Table 4. — Correlation coefficients between the different morpho-physiological attributes.

	LA	LWR	SLW	LAR	ht	dia	leaves/plant	leaf length	leaf breadth	l/b ratio
DMP	0.711**	0.164	0.779**	-0.656**	0.804**	0.349	0.200	0.804**	-0.033	0.067
LA		0.323	0.158	0.005	0.631**	0.598**	0.463*	0.424*	-0.518**	-0.408*
LWR			0.125	0.096	0.004	0.035	0.311	0.292	-0.094	0.213
SLW				-0.921**	0.532**	0.054	-0.029	0.805**	-0.501**	0.529**
LAR					-0.570**	0.142	0.221	-0.741**	0.551**	-0.548**
ht						0.233	-0.066	0.641**	0.154	-0.144
dia							-0.607**	0.145	0.494**	-0.340
leaves/plant								0.179	0.087	0.140
leaf length									-0.262	0.468*
leaf breadth										-0.861**

bility values, according to JOHNSON, ROBINSON a. COMSTOCK (1955) and SWARUP a. CHAUGALE (1962), high heritability coupled with high genetic advance would be the true index for effective selection. Measured by these yardsticks, DMP and SLW, besides l/b ratio are brought into focus.

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Genetic variation in the Wood Density and Ring Width Trend in Coastal Douglas-Fir

By M. D. McKIMMY and R. K. CAMPBELL[1])

Summary

Stem strength of Douglas-fir (Pseudotsuga menziesii var. menziesii (MIRB.) FRANCO), was studied indirectly by examining genetic variation of the trend in wood density and ring width with age along a stem radius. Juvenile and mature wood from increment cores (12 mm) were analyzed from 64-year old progeny of three families from each of 10 provenances (sources) grown in two plantations. Ring width varied among families-within-sources and among interactions of families-within-sources and plantations. Specific gravity varied among sources and among interactions of families-within-sources and plantations. Sources did not differ significantly in ring width, nor did families-within-sources differ in specific gravity. However, wood-specific gravity varied considerably among sources at given ring widths. This genetic structure apparently resulted because the rate of increase of specific gravity with increasing age and decreasing ring width along the stem radius varied among families. The biological basis for such a response and evidence that source differences are adaptive are discussed. Conclusions are: (1)

[1]) The authors are Professor, Forest Products, School of Forestry, Oregon State University and Principal Plant Geneticist, U.S.D.A. Forest Service, Forestry Sciences Laboratory, Corvallis, Oregon 97331, USA.

differences in the density and ring width trend indicate that there are genetic differences in stem strength properties, (2) among families of Douglas-fir the strong family × plantation interaction in the density and ring width trend should be a consideration in tree-breeding decisions.

Key words: provenance specific gravity, stem strength, genotype-environment interaction, adaptation.

Zusammenfassung

Bei Douglasie, *Pseudotsuga menziesii* MIRB. FRANCO, wurde die Stammstärke indirekt durch eine Untersuchung des Trends der genetischen Variation der Holzdichte und Jahrringbreite mit zunehmendem Alter entlang des Stammradius studiert. Anhand von 12 mm Bohrkernen wurde bei 64 Jahre alten Nachkommenschaften von 3 Familien von je 10 Herkünften, die an zwei Standorten angebaut worden waren, das Holz der Jugend- und Altersphase analysiert. Die Ringbreite variierte zwischen Familien innerhalb der Herkünfte und zwischen Interaktionen der Familien innerhalb der Herkünfte und Pflanzungen. Das spezifische Gewicht variierte zwischen Herkünften und zwischen Interaktionen zwischen Familien innerhalb der Herkünfte und Pflanzungen. Die Herkünfte differierten nicht signifikant in der Ringbreite, desgleichen die Familien innerhalb der Herkünfte im spezifischen Gewicht. Jedoch variierte das spezifische Gewicht beträchtlich zwischen den Herkünften bei gegebener Jahrringbreite. Diese genetische Struktur entstand scheinbar, weil die Rate des Anstiegs im spezifischen Gewicht mit zunehmendem Alter und abnehmender Jahrringbreite entlang des Stammradius zwischen Familien variierte. Die biologische Basis für solch eine Reaktion und einen Beweis, daß Herkunftsunterschiede anpassungsfähig sind, wird diskutiert. Schlußfolgerungen sind: 1) Unterschiede in den Trends bei Dichte und Jahrringbreite zeigen an, daß dort genetische Differenzen im Merkmal Stammstärke auftreten. 2.) Innerhalb der Familien bei Douglasie sollten die starken Familien × Standort-Interaktionen in den Trends für Dichte und Ringbreite bei Züchtungsentscheidungen in Erwägung gezogen werden.

Introduction

In regions with mountainous topography, wet snows, and strong winter winds, such as the Pacific Northwest, stem strength may be an important factor in seed transfers and in delimiting seed zones, though it is rarely considered. The genetic attributes of the trait in Douglas-fir have not been studied. Because strength tests usually rely on destructive sampling that can seldom be accepted in progeny tests, our purpose was to take a nondestructive, indirect approach to examining the genetics of wood density and ring width and their combined effects on stem strength.

