La présence de branches laterales au dessous du point d'annelation est nécessaire a la survie des greffes de mélèze de 6 ans parce qu'elles permettent le maintien en vie des racines. Par contre, ni le diamètre de la greffe (s'il est superieur a 0,5 cm), ni la position de l'annelation (0,9 cm de large) n'affectent la survie de la greffe.

L'effet de l'annelation avec une griffe differe significativement de l'annelation avec deux couteaux paralleles en ce qui concerne le nombre de fleurs femelles produites; mais le nombre total de fleurs est superieur avec le premier traitement. L'emploi de la griffe présente des risques d'endommager le bois mais il est plus rapide.

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Phenotypic Variation and Some Estimates of Repeatability in Branching Characteristics of Douglas-Fir*)

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Introduction

Presently, at least in the western United States, phenotypic variation of wild populations is the main resource available as raw material for tree-breeding. Tree-improvement-breeding programs are typically started by selecting from such populations. Choice of the most appropriate first generation selection method depends on: (1) pattern of variation in existing populations; and (2) some estimate of heritabilities to be expected in these populations. Controlled pollination normally follows selection; concurrently progeny tests may be designed and established. Progeny tests are expensive under the most favorable conditions; consequently, a breeder usually attempts to provide optimum field conditions and the most efficient field design for every progeny test. Test efficiency can be greatly increased if ranges of variation to be anticipated under various field conditions can be considered while field tests are being designed. Accordingly, between-tree and between-population variation estimates may be particularly valuable to the tree breeder engaged in the initial selection and progeny test phases of an improvement program.

In this paper phenotypic variations in crown form attributes of Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO var. menziesii) are quantitatively described. The description is based on measurements made in ten populations of young Douglas-fir native to the southwestern part of the State of Washington.

Crown attributes measured for the study are basic components of the Douglas-fir crown: number and length of branches, branch angle and branch diameter. Stem diameter and stem length measurements were also made within the portion of the crown considered in this study. From diameter and length measurements, stem volume estimates were calculated, and these estimates were used to study the relationships between the four branching characteristics and stem volume.

With the possible exception of branch length, the four crown components (necessarily considered in relation to stem volume) affect quality of wood produced by the tree (JACOBS, 1955; ENTRICAN, 1957; PAUL, 1957). Whether thought of separately as individual characteristics of a crown or collectively as "branchiness" or "knottiness", these attributes are usually treated as major factors to be considered in selection (ARNBORG and HADDERS, 1953; JENSEN, 1954; ISAAC, 1955).

Since most modern breeding practices are based on quantitative assessment of the phenotype, no description of the tree crown, other than quantitative, has been attempted in this study. But for the quantitative description of a phenotype, one measurement value per attribute per tree is preferable. To assign appropriate values to each tree without misrepresenting the phenotype, within-organism variation must be taken into account. This is particularly important in large perennial plants that produce new plant organs or extensions on existing organs each year. For this reason, a description of within-tree variation, based on a sample of 240 whorls in 30 trees is also presented. In addition, a method for estimating the upper limits of heritabilities in branch characteristics that may be anticipated in young stands of Douglas-fir is discussed.

Procedure

Qualitative observations made on several hundred trees suggest that the crown of Douglas-fir first develops its characteristic features at about 15 years of age, and in open stands it retains these same features for about 25 to 30 years. After this period, crowns become increasingly modified by branch-breakage and by forking of the stem.

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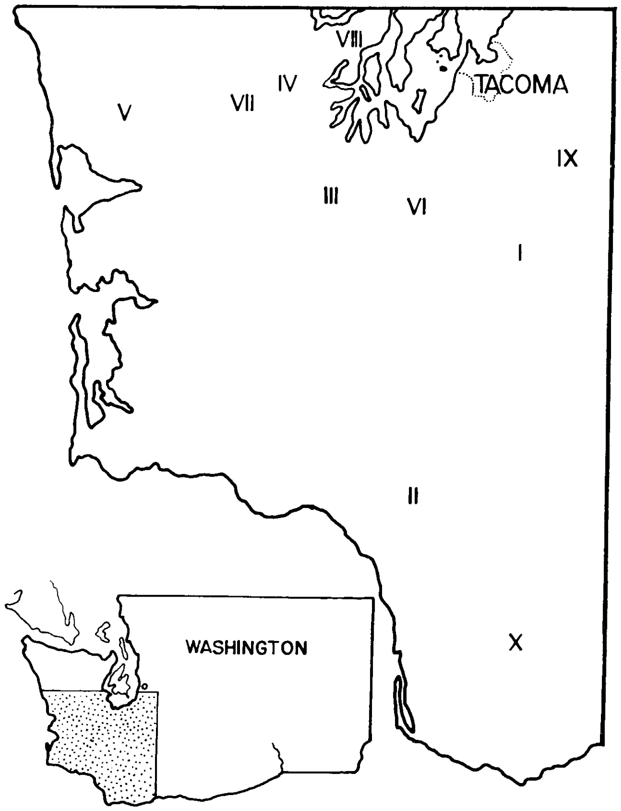

Figure 1. — The ten Douglas fir stands sampled for the study of crown variation were located in southwestern Washington State of the United States of America.

Trees measured for the study sampled this transition period. Their ages ranged from approximately 20 to 40 years, *i. e.*, number of annual rings 4.5 feet above ground level varied from 15 to 35.

Three hundred trees, located in ten geographically separated stands in southwest Washington were measured to provide between-tree and between-population variation data. Procedures developed for selecting areas to sample, trees to measure, and portions of the crown to measure were all designed to minimize variation due exclusively to environmental differences between areas or trees. This region is geographically small enough to disallow any major environmental influence on the hereditary constitution of a tree species due to latitudinal differences. The locations of the areas sampled are shown in *Figure 1.*

Average ages of the selected stands ranged from 18 to 34 years. A considerable proportion of the trees in the stands were open-grown, *i. e.*, stand conditions were such that the lowest, first-formed branches in the crown of the semi-intolerant Douglas-fir were still living. Presence of such was considered evidence that there was little or no crown competition between trees.

Sample populations were chosen in locations with reasonably flat topography to minimize environmental differences which usually accompany differences in topography. Soil type and altitude varied between areas. However, within each of the study areas, these factors were superficially homogeneous, as judged by examination of the surface soil and of the vegetation present.

After an appropriate population of Douglas-fir had been chosen on the basis of the above criteria, thirty individual trees suitable for measurement of crown characteristics were selected as a sample. Criteria for selecting the thirty trees were: (1) the crown could show no apparent damage due to wind breakage, falling trees, or other causes; (2) no major forks were allowed in the main stem from whorl[1]) 2 to 11, the measured portion of the crown, nor were stem forks which interfered with crown development permitted below whorl 11; (3) no obvious crown competition was permitted between the portion of the crown to be measured and other trees or brush. In almost all cases, this last requirement meant there was no contact with other trees or brush from whorl 11 upward.

