the same for all trees. The age at which a tree starts forming mature wood is thought to be 10-20 years, but may be longer in some cases. This period of time is too great for one wishing to determine the influence of genetics on wood properties, consequently most such studies have analyzed the juvenile wood of young seedlings.

To alleviate this problem it would be helpful to have an indicator of mature wood properties that could be measured at a young age. Phenological characteristics such as bud bursting, bud set, and needle length are to some extent genetically controlled and may have an influence on wood formation. Phenological characteristics can be easily measured at a young age. If phenological characteristics could be correlated with mature wood properties, such relationships could be used as selection criterion for out planting seedlings with a high probability of having desirable wood properties, or as an early indicator of the genetic influence on wood properties.

II. OBJECTIVES

The primary objective of this study was to find an early stage predictor of mature wood properties in Douglas-fir (*Pseudotsuga menziesii*, var. *menziesii*). The relationships of seed source location and phenological characteristics with some of the more important wood quality traits were tested from a young Douglas-fir provenance plantation. The characteristics used were:

1. Elevation of seed source
2. Latitude of seed source
3. Bud bursting time (during second growing season)
4. Bud set time (during second growing season)
5. Needle length (during second growing season)

These data were measured in an earlier study (Ching and Bever, 1960).

The wood quality traits measured in this study were:

1. Wood density
2. Uniformity of wood density
3. Percentage latewood
4. Runkel ratio
5. Fiber length
6. Holocellulose content

As an estimate of mature wood properties, these wood quality traits were measured in the outer three annual rings of each sample. Most of the samples collected contained 10 annual rings, and although not mature wood by definition, the outer three annual rings should have exhibited properties approaching those of mature wood. Also, the average sample wood density, uniformity of wood density, and percentage latewood were measured. In an attempt to explain some of the variation encountered, these three traits along with growth rate (ring width) were measured in each individual growth ring from pith to bark.

III. LITERATURE REVIEW

Definition of Wood Quality

Wood quality can be defined as those characteristics and properties of wood which make it desirable for certain end uses. Thus, many properties and criteria must be considered in evaluating wood quality. The constitution and arrangement of the wood cells and fibers have a significant influence on the behavior of wood when subjected to certain end uses.

Many wood properties show a significant amount of natural variation. Environment, tree age, position within the tree, and even genetic differences have all been shown to have an influence on the variation in wood properties. The variation in several of the more important wood quality traits will be discussed below.

Variation in Wood Density

The sources of variation in wood density have received more attention than any other aspect of wood structure. This is due primarily to the association of density with many other wood properties. Basic wood density (ovendry weight/saturated volume) is a measure of the relative proportions of cell wall substance and air in wood and is influenced by cell diameter, cell wall thickness, and to a lesser extent in conifers by the relative numbers of different cell types (Cown, 1976). Wood density influences strength properties, machinability, and pulp yields, and is a major factor in determining the final end uses for a particular wood.

In general, density increases from the pith outwards. The inner zone of lower density is referred to as juvenile wood or core wood. The extent of this juvenile wood is known to vary between species and even between trees, but cannot be precisely defined because its characteristics are not dependent solely on wood density (Cown, 1976). McKimmy (1966) measured the effect of tree age on wood density in Douglas-fir and found an initial decrease through the first ten rings or so (the juvenile wood zone), then a steady increase for the next twenty years. The general consensus of the literature seems to be that the juvenile or core wood zone tends to contain the first 10-20 rings from the pith.

The dimension of wood cell walls varies appreciably across growth rings. This variation is due to both genetic and environmental factors. The wood formed early in the growing season is characterized by large diameter tracheids with thin cell walls and is referred to as springwood or earlywood. Tracheids formed later in the growing season are characterized by narrower radial diameter and thicker cell walls. This zone is referred to as summerwood or latewood. Echols (1970, 1973) used radiation densitometry to show that density within the same annual ring of Douglas-fir can vary from 0.20 g/cm^3 (earlywood) to 0.85 g/cm^3 (latewood).

Earlywood and latewood are subject to variation in both density and their proportions within the annual ring. As a result, the average density of annual rings is subject to wide variation.

Several authors have attempted to correlate growth rate, i.e., ring width, with wood density but have had little success. Zobel and Rhodes (1955) working with Southern pine found little correlation between growth rate and wood density. Mozina (1960) found no relationship between ring width and wood density in Douglas-fir. McKimmy (1959) also found that growth rate had no statistically significant effect on the wood density of Douglas-fir; however, it was suggested that growth rate may effect the wood density of various species but these effects may be modified by such factors as moisture holding capacity of soil, nutrients in soil, site, and age of the tree. Alterations in ring width alone cannot effect wood density unless accompanied by regular changes in the proportions or densities of the earlywood and latewood components (Cown, 1976).

Environmental and Geographic Sources of Variation in Wood Density

It has been conclusively established that environmental and geographic conditions can have a significant effect on wood density. The two distinct varieties of Douglas-fir (Pseudotsuga menziesii, var. menziesii, and Pseudotsuga menziesii, var. glauca) have already been mentioned. The subdivision of the species into these two varieties is the result of the large variation in geographic and environmental conditions encountered within the range of Douglas-fir. In addition to morphological and physiological differences encountered between these two varieties there are also differences in wood density. The Pacific Coast variety (var. menziesii) is generally considered to have higher wood density than the Rocky Mountain variety (var. glauca) (Panshin and deZeeuw, 1970).

Geographic location in itself does not effect wood quality but it reflects certain environmental factors (soil, rainfall, length of growing season, temperatures, etc.) that do have a more direct influence on wood density (Mitchell, 1964). Many studies have attempted to correlate specific environmental factors with wood density; however, due to a strong genetic component of variation in wood density, the effects of environment are sometimes masked (Cown, 1976). Lassen and Okkonen (1969) found a significant negative relationship between wood density and summer rainfall. It was also found that wood density varied with elevation in a non-linear relationship. Trees from the lowest elevations had the highest wood density while trees from middle elevations had the lowest wood density. McKimmy (1959) found little effect on wood density caused by site class or crown class. McKimmy and Nicholas (1971) found a significant environmental (plantation) effect on wood density among three provenance plantations of Douglas-fir. Heger, et al. (1974) used radiation densitometry to relate weather data to growth ring component variables. Average latewood density and maximum ring density varied most and were correlated positively with temperature and negatively with precipitation.

Genetic Variation in Wood Density

It is generally accepted that genetic variation in wood density can exist within a species. This fact becomes evident when seed lots from different geographic sources (provenances) are planted together in the same environment (Cown, 1976). McKimmy (1966) and McKimmy and Nicholas (1971) have shown significant differences in wood density between seed sources in Douglas-fir provenance plantations. Nicholas (1963) found that both genetic and environmental effects were important factors in explaining the total variation of wood density in Douglas-fir. However, it appeared that the environmental component of variation was considerably greater than the genetic component of variation. Many other authors have mentioned large between tree variation under constant environmental conditions and have attributed this variation to genetic differences (Zobel, 1960; McKimmy, 1966).

Juvenile-Mature Correlation

There is a need in forest genetics research to establish criteria whereby specific wood characteristics of the mature tree will be predictable from juvenile characteristics of a seedling or young tree. As previously mentioned the tree forms juvenile wood or core wood during its first 10 to 20 years of growth. The properties of this wood are different from those of mature wood. Thus, it is necessary to wait the number of years a tree needs to start forming mature wood before evaluating the properties of such wood. This period of time is undesirable when one wishes to evaluate the influence of genetics on wood properties.

Zobel and Rhodes (1956) found a highly significant positive correlation between juvenile wood density (first eight rings) and mature wood density in loblolly pine (*Pinus taeda* L.). McKimmy (1966), on the other hand, found that juvenile wood density was not reliable in predicting the density of mature wood in Douglas-fir.

Variation in Percentage Latewood

The first and most popular definition of the earlywood-latewood boundary is Mork's definition. Based on this definition, latewood begins when twice the double cell wall thickness exceeds the lumen diameter in the radial direction. This criterion involves microscopic examination and is very tedious to use. Several attempts have been made to determine a less tedious technique to determine the early-wood-latewood boundary. These techniques have had little success with the exception of radiation densitometry. Phillips (1960) used beta-ray densitometry to determine a lower limit for the density of latewood. The proportion of wood above this level was then measured as percentage latewood. The basis for this determination was Mork's definition.

It is generally accepted that there is a close relationship between percentage latewood and wood density in Douglas-fir (Cown, 1976). This relationship is an intuitively obvious one since in Douglas-fir the latewood density is generally about two to three times that of the earlywood.

Although there is a definite relationship between percentage latewood and wood density, this relationship cannot be assumed to be constant under all conditions. This is because not only are the proportions of earlywood and latewood subject to variation, but the relative densities of earlywood and latewood may vary independently of one another. As an example, Drow (1957) found that the relationship between percentage latewood and density was different for different growth rate classes.

As would be expected, several researchers have found the variation in percentage latewood to follow trends similar to those of wood density. Lassen and Okkonen (1969), working with sources of environmental variation in Douglas-fir, found percentage latewood decreased with increasing summer rainfall in a linear trend similar to that of wood density. Percentage latewood was also found to be highest in the low elevation-low precipitation combination, and lowest in the high elevation-high precipitation category. As was the case with wood density, McKimmy (1966) found both the environmental and genetic sources of variation of percentage latewood in Douglas-fir to be highly significant.