The mechanistic theory of stem form (discussed in detail by LARSON 1963) is the basis for assuming that wood density and ring width interdependently determine stem strength. A stem is so formed that it provides equal resistance to bending moments produced by wind load in the crown and to gravitational force of the tree mass (SCHWENDENER 1874, METZGER 1893, 1894). Resistance depends strongly on the quality as well as the quantity of wood at various stem heights. A stem is strengthed either by a large volume of low-density wood or a small volume of high-density wood (TRENDELENBURG 1932, 1935). At a given stem height, the volume-to-density relationship changes as the tree grows, in a way apparently optimizes allocation of wood substance for strengthening the stem (SCHNIEWIND 1962). The inherent pattern, established by many investigators, is one of increasing wood density and decreasing ring width with age along a stem radius. This trend, culminating at an unspecified age, is strongly influenced by crown size and development (LARSON 1962).

There is reason to hypothesize that the trend of density and ring width is genetically variable among Douglas-fir populations in the Pacific Northwest. Strong onshore winter winds are channeled by mountains so that the factors influencing wind and snow loads on trees vary. Consequently, maximum bending moments of stems depend partly on stand location. Sites also differ in potential productivity and the competitive stresses favoring natural selection for rapid height growth. Hypothetically, natural selection optimizes allocation of wood substance for height growth and stem strength. This must be done within the context of differing strength requirements in different stands. Therefore, the inherent density and ring-width pattern may be expected to vary among Douglas-fir populations.

Evidence for genetic variation in the density and ring-width trend in Douglas-fir does not exist. Average specific gravity of a radial core differed among provenances in a test by McKIMMY (1966) but not in one by COWN and PARKER (1979). In the latter, ring width among provenances also did not differ significantly.

In this paper, we examine genetic variation in the two traits, ring width and specific gravity, among 64-year-old open-pollinated progeny from ten provenances (sources) grown in two plantations. We then examine genetic variation as expressed by coefficients for change in density with ring width and age. The questions asked were:

(1) Is genetic structure (the allocation of genetic variation among and within sources and among interactions with plantations) similar for density and ring width?
(2) Does genetic structure change as trees age?
(3) Is there genetic variation in the density and ring-width trend?

We believe answers to these questions can help evaluate whether stem strength is a factor to be considered in seed transfer and in delimiting seed zones.

Materials and Methods

Sampling

The trees sampled were established as a genetics experiment in Washington and Oregon in 1912 (MUNGER and MORRIS 1936). Genetic entries were open-pollinated families from 13 native populations from western Washington and northwestern Oregon. Entries were planted as 2-year-old seedlings in two blocks (1915, 1916) in six plantations. Seedlings were planted by family in row plots at 2.1 × 2.1 m spacing.

We studied a small subsample of the original experiment because our resources limited the number of wood samples we could process, and because we wanted a balanced sampling design that allowed straightforward treatment of interactions. Because substantial mortality had occurred at most plantation sites by 1975, we settled on three trees for each of three families from each of ten sources grown in two plantations.

Four of the ten sources sampled were from the Stillaguamish River drainage in northwestern Washington (Darrington, Granite Falls, Hazel, and Fortson, ~48° N latitude); three were from the Wind River drainage in southwestern Washington (Carson, Racetrack, and Wind River, ~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 Palmer, 45.2° and 45.8° N latitude, respectively). All except that from Lakeview were from the western slopes of the Cascade Mountains. Trees from the ten sources were sampled at two plantations, Wind River in southwestern Washington (335 m elevation, 45.25° N latitude) and Mt. Hood in northwestern Oregon (850 m elevation, 45° N latitude). These plantations have previously been studied for genetic variation in height growth (NAMKOONG, et al. 1972).

We sampled each tree with two 12-mm increment cores (at north and south cardinal directions) 1.4 m from the ground. Cores were further subdivided into juvenile sections (10 rings closest to pith) and mature sections (10 rings closest to bark). Specific gravity, a relative measure of wood density, was determined for each section by maximum moisture content (SMITH 1954). The terms specific gravity and wood density are used interchangeably in this paper. Ring width was measured in inches (25.4 mm).

Analysis

We analyzed data for juvenile and mature sections separately, except when both contributed to indexes of the density and ring-width trend, because their error variances differed greatly and variances could not be equalized by data transformation. Analysis of variance was constructed from a split plot, random model *(Table 1)*. It was necessary to synthesize some of the denominators (SNEDECOR and COCHRAN 1967) for approximate F tests and for estimating components of variance.

Because the magnitude of variance components depends partly on the mean for the trait, we transformed them to coefficients of variation (CV) for some comparisons. For comparing variance components of two traits or of two ages for a single trait, we transformed the ith component of the jth trait ($\hat{\sigma}_{ij}^2$) to its coefficient of variation by the relationship:

$$CV_{ij} = 100\ \hat{\sigma}_{ij}/\overline{X}_i \qquad (1)$$

where $\overline{X}_i$ is the experimental mean of the jth trait.

To examine the trend of density and ring-width with age along a stem radius, we assumed that wood specific-gravity (Y) is a linear function of $\log_e$ ring-width (X), that is, $Y = a + b\ X$, where a and b are coefficients estimated from the data. The data for second-growth coastal Douglas-fir from DROW (1957), eight points of specific gravity and ring width averaged over 1,128 wood samples, fitted this relationship well *(Figure 1)*. The range of ring-width and density in Drow's data was somewhat greater than in our study. Data from a 16-tree sample of Douglas-fir (WELLWOOD and SMITH 1962) fitted a linear regression line less well ($R^2 = 0.44$) but with no evidence of curvilinearity or other lack of fit.

In our analyses of trend, ring age and ring width were inextricably confounded. The confounding, however, should cause no appreciable bias. Sampled trees were of identical age and samples were taken from the pith to the bark at the same height above ground. Therefore, rings in the juvenile sample represented a comparable set of ages in all trees, as did rings in the mature sample.