Using a modification of the method developed by SQUILLACE and BINGHAM (1954), measurements were made in eight successive branch whorls for each tree. Since 20 to 40-year-old Douglas-fir normally produce only one whorl of branches each growing season, eight growing seasons are usually represented by eight consecutive whorls. To insure that branches in a succession of whorls have developed under somewhat comparable climatic conditions, branches produced during the same series of calendar years were assessed by measuring whorls 4 through 11 of every tree. As a result, differences in branch characteristics attributable to yearly variations in climate were minimized. Also, measuring the top of the crown reduces variation due to differential side competition with other tree crowns since crown tops are usually far removed from the crowns of other trees. Other advantages of relating the age of a whorl to the top of the crown instead of to the soil have been demonstrated by SQUILLACE and BINGHAM (1954) and DUFF and NOLAN (1953).

Measurements taken within the crown of each tree were:

(1) The length of each interwhorl[2]) from whorl 4 to whorl 11 was measured to the nearest tenth of a foot. In addition, a single measurement was made of the total length of the stem between whorl 1 and whorl 4.

(2) The diameter outside bark of the stem 0.5 inch above every whorl from whorl 4 to whorl 11 was measured to the nearest tenth of an inch.

(3) The diameter outside bark at a point 3.6 inches from the stem surface was determined for all branches above 0.350 inches in diameter. The lower limit of diameters to measure was chosen arbitrarily. However, contributions of smaller branches to knot formation are negligible; and due to their inferior position in whorls, it is doubtful if they contribute, in any significant way, to crown development. All branch measurements were made with a fork diameter gauge calibrated to 0.1 inches.

(4) The lengths of all undamaged, major[3]) branches in whorls 4 through 11 were measured to the nearest tenth of a foot. The length of a branch was considered as the distance from the center of the stem at the point of insertion of the branch, to the point where elongation for the current year had started.

(5) The angles of all undamaged, major branches in whorls 4 through 11 were measured to the nearest five

[1]) Throughout the text, whorl number is counted from the top of the tree. In this instance, whorl 11 is the eleventh whorl from the tip of the stem in the downward succession of whorls.

[2]) Interwhorl length was measured from the top surface of the uppermost branches in a whorl to the top surface of the uppermost branches in the whorl immediately below.

[3]) The branches constituting each whorl were separated into "major" and "minor" branches. This was necessary because Douglas fir does not have the definite whorl pattern of branch insertion that many other conifers possess. Instead, each whorl appears to be composed of two "types" of branches that differ from each other in degree of vigor, and position of insertion into the stem. There is a dominant, upper portion of the whorl composed of branches which originated from the one to five lateral buds which sur-

Table 1. — Within-tree variation in three crown characteristics for thirty randomly selected trees.

Area No.	Tree No.	Number Branches Per Whorl: Units in Mean	Mean X	Standard Deviation s	Coefficient of Variation CV = (s/X)	Between-Whorl Stem Length (Inches): Units in Mean	Mean X	Standard Deviation s	Coefficient of Variation CV (s/X)	Knottiness Ratio: Units in Mean	Mean X	Standard Deviation s	Coefficient of Variation CV (s/X)
VII	5	8	7.0	1.77	25%	7	28.3	3.21	11%	7	119	22.3	19
	6	8	8.9	2.23	25	7	32.3	4.65	14	7	100	24.1	24
	8	8	6.4	1.85	29	7	24.0	4.28	18	7	92	24.5	27
	16	8	9.8	2.26	23	7	30.0	5.77	19	7	66	17.3	26
	18	8	8.5	1.19	14	7	35.7	5.35	15	7	145	15.7	11
	19	8	7.5	1.92	26	7	30.4	4.06	13	7	91	19.2	21
	22	8	6.9	3.18	46	7	28.6	5.46	19	7	119	53.3	45
	24	8	11.8	3.62	31	7	30.3	5.92	20	7	74	18.7	25
	27	8	8.4	2.51	30	7	31.7	6.65	21	7	128	37.3	29
	29	8	5.5	1.31	24	7	25.9	3.67	14	7	125	32.0	26
	Average	8	8.1	2.18	27	7	29.7	4.90	16	7	106	26.4	25
IX	2	8	6.9	1.81	26	7	23.1	7.12	30	7	94	22.2	29
	5	8	6.6	1.92	29	7	23.6	6.59	28	7	134	32.4	24
	6	8	7.0	1.61	23	7	27.0	6.55	24	7	128	25.9	20
	7	8	5.9	1.00	17	7	26.0	6.08	23	7	147	23.3	16
	10	8	5.4	1.19	22	7	27.3	8.94	33	7	119	25.3	21
	11	8	6.5	1.51	23	7	28.0	2.08	7	7	117	14.3	12
	12	8	7.1	1.25	18	7	24.4	2.12	9	7	115	28.7	25
	18	8	7.9	2.70	34	7	29.1	9.44	32	7	120	58.5	49
	23	8	6.9	1.00	15	7	25.6	6.07	24	7	136	54.2	40
	26	8	6.9	3.05	44	7	25.7	11.45	45	7	120	23.5	20
	Average	8	6.7	1.70	25	7	26.0	6.64	25	7	123	30.8	25
X	2	8	12.0	2.39	20	7	39.6	4.98	12	7	111	21.8	20
	9	8	9.5	2.65	28	7	35.7	1.91	5	7	110	23.8	22
	12	8	12.1	2.09	17	7	36.8	4.64	13	7	90	21.0	23
	15	8	12.2	1.46	12	7	35.3	3.91	11	7	99	39.4	40
	16	8	9.6	2.93	30	7	35.4	5.37	15	7	129	96.1	74
	17	8	13.1	2.30	18	7	36.7	4.83	13	7	95	41.7	44
	18	8	10.8	3.44	32	7	37.0	8.28	26	7	92	27.3	30
	21	8	11.1	2.62	24	7	38.3	10.25	27	7	100	57.2	57
	22	8	12.0	4.14	35	7	36.9	4.45	12	7	118	86.0	78
	23	8	10.6	2.45	23	7	35.9	3.08	9	7	94	31.5	34
	Average	8	11.3	2.65	24	7	36.3	5.17	14	7	104	44.6	42

degrees. Points one foot above the whorl on the main stem and one foot out on the branch were used in measuring branch angle.

Results

Within-tree variation

Within-tree variation is defined as the variation that exists between the seven or eight whorls measured for every attribute in each tree.