Uniformity

Very little is known about the variation patterns in uniformity from ring to ring or from tree to tree. However, uniformity is an important factor in determining suitable end uses for a particular wood. Echols (1972) proposed a hypothetical guide to the utilization of Ponderosa pine (Pinus ponderosa Laws) on the basis of mean wood density and density distribution (Figure 1). A density distribution coefficient was used to quantify the amount of variation about the mean. The derivation of this index is discussed in the Appendix. A high density distribution coefficient indicates a great deal of variation about the mean, while a low density distribution index indicates little variation about the mean.

Fiber Length

Fiber length has a very important influence on pulp and paper properties. Dadswell, et al. (1959) found that an increase in fiber length showed a direct linear relationship with tearing strength and also caused improvement in both fold endurance and tensile strength. Wangaard, et al. (1966) also evaluated the influence of fiber length on pulp sheet properties and found fiber length to have a significant effect on sheet density, burst factor, breaking length, and tear factor.

Fiber length has also been related to permeability in Douglas-fir (Krahmer, 1961). Kennedy and Ifju (1962) found a statistically significant relationship between fiber length and micro-tensile strength but attributed this to a correlation that was found between fiber length and microfibril angle.

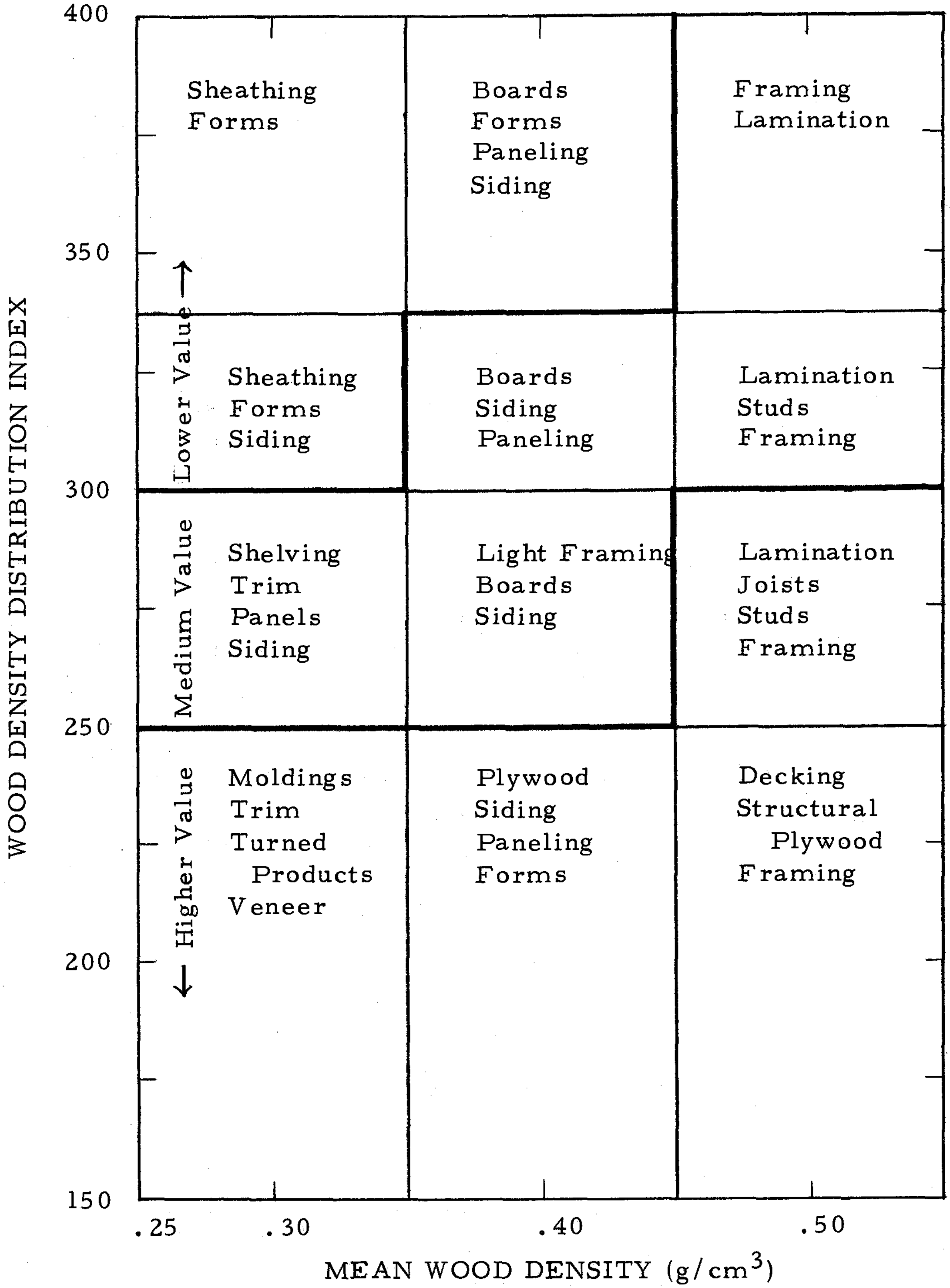

Figure 1. Product Suitability of Ponderosa Pine (based on wood density and density distribution).

A great deal of work has been done concerning both genetic and environmental components of variation in fiber length. Zobel et al. (1960) obtained a highly significant variation between trees on a specific plot of Southern pine. This variation could be due to genetic differences. A highly significant difference was also obtained between sites which was accounted for by an environmental component of variation. Nicholas (1963), working with 50 year old provenance plantations of Douglas-fir, found that provenances retained the same relative ranking of fiber length in all plantations. This indicated a strong genetic component of variation. However, there was a considerable variation in fiber length from one plantation to another. This environmentally caused variation ranged from 3.0 to 3.7 mm. Echols (1958), working with Scotch pine (*Pinus sylvestris* L.) from different geographic locations, found a significant correlation between fiber length and latitude.

Holocellulose

Holocellulose is a term which describes the chemical portion of the wood containing the cellulose and hemicelluloses. In other-words, it is the portion of the wood remaining after the lignin and extractives are removed. Due to the difficulty of removing all the lignin without removing some cellulose, most holocellulose figures presented in the literature include 2-3% lignin (Erickson, 1962).

Delignifying below 2-3% residual lignin can be detrimental to the cellulose fractions. However, even with this residual lignin, consistent measurements allow holocellulose comparisons to be made between samples.

Little work has appeared on the variation of holocellulose in Douglas-fir. Kennedy and Jowarsky (1960) attempted to relate several factors to cellulose content (Cross and Bevan) in Douglas-fir. It was found that site, crown class, radial position, and their interactions were all insignificant factors in regulating cellulose content. Growth rate and percentage latewood were also insignificant in explaining cellulose variation. Since the variation in cellulose content between individual trees could not be attributed to any of the growth or environmental factors studied, it was speculated that the cellulose variation between trees may be an inherent one under genetic control. Schütt (1958) determined the cellulose content in several provenances of *Pinus contorta* Dougl. grown in Western Germany and also concluded that the variation in cellulose yields depended more on the genetic or provenance effect than on site conditions and climatic differences.

Zobel, *et al.* (1966) determined patterns of holocellulose variation in loblolly pine. Holocellulose was found to be low near the center of the tree and to increase outwardly. Juvenile values were indicative of mature wood values but not with sufficient accuracy to base major decisions on this relationship. Differences in holocellulose among trees of the same age from the same site and growing at the same rate were found to be quite large. However, a small degree of inheritance was found. It was concluded that breeding for holocellulose by simple selection methods would show little improvement in loblolly pine.

Relationships Between Phenological Characteristics and Wood Density

The relationship between wood density and percentage latewood was discussed earlier. The proportion of the growing season involved in the production of earlywood and latewood will have a direct effect on the proportions of each formed. This relationship, however, cannot account for all the variation encountered in wood density because, in addition to differences in the proportions of earlywood and latewood formed, there may be relative differences in the densities of each zone from tree to tree. Also, the rate of production of both earlywood and latewood may be different from tree to tree.

Larson (1960) relates the earlywood - latewood differentiation to physiological processes. In the so called "hormonal theory" of differentiation, large diameter, thin walled tracheids will be produced during the period of active elongation growth and high auxin synthesis. Auxin is a growth hormone produced in the elongating buds. The initial wall thickness is influenced by the rate of cell division as well as by an inherent response to the water and nutrient supply, crown size, and general physiological efficiency of the tree. After the early period of growth (earlywood formation), a balance is achieved where reductions in cell division rate follow the increasing water stress conditions. This stage has been related to the cessation of shoot growth. Latewood tracheids with narrow diameter are produced following the cessation of terminal growth and the consequent reduction in auxin synthesis; a growth inhibiting system may become more prominently active at this time. As the inhibition of cell division begins before the supply of nutrients from the crown tapers off, the resulting cell wall material produced causes thicker cell walls. Under the same conditions, some trees continue this process longer than others resulting in a higher proportion of latewood.

Several workers have attempted to relate activity of the apical meristem to wood density. McKimmy (1966) found a relationship in Douglas-fir provenances between early bud bursting and high wood density. Kennedy (1970), also working with Douglas-fir, found similar results and offered the following explanation: early flushing trees may terminate their grand period of growth (period between bud burst and cessation of leader elongation) before the late flushers, and since there was no apparent difference in the rate of xylem production, the early flushing trees will have a somewhat longer period for the formation of wood under conditions of reduced crown activity and hormone production. This physiological state would encourage a proportionately larger amount of latewood to be formed.