Table 1. — Analyses of ring width and wood specific gravity.

Source of variation	d.f.	Expected mean squares [1]									
		σ_c^2	σ_w^2	σ_p^2	$\sigma_{lf(s)}^2$	$\sigma_{f(s)}^2$	$\sigma_{r(l)s}^2$	σ_{ls}^2	σ_s^2	$\sigma_{r(l)}^2$	σ_l^2
Plantation (L = 2)	1	1	2	6	12		18	36		180	360
Replications in plantations (R(L))	2	1	2	6			·18			180	
Sources (S = 10)	9	1	2	6	12	24	18	36	72		
Plantation x source	9	1	2	6	12		18	36			
Replications in L x S	18	1	2	6			18				
Families within-sources (F = 3/S)	20	1	2	6	12	24					
Plantation x F(S)	20	1	2	6	12						
Plot error R(L) x F(S)	40	1	2	6							
Within-plot (W = 3/F(S))	240	1	2								
Cores in trees within plots (C = 2/W)	360	1									

[1] Numerals are coefficients for extracting components of variance from observed mean squares.

σ_c^2 = Variance of core effects within trees.

σ_w^2 = Sum of within-plot environmental effects and variance among "half sibs" (open-pollinated).

σ_p^2 = Variance of subplot effects.

$\sigma_{r(l)s}^2$ = Variance of main plot effects.

$\sigma_{r(l)}^2$ = Variance of replications within plantations.

σ_s^2 = Variance of source effects.

$\sigma_{f(s)}^2$ = Variance of family-within-source effects.

σ_{ls}^2, $\sigma_{lf(s)}^2$ = Interaction variances among sources and families within-sources × plantations.

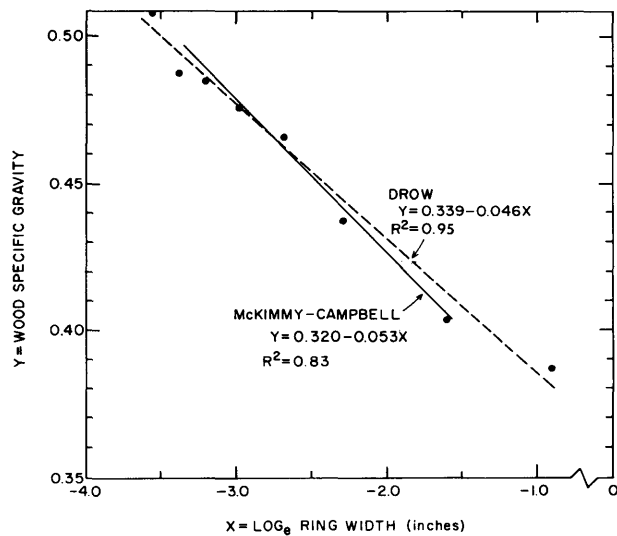σ_l^2 = Variance of plantation effects.

Figure 1. — Relationship between wood specific gravity and ring width as shown by this study and by data for coastal, second-growth Douglas-fir from Drow (1957, *Figure 3*). Data points (●) are from Drow.

We used two indexes (b and $\hat{Y}$) for trend analyses. Indexes were estimated for every core, two per tree. We estimated *trend slope* (b) by the equation:

$$b = \text{(juvenile specific gravity-mature specific gravity)/(juvenile log}_e \text{ ring width-mature log}_e \text{ ring width).} \quad (2)$$

We estimated $\hat{Y}$ by the equation:

$$\hat{Y} = a + b \,(-2.52316) \quad (3)$$

where $a = \bar{Y} + b \,(-\bar{X})$, and

b = is as defined above

$\bar{Y}$ = (juvenile specific gravity + mature specific gravity)/2

$\bar{X}$ = (juvenile log$_e$ ring-width + mature log$_e$ ring-width)/2.

$\hat{Y}$ is an estimate of *trend elevation* at the experimental mean (log$_e$ ring-width = −2.52316). $\hat{Y}$ was used rather

than a because it generally supplies the same information and, being centered in the data, does so with less extrapolation error. Index values were then analyzed by the model given in *Table 1*.

Results

The indirect procedure for evaluating stem strength as an adaptational trait produced two important new observations: (1) the genetic structure differs for the two traits, wood specific gravity and ring width; (2) genetic variation exists in the density and ring-width trend.

Structure of Genetic Variation

Analyses indicated significant genetic variability in specific gravity and ring width, but the structure of the variability differed. For example, wood specific gravity differed among sources but apparently not among families-within-sources *(Table 2)*; ring width apparently did not differ among sources, but did differ among families-within-sources. The latter inference (validity will be discussed later) is not nearly as strongly based as are inferences for specific gravity because decisions pertaining to ring width were made at a lower probability level *(Table 2)*.

Analysis also indicated significant genotype-plantation interactions for both traits. Like average genetic variability, the structure of the interaction differed. Specific gravity appeared to be similar for sources at Wind River and Mt. Hood plantations, but for families-within-sources it was not *(Table 2)*. For example, six of the ten sources (Wind River, Darrington Granite Falls, Hazel, Gates, and Palmer) produced a family with the highest mature specific gravity at one plantation and the lowest at the other *(Figure 2A)*. In ring width, sources rather than families-within-sources differed between plantations. Darrington and Granite Falls produced mature rings considerably wider than those of other sources at Wind River but narrower than those of all sources except Lakeview at Mt. Hood *(Figure 2B)*.

Table 2. — Mean squares, means, and significance tests for six traits.