In the succeeding *between-tree variation* section of this paper, it will be shown that measurement values for many of the crown characteristics are statistically correlated with size of tree as measured by stem length or stem volume. To determine if within-tree variation is also influenced by differences in size of tree, it was expedient to select study trees from areas indicating extremes of growth. For the description of within-tree variation, measurements from crowns of thirty trees, representing ten randomly selected trees from each of three areas, were utilized. The three areas chosen are examples of medium, low, and high site quality within the limits of the ten areas sampled. Area VII had an average ten-year height increment (the average length of the stem from whorl 1 to whorl 11 for the thirty sample trees within each area) of 25.5 feet, area IX of 22.0 feet, and area X of 28.9 feet. Crown attribute measurements were made in these areas during a short period in late summer of 1957.

round the tip of the leader immediately below the apical bud ("major" branches). There is also a lower portion of the whorl consisting of the branches which originated from lateral buds in the upper group of the so-called "internodal" buds ("minor" branches). Major and minor branches are borne between two successive terminal-bud scale scars (oftentimes visible 12 to 15 whorls down from the top of the stem in Douglas fir) and should not be confused with "double whorls" which develop as a result of lammas growth. The topmost minor branches are occasionally equal in vigor to the upper branches of the whorl, and can be distinguished from the upper branches only by checking the point of branch insertion on the main stem. Because the minor branches are extremely variable, measurements of angle and length were made only on the major or dominant branches in a whorl.

The standard deviation (s) and coefficient of variation (CV) are used to describe within-tree variation in number of branches per whorl, interwhorl stem length, and cross-sectional area of branch bases. The other two crown attributes measured, namely branch angle and branch length, showed a definite linear relationship to whorl number. Hence, for these, the standard deviation from regression ($s - y \cdot x$) of the attribute measurement (y) on whorl number (x) was used in preference to s as a measure of within-tree variation.

Within-tree variation in number of branches per whorl, interwhorl stem length, and cross-sectional area of branch bases is summarized in *table 1.*

Number of branches per whorl is considered as the number of measured branches inserted in the stem between two successive bud scale scars which, in Douglas-fir, denote inception of two successive years of stem growth.

The comparatively large within-tree variation in number of branches ($\overline{CV} = 25\%$) is apparently due, at least in part, to the procedure used for determining number of

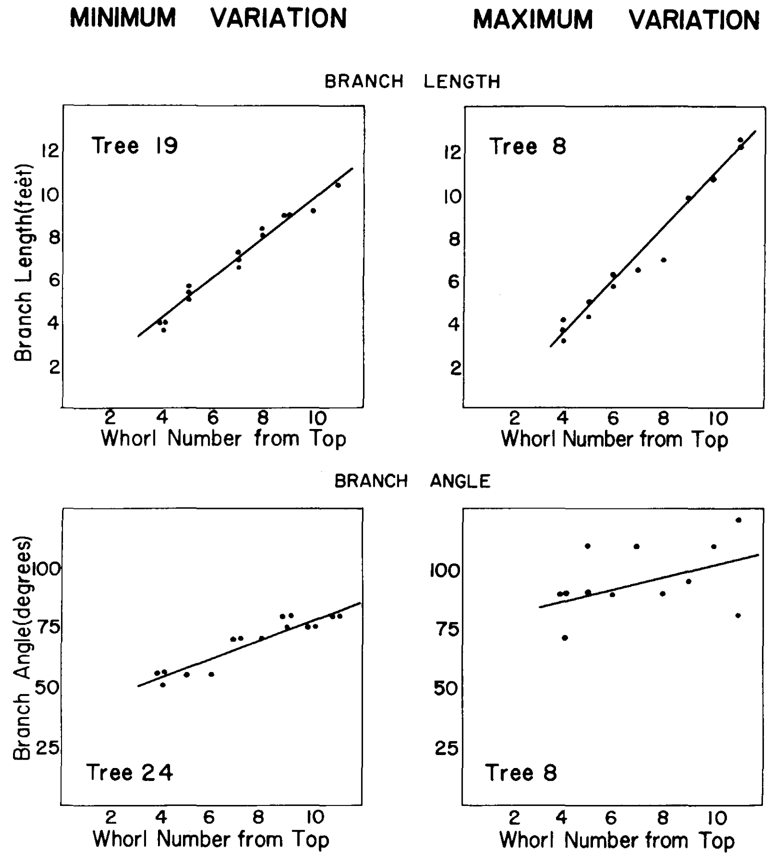

Figure 2. — Regression lines fitted to data from the trees of area VII which demonstrated least and greatest within-tree variation (see *table 2*) in branch length and angle. The linear relationship between branch length, or angle, and whorl number is clearly demonstrated.

branches per whorl. As noted above, branch enumeration included only measured branches, *i. e.*, only branches above 0.350 inches in diameter. Consequently, as the average branch diameter increases, the number of branches in a whorl increases — branches formerly below the minimum measured diameter eventually reach measurable size. Concomitantly, upper whorls in a tree tend to have fewer tallied branches. Although this effect of ingrowth is not constant from tree to tree, sample trees with a low number of branches in upper whorls and a high number of branches in lower whorls tend to increase average within-tree variation. Regardless of tree size or site quality of an area, no effect due to branch ingrowth could be noticed below the sixth whorl.

There is considerably more within-tree variation of interwhorl stem length in area IX than in areas VII and X *(table 1)*. In area IX, an abrupt decrease in annual height growth increment occurred during, or just preceding, the 1951 growing season. Shortened height growth persisted for the 1952 and 1953 growing seasons. As result, three of the seven interwhorl lengths were shorter than the others in most of the 30 trees measured in this area. It is apparent that persistent, unaccountable, environmental factors which adversely influenced height growth have greatly increased within-tree variation of interwhorl length.

Total cross-sectional area of branch bases per whorl is related to the number, or age, of the whorl in which the branches are inserted. On the average, in the upper crown of Douglas-fir, older whorls have larger branches. An adjustment which partially takes this relationship into account, and consequently reduced within-tree variation, was made by using a ratio of the surface area of each interwhorl to the cross-sectional area of branch bases inserted in that particular interwhorl. Numerically, each ratio equals the number of square inches of stem surface per square inch of branch base inserted in this stem surface. Therefore, this ratio estimates variation in knot formation.

In each tree selected for the within-tree variation study, the above ratio was computed for seven interwhorl stem segments. Surface area of the stem for each segment was calculated as the surface area of a cylinder with length equivalent to the interwhorl length and diameter equal to the diameter of the stem at the base of the same interwhorl. The cross-sectional area of the base of branches borne on a one-whorl segment was calculated by totaling the cross-sectional area of all branches above 0.350 inches in diameter that were inserted in the one-whorl segment. Thus, seven ratios were computed for each tree. *Table 1* includes a description of within-tree variation in this ratio (knottiness ratio).[4])

High ratios in whorls 4 and 5 of almost every tree account for much of the large average coefficient of variation in the knottiness ratio for area X (42% compared to 25% for other two areas). Although this trend was especially evident in the ten tree sample from area X, data from the twenty other trees used for description of within-tree variation exhibited similar tendencies. This suggests that sampling for knottiness ratio, as well as for number of branches above 0.350 inches diameter, should preferably be restricted to whorls below number 5 in Douglas-fir.

The length of a major branch is partially dependent upon its age. Moreover, the branch angle of major branches is again partially dependent on the lengths and diameters of the branches. Accordingly, in the upper crown of young Douglas-fir, there is a relationship between length of branch, or angle of branch, and the age of the whorl in which the branch is inserted. Since both relations are direct, linear regressions of branch length, or angle, on the number of the whorl from the tip of tree (age of whorl) may be employed to minimize variation in branch length, or angle, that is due to branch age differences.