Mergen, et al. (1964), on the other hand, working with Norway spruce (Picea exelsa Link.), found that trees with early bud bursting had more rapid growth, lower latewood percentage, and lower density. This was attributed to a longer period available for earlywood formation. Worrall (1970) found a relationship between bud bursting and density in Norway spruce similar to that found by Mergen et al. In this study, however, the cessation of leader elongation and cessation of radial growth were also measured and the proportions of the growing season available to earlywood and latewood production were estimated. The proportion of the growing season from cessation of leader elongation to cessation of radial growth was highly correlated with percentage latewood and density, providing support for the hormonal theory.

From these studies it appears the effect of crown phenology on wood quality must be different for different species.

X-Ray Densitometry

For this study, more detailed information than just the overall or average density of samples was desired. Information regarding the variation of density within growth rings was necessary.

X-ray densitometry is an indirect technique of measuring wood density on a continuous basis. It allows the rapid and accurate assessment of wood density both within and between individual growth rings. The general procedure is to: (1) produce a negative image of the cross section of a wood sample by projecting x-rays onto x-ray film through the wood sample; (2) develop the film under standard conditions to ensure consistent results and uniform comparisons between exposures; (3) scan the x-ray negative with a micro-densitometer which converts the optical density of the film to a continuous chart recording representative of wood density (see Fig. 6). This chart recording then serves as the basis for determining average sample wood density, the density distribution index, and percentage latewood. The equipment allows for the measurement of these characteristics over the entire sample or any segment of the sample; e.g. individual growth rings. The calculation of these properties are discussed in the Appendix.

Wood is composed of chemical elements with a low atomic weight (principally carbon, hydrogen, and oxygen) and as a result does not readily absorb x-rays. Soft x-rays are therefore adequate for densitometric investigation of wood samples (Polge, 1966). Soft x-rays are rays of long wave length produced under low voltage and thus possessing low energy.

If sample thickness is uniform the amount of x-rays absorbed by the wood sample will be related exponentially to its density according to the formula:

$$I = I_o e^{-\mu td}$$

Where I_o = intensity of radiation reaching the sample

I = intensity of radiation passing through the sample

μ = mass-absorption coefficient of material (wood)

t = sample thickness

d = sample density

The intensity of radiation reaching the x-ray film will be approximately equal to the radiation passing through the sample. When exposing x-ray film for low optical densities, providing exposure and development are uniform, darkening of the film is proportional to the incident energy on the film. If O and O_o are the opacities and D and D_o are the optical densities, respectively corresponding to I and I_o, we have in these conditions:

$$O = O_o e^{-\mu td}$$

or

$$\log_{10} O = \log_{10} O_o - \frac{\mu td}{0.434}$$

i.e.

$$D = D_o - \frac{\mu td}{0.434}$$

Thus, optical density is inversely related to wood density in the impact area of radiation. A densitometer analysis of the x-ray film then provides a linear response directly related to wood density (Polge, 1966).

There are three parameters that are specimen dependent and have an effect on the accuracy of the technique. These parameters are:

1. specimen thickness
2. specimen moisture content
3. fiber axis in relation to the x-ray beam

The specimen thickness must be controlled very closely since the absorbed x-radiation will be proportional to specimen thickness. Any deviations in thickness will cause aberrations in the radiation received by the film affecting the linearity of the relationship between optical density of the film and actual wood density. It may help to visualize the optical density of the film as representative of a wood density per unit area which has been calibrated to a given specimen thickness.

Moisture contained in the wood will also absorb x-rays, so any fluctuations in moisture content will cause erroneous results. A constant and uniform moisture content must be maintained in all specimens in order to allow comparison between specimens.

The fiber axis of the specimen must be as closely parallel to the x-ray beam as possible. If the fiber axis is not parallel to the x-ray beam, the abrupt changes in density between earlywood and latewood will appear more gradual due to an averaging affect caused by the beam passing through both earlywood and latewood.

IV. BACKGROUND

In 1954, planning began on a region-wide provenance study of Douglas-fir (Ching and Bever, 1960; Rowe and Ching, 1973). Sixteen seed sources from the west side of the Cascade Mountains in Oregon, Washington, and British Columbia were selected. A uniform latitudinal and altitudinal distribution of seed collection was planned in the natural growing range of this species type in order to include as many different provenances as possible.

Geographic locations of the seed provenances are given in Table 1. The provenances range in latitude from southern Oregon to the northern part of Vancouver Island, British Columbia; and in elevation from 100 ft. to 4100 ft.

Cone collections were started in the fall of 1954 in some localities, but due to the different periodicity of seed years in the various seed source locations, the last seed was not collected until the fall of 1957. Seed from all but two of the seed sources had arrived by the spring of 1957 for planting. These two late seed sources were planted a year later. Each cone collection was confined to a designated area with a radius of 25 miles, and the number of trees sampled in these areas ranged from 14 to 89. Before sowing, seeds were cleaned and stored in a cold storage room at $0^{o}F$ at the Oregon Forest Nursery, Corvallis. Sowing was performed from May 15 to

May 17, 1957. Care was taken to obtain uniform density of seedlings in all seedbeds.

During the second growing season (1958) the phenological characteristics of needle length, bud bursting time, and bud set time were measured. For needle length, five needles were measured from each of 40 seedlings per provenance to obtain an average needle length for each provenance. The terminal buds of the seedlings were examined at bi-weekly intervals from March 29 to April 25, 1958. Bud bursting was expressed as the cumulative percentage of buds burst for each seed source at the time of each inspection. Data for bud set were taken at weekly intervals from August 1 to August 22, 1958. Bud set data were expressed as a cumulative percentage of seedlings with distinctly formed terminal buds. These data are summarized in tables 2, 3, and 4.

At the end of the second growing season the seedlings from the various seed sources were outplanted at provenance plantations established at or near the sixteen seed collection areas. Each plantation consists of sixteen seed sources in a randomized block formation with at least two replications. Each block originally consisted of 121 trees from a seed source in an 8' x 8' spacing.

A thinning operation was performed on one of these plantations near Dorena Dam, Oregon at the end of the 1975 growing season.

Table 1. Geographic Locations of Seed Sources.

Seed Source	Latitude	Average Elevation (ft)	Location
C	49°10'	2750	Sugar Loaf Mountain, B.C.
H	46°45'	1925	Elbe Area, WA
J	45°10'	1800	Molalla Area, OR
K	45°10'	3500	Molalla Area, OR
M	44°30'	1900	Corvallis Area, OR
P	42°20'	2850	Butte Falls, OR

Table 2. Needle Length at End of Second Growing Season.

Seed Source	Needle Length (mm)
C	25.4
H	22.7
J	23.0
K	22.7
M	21.8
P	23.1

Table 3. Order and Cumulative Percentages of Bud Burst in Bi-weekly Intervals.

March 29		April 11		April 25	
Source	% Open	Source	% Open	Source	% Open
P	11.3	H	54.8	H	92.8
H	9.4	P	44.0	C	92.7
M	3.9	M	38.5	K	91.4
K	2.7	C	34.5	P	88.7
J	0.3	K	22.2	J	83.9
C	0.0	J	19.9	M	70.7

Table 4. Order and Cumulative Percentages of Bud Set in Weekly Intervals.

August 1		August 8		August 15		August 22	
Source	% Set	Source	% Set	Source	% Set	Source	% Set
P	31.0	P	52.9	P	81.6	C	96.1
C	24.5	C	37.4	C	80.6	P	95.6
M	20.9	K	31.8	K	57.6	M	87.8
K	19.1	M	28.6	M	48.8	K	87.7
J	13.3	H	26.0	H	43.2	H	84.2
H	10.3	J	16.5	J	33.1	J	73.0

Wood samples obtained from these thinnings provided the opportunity to correlate wood properties with the phenological characteristics previously mentioned.

V. METHODS AND MATERIALS

Sampling

Samples were collected from six seed sources after the thinning operation of the Dorena Dam provenance plantation. The seed sources were chosen to provide a wide range of phenological data with which to work. The seed sources selected for the study were: C, H, J, K, M, and P. Ten sample trees from each of these seed sources were desired, however, thinnings in some seed sources were limited and this was not possible. Nine trees were sampled from seed source C and only four from seed source P; all other seed sources had the desired number of ten sample trees.

Cross sectional disks, about two inches in thickness were cut from the thinned trees at approximately breast height. The disks were numbered for identification purposes, placed in plastic bags, and stored in a cold storage room until work was begun.

X-Ray Densitometry

Equipment

The x-ray densitometry technique described earlier was used in this study to determine wood density, density distribution, and percentage latewood. The equipment used was developed at the

Pacific Southwest Forest and Range Experiment Station, Berkeley, California, and has been described by Echols (1970).

This equipment consisted of a Profexray x-ray unit with a rating of 60 KVP and 10 ma. The x-ray stabilizing circuit was modified to provide a smoother output. To overcome the problem of parallax, caused by x-rays eminating from a virtual point source, Echols incorporated a moving slit principle. The x-ray unit was enclosed in lead shielding with a two mm slit 20 cm directly below the x-ray source. This reduced the effective beam spread angle to less than one degree. To make the exposure the x-ray unit and lead shield were traversed at a controlled constant speed over the sample and film. This provided a very uniform exposure with nearly parallel rays.

The densitometer developed by Echols incorporated a film carriage for traversing the negative past a light source at a controlled constant speed, an optical focusing system, a photomultiplier tube, and the necessary preamplifier and amplifier circuitry to feed the signal into a chart recorder. Controls were designed into the circuits to vary the essential parameters such as linear spread, input level, and calibration. The signal received by the chart recorder produces the chart trace described earlier.