Sources of variation	d.f.	Specific gravity		Log$_e$ (Ring width)		Density ring-width trend	
		Juvenile	Mature	Juvenile	Mature	Slope(b)	Elevation (Y)
Plantation	1[1]	0.0046869	0.047727*	29.579400**	4.008190	0.010383	0.123327*
Replications in plantations	2[1]	0.0059698*	0.004114	0.049708	3.656000**	0.018191	0.009956
Source	9[1]	0.0090766*	0.0182575**	0.151055	0.308725	0.002279	0.008899*
S x P	9[1]	0.0006325	0.0020855	0.135757†	0.471116	0.003705	0.002317
Main plot error	18	0.0012028	0.0030397	0.078192	0.369648	0.003348	0.003001
Families-within-sources	20	0.007561	0.0025559	0.112776†	0.253443	0.003666	0.001495
F(S) x L	20	0.0018122**	0.0026968†	0.049075	0.161467	0.005042**	0.001878
Subplot error	40	0.007387	0.0017919	0.094208*	0.258399	0.001713	0.002012
Within-plot	240	0.0008794**	0.0015751**	0.060626**	0.213121**	0.002605**	0.001596**
Cores in trees	360	0.0006912	0.0005961	0.021414	0.059491	0.001905	0.000815
Means		0.4162	0.4900	−1.8571	−3.1883	−0.0613	0.4560

[1] Approximate F Tests (SNEDECOR and COCHRAN 1967, p. 365—369). Degrees of freedom were synthetic, appropriate to each test, and not as indicated in this table.

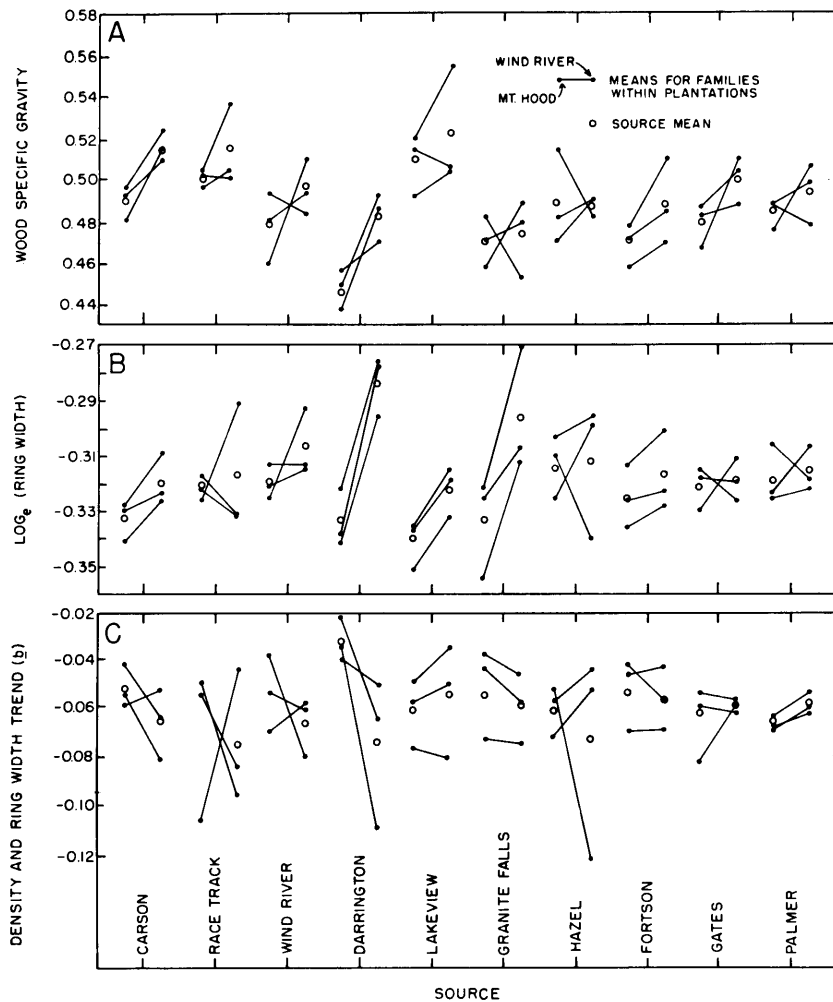† p $\leq$ .08

* p $\leq$ .05

** p $\leq$ .01

Figure 2. — Means for specific gravity, ring width, and the density and ring-width trend for sources and families-within-sources at the Mt. Hood plantation (left, each column) and Wind River plantation (right each column).

Genetic Structure and Tree Age

A previous report on 53-year-old progenies grown at the Wind River and Mt. Hood plantations noted that Wind River produced considerably taller trees (27.92 m vs. 18.28 m; NAMKOONG, *et al.*, 1972). In our experiment, the differing capacity of the two sites for producing wood substance was shown in juvenile ring width and in mature wood density. Wind River produced the wider growth rings in the juvenile sample (4.86 mm vs. 3.24 mm, p < 0.01) and the higher specific gravity in the mature sample (0.498 vs. 0.482, p < 0.05) *(Table 2)*. Plantations differed slightly, if at all, in juvenile specific gravity (0.416 vs. 0.418, non-significant) and in mature ring width (1.13 mm vs. 0.99 mm, nonsignificant) *(Table 2)*.