In *figure 2* regression lines, fitted to data from those trees of area VII which demonstrated least and greatest within-tree variation in branch length and angle, are presented. The linear relationship between branch length, or angle, and whorl number is clearly demonstrated in both cases.

Table 2 summarizes within-tree variation in branch length and angle.

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4) A. E. SQUILLACE has suggested, in personal communication, that the reciprocal ratio (branch cross-sectional area to interwhorl surface area) might be preferable. If a sample contains a whorl with exceptionally few or small branches, the corresponding knottiness ratio would be very large and could even approach infinity. On the other hand, ranges between upper and lower limits of the ratio suggested by SQUILLACE would usually be less; consequently, lower coefficients of variation (CV) should result.

Table 2. — Within-tree variation in branch length and branch angle for 30 randomly selected trees

Area No.	Tree No.	Branch Length (Whorls 4 to 11) n	Regression Equation $y = a + bx$[1]	Standard Deviation From Regression ($s_{y.x}$)	Σx^2	Branch Angle (Whorls 4 to 11) n	Regression Equation $z = a + bx$[1]	$s_{z.x}$	Σx^2
VII	5	13	$y = 2.24 + .549x$	.348	67	13	$z = 55.2 + 2.60x$	4.8	67
	6	19	$y = 1.95 + 7.49x$	.401	78	19	$z = 41.3 + 5.00x$	9.2	78
	8	13	$y = -1.58 + 1.240x$	.607	83	13	$z = 79.6 + 2.17x$	13.4	83
	16	18	$y = .61 + .975x$	.357	77	18	$z = 58.4 + .83x$	6.9	77
	18	11	$y = 1.57 + .560x$	.266	67	13	$z = 55.8 + 2.51x$	5.0	81
	19	16	$y = .40 + .936x$	.217	79	17	$z = 26.0 + 4.60x$	4.7	79
	22	15	$y = -.34 + .957x$	.515	77	15	$z = 46.8 + 3.43x$	5.2	77
	24	13	$y = .89 + .796x$	.486	75	15	$z = 37.0 + 4.13x$	4.0	90
	27	17	$y = 1.68 + .583x$	.365	92	17	$z = 64.9 + 1.59x$	6.7	92
	29	16	$y = 1.91 + .550x$	.272	74	16	$z = 45.5 + 3.32x$	5.9	74
	Average	15.1	.93 .790	.383	77	15.6	51.0 3.02	6.6	80
IX	2	17	$y = 1.84 + .472x$	.271	102	17	$z = 52.2 + 1.40x$	5.5	102
	5	18	$y = 1.13 + .507x$	.289	84	19	$z = 73.4 + 1.34x$	5.2	95
	6	11	$y = 1.68 + .628x$	.369	69	13	$z = 54.2 + 1.29x$	7.0	75
	7	15	$y = .33 + .641x$	.525	71	16	$z = 53.2 + 1.83x$	6.0	72
	10	13	$y = 1.29 + .553x$	.522	49	14	$z = 34.7 + 3.54x$	8.8	54
	11	19	$y = 2.61 + .528x$	.361	93	20	$z = 45.6 + 1.32x$	5.0	95
	12	17	$y = 1.40 + .608x$	.401	76	17	$z = 48.2 + 2.69x$	6.8	76
	18	11	$y = .71 + .841x$	.539	55	15	$z = 70.6 + .92x$	6.0	79
	23	13	$y = 1.12 + .641x$	.313	57	13	$z = 39.1 + 2.60x$	7.0	57
	26	14	$y = 1.33 + .582x$	.615	69	14	$z = 36.0 + 4.29x$	5.8	69
	Average	14.8	1.34 .600	.420	72	15.8	50.7 2.12	6.3	77
X	2	18	$y = 1.84 + .701x$	.527	86	22	$z = 81.7 + 1.46x$	4.2	107
	9	15	$y = 2.60 + .465x$	.365	84	16	$z = 44.3 + 3.84x$	8.3	85
	12	16	$y = .58 + .750x$	.516	78	17	$z = 52.4 + 2.98x$	6.5	90
	15	21	$y = 1.00 + .765x$	.417	93	23	$z = 51.4 + 3.07x$	3.4	111
	16	12	$y = -.50 + 1.050x$	.794	82	12	$z = 34.4 + 3.85x$	3.0	82
	17	18	$y = 1.26 + .754x$	.475	92	19	$z = 56.3 + 3.48x$	4.4	94
	18	11	$y = .75 + .716x$	.506	72	11	$z = 78.9 - .04x$	7.5	72
	21	18	$y = 2.32 + .840x$	.861	74	19	$z = 73.9 + 2.43x$	4.3	83
	22	10	$y = -1.06 + 1.060x$	.361	54	14	$z = 67.4 - .35x$	4.5	71
	23	15	$y = .28 + .896x$	.234	77	18	$z = 89.7 - 1.02x$	4.0	93
	Average	15.4	.91 .800	.506	79	17.1	63.0 1.97	5.0	89

[1]) x = Whorl number — counted from tip of tree
y = Branch length in feet
z = Branch angle in degrees

Between-tree Variation

To estimate differences between trees, a single descriptive value for each characteristic had to be determined for every tree in the study. The values are used in this section to describe variation between trees within the ten separate Douglas-fir populations, and in the succeeding section to examine apparent differences between population averages. Measures used as individual tree values are:

(1) Length of the stem from whorl 1 to whorl 11.

(2) Total number of branches above 0.350 inches diameter outside bark, found in whorls 4 through 10 of the tree.

(3) Cross-sectional area of branch bases of all branches with diameters greater than 0.350 inches located in whorls 4 through 10.

(4) Branch length and branch angle of a tree derived from a linear regression using the length (or angle) of the major branches at a whorl plotted against the number of the whorl. Regression formulae for each tree for the two characteristics were obtained from these data. The length of the average branch at the eleventh whorl and the angle of the average branch at the seventh whorl was calculated from the regression formulae to be used as unit-values for a tree (see *figure 2* for linear regression lines fitted to individual tree data).[5])

Differences in size of tree within thirty-tree samples was associated with number of branches (association between stem length and number of branches as determined by combining correlation coefficients from nine areas to get combined $r = 0.41$[6])) and length of branches (combined correlation coefficient of branch length and stem length from ten areas is $r = 0.26$[7])). Branch angle was not associated with stem length (combined r for ten areas = 0.07).

To reduce variation in branch length and number of branches, due only to size differences between trees, a linear regression was used to adjust all attribute values to the same tree size — as measured by stem length. On the other

[5]) Branch length, estimated at the eleventh whorl, includes a certain amount of bias. The reliability of values derived from the regression of branch length on whorl number depends on the correlation between the two variables in each tree. If correlation is strong, regression will estimate branch length precisely. If correlation is weak, the regression coefficient is accordingly smaller and will cause branch length to be underestimated in lower whorls. Because branch length and whorl number are closely associated (*table 2* and *figure 2*), branch length bias is relatively small. For this study, the author wished to relate branch length at a given whorl to total stem length above the whorl. Interwhorl stem length is particularly subject to modification by year to year differences in climate. To minimize between-tree stem length variation caused by environmental differences, a ten-whorl stem segment (whorl 1 to 11) was measured. Correspondingly, branch length was estimated at the eleventh whorl. For future studies an estimate at whorls more centrally located on the regression line may be desirable.