By means of a transducer, a digitising unit was connected to the chart recorder. This digitiser was essentially a 14 channel density component integrator which accumulates values representative of the total amount of wood in a sample at each of 14 successive 0.05 g/cm^3 density levels from 0.20 - 0.25 g/cm^3 to 0.85 - 0.90 g/cm^3, the normal range of densities encountered in wood. The values accumulated by the digitiser were then used to calculate average density, density distribution index (DD Index), and percentage latewood in the sample (see Appendix).

Calibration

In x-ray analysis, the linearity of the density response involves not only microdensitometer calibration but also depends on the combination of kilovolt potential and miliamps used in making the x-ray exposure (Echols, 1973). Kilovolt potential refers to the strength or penetrating power of the radiation while miliamps refers to the amount of radiation produced. Certain combinations yield a linear response over the range of density found in wood, other combinations yield curves. Echols found that a density wedge with a linear gradient was very useful for determining correct exposures.

Echols calibrated the microdensitometer to actual wood densities so that they could be read directly from the linear chart scale. Thirty-five selected wood samples covering a range of wood densities were x-rayed. By adjusting the densitometer to the known density values a true calibration was reached. By running a series of comparative analyses on the wood and varying thicknesses of plexiglass a three step plexiglass chip was produced having representative wood densities of 0.22 g/cm^3, 0.51 g/cm^3, and 0.85 g/cm^3. This chip served as the basis of calibration on individual densitometer runs.

Specimen Preparation

In the preparation of the specimens for x-ray densitometry, the disks were first split in half. One half was returned to the cold storage room for future measurements and the other half retained for densitometry specimen preparation. From this half disk a piece two inches wide was cut, using a band saw, so as to contain the radius from pith to bark. This cut was made to reduce drying stresses caused by the differential shrinkage between the tangential and radial directions, and to reduce the resultant checking of the specimens. The specimens were then placed in a constant temperature, constant relative humidity chamber. They were conditioned for two months and allowed to come to an equilibrium moisture content of approximately 12%. The specimens were then machined down to the final dimensions of 12 mm square containing the radius from pith to bark. The specimens were then allowed to condition for another two months in the constant temperature, constant relative humidity chamber. This was to insure a constant and uniform moisture content in the samples. When machining the samples, care was taken to make the fiber axis, during exposure, as nearly parallel to the x-ray beam as possible.

Exposure

The film used to make the x-ray exposure was Kodak 70 mm type AA Industrex film which comes in 200 ft rolls encased in a continuous light proof envelope. The film was cut into 30 cm lengths and the ends of the envelope sealed with black tape before handling in light. To make the x-ray exposures, a piece of film was placed on a table a set distance from the x-ray unit. The calibration chip, the specimen, and lead identification numerals were placed on the film. The x-ray unit was then traversed directly over the film and specimen at a constant rate of 4.2 cm/sec. The settings on the x-ray unit were 30 KVP and 7 ma. One entire exposure took 90 seconds and the unit shut off automatically at the end of each exposure. The exposures were made inside a lead lined cabinet to protect the operator from radiation effects.

Individual Ring Data

Using the x-ray densitometry technique it was possible to obtain data from each individual ring of the samples for average ring density, DD index, percent latewood, and ring width. The densitometer was stopped after each individual ring by using a limit switch on the chart recorder. The switch was set in a position so that it would break the circuit of the densitometer drive, the chart paper drive, and the digitizer as the pen was traveling from the latewood zone of one ring to the earlywood zone of the next ring. Readings were then taken from the digitizer and calculations performed as described in the Appendix.

The ring width was calculated from the total number of pulses recorded by the digitizer. Knowing the densitometer film carriage speed (18/25 in/min) and the number of pulses per unit time (10 pulses/sec) in the digitizer, ring width was calculated by the following formula:

$$\text{ring width (mm)} = \text{total pulses} \times \frac{\text{film speed (in/min)} \times 25.4 \text{ mm/in}}{\text{pulse rate (pulses/sec)} \times 60 \text{ sec/min}}$$

Fiber Length

The material used for fiber length determination contained only the outer three growth rings of each sample. Using a razor blade, this material was split into match stick size pieces and placed in 25 ml erlenmeyer flasks (one sampling unit per flask). Approximately 20 ml of distilled water was then added to each flask and the samples were allowed to soak overnight. The water was then decanted off and 20 ml of a solution containing 700 ml H_2O, 600 drops HOAc, 100 gms $NaClO_2$ were added. The samples were cooked in this solution at

$85^{o}C$ for one hour and then allowed to stand at room temperature overnight. At the end of this time the solution was decanted off and 20 ml of a fresh solution containing 700 ml H_2O, 120 drops HOAc, and 20 gms $NaClO_2$ were added and the samples were allowed to stand at room temperature for another three hours. The solution was then decanted from each flask and the samples were washed twice with 25 ml quantities of distilled water. Five ml of distilled water and 1 ml of a 2.5% solution of acid Fuschin stain were added and the samples allowed to stand overnight. The excess stain was then poured off and the samples were washed twice with 25 ml quantities of distilled water. The samples were then diluted with 20 ml of distilled water and the flasks shaken vigorously to separate the fibers.

To prepare the microscope slide a small wad of fibers was removed from a flask using teasing needles. The fibers were spread out on the slide with one or two drops of glycerin and covered with a cover glass. The slide was then placed under an ampliscope which projected an image on a screen at 40X magnification. Fiber lengths were measured from this image using a calibrated scale. Three strings were stretched across the ampliscope screen and were used for randomization. Starting with the top string and proceeding from left to right, and top to bottom, the first 25 tracheids crossing the strings were measured for each sample. Care was taken to measure only whole fibers and to avoid those that had been broken or cut during processing.

Runkel Ratio

The Runkel ratio is a calculated value defined as the ratio between double cell wall thickness and lumen diameter of the fibers. The macerated fibers used for fiber length determination were also used to determine the Runkel ratio. Microscope slides were prepared in the same manner as described above. The fibers were observed under a microscope at 100X magnification. The lumen diameter and cell diameter were measured using an eyepiece micrometer. From these data the double cell wall thickness and Runkel ratio were calculated. Care was taken to measure these dimensions in the radial direction only. All measurements were taken away from bordered pit areas and away from the fiber ends to avoid any bulging or taper in the fiber walls. Ten fibers from the earlywood and ten from the latewood were selected at random for these measurements. Mork's principle was used to distinguish between earlywood and latewood fibers. Using the average percentage latewood for the outer three rings determined from x-ray densitometry, a weighted average Runkel ratio was calculated.

Holocellulose

The basis for the holocellulose procedure was described by Erickson (1962). A few modifications were implemented so the procedure will be described in detail. Wood from the outer three rings of the sample was removed. This wood was ground in a Wiley mill to pass a 40 mesh screen. To avoid any mixing of the samples, the Wiley mill was vacuumed after each sample to remove any residue left behind. The wood flour was then extracted in a Soxhlet extraction apparatus acccording to ASTM standard D1105-56 (1972). The wood flour was extracted for four hours with each of the following solutions: (1) a 2:1 benzene-ethanol solution, (2) 95% ethanol, and (3) water. Following extraction, the wood flour was allowed to dry for four weeks and come to equilibrium moisture content in a constant temperature, constant relative humidity room.

Approximately 0.6 gms of each sample were weighed out in 50 ml erlenmeyer flasks. Six control samples were chosen randomly for moisture content determination. The average moisture content was used to calculate the amount of dry wood substance in each sampling unit. Ten ml of a stock solution (premeasured) consisting of 60 ml acetic acid and 1.3 gms of NaOH per liter were added to each flask from test tubes. The flasks were then placed in a constant temperature hot water bath previously heated to 75°C. One ml of a 20% sodium chlorite solution was added to each flask using a 5 ml glass syringe. The flasks were then covered with inverted 2 dram screw cap vials. An additional 1 ml of the sodium chlorite solution was added after 0.5 hr., 1.0 hr., 1.75 hr., and 2.5 hr. The flasks were swirled after each sodium chlorite addition. The total cooking time was 3.25 hours. At the conclusion of the cook the flasks were removed from the hot water bath and the contents transferred to Pyrex fritted-glass-bottom crucibles of 30 to 35 ml capacity and coarse porosity. The flasks were rinsed with 20 ml portions of distilled ice water which was also added to the crucibles. The excess solution was removed by suction and the samples were washed with four 25 ml quantities of 1% acetic acid solution and two 10 ml quantities of acetone. The samples were allowed 36 hours to reach equilibrium moisture content and the final sample weights were obtained. Moisture contents were determined on six randomly chosen samples. The percent holocellulose was determined from the initial dry weights of the samples and the dry weight of the samples after treatment.

Statistical Analysis

The analysis of the data was performed using the Statistical Interactive Programming System (SIPS) on a CDC 3300 computer at Oregon State University.

The wood property data from each of the samples were pooled for each seed source. A simple least squares regression analysis was used to determine the relationships between each of the wood properties and phenological and seed origin variables. The phenological and seed origin characteristics were used as the independent variables in the analysis. The significance of the relationship was determined by the F statistic of mean square regression divided by mean square error ($F = \frac{MSR}{MSE}$) with 1 and n-2 degrees of freedom. For those relationships found significant the correlation coefficient (r) and the coefficient of determination (r^2) were determined.

In addition, suitable multiple regressions and their significance were determined by the stepwise regression procedure. This procedure involves adding independent variables to the model one at a time. At each stage, the next variable to be added is that having the highest partial correlation coefficient with the response (given the previous variables already in the model).

The individual ring data were also pooled for each seed source and plotted against age (rings from pith). It was hoped that differences in the relationships with age could be determined between seed sources through confidence intervals on the regression coefficients. However, due to the non-linearity of most of the relationships this was not possible. Visual observations were made on these plots and will be discussed later.