Coefficients of variation based on components of variance indicated that genetic structure did not change appreciably from juvenile to mature stages. Coefficients for genetic effects--sources, $\hat{\sigma}^2_s$; source $\times$ plantation, σ^2_{sl}; families-within-sources, $\sigma^2_{f(s)}$; and families-within-sources $\times$ plantations, $\sigma^2_{f(s)l}$--remained remarkably similar from juvenile to mature samples *(Figure 3)*. Coefficients for error deviations--replications in plantations, $\hat{\sigma}^2_{r(l)}$; main plot,$\hat{\sigma}^2_{r(l)s}$; subplot, σ^2; and among cores within trees, $\hat{\sigma}^2_c$--were less consistent. Error deviations usually were larger for ring width than for specific gravity. Coefficients of variation

for error components also generally increased with sample age *(Figure 3)*.

That genetic structures did not differ between juvenile and mature samples does not imply that juvenile and mature genotypic values were strongly correlated. For example, correlations of ring width in juvenile and mature samples based on means of ten sources were low, r = 0.60, 0.01, and 0.22 for Mt. Hood, Wind River, and the combined plantations, respectively. In contrast, comparable correlations for wood specific gravity were r = 0.74, 0.90, and 0.95. The only substantial rank change for specific gravity was from the Palmer source, which ranked tenth in the juvenile sample in both plantations and fifth and sixth in the mature sample.

Density and ring-width trend

We analyzed the wood density and ring-width trend by two procedures, the first designed to describe the average trend over the experiment, the second the genetic structure. First, a regression line was calculated for 40 points (10 source means, 2 sample ages, 2 plantations) to describe specific gravity of juvenile and mature samples as a function of sample ring width. Ring widths explained about 83% of the variation in specific gravity. The line deviated only slightly from the line based on Drow's data *(Figure 1)*; thus, the average density and ring-width trend
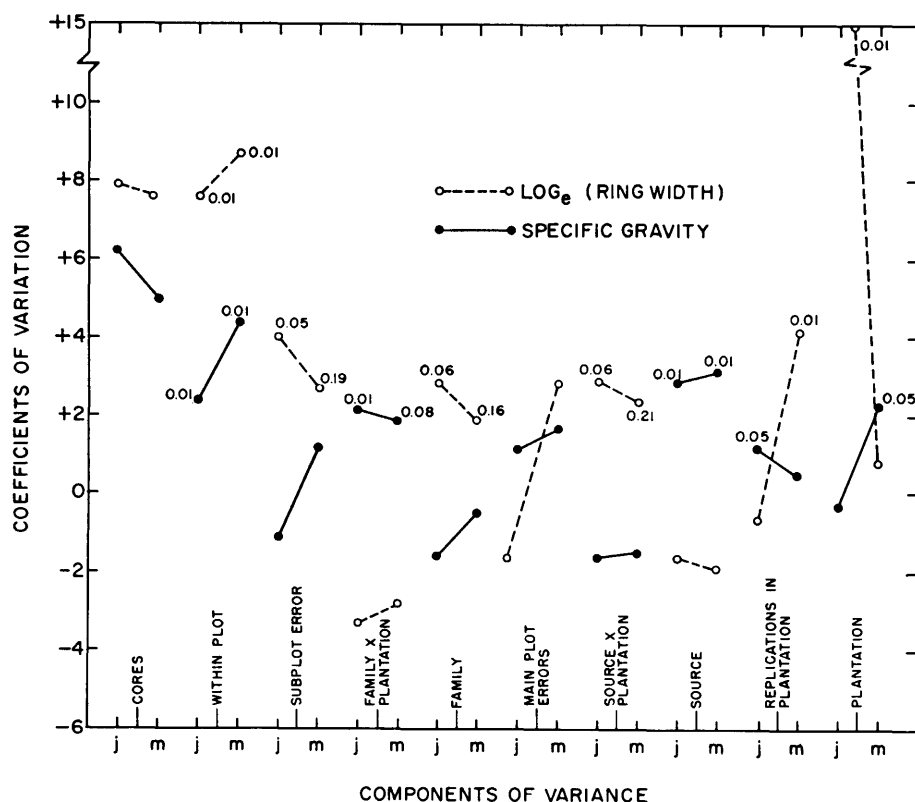
Figure 3. — Coefficients of variation based on variance components from the classification model (Table 1) for juvenile (j) and mature (m) samples. Negative coefficients of variation resulted from negative estimates of variance components. Variance components of coefficients were significantly different from zero at the probability indicated.

for this study followed the pattern of samples from naturally regenerated stands.

Second, we analyzed the trend indexes, b and Ῡ. The first, b, gives the rate at which specific gravity increases with age and decreasing ring width, that is, the trend slope. Analyses of variance showed no significant differences among sources and no significant source × plantation interaction (Table 2).

In contrast, slopes for families-within-sources varied greatly from plantation to plantation. Families with the highest slope in one plantation often had the lowest slope in the other (Figure 2C). This rank change shows in the analysis as a highly significant interaction of family-within-source × plantation (Table 2). Also, the wide rank change minimized average family differences when family means were calculated over both plantations. The analysis, therefore, indicated no significant genetic variation among families-within-sources (Table 2).

Although sources did not differ in the rate at which specific gravity increased with decreasing ring width, they did differ in specific gravity at given ring widths (trend elevation, Table 2). Specific gravities for some sources were consistently higher or lower than for others over the range of ring widths.

Trend elevations apparently are related to factors associated with the geographic origin of the source. Wood specific gravity at all ring widths for the four sources from the Stilliguamish river drainage were generally lower than the experimental average (Figure 4A). (To simplify the figure, we did not plot the Hazel source from the Stillaguamish River drainage). Specific gravity of the three sources from the Wind River drainage generally exceeded the experimental average (Figure 4B). The relationships,

however, cannot be construed to depend solely on source latitude. Of the three sources not plotted, Lakeview, located midway between the two drainages, had highest specific gravity (Figure 2A); Gates and Palmer, south of the two drainages, had average specific gravity.