[6]) Significant at the 0.1 per cent level.

[7]) Significant at the 1.0 per cent level.

Table 3. — Variation between trees, within areas, after variation due to different tree size, as expressed by stem length or surface area of stem, has been removed by regression

Area No.	No. Trees Measured	Branch Length (Feet)			No. Branches			Cross-sectional Area of Branch Bases (Square Inches)		
		Regression Formula $L = a + bx$[1]	$s_{l.x}$	Σx^2	Regression Formula $N = a + bx$[1]	$s_{n.x}$	Σx^2	Regression Formula $Y = a + bz$[1]	$s_{y.z}$	Σz^2
I	30	$L = 3.20 + .255x$	0.990	124.7	—	—	—	—	—	—
II	30	$L = 2.61 + .211x$	1.308	201.5	$N = 36.0 + 0.40x$	8.43	201.5	$Y = -12.99 + .012z$	6.24	12.4×10^6
III	30	$L = 7.82 + .087x$	1.591	308.6	$N = 6.8 + 1.69x$	8.47	308.6	$Y = 3.02 + .011z$	8.00	16.7×10^6
IV	30	$L = 3.25 + .238x$	1.058	156.0	$N = 15.0 + 1.67x$	7.87	156.0	$Y = -10.16 + .016z$	8.78	8.0×10^6
V	30	$L = -0.14 + .328x$	1.100	264.5	$N = 4.7 + 1.89x$	8.94	264.5	$Y = 3.08 + .010z$	8.00	13.7×10^6
VI	30	$L = 7.04 + .123x$	1.127	96.6	$N = 1.1 + 2.36x$	6.90	96.6	$Y = -2.95 + .018z$	6.32	2.9×10^6
VII	30	$L = 12.04 - .108x$	1.407	124.3	$N = 12.6 + 1.83x$	8.67	124.3	$Y = -19.79 + .018z$	6.48	6.8×10^6
VIII	30	$L = 2.75 + .213x$	0.804	121.0	$N = 27.0 + 1.20x$	5.96	121.0	$Y = -1.50 + .010z$	3.00	4.1×10^6
IX	30	$L = 3.89 + .160x$	0.846	114.6	$N = 30.5 + 0.74x$	5.17	114.6	$Y = -2.43 + .010z$	4.47	3.0×10^6
X	30	$L = 5.78 + .115x$	1.082	151.8	$N = 31.1 + 1.54x$	8.96	151.8	$Y = -3.63 + .012z$	6.63	6.4×10^6

[1]) L = Length of branch, per tree, at the eleventh whorl from tip, in feet.
N = Number of branches in whorls 4 through 10 per tree.
x = Length of stem from whorl 1 to whorl 11 in feet.
Y = Cross-sectional area of the base of all branches above 0.350 inches diameter per tree in whorls 4 through 10, in square inches.
z = Surface area of stem from whorl 1 to whorl 11 in square inches.

hand, cross-sectional area of branch bases was adjusted to an average surface area of stem (combined r for 10 areas = 0.71[8])). Surface area of stem per tree was defined as the surface area of a cone with height equal to the length of the stem from whorl 1 to whorl 11 and basal diameter equal to the diameter of the stem one inch above whorl 11.

Tree age was not significantly correlated with any of the crown characteristics. Therefore, no adjustment was made for age differences between trees within areas.

Ranges of differences between trees in branch length, number of branches, and cross-sectional area of branch bases are described by corresponding standard deviations from regressions in *table 3*. Since variation as expressed by standard deviation from regression is difficult to interpret, areas with greatest and least between-tree variation in the three crown attributes are shown graphically in *figure 3*. Ninety-five per cent confidence limits of the individual observations (SNEDECOR 1956, pp. 138—139) are shown on these graphs. *Table 4* summarizes between-tree variation in branch angle and stem length.

Between-Area Variation

Averages for each crown attribute for each area were calculated from individual tree values obtained as outlined in the between-tree variation study. Each average is based upon a thirty-tree sample.

Site quality of the ten areas, as measured by stem length *(table 4)*, was quite variable. Covariance analysis, using stem length as a measurement of environmental differences between areas, was used to partially eliminate the effect of site quality differences between areas from the crown-characteristic averages. In the covariance analyses, crown characteristic variances for the several areas sometimes proved to be heterogeneous. Homogeneity was restored by square-root transformation of measurement values for the dependent variables (crown characteristics). With cross-sectional area of branch bases, the surface area of the stem was used as a measure of environmental differences between areas.

The correlation coefficient (r = 0.80[8])), computed from average branch angles and average stem lengths *(table 4)* of the ten areas, indicates a statistically highly-significant association between average branch angle for an area and its corresponding average stem length. On the other hand, branch angle and stem length are apparently not associated within the individual trees of a thirty-tree sample. Ten correlation coefficients, computed for the thirty trees in each of the ten separate areas, were found not significantly different. Accordingly, they were combined to provide a single, more reliable estimate of the association between branch angle and stem length within areas (r = 0.07, non-significant). It is plain that if area averages are considered, branch angle and stem length are associated; if individual trees growing within one area are considered, angle and stem lengths are not associated. In the absence of any plausible explanation for this, no adjustment for the effect upon branch angle of growth differences between areas was considered to be justified.

Average measured values for other crown characteristics, compared to values adjusted for site quality differences *(table 5)*, show the considerable effect of size differences between trees upon the quantitative expression of crown characteristics. Results of statistical tests of significance for differences between areas may be examined in *figure 4*. Tests for differences in the average number of branches, length of branches, and cross-sectional area of branch bases are all based on analyses of covariance, using transformed data. Differences in the average values for these attributes were judged significant if there was less than one chance in 100 that a comparable difference could occur due to chance. Analysis of variance was used on branch angle data. Branch angle data were extremely variable. Few distinctions between populations could have been made

Table 4. — Average stem lengths (Whorls 1—11) and branch angles (Whorl 7) from 30 tree samples of 10 areas.

Area	Branch Angle (Degrees)		Stem Length (Feet)	
	$\bar{X}$	s	X	s
I	69	7.5	23.0	2.1
II	77	7.9	31.4	2.6
III	71	8.5	26.7	3.3
IV	71	7.9	26.2	2.3
V	77	9.8	28.0	3.0
VI	71	7.8	20.3	1.8
VII	71	9.6	25.5	2.1
VIII	64	6.4	22.7	2.0
IX	67	8.0	22.0	2.0
X	76	8.6	28.9	2.3

[8]) Significant at the 1.0 per cent level.

using the same level of probability as above. Therefore, differences in average branch angles were judged significant if there were less than five chances in 100 for comparable differences to occur due to chance. A modification of TUKEY's Q test was used to make all comparisons among population means (SNEDECOR, 1956).