VI. RESULTS AND DISCUSSION

In the following discussion, subscripts were used to denote the first, second, third, etc. bud burst and bud set measurements. In addition, an average was calculated from all different measurement dates for bud burst and bud set, and was used in the regression analysis. A listing of the correlation coefficients of all the regressions of seed origin and phenological characteristics with wood quality are given in Table 5. A complete listing of the wood quality data for each seed source is given in Table 6.

There was a serious problem in the analysis due to the manner in which bud burst and bud set data were measured. There was a great deal of inconsistency in the ranking of the seed sources from one bud burst measurement time to the next (Table 3). This was most likely the result of differences in the variation about the mean bud bursting time in each seed source. Measurements taken as cumulative percentages of buds burst or buds set, on different dates, reflect both the mean bud burst or bud set time and the variation around this time of the trees within a seed source. As a result, there was a serious confounding of the data. The problem with bud set data (Table 4) was not as great since the degree of inconsistency in the rankings from one measurement time to the next was much less than that shown in the bud burst data. Correlations were made using

Table 5. Correlation Coefficients of Seed Origin and Phenological Characteristics with Wood Quality Characteristics.

	Correlation Coefficient					
	Average Density	Density Outer 3 Rings	Average DD Index	DD Index Outer 3 Rings	Average % Latewood	% Latewood Outer 3 Rings
Latitude	-0.676	-0.471	0.155	-0.070	-0.313	-0.065
Elevation	-0.087	0.210	0.762	0.431	0.389	0.637
Needle Length	-0.979**	-0.760	-0.456	-0.441	-0.794	-0.433
Bud Burst 1	0.348	0.197	0.389	0.147	0.017	0.079
Bud Burst 2	0.017	-0.210	-0.370	-0.406	-0.170	-0.328
Bud Burst 3	-0.488	-0.044	-0.187	-0.185	-0.455	0.208
Average Bud Burst	0.258	0.376	-0.244	0.383	-0.106	0.057
Bud Set 1	-0.276	-0.459	-0.560	-0.731	-0.317	-0.472
Bud Set 2	-0.225	-0.335	-0.594	-0.634	-0.337	-0.348
Bud Set 3	-0.536	-0.565	-0.552	-0.706	-0.480	-0.406
Bud Set 4	-0.368	-0.495	-0.378	-0.722	-0.258	-0.326
Average Bud Set	-0.401	-0.495	-0.554	-0.721	-0.394	-0.402

* Significant at 95% Level of Probability

** Significant at 99% Level of Probability

Table 5. Continued.

	Correlation Coefficient				
	Fiber Length	Earlywood Runkel Ratio	Latewood Runkel Ratio	Average Runkel Ratio	Holocellulose Content
Latitude	0.977**	-0.730	0.496	0.065	-0.240
Elevation	0.678	-0.845*	0.837*	0.699	0.033
Needle Length	0.540	-0.129	-0.066	-0.375	-0.076
Bud Burst 1	-0.632	0.375	-0.199	-0.039	0.441
Bud Burst 2	-0.079	-0.017	0.009	-0.174	0.377
Bud Burst 3	0.233	-0.204	0.249	0.240	-0.007
Average Bud Burst	-0.661	0.763	-0.639	-0.174	-0.492
Bud Set 1	-0.422	0.461	-0.426	-0.453	0.659
Bud Set 2	-0.457	0.380	-0.283	-0.290	0.760
Bud Set 3	-0.107	0.164	-0.163	-0.321	0.673
Bud Set 4	-0.038	-0.043	0.053	-0.178	0.848*
Average Bud Set	-0.242	0.238	-0.204	-0.320	0.751

* Significant at 95% Level of Probability

** Significant at 99% Level of Probability

Table 6. Complete Listing of Wood Quality Data by Seed Source.

Seed Source	Average Wood Density (g/cm^3)	Average DD Index	Average % Latewood	Density Outer 3 Rings (g/cm^3)	DD Index Outer 3 Rings	% Latewood Outer 3 Rings
P	0.3929	249.60	22.71	0.3833	290.30	24.58
J	0.3921	269.51	23.45	0.3906	331.80	26.56
M	0.4029	279.12	26.46	0.3866	297.29	25.96
H	0.3957	273.30	24.33	0.3936	325.37	27.98
C	0.3722	262.44	21.65	0.3610	283.89	24.12
K	0.4008	290.87	26.74	0.4079	342.30	32.15

	Fiber Length (mm)	Earlywood Runkel Ratio	Latewood Runkel Ratio	Average Runkel Ratio	% Holocellulose	Average Ring Width (mm)
P	2.82	0.195	1.253	0.4548	73.349	6.22
J	3.23	0.180	1.306	0.4792	72.536	7.32
M	3.22	0.163	1.443	0.4995	73.269	6.69
H	3.37	0.153	1.534	0.5489	73.021	7.12
C	3.62	0.154	1.458	0.4666	73.129	6.53
K	3.24	0.151	1.608	0.6230	73.281	6.40

each measurement of bud burst and bud set to see if any relationships might exist. However, it was necessary to consider this confounding problem before drawing any definite conclusions as to the effects of bud bursting time and bud set time on wood properties.

Wood Density

Needle length showed a very highly significant correlation ($P > .99$) with average wood density. Although the correlation between needle length and wood density in the outer three growth rings was not statistically significant ($P < .95$) it was related at the 90% level of probability. This indicates that needle length, measured at an early age, may be related to wood density in the juvenile zone but that the needle length of young seedlings may not be a good predictor of future mature wood density.

Needle length is a characteristic which may vary greatly due to differences in environmental factors. For this study, needle length was measured from two year old seedlings grown under optimum conditions in fertilized nursery seed beds. Very little is known about the genetic heritability of needle length in Douglas-fir and it cannot be assumed that the seed sources would maintain the same ranking of needle length under different environmental conditions. More research is required to evaluate the genetic heritability of needle length in

Douglas-fir and to measure the consistency of the needle length-wood density relationship under different environmental conditions and at different ages.

No significant relationships ($P < .95$) were found between wood density and other phenological or seed origin characteristics. This does not prove, however, that a relationship between wood density and bud burst or bud set does not exist. Due to the confounding problem in the data, no definite conclusion may be drawn on this point.

Uniformity

Although non-significant ($P < .95$), elevation of seed origin showed the strongest correlation with the average DD index (uniformity). This was a positive correlation and accounted for 58% of the variation in DD index. Elevation and needle length together showed a highly significant correlation ($P > .99$) with the average DD index (see Table 7). The highest density distribution indices were associated with high elevation and short needle length and the lowest density distribution indices were associated with low elevation and long needle length.

As was the case with the wood density-needle length relationship, neither elevation nor elevation and needle length combined showed any statistically significant ($P < .95$) relationship with the density distribution index in the outer three annual rings. Thus, it appears that neither of these characteristics would be a good predictor of mature wood uniformity.

Percentage Latewood

Needle length showed the highest correlation with average percentage latewood; however, this relationship was not significant above the 95% level of probability. Needle length combined with elevation of seed origin showed a very highly significant ($P > .99$) relationship with average percentage latewood (see Table 7). The highest percentages of latewood were associated with short needle length and high elevation of seed origin; the lowest percentages of latewood were associated with long needle length and low elevation.

The relationship between needle length and elevation together and percentage latewood of the outer three rings was not significant ($P < .95$). None of the other phenological or seed origin characteristics (or combinations) showed any significant correlations with the percentage latewood of the outer three rings. Thus, it appears that none of the characteristics studied could be used as predictors of mature percentage latewood.

Individual Ring Analysis

The relationship between wood density and age showed a sharp decrease in density in the first six annual rings from the pith, then a

Table 7. Summary of Significant Relationships of Seed Origin and Phenological Characteristics With Wood Quality Characteristics.

Wood Quality Characteristics	Phenological Characteristics	R	R^2	Signif.
Average Density	Needle Length (-)	0.979	0.959	$P \geq .99$
Average DD Index	Elevation (+) + Needle Length (-)	0.994	0.988	$P \geq .99$
Average % Latewood	Needle Length (-) + Elevation (+)	0.981	0.963	$P \geq .99$
Density Outer 3 Rings	Needle Length (-)	0.760	0.577	$P \geq .90$
DD Index Outer 3 Rings	--			
% Latewood Outer 3 Rings	--			
Fiber Length	Latitude (+)	0.977	0.954	$P \geq .99$
Earlywood Runkel Ratio	Elevation (-)	0.845	0.714	$P \geq .95$
	Elevation (-) + Bud Burst 2 (-)	0.975	0.951	$P \geq .95$
Latewood Runkel Ratio	Elevation (+)	0.837	0.700	$P \geq .95$
Average Runkel Ratio	--			
Holocellulose Content	Bud Set 4 (+)	0.849	0.720	$P \geq .95$
	Bud Set 4 (+) + Needle Length (-)	0.979	0.958	$P \geq .99$

slight increase through the remaining rings in the samples (Figure 2). This agrees with the results of McKimmy (1966) who found a decrease in density through the first ten or so annual rings, then a steady increase over the next twenty rings. McKimmy measured wood density in five ring increments, so this implies that the minimum density occurred between the fifth and tenth annual rings from the pith.

Although the general trends appeared fairly consistent between seed sources (initial decrease followed by a slight increase) there did seem to be some differences in the range of densities encountered over the first six years. Seed sources M, J, and C showed the greatest decrease in density over the first six annual rings, while seed sources P, H, and K showed the smallest decrease. Those seed sources with the greatest initial density showed the greatest decrease. These differences may explain why needle length was highly correlated with average wood density but not with the density of the outer three rings, i.e. the relationship between juvenile and mature wood density is not consistent between seed sources. Needle length, measured at age two, may be related to juvenile wood density, but does not show the same relationship with future mature wood density.