Discussion

Wood substance is theoretically distributed jointly to density and ring width as components of stem strength; therefore the observation of this study that genetic structure differs for the two traits may not seem reasonable. Natural selection might be expected to produce mechanisms for optimizing joint allocation, thus to produce similar genetic structures. The explanation for the dissimilarity must lie in the biology of wood-substance allocation.

Wood Substance Allocation

Discussion of the factors affecting allocation provides a useful background for evidence that differences in trait response are adaptive and that the density and ring-width trend indicates strength variation among sources.

Growth of the stem is by successive, yearly additions of incremental sheaths laid down by the cambium. Sheaths so laid down may be considered as a nest of inverted cones of varying wall thickness, the cone-wall thickness corresponding to ring width, which varies, depending partly on the distance of the ring cross-section from the stem tip (DUFF and NOLAN 1953, SMITH and WILSIE 1961). The dimension of each sheath is further determined by available wood substance, stem height increment, and porosity requirements for water and nutrient conduction.

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The distribution of wood substance within a tree apparently represents an allocation mediated by responses to seasonal pattern. The tree crown supplies material for wood substance but also acts as the regulating center allocating substance to the different vertical levels in the sheath and to earlywood and latewood components of the radial dimension (LARSON 1962). According to the hormonal theory, bursting of spring vegetative buds initiates cambial activity, cessation of terminal height growth initiates latewood formation, and development of vegetative dormancy terminates cambial growth (WORRALL 1970). Because wood density of conifers is largely a function of the earlywood-latewood ratio (LARSON 1962), phenology of the vegetative cycle influences wood density as well as ring width and terminal shoot growth (WORRALL 1970).

In Douglas-fir, timing of the vegetative cycle depends on environmental cues provided by the seasonal climatic and photoperiodic cycle. Provenances respond to these cues somewhat differently. For example, a given environmental pattern may advance bud burst more rapidly in one provenance than in another (CAMPBELL and SUGANO 1979). Thus, we may expect a difference in allocation of wood substance among provenances grown at a single plantation site, just by nature of unique phenological responses to environmental cues.
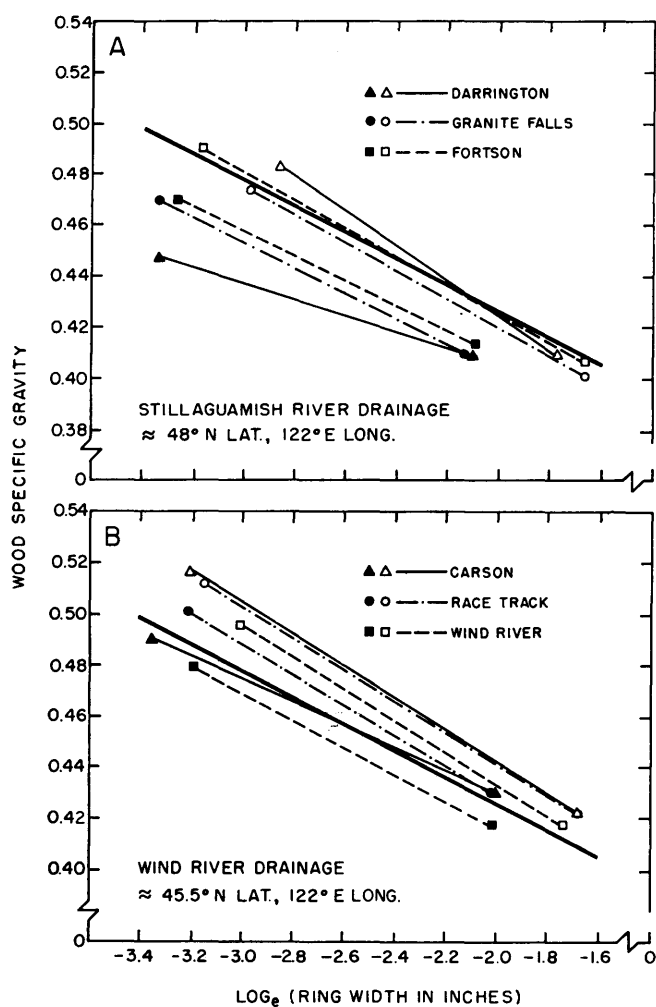
Hypothetically, response of a provenance to environmental cues arises by natural selection to optimize allocation of wood substance (among other functions) within the native environment. Optimization may be exceedingly complex, encompassing variable responses within an individual and population. Environmental cues influence some parts of the vegetative cycle in an individual plant more strongly than other parts. Date of bud burst, for example, mainly reflects winter and spring temperatures (LAVENDER and HERMANN 1970, CAMPBELL and SUGANO 1975). Duration of height growth and dormancy initiation seem more responsive to soil moisture and photoperiod (LAVENDER et al. 1968). Mechanisms for regulating bud burst timing, therefore, must accommodate highly variable spring temperatures; dormancy initiation apparently relies more on the relatively invariable photoperiodic cycle. Phenotypic plasticity of individuals, however, cannot preadapt plants to all situations because of physiologic limitation--some genetic differentiation is needed. Presumably, the resulting genetic pattern also must accommodate various controlling environmental factors. Since these factors and, consequently, variability, may differ for each phenologic trait, the genetic patterns for different traits need not be identical. If, as hypothesized, allocation of wood substance is at least partially controlled by vegetative phenology, then the mechanisms for optimizing wood density and ring width also need not be identical. They apparently are not in coastal Douglas-fir. Our perception of the pattern of genetic variation differed, depending entirely on whether we viewed it in terms of specific gravity or in terms of ring width.

