INTRASPECIFIC VARIATION IN

THE IUFRO 16 YEAR OLD DOUGLAS-FIR

(*PSEUDOTSUGA MENZIESII (MIRB.) FRANCO*)

PROVENANCE-PROGENY TRIAL

IN HANEY, BRITISH COLUMBIA

by

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ABSTRACT

Variation in height, dbh and volume was analyzed after 16 years of growth. Results were compared with the 4th and 7th growing season measurements for height. This trial comprised 464 open-pollinated families representing 58 provenances planted at the University of British Columbia Research Forest in Haney, B.C. in 1971.

Phenotypic variations between and within provenances, additive genetic variances, heritabilities, genetic gain and juvenile * mature correlations were estimated for the three growth variables according to zone groupings.

The effects of provenance by block and family by block interactions were evaluated. Expected reductions from the genetic gain caused by the interactions were calculated.

Relationships among growth variables and growth variables versus geographical variables were investigated by simple and multiple linear regression analyses.

An attempt was made to classify provenances according to their adaptation to the Haney planting site, on the basis of their performance over the years.

Within provenance variation for height was compared among provenances and was related to the geography of origin of provenances. Explanations from the point of evolutionary biology were discussed.

High values of calculated genetic gain indicated that significant improvement could be achieved by selection. Age - to - age correlations for height were highly significant ($p \leq 0.01$) over time and therefore it was concluded that selection is possible after age 7. However, if we

consider the importance of the time factor in improvement programs, it is feasible to select after age 5.

Differential results obtained by regression analysis between height and dbh according to zone grouping suggest that volume will be a better criterion for selection purposes than height alone.

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INTRODUCTION

Good forest management looks at the genetic quality of trees and follows certain fundamental principles that will permit the maintenance or even an increase of the quality and quantity of forest production. For this purpose, an understanding of the variability at the species, population or individual level is necessary in order to implement an appropriate improvement program and healthy forest management.

As early foresters mentioned, every tree has a different appearance in a naturally regenerated forest. Patterns of this variability differ from region to region; thus different geographical subgroups of trees exhibit different spectra of variation. Maximization of genetic diversity is probably the strategy of nature to optimize the chances that a species can withstand changes in the environment, and differences between populations are the result of a long evolutionary process.

Today, deforestation, pollution and climatic change are major threats to the diversity and the collective entity of forest ecosystems. And, because forests are the habitats for diverse organisms, the threat is extended to all the flora and fauna associated with forests. Ledig (1988) stated the importance of the issue, "Immediate loss of species is not the only danger. Among the surviving species, many populations will be lost, taking with them much of the genetic diversity upon which long-term survival and evolution depend."

Increased reforestation programs brought forward a problem of seed movement between localities. Transfer of forest seed from the collection site to another location without considering the adaptation

of the seed to the non-native area may prove to be unproductive. It is therefore important to understand variation at the provenance level in order to establish transfer rules and to delineate the limits of seed and planting zones. In other words, the perpetuation of highly resilient, healthy future forest generations depends on our understanding of their diversity and the association of this diversity with different environmental factors.

At the moment, means for assessment of genic and geographic variability are biosystematic, genecologic, biochemical and molecular studies. In this study the results of the analysis of data obtained in 1986 from a provenance/progeny trial of Douglas-fir, which is a type of genecological study, will be presented and these results will be compared to the previous analyses.

History:

The International Union of Forestry Research Organizations (IUFRO) Section 22 organized seed collections in 1966 and 1968 from the natural range of Douglas-fir to provide material for provenance tests in co-operating countries. The collection of cones was supervised by the Faculty of Forestry, UBC, and as a contribution towards further studies of variability in Douglas-fir on average, fifteen cones per tree from a total of 1818 trees were provided.

Yao (1971) studied the biosystematic relationships among families, provenances, sub-regions and regions using thousand-seed weight, (TSW) cone-scale characteristics and germination percent of this material. Differences between and within provenances were revealed at various confidence levels. Therefore UBC maintained the identity of individual

trees (families) within each provenance in a nested design in an experiment to test the same material under field conditions, whereas the majority of co-operators established provenance tests from bulked seed. Therefore the identity of the families was not preserved.

Seedlings from eight trees per provenance were grown by the Canadian Forest Service (CFS) in 313 styroblock containers in Victoria, 1970. The 1 + 0 containerized seedlings were outplanted at the UBC Research Forest during April, 1971 (Kvestich, 1976).

Objectives:

1 - To estimate the amount of genetic variation for height growth, dbh and volume among and within various provenances, when grown at Haney, British Columbia (B.C.).

2 - To estimate the additive genetic component of variation and narrow sense heritabilities for open-pollinated progenies.

3 - To investigate the juvenile-mature correlations of traits, that is, the consistency of traits over time, in order to recommend the best selection strategy for the Haney planting site.

4 - To investigate the adaptation of provenances to the Haney planting site.