The relationship between density distribution index and age showed a rapid increase (larger difference between earlywood and latewood density) over the first six to seven annual rings, then a tendency to level off in the remaining rings (Figure 3). There were no apparent differences in these trends between seed sources.

The relationship between percentage latewood and age showed a sharp decrease in the first few rings, then a tendency to level off, followed by a slight increase in the outer few rings (Figure 4). Seed source K showed a shorter leveling off period and a greater increase in the outer rings than any other seed source.

The relationship between ring width and age showed a very rapid increase in ring width through the first four to five annual rings, then a sharp decrease through the remaining rings (Figure 5). There did appear to be a slight tendency toward leveling off in the outer annual rings of some of the seed sources. Seed source P showed a marked difference in the relationship; there was very little variation in ring width from pith to bark and the first three annual rings showed a slight decrease in ring width rather than the sharp increase shown by the other seed sources.

It was evident from the individual ring data that all of the wood properties included showed a definite change in their relationship with age at about five to seven rings from the pith. These changes may actually be a reflection of changes in the growth patterns of the trees.

A very young seedling, just beginning growth, will have a very small crown and root system. In later years, crown and root

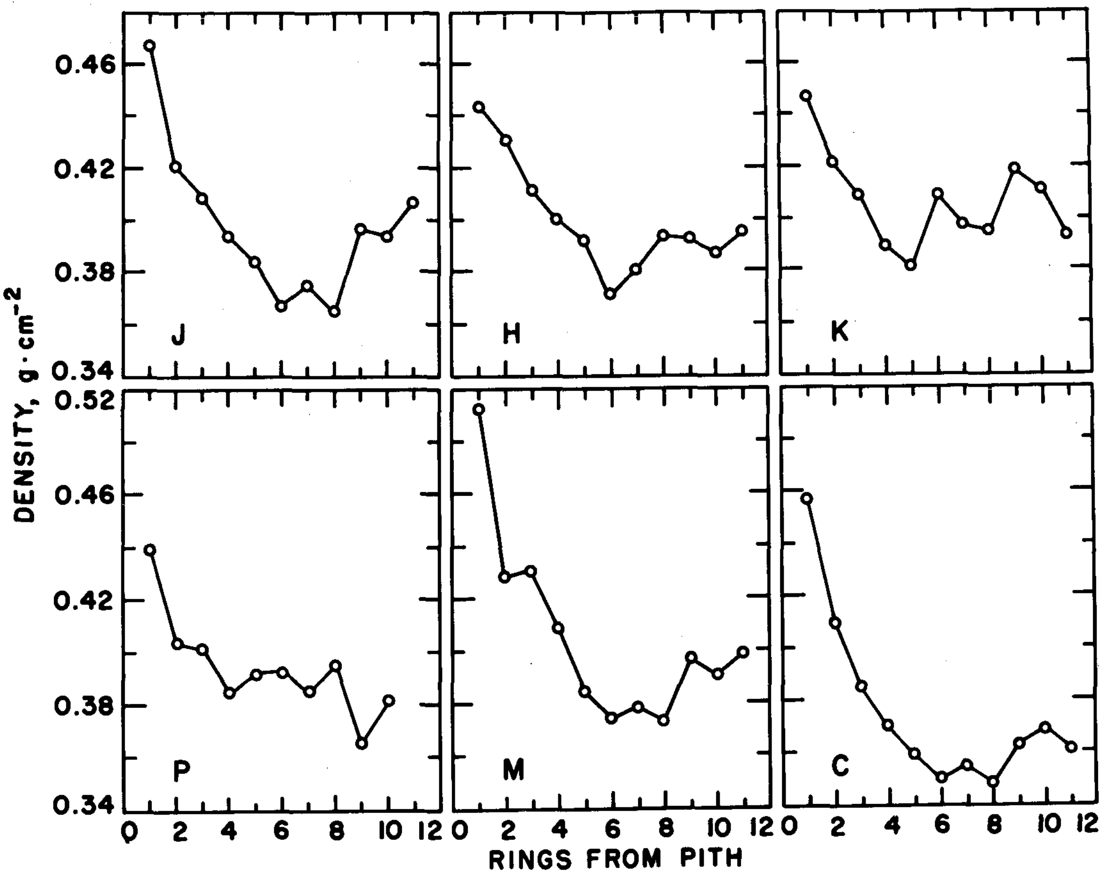

Figure 2. Density vs. Age in Each Seed Source.

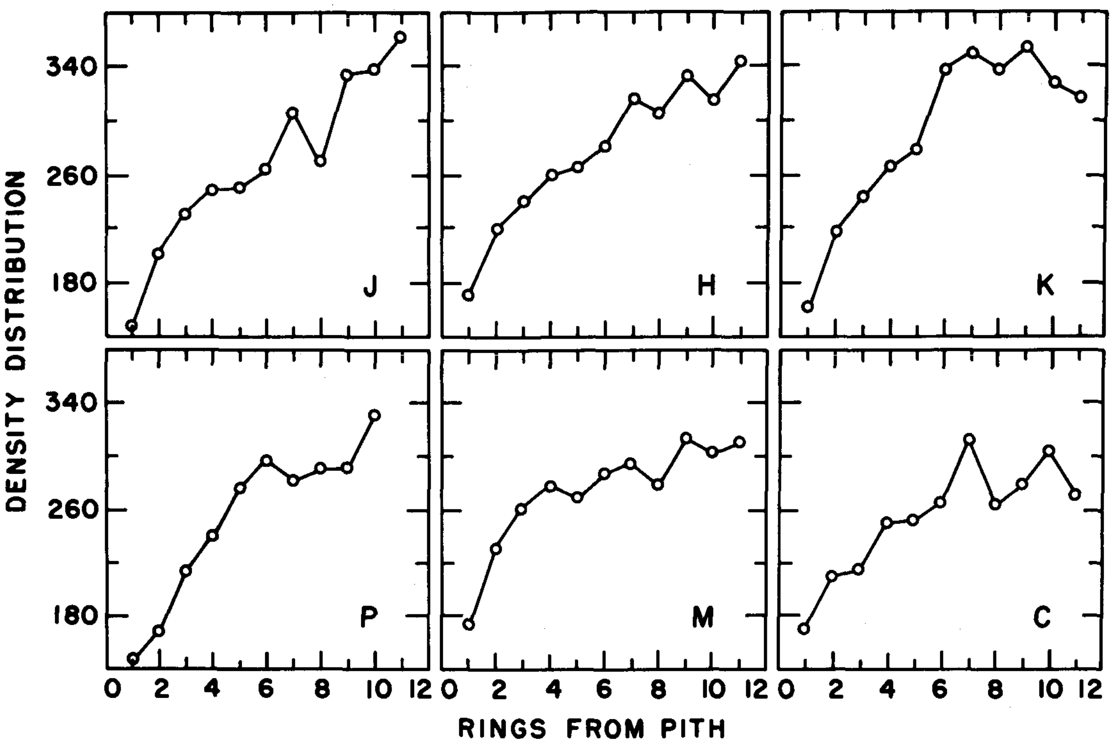

Figure 3. Density Distribution vs. Age in Each Seed Source.

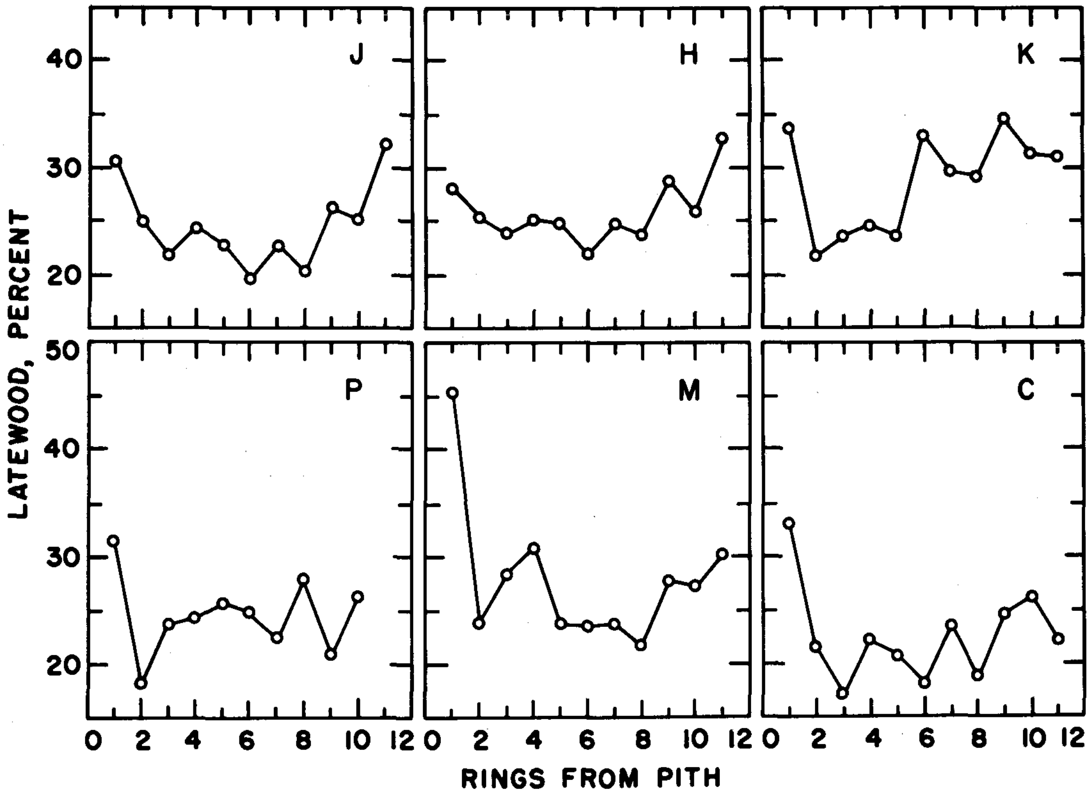

Figure 4. Percentage Latewood vs. Age in Each Seed Source.