Adaptive Significance of Trait Response

The multidimensional structuring of genetic variation found here is difficult to explain except as a reflection of natural selection. The pattern of variation in the density and ring-width trend is of most interest for evaluating stem strength as a potential adaptive trait. Evidence for adaptation hinges on two points: (1) that genetic mechanisms appear to exist for maintaining the consistency revealed in average trend slopes and the difference revealed in average trend elevations among sources, and (2) that trend elevations are apparently related to factors associated with the origin of sources.

A trend slope close to the average found in this experiment may be important for adaptation of Douglas-fir. The trend slope did not vary, averaged over both plantations, among sources or among families-within-sources. Behind this seeming consistency are great differences in the response of genotypes of families-within-sources to plantation environments. The average genotype of families often dictated the fastest increase in specific gravity with decrease in ring width in one plantation but the slowest increase in the other, which resulted in an average trend slope that was fairly constant among sources.

The constant trend slope depends on responses to the environment reflected concurrently in ring width and specific gravity. The genetic bases for response control appear different for the two traits. Change in ring width appears to be based on an environmental response varying from source to source but not among families-within-sources. Change in specific gravity, in contrast, appears to be based on an environmental response varying among families-within-sources but not among sources. Average ring width differed among families-within-sources, and average

Figure 4. — Wood density and ring-width trends for six sources grown in the Wind River (△ ○ □) and the Mt. Hood (▲ ● ■) plantations. The bold line is the experimental mean for all ten sources of the experiment grown in both plantations.

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specific gravity differed among sources. Therefore, although the trend slope did not vary among genetic entries, the elevation did vary among sources.

We suggest that the trend elevations for sources reflect an adaptive response to environment such that at given ring widths some have lower wood densities than others. Genetic mechanisms provide a relatively consistent ranking of sources that is maintained regardless of plantation. Sources from similar geographic origins have similar trend elevations that remain consistently higher or lower in both plantations than trends of sources from dissimilar origins (compare *Figures 4A* and *4B*). Thus, the allocation of wood substance into various stem components is apparently a consistent response, perhaps optimized for the environment at source origin.

Inferences for Stem Strength

Some sources in this study had lower specific gravities at all ring widths. We interpret this to indicate that sources differed in stem strength. Many investigators have shown that wood strength properties (maximum crushing strength, moduli of rupture, elasticity) vary with wood density. Strength is generally presumed to increase by some power of wood specific gravity (Drow 1957). Since all aspects of strength and a power function appear to contribute, a slight variation in density may considerably influence breaking strength under natural conditions.

To increase stem strength, greater volumes of wood along the stem radius can compensate for lower density wood (Trendelenburg 1935). A comparison of Stillaguamish and Wind River sources shows that this did not occur. In juvenile samples, the four Stillaguamish sources ranked lower than the three Wind River sources both in specific gravity (average ranking 7.3 vs. 3.0; 1 highest, 10 lowest) and in ring-width (8 vs. 5.3; 10 narrowest). In mature samples, Stillaguamish sources ranked lower in specific gravity (8.3 vs. 4.0) but slightly higher in ring width (4.3 vs. 5.3) because of better performance at the Wind River plantation. Stillaguamish sources, therefore, did not produce greater wood volume to compensate for low density, except, perhaps, in maturity at the Wind River plantation.

The important adaptive aspect of stem strength is relative to bending moments in the stem. Do bending moments vary for the sources in this experiment? If, because of inherited properties, Stillaguamish sources, for example, encounter lower bending moments than those for Wind River sources, they may need less strength. This is doubtful, however, if bending moments are directly related to stem height, as it seems they should be. Reported heights from this progeny trial (Munger and Morris 1936, Namkoong et al. 1972) show Stillaguamish sources are consistently taller than Wind River sources. Therefore, Stillaguamish sources had stems as tall or taller, stem diameters as small or smaller, and wood densities considerably lower at the sampling point than Wind River sources. From this we infer that Stillaguamish sources have potentially higher bending moments and weaker stems, at least in lower sections.

The sampling constraints in this experiment made results more ambiguous than we would have wished, particularly in analysis of ring width, which consistently produced higher coefficients of variation for error components than did analyses for specific gravity. Also, because coefficients generally increased with tree age, fairly large differences among genetic entries could exist without being statistical-

ly significant. The probability of committing an inferential error of the second kind (accepting the null hypothesis, no genetic variation, when it was false) was high in the juvenile sample and even higher in the mature sample. In spite of this and increasing error, coefficients of variation for genetic effects remained consistent in juvenile and mature samples. Therefore, we felt justified in inferring significant genetic effects when some such inferences were not indicated at the 0.05 probability level by isolated statistical tests.

We believe our indirect procedure is a productive first step in evaluating stem strength as a trait affecting seed transfer or delineation of Douglas-fir seed zones. Direct results from strength tests, however, would be more convincing. Apparently, from our results, such tests on 10- to 15-year-old material could provide information applicable to older material.

We suggest that, because of the strong family $\times$ plantatio interaction shown here, the density and ring-width trend should be considered in many tree breeding decisions. Because of the apparent control of wood density and ring width by shoot-growth phenology, it may be possible to substitute phenological information for information on the density and ring width trend. However, before phenological observations can be used to predict the trend, much experimental work needs to be done.