In *figure 4*, all blank, small-squares indicate significant differences. Thus, only completely blank large-squares show that the two areas being compared belong to two distinct populations for the four characteristics considered.

Discussion

Performance, in any generation of an organism undergoing improvement breeding, can be estimated by a general formula: performance, or the hereditary potential of progeny from selected parents = average phenotype of parent population ± (selection differential × heritability in the narrow sense) (ROBINSON, COMSTOCK, and HARVEY, 1949; WARWICK, 1951). Choice of an appropriate selection method, for any characteristic within any species, is impossible without considering all components of this performance formula.

Estimation of Heritability in Wild Populations of Douglas-Fir

All methods used to estimate heritability depend on measuring how much more closely-related-organisms resemble each other, in a given environment, than do less-closely-related organisms, in the same environment. Hereditary relationship between trees in a wild population cannot be determined. However, animal breeders have developed a method which estimates the upper limit of heritability in the broad sense and does not require a knowledge of familial relationship between organisms. This method applies only to characteristics for which an animal may have a number of discrete production records throughout its lifetime, *i. e.*, milk production per lactation, birth weight of calves, etc. The constancy of the production records may be measured by intraclass correlation — LUSH (1945) has termed this measurement "repeatability".

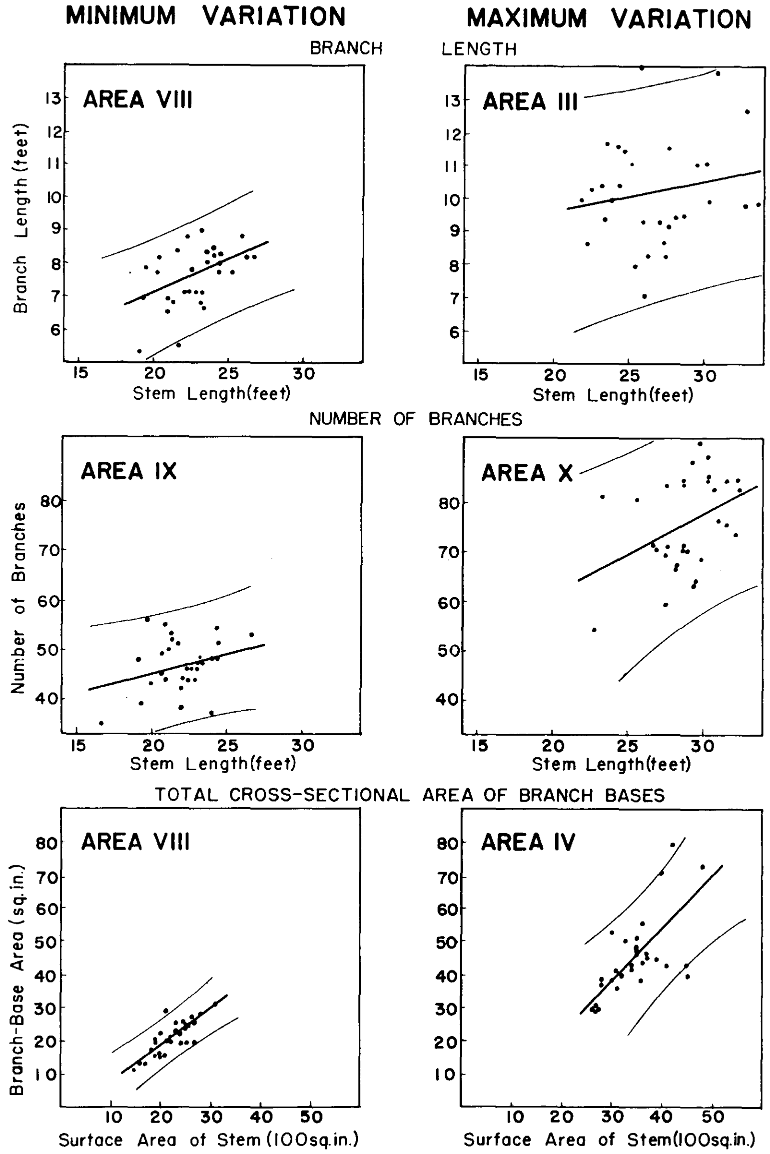

Figure 3. — Areas, of the ten sampled, showing the greatest and least between-tree variation in branch length, number of branches and total cross-sectional area of branch bases. Regression lines and ninety-five per cent confidence limits of the individual tree values were computed from data presented in *table 3*.

Since a new set of crown characteristics are produced each growing season, the phenotype for crown manifests the joint action of the genotype, which remains constant in a tree, with the environment, which changes yearly from site to site, tree to tree, and from whorl to whorl. If no permanent non-random environmental differences existed between trees, heritability estimates could be obtained by relating variation between trees (representing differences due to heredity) to variations between all whorls within all trees (representing differences due to heredity and environment). Of course, this assumption cannot be made. However, by correlating records for branch characteristics from successive whorls within a tree, an idea of the repeatability of the trait may be obtained. Repeatability, therefore, equals heritability in the broad sense plus any between-tree environmental effects which persist over the period during which the measured whorls were produced. Consequently, repeatability is the upper limit of heritability in the broad sense (WHEAT and RIGGS, 1958).

It must be assumed that permanent environmental influences, differing from one individual to the next are much more prevalent in forest trees than would be expected in animal herds. Individual animals of a herd may move from place to place, perhaps sampling a different portion of the environment at every movement. In contrast, the forest tree partakes only of environment that occurs in a limited, fixed area, e. g., it probably has much the same soil conditions throughout its life. Certainly, the individual tree does not have a chance to average out environmental differences over an area as does the animal. Moreover the tree cannot choose its environment whereas the animal may to a limited extent. For this reason, repeatability may under some circumstances far overestimate broad-sense heritability, particularly in forest trees; it can never underestimate heritability values peculiar to any specific stand. Since heritability in the narrow sense seldom is greater than two-

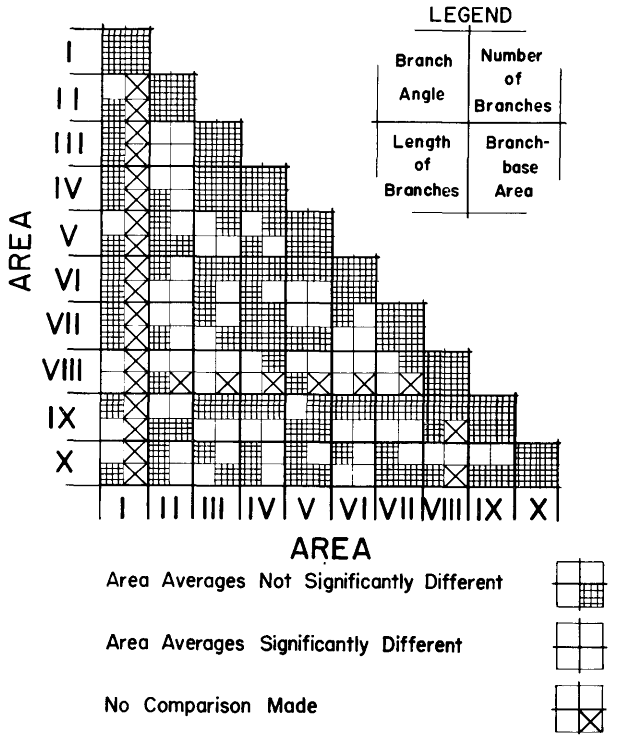

Figure 4. — Statistical significance of differences, for four crown characteristics, between means of 30-tree samples of ten areas.

thirds of the repeatability, even in relatively homogeneous animal herds (LUSH and ARNOLD, 1937; BOTKIN and WHATLEY, 1953), the tree breeder will be fortunate if narrow-sense heritability approaches one-half of repeatability.