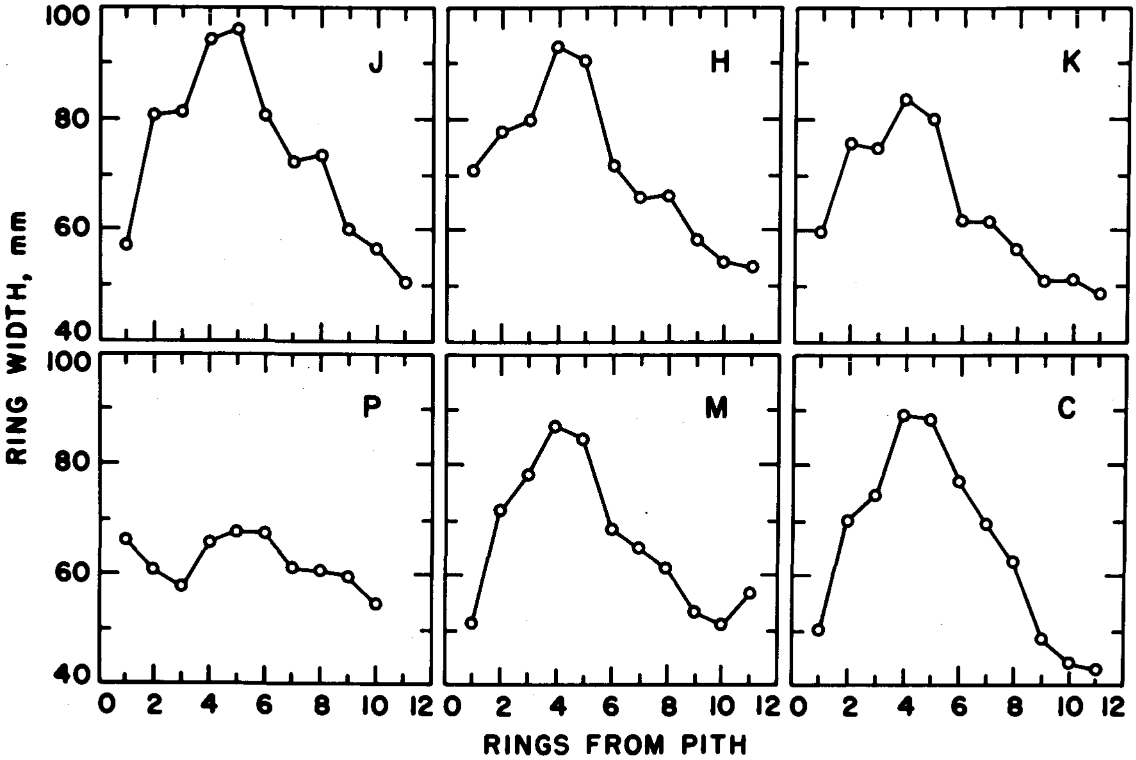

Figure 5. Ring Width vs. Age in Each Seed Source.

development increases rapidly and many new lateral buds are formed. With the increase in the number of buds, there should also be an accompanying increase in auxin (a growth hormone produced in the buds) production. This increased auxin level would result in an increased growth rate (from year to year) in the early part of the growing season. This would result in a higher percentage of earlywood formation, lower percentage latewood, and a lower overall density. Also, if the increase in auxin production is greater than the concomitant increase in photosynthate production, a lower density earlywood portion may be formed. This was indeed the case as shown by the densitometric scans (example scan, Figure 6). After the period of shoot elongation (bud set), latewood formation begins (based on the hormonal theory). With the crown enlarged, from the previous year, there should be a greater amount of photosynthates produced; and these would be deposited as thicker cell walls and increased latewood density. The increase in latewood density along with the decrease in earlywood density would be reflected as an increase in the DD index (uniformity).

As the tree continues to grow, there comes a time when competition and crowding from adjacent trees begins to limit further crown development. With fewer new buds being formed the level of auxin production would remain more or less constant. Some of the buds may actually be lost due to friction from the branches of

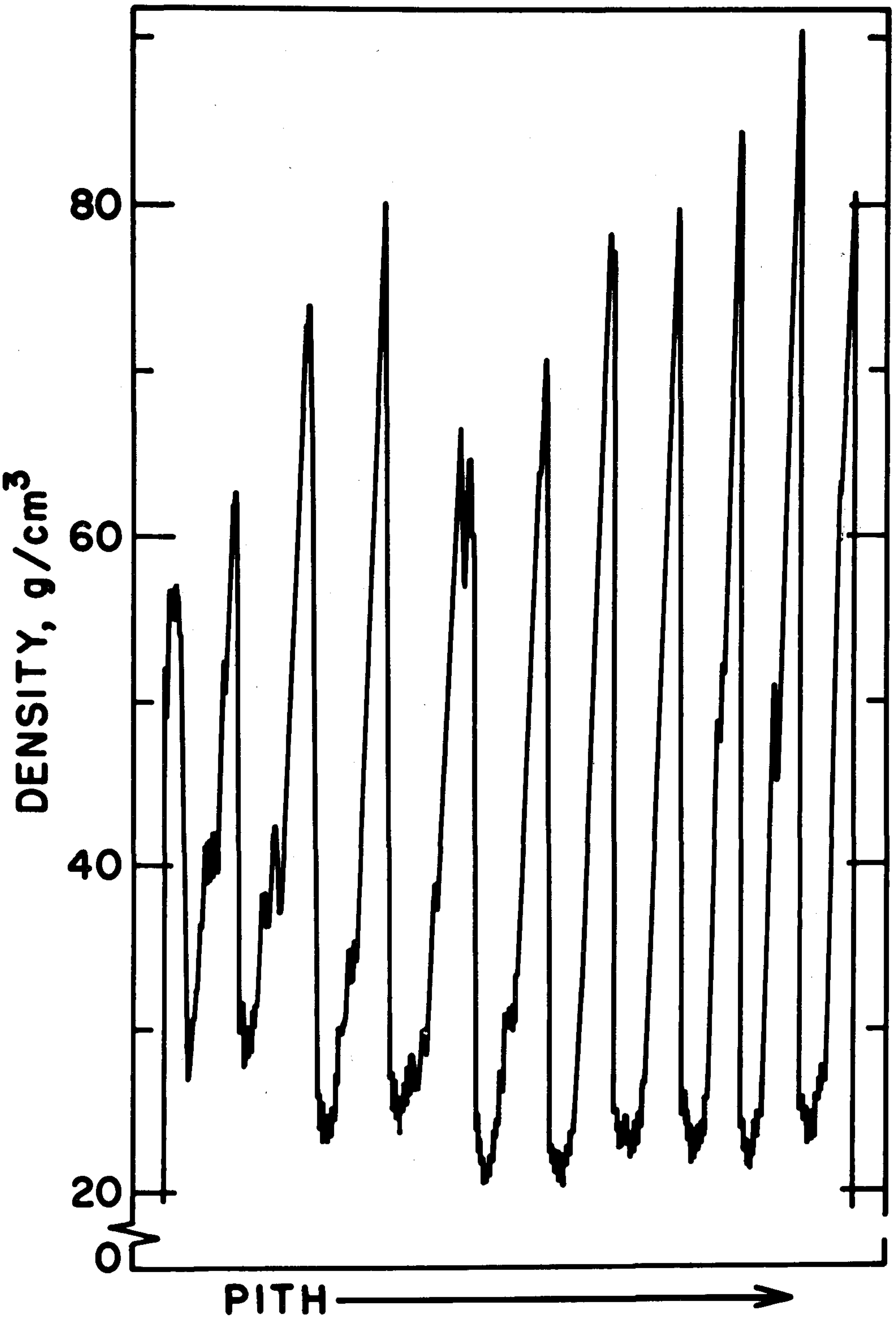

Figure 6. Example Densitometer Scan.

surrounding trees or to the shading of the buds on lower limbs. This would cause a lowering in the production of auxin and an accompanying reduction in ring width and earlywood formation. This also could cause a slight increase in wood density from the greater proportion of latewood. With limited crown development, more of the photosynthates produced in the crown may be distributed to the cambium and used as precursors in cell wall formation and resulting in thicker cell walls. These thicker cell walls would result in higher density wood. When the crown size and the production of auxin and photosynthates level out there should be no further changes in the densities of earlywood and latewood. This would result in a tendency for the density distribution index to reach an equilibrium point.

The above discussion is offered as a possible explanation for the annual variation in wood density, uniformity, percentage latewood, and ring width encountered. The data show a definite change in relationships between the fifth and seventh rings; it may be that competition effects become evident at this time. Although this effect was shown in the fifth to seventh ring, the actual tree age at that point was approximately ten to twelve years. With the spacing used it is conceivable that competition could become important at this age.

It should be pointed that crown size in itself could not be used as a predictor of wood properties. Rather, changes or trends in crown development may give some indication of changes in wood density. It should also be pointed out that this hypothesis is based on measurements from one level in the stem and unless other levels show the same trends at the same tree age (not number of rings from the pith) the hypothesis would not be valid.