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The Bud Enzymes of Beech (Fagus sylvatica L.) Genetic Distinction and Analysis of Polymorphism in Several French Populations

By B. Thiebaut*), R. Lumaret** and Ph. Vernet**)(⁺)

Summary

This paper describes the methods used to study enzymatic genetic markers in Beech *(Fagus sylvatica* L.), and indicates the reasons which led us to work particularly on buds.

Starch gel electrophoresis was used to study the genetics of 3 loci, two coding for peroxidases (Px1 and Px2) and one coding for a glutamate-oxaloacetate transaminase (GOT₁), in Beech buds. The peroxidases are monomeric enzymes in both cases, the first locus is composed of 2 alleles $Px_1^{1.00}$ and $Px_2^{1.05}$ (with existence of silent alleles in certain cases) and the second of 3 alleles $Px_2^{1.13}$, $Px_2^{0.26}$ and $Px_2^{0.40}$. The glutamate-oxaloacetate transaminases are dimeric enzymes specified by one locus composed of two alleles: $GOT_1^{1.00}$ and $GOT_1^{1.05}$.

Using 11 Southern and 2 Northern populations, polymorphism is examined simply for the peroxidases (2 loci). The variation of allelic frequencies show clearly the influence of climate; in the first locus the moisture regime seems to be involved, and in the second the temperature regime.

Key words: Beech, genetic determinism, peroxydases, glutamate-oxaloacetate-transaminases, polymorphism.

Zusammenfassung

Diese Arbeit beschreibt die Methoden, die zur Untersuchung enzymatischer genetischer Marker bei Buche *(Fagus sylvatica* L.) verwendet wurden und zeigt auf, warum wir insbesondere mit Knospen gearbeitet haben. Für die Untersuchung der Genetik von Loci, von denen 2 für Peroxidasen (Px1 und Px2) und einer für Glutamat-oxalacetat Transaminase (GOT₁) codieren, wurde Stärkegelelektrophorese bei Buchenknospen angewendet. Die Peroxidasen sind in beiden Fällen monomere Enzyme, der erste Locus besteht aus den 2 Allelen $Px_1^{1.00}$ und $Px_2^{1.05}$ (wobei die Anwesenheit von Nullallelen nicht auszuschließen ist), der zweite Locus aus den 3 Allelen $Px_2^{0.13}$, $Px_2^{0.26}$ und $Px_2^{0.40}$. Die Glutamat-oxalacetat Transaminasen sind dimere Enzyme, gekennzeichnet durch einen Locus mit 2 Allelen: $GOT_1^{1.00}$ und $GOT_1^{1.05}$.

In 11 südlichen und 2 nördlichen Populationen wurden lediglich die Polymorphismen für die Peroxidasen (2 Loci)

untersucht. Die Variation der Allelfrequenzen zeigte deutlichen Klimaeinfluß; beim ersten Locus schienen die Feuchtigkeitsverhältnisse, beim zweiten die Temperatur von Einfluß zu sein.

Introduction

Beech is widely distributed over much of Northern Europe. At its southern limit, in the mediterranean region it can be found in various habitats with differing climates. In SE France, while the majority of Beechwoods occur at some altitude, in a fairly humid climate, some isolated islands of fully developed Beech can be found at low altitude, under a drier climate (Thiebaut, 1978 and in prep.).

The diversity of environments, and fragmented distribution of Beech at its southern limit could have favoured genetic differentiation within the species. This hypothesis, upon which our work is based, is substantiated by the many publications on the morphological and phenological variations of Beech in northern and central Europe. Cultural experiments have shown a genetic basis for some of these variations (Czeczottova, 1933; Hølm, 1937; Krahl-Urban, 1952; Dimitriu-Tatarani, 1959; Arnswaldt, 1959; Dajoz, 1961; Smagljuk, 1964; Gøhrn, 1972; Abashidze, 1973 and 1974; Garelkova, 1977; Istrath, 1977; Tyshkevitch, 1977 a, b, c, d; Teissier du Cros, 1977, 1980).

These morphological and phenological variations, often of a quantitative nature, and under polygenic control, are not easy to use as markers, Meanwhile, biochemical characters, such as presence or absence of allozymes, are usually monogenic in control, and much easier to use. Electrophoresis allows study of enzymatic variability, and thus the genetic structure of natural and artificial populations of forest trees. In effect the allelic and genetic frequencies observed can be used to characterise genetic variations. For these reasons, these techniques have a great potential in forestry research (Rudin et al., 1974; Hayashi et al., 1975; Bergmann, 1978; Bonnet-Masimbert and Bikay-Bikay, 1978; Lundkvist, 1979).

In fact, biochemical studies on beech are very few. Paganelli et al. (1973) examined variation of deshydrogenases in winter buds; Zin-Suh-Kim (1979) studied the genetic determination of leucine-amino peptidases (LAP) and acid-phosphatases in the young leaves. Thus, it interested us, to try to investigate, in a more systematic manner a range of enzymes of various functions: peroxidases, glutamate-oxaloacetate-transaminases (GOT), leucine-aminopeptida-

*) Institut de botanique, laboratoire de systématique et d'écologie méditerranéennes, 163 rue Auguste Broussonet, F-34000 Montpellier.

**) Centre d'études phytosociologiques et écologiques L. EMBERGER, Laboratoire de génétique écologique, C.N.R.S., B.P. 5051, F-34033 Montpellier Cedex.

(⁺) Present adress: Université des sciences et techniques de Lille, Laboratoire de génétique végétale, F-59655 Villeneuve d'Asco Cedex.