Intraclass correlation coefficients, calculated from data used for the within-tree variation study, are shown in *table 6*. The coefficients indicate repeatability of branching characteristics, hence heritabilities, to be low or lacking in the three stands sampled. From a topographic and soil standpoint, IX and X were located on two of the least uniform areas, and VII was one of the most uniform areas of the ten sampled for the study. Apparently intense individual tree selection for crown characteristics will be effective only if practiced in stands located on extremely uniform sites. Heritabilities may be so low in stands on variable sites that a high selection differential will be meaningless.

Low repeatability values further indicate that branching characteristics of a tree should not be estimated from measurements taken at a single whorl. LUSH (1945) predicts that

Table 6. — Intraclass correlation coefficients (repeatabilities) of three crown characteristics for ten trees from three areas.

Area	VII	IX	X
Stem interwhorl lengths (above whorls 5 through 11)	.302[2])	.020	.021
Number of branches per whorl (whorls 6 through 11)	.385[2])	.088	.142
Knottiness ratio (whorls 7 through 11)	.356[2])	.163	.233[1])

[1]) Significant at 95% level.
[2]) Significant at 99% level.

breeding progress per generation, when selecting on an average of n records per organism is $\sqrt{\frac{n}{1 + (n-1)\,r}}$ times as much as if selecting on only one record per organism. Particularly where r (repeatability) is low, three or four observations per tree may foster a considerable increase in efficiency of selection. Also substantial benefit may be obtained by consideration of repeatability in the design and measurement of progeny tests where a number of measurements might be made on a single organism instead of a single measurement on several.

Population Structure in Douglas-Fir

It is injudicious for several reasons to consider statistically significant differences between areas *(figure 4)* to be bona fide evidence for existence of hereditarily distinct local populations in Douglas-fir. First, although, admittedly, estimates are based on limited quantitative evidence *(table 6)*, it appears that heritabilities are low in wild populations — at least for crown characteristics collateral to branch size and number.

From this, and from other reported observations, it can be gathered that crown phenotypes are particularly susceptible to environmental modifications. Stand density has profound effect on crown characteristics. Branch diameter (EVERSOLE, 1955) and number of branches (KUNZ, 1953) are especially altered in the crown region where active competition between neighboring trees occurs. JACOBS (1938) suggests that in *Pinus radiata* branch length is affected above the actual zone of contact as well; at the same time, cross-sectional area of branch bases is not.

Environment may also have a differential influence on the growth of separate crown attributes. GESSEL and WALKER (1956), LEYTON (1956) and others have demonstrated positive correlation between length increase of the terminal shoot and nutrient concentration in the foliage. WILL (1957) showed that nutrient levels in the foliage of *Pinus radiata* vary considerably, but variation patterns within the crown are distinctive and fairly consistent for each nutrient. From

Table 5. — Observed and adjusted thirty-tree average values for three crown characteristics.

Area	Cross-sectional Area of Branch Bases (Square Inches)			Branch Length (Feet)			Number of Branches		
	As Measured		Adjusted to Average Surface Area of Stem	As Measured		Adjusted to Average Stem Lengths	As Measured		Adjusted to Average Stem Lengths
	$\bar{X}$	s	$\hat{X}$	$\bar{X}$	s	$\hat{X}$	$\bar{X}$	s	$\hat{X}$
I	—	—	—	9.1	1.1	9.4	—	—	—
II	35.91	9.79	26.11	9.2	1.4	8.4	48.5	8.5	40.6
III	40.89	11.52	37.70	10.1	1.6	9.9	51.9	10.0	50.0
IV	44.88	12.09	41.60	9.5	1.2	9.3	58.7	8.6	57.8
V	40.89	10.54	33.76	9.0	1.2	8.7	57.5	10.5	53.9
VI	41.58	8.34	51.84	9.5	1.1	10.3	49.1	8.0	56.7
VII	33.56	10.57	36.24	9.3	1.4	9.2	59.3	9.3	59.1
VIII	20.91	4.82	—	7.6	0.9	7.9	54.3	6.3	58.4
IX	17.84	5.45	28.41	7.4	0.9	7.9	46.8	5.3	51.8
X	41.33	8.62	34.69	9.1	1.1	8.6	75.6	9.5	70.1

these patterns it appears possible that a nutrient deficiency may limit shoot elongation in one portion of the crown and, at the same time, in another portion of the crown the same nutrient may not be limiting.

An actual case, demonstrating the differential effect of a nutrient deficiency on branch elongation versus stem elongation, is found in a study reported by HOLMBÄCH and MALMSTRÖM (1947). During an irrigation test, the nutritional status of *Pinus sylvestris* was increased on one plot relative to an adjacent plot which was not treated. Branch length was increased comparatively more than stem length on the treated plot. The resulting trees had noticeably broader crowns. From this, it would appear that soil environment (nitrogen nutrition, in this case) which limits branch elongation does not always limit stem elongation to a like degree.

In the present study of variation in crown characteristics, some between-area differences could well be an expression of this phenomenon. In fact, a very reasonable hypothesis to explain phenotypically dissimilar trees growing on two of the adjacent study areas can be developed from this assumption. Although areas VI and VIII have very similar average stem lengths *(table 4)*, they have quite divergent average branch lengths *(table 5)*. For area VI, average branch length at the eleventh whorl is almost two feet greater than the average length of similarly located branches in area VIII. Trees growing on area VIII have narrow, spire-like crowns with the light green foliage which typically indicates nitrogen deficiency in Douglas-fir (GESSEL, WALKER, and HADDOCK, 1951). Trees from area VI have a broad crown with dark green foliage. But area VI is located on a soil characterized by excessive drainage, and CARMEAN (1956) suggests that in Douglas-fir stands on excessively drained soils height-growth practically ceases at 60 to 70 years. This indicates that soil moisture may be limiting height growth elongation in area VI. On the other hand, lower-branch elongation does not cease if the branches have no lateral competition. From these observations, it appears possible that branch and stem elongation may have been affected differentially by nutrient and soil moisture conditions prevalent at the two areas.