This relationship could be important to the forest manager. If high density wood is desired, on the basis of the above discussion competition with surrounding trees should be imposed as early as possible. This could be done by using a closer spacing of trees in the young plantation and using more thinnings.

Fiber Length

Fiber length showed a highly significant ($P > .99$) correlation with the latitude of seed origin. Since fiber length measurements were taken from the outer three rings of the samples, it appeared as if latitude of seed origin may be a good predictor of mature wood fiber length. Longer fiber lengths were associated with the more northerly seed origin sites.

Seed source P, from the southern most latitude, exhibited a much slower growth than any other seed source. Samples from this seed source had an average of 8.5 annual rings (at breast height) while samples from other seed sources had an average of ten or more annual rings (at breast height). In the juvenile zone, fiber length is known to increase with the number of annual rings from the pith. Thus, the slow growth exhibited by seed source P may partially account for the short fiber lengths obtained from this seed source. The influence of latitude of seed origin may not be as strong as indicated here due to the age differences in some of the samples and should be studied more intensively.

Echols (1958) found a similar relationship between fiber length and latitude of seed origin in provenances of scotch pine. A faster radial growth rate was also found in the lower latitude provenances and it was proposed that shorter fiber lengths were due to a greater number of anticlinal cambial divisions in the fast growing seed sources. In this study, however, no relationship was found between latitude and radial growth (average ring width). Thus, the differences in fiber length must be due primarily to genotypic variation or a genotype-environment interaction.

Runkel Ratio

The Runkel ratios of earlywood and latewood in the outer three annual rings were measured separately. Also, a weighted average Runkel ratio was calculated on the basis of the percentage latewood in the outer three rings of the samples. The earlywood Runkel ratio showed a significant ($P > .95$) negative correlation with elevation of seed origin, while the latewood Runkel ratio showed a significant ($P > .95$) positive correlation with elevation of seed origin. This indicates that the greatest range in the Runkel ratio within a growth ring occurs in those seed sources from the highest elevations. Seed sources from low elevations should then have the smallest range in Runkel ratio and more uniform wood within a given annual ring. To test this relationship further, it was determined that the range in Runkel ratio between earlywood and latewood was significantly correlated with the density distribution coefficients measured.

Elevation alone explained 71% of the variation in earlywood Runkel ratio. Elevation and the second bud burst measurement (bud burst 2) combined, accounted for 95% of the variation in earlywood Runkel ratio, however, there was no increase in the level of significance (see Table 7). Due to the confounding problem in the bud burst data, no conclusions can be drawn as to the influence of bud bursting time on earlywood Runkel ratio.

Although non-significant ($P < .95$), average Runkel ratio showed the strongest correlation with elevation of seed origin. This was a positive relationship and accounted for 48% of the variation in average Runkel ratio. The reason for this non-significance is most likely due to the opposite direction of the earlywood and latewood Runkel ratio correlations with elevation of seed origin.

Holocellulose

The only significant correlation with holocellulose content was the fourth bud set measurement. This was a positive correlation and accounted for 72% of the variation in holocellulose content. Due to the confounding problem in the bud set data discussed earlier, it is very difficult to draw any conclusions concerning this relationship. However, the seed source ranking in terms of bud set is consistent enough that it appears likely that bud set time may indeed have some influence on the holocellulose content in Douglas-fir.

The fact that a positive correlation was obtained means that a high percentage of holocellulose content was related to a high cumulative percentage of bud set; or in otherwords, the earlier bud setting seed sources showed the highest degree of holocellulose content. This relationship could be explained by the hormonal theory of earlywood and latewood differentiation. The earlier the buds set the more time available in the growing season for latewood formation. Barring any differences in the rate of latewood formation, this would result in greater amounts of latewood formed. The S2 cell wall layer contains the greatest proportion of cellulose and since this layer is the thickest in latewood tracheids it would follow that the greater the amount of latewood the greater the holocellulose content. However, there appeared to be no consistent relationship between holocellulose content and percentage latewood. Since the percentage of holocellulose was measured on a weight basis, perhaps the percentage latewood on a weight basis would show a more consistent relationship.

In a multiple correlation the fourth bud set measurement combined with needle length accounted for 96% of the variation in holocellulose content. This relationship was significant above the 99% level (see Table 7).

VII. SUMMARY AND CONCLUSIONS

A summary of significant relationships of seed origin and phenological characteristics is shown in Table 7. The significant conclusions of this study may be summarized as follows:

1. Needle length (measured at age two) showed a very strong negative correlation with average wood density. However, needle length showed a considerably weaker correlation with the density in the outer three rings. This indicates that needle length, measured at this age, may be a good predictor of juvenile wood density but not mature wood density.

2. A combination of elevation of seed origin and needle length at age two showed a significant multiple correlation with the average DD index. The higher density distribution coefficients were associated with high elevations of seed origin and short needle lengths. This relationship was not significant with the outer three rings which indicates it would be a poor predictor of mature wood uniformity.

3. Needle length and elevation combined showed a significant multiple correlation with average percentage latewood. The highest percentage latewood was associated with high elevation of seed origin and short needle lengths. This relationship was not significant with the outer three rings which indicates it would be a poor indicator of mature wood percentage latewood.

4. There were no relationships which appeared to be good predictors of mature wood density, uniformity, or percentage latewood.

5. Latitude of seed origin showed a significant relationship with the fiber length of the outer three rings. This is most likely due to either genetic differences between the seed sources or to a genotype-environment interaction.

6. Although elevation of seed origin showed no correlation with the average Runkel ratio for tracheids in the outer three rings it did show a significant negative correlation with earlywood Runkel ratio and a significant positive correlation with latewood Runkel ratio.

7. Due to confounding of the data for bud burst and bud set data, no specific conclusions could be drawn regarding these characteristics, however, it appeared that time of bud set may have a significant influence on holocellulose content of mature wood. More research is required to verify this relationship.

8. There was evidence which suggested growth and crown development could have a significant effect on the physiology of wood formation. More research is required in this area, however.

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APPENDIX

APPENDIX

Calculation of Wood Density, Uniformity of Wood Density and Percentage Latewood from Digitized X-ray Densitometry Data

The values accumulated by the digitiser are converted to percent figures in a numerical table. The percentage of wood in each density class is then multiplied by the midpoint of that class and divided by 100 to produce the wood density increment (see example x-ray analysis sheet, Fig. 7). The wood density increments are then summed over all the classes to obtain the average wood density.

As an expression of uniformity, the density distribution index used by Echols (1972) was used in this study. The departure from mean density is calculated by a weighting process based on Echols concept of an ideally uniform wood. The density of such wood would vary $\pm$ 0.075 g/cm^3 about the mean for a total range of 0.15 g/cm^3. To obtain the DD index, the percent of wood in each density class is multiplied by a weighting factor. The weighting of only three of the 0.05 g/cm^3 classes (percent of wood in the mean density class, the class above, and the class below) by a factor of one would produce a density distribution index of 100. When variation exceeds the mean density by more than one 0.05 g/cm^3 increment on each side, the successive levels above and below are weighted by multiplier factors of 2, 3, 4, etc.. Thus the greater the variation in density, the greater the density distribution index (see sample calculation sheet).

For percentage latewood calculation, a density value corresponding to the lower limit for latewood was determined by Phillips (1960). Phillips used Mork's criterion to determine the points of demarcation between earlywood and latewood and the corresponding density was found from chart traces produced from beta-ray densitometry. The values obtained for the density boundary between earlywood and latewood ranged from 0.50-0.59 g/cm^3 with an average of 0.54 g/cm^3. In this study a value of 0.55 g/cm^3 was chosen, for the sake of simplicity, as the demarcation between earlywood and latewood. The percentage latewood is then determined from the sum of the percentages of wood in each density class above this 0.55 g/cm^3 level.

The generally accepted method of determining percentage latewood involves Mork's criterion, which states, that latewood begins when twice the double cell wall thickness exceeds the lumen diameter. Mork's criterion involves microscopic examination and is subject to personal judgement in deciding the exact position of the boundary between earlywood and latewood. Using a lower limit of wood density in determining latewood proportions eliminates personal bias and renders observations strictly comparable (Phillips, 1960).

Species: Douglas-fir

X-RAY ANALYSIS SHEET

Sample: M-6

Density* Class	Counts in Class	(a) Percent of Total Counts in Class	(b) Midpoint of Class	Wood Density Increment =(a)(b)/100	(c) Multi-plier	DD Increment =(a)(c)
.85 - .90	15	0.57	.875	0.0049	9	5.09
.80 - .85	43	1.62	.825	0.0134	8	12.96
.75 - .80	104	3.92	.775	0.0304	7	27.43
.70 - .75	86	3.24	.725	0.0235	6	19.44
.65 - .70	100	3.77	.675	0.0254	5	18.84
.60 - .65	135	5.09	.625	0.0318	4	20.35
.55 - .60	178	6.71	.575	0.0386	3	20.12
.50 - .55	151	5.69	.525	0.0299	2	11.38
.45 - .50	155	5.84	.475	0.0277	1	5.84
.40 - .45	214	8.06	.425	0.0343	1	8.06
.35 - .40	244	9.19	.375	0.0345	1	9.19
.30 - .35	286	10.78	.325	0.0350	2	21.55
.25 - .30	464	17.48	.275	0.0481	3	52.45
.20 - .25	479	18.05	.225	0.0406	4	72.19
Total	2654	100	Mean Wood Density	0.4180	DD Index	304.90

*Density in g/cm^3

Figure 7. Example X-Ray Analysis Sheet.