Finally, in this study, there usually was a positive correlation between branch characteristics and tree size. When testing differences between areas, variation due to different average size of tree can be partially removed by statistical control. An attempt has been made to do this by using average stem length of an area as a measurement of the environment of the area. But, if speculations in the previous paragraph are correct, similar stem lengths may be produced by very dissimilar environments which may have radically different effects upon the expression of the separate branch characteristics. Therefore, extreme caution must be used in interpreting average differences in crown characteristics where differences in size of tree exist between areas.

It is probably equally unwise to consider all differences between populations as being due only to environmental modification. Areas II and X, with almost identical height growth and located at similar altitudes on similar soils, have greatly different numbers of branches per whorl *(tables 4, 5)*. It is extremely unlikely that this is due to modification alone. Also, there is some slight evidence for the presence of clines or "population centers" for some branch characteristics. For example, when the areas with their corresponding adjusted branch length *(table 5)* are placed on an outline map *(figure 1)* to indicate their relative geographic position, a possible pattern arises. Areas VI and III seem to represent a population center of long-branched trees. Departure from the center in any direction produces a decrease in average branch length. This may be evidence for geographic clinal variation, or on the other hand, it may be evidence of a gradation in environment affecting branch length. Similar population centers for high number of branches, and large average cross-sectional area of branch bases can also be discerned.

Selection for Branch Characteristics in Wild Populations

In theory, intensive selection is ineffective where heritabilities are very low; in this case progeny tests should be used as aids to selection (LUSH 1948). So if heritabilities for branching characteristics in Douglas-fir are as low as the repeatability data indicate, selection for these characteristics should be based on progeny tests. Furthermore, "races" with desirable branching attributes should also be chosen on the basis of progeny tests or provenance trials. Clearly, if heritabilities are low, phenotypic differences between local populations are doubtful evidence for racial or clinal variation.

On the other hand, phenotypic selection is far less expensive than progeny testing. With forest trees, progeny tests are particularly costly in terms of space and time required to complete each test — far more so than with animals or agricultural crops. Consequently, fairly intensive phenotypic selection may be justified as a preliminary step to progeny testing of forest trees. This may be true even under conditions where very low heritabilities generally prevail, if only to increase the probability that trees with better than average heredity will be tested. If phenotypic selection for branching characteristics of Douglas-fir is used to increase this probability, only the more desirable trees should be chosen from the phenotypically better local populations growing on extremely uniform sites.

Larger heritabilities should be found in such populations, and genetic variation due to both racial and individual tree differences is exploited by testing the better trees from the better races (WRIGHT, *et al.*, 1958).

Summary

Three hundred 15 to 35 year old Douglas-firs, located in ten native stands in Southwestern Washington were measured to provide quantitative estimates of phenotypic variation in branching characteristics. Measurements of stem length and diameter, branch diameter, angle, length and number were restricted to eight consecutive whorls in the upper crown of each tree. From these measurements, estimates of the variation to be expected within trees, between trees within-populations, and between populations, have been calculated and are presented in tabular form to be used as basic variation information, *e. g.*, information that may be helpful in the proper design of Douglas-fir progeny tests.

A method which may be used to estimate upper limits of broad sense heritabilities for crown characteristics in populations of trees for which parentages cannot be ascertained is also discussed. Application of this method (based upon the idea of "repeatability" used for many years by animal breeders) to measurement data from ten trees from each of three widely separated stands indicates that broad sense heritability of crown characteristics may be very low in wild populations of Douglas-fir. This suggests that intensive selection for phenotypic "plus" trees, where crown characteristics are being considered, is extremely

inefficient in species such as Douglas-fir which are found growing on many sites within a relatively small geographic range.

Zusammenfassung

Titel der Arbeit: *Die phänotypische Variation bei Douglasfichte und einige Schätzungen über die Wiederholbarkeit von Verzweigungsmerkmalen.*

Dreihundert 15- bis 35jährige Douglasien aus 10 autochthonen Beständen Südwestwashingtons wurden vermessen, um quantitative Schätzungen phaenotypischer Verzweigungsmerkmale zu bestimmen. In der oberen Krone eines jeden Baumes wurden an acht aufeinanderfolgenden Astquirlen Stammlänge und -durchmesser, sowie Astdurchmesser, -winkel, -länge und -anzahl festgestellt. Aus diesen Werten wurden Schätzungen der Variation innerhalb der Bäume, zwischen den Einzelbäumen innerhalb der Population und zwischen den Populationen errechnet. Diese werden in Tabellenform vorgelegt, um als grundlegende Information über die Variation benutzt zu werden, d. h. als eine Information, die als Hilfsmittel bei einer exakten Anlage von Douglasienprovenienzversuchen dienen könnte.

Außerdem wird eine Methode diskutiert, mittels der die obere Grenze der Heritabilität im weiteren Sinne von Kronenmerkmalen in Waldbaumpopulationen, deren Abstammung unsicher ist, geschätzt werden kann. Die Anwendung dieser Methode (die seit vielen Jahren von Tierzüchtern benutzt wird und die auf der Wiederholbarkeit = "repeatability" basiert) bei Vermessungswerten von je 10 Bäumen von 3 weit auseinanderliegenden Beständen zeigt, daß die Heritabilität im weiteren Sinne der Kronenmerkmale in einer Wildpopulation von Douglasien sehr niedrig zu sein scheint. Dies legt die Vermutung nahe, daß eine intensive phaenotypische Plusbaumselektion nach Kronenmerkmalen in Arten wie Douglasie, die auf vielen Standorten in einem relativ kleinen geographischen Verbreitungsgebiet vorkommt, sehr unwirksam ist.

Résumé

Titre de l'article: *Variation phénotypique et estimation de la constance dans les caractéristiques des branches du douglas.*

300 douglas âgés de 15 à 35 ans situés dans 10 peuplements naturels dans le Sud-Ouest de l'Etat de Washington ont été mesurés dans le but d'obtenir une estimation de la variation phénotypique des caractères des branches. Les mesures de longueur et diamètre du tronc, diamètre, angle d'insertion, longueur et nombre des branches n'ont porté que sur les 8 derniers verticilles de chaque arbre. D'après ces mesures on a pu calculer la variation probable à l'intérieur d'un arbre, entre des arbres d'une même population, et entre des populations; les résultats sont présentés sous forme de tables pour servir de base aux estimations de variabilité utiles en particulier pour déterminer les dispositifs des tests de descendance de douglas.

On étudie également la méthode qui permettrait d'estimer les limites supérieures de l'héritabilité au sens large pour les caractéristiques de la cime dans des populations où la filiation n'est pas connue avec certitude.

L'application de cette méthode (basée sur l'idée de »répétabilité« employée depuis de nombreuses années en amélioration du bétail) aux mesures de 10 arbres pris dans trois peuplements éloignés indique que l'héritabilité au sens large des caractères de la cime paraît très faible dans les populations naturelles de douglas. Cela suggère qu'une sélection phénotypique intensive d'arbres »plus« basée sur des caractères de la cime est tout à fait inefficace pour des espèces comme le douglas qui pousse dans de nombreuses stations différentes à l'intérieur d'une région relativement peu étendue.

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