Experimental Design:

The environmental component in progeny tests is controlled by the use of experimental designs which seek to reduce the non-genetic effects. The use of blocks facilitates control of local variability, exposing the progeny to fairly standard site conditions within a block. Randomization is used to avoid systematic errors in calculation of experimental error. The testing site should be representative of the

area where the seed will eventually be used in a normal plantation. The experiment was originally laid out in a randomized complete block design.

LITERATURE REVIEW

Douglas-fir (*Pseudotsuga menziesii [Mirb.] Franco*) is one of the most studied species in North America and Europe. Soon after the species was introduced to Europe, the important differences in growth potential and other characteristics between origins of Douglas-fir were recognized. In Livonia, Russia the coastal form was particularly susceptible to cold injury, but the Rocky Mountain forms were inferior in growth rate (Zon, 1913).

Isaac (1943) summarized the reproductive habits and silvics of Douglas-fir as well as other aspects of variability and outlined a proposal for tree improvement research in this species (Isaac, 1949).

The typical coast, or green, variety, *menziesii*, grows better and is commercially more valuable than the other recognized variety, *glauca*, Rocky Mountain or blue. Fowells tried to delineate the ranges of the two forms separately, and noted that the Rocky Mountain form mixes with the coastal form in southern British Columbia and northeastern Washington (Fowells, 1965).

The studies (provenance trials or common garden methods) of screening geographical variation in Douglas-fir can be reviewed in two phases. The first phase is the period between 1827, when Douglas first introduced the species to Europe, and 1966. IUFRO Section 22 started expeditions in 1966 on natural range-wide cone collection and distributed the seed to 59 institutes in 36 countries for provenance research. This marks the beginning of the second phase.

Early European experiments were mostly focussed on growth, survival and disease and insect resistance of different origins. Wood (1955)

described the general ecological conditions best suited to Douglas-fir and concluded that the "Fraser River type" seed source is the most suitable to use in Britain. In general, the coastal form is better suited to conditions in western Europe and the British Isles than the interior form.

One of the oldest extensive studies of thirteen coastal origins in North America was initiated in 1912. Munger authored the plan, and phases of the study have been reported by various authors (U.S.F.S. 1962, 1964). In this study, gene-environment interactions were encountered. The two most important outcomes of these studies were that, first, progeny testing at a site different from that to be outplanted is a questionable practice, and secondly, that seed origin is more critical at high elevation than in low elevation plantations.

Later, summarizing fifty year results of the same experiment, Silen (1965) proposed a hypothesis to explain the differing pattern of results of each planting site, based on survival, inherent rates of growth, planting site exposure, weather extremes and time. He stated that "inherent growth rate of a race had developed towards the maximum that could be sustained in each locality against the impacts of long-term weather extremes. Further, these inherent differences in rates of growth for each environment are expressed until climatic extremes intervene at an unpredictable frequency to reduce growth, or damage, or kill." He also entered the time factor to the hypothesis and concluded that, "at the most severe site in this study, both survival and growth rate began to strongly favor the adopted local race by the end of the second decade. At the most sheltered site, where most planted trees

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have survived, the growth patterns displayed during the first decade were maintained to age 50, with non-local races superior in growth." (Silen, 1965).

Sorensen (1967) reported important and rather sharp transitions in seedling growth habits associated with the eastern slopes of the Coast and Cascade Ranges in the Pacific Northwest of the U.S.A., investigating the west-east transect of the same area.

Finally, the changes in genetic parameters over time were investigated in the same experiment and three periods in the development of genetic variances in height growth were identified. In the juvenile period, variances in environmental error increased logarithmically while genetic variance within populations existed at moderate levels, and variance among populations was low but increasing; in the early reproductive period, the response to environmental sources of error variance was restricted, genetic variance within populations disappeared, and strong populational differences emerged; in the later period, environmental error again increased rapidly, but genetic variance within populations did not reappear and population differences were maintained at about the same level as established in the early reproductive period (Namkoong *et al.*, 1972).

In 1954, the Forest Research Laboratory at Oregon State University and several co-operators initiated a Douglas-fir provenance study based on seed collected from 16 locations throughout the west side of the Cascades in the Pacific Northwest of the U.S.A. Two year-old seedlings of these provenances were outplanted in plantations established at or near each seed collection site in 1959. Twenty and twenty-five year

results have been reported (Ching and Hinz, 1978 and Ching and White, 1985). Significant correlations between growth variables and geographic variables were found, and correlation analyses conducted by individual planting location indicated that different clinal expressions might be exhibited in different plantation environments. The study also drew attention to the observation that local provenances have greatly increased their height rankings as these tests aged. Age-to-age correlations decreased from 0.91 between ages 5 and 9, to 0.48 between ages 5 and 25. They also found that faster growth was positively correlated with early survival before thinnings.

In British Columbia, a provenance study employing 16 different coast and interior origins was reported (Haddock et al., 1967). Cold resistance records for two year-old seedlings in the nursery in Vancouver were presented, and the important influence of topography on climate and consequent variation in Douglas-fir was emphasized.

The majority of these early provenance experiments employed coastal populations. In 1962 in East Lansing, Michigan, in order to determine the geographic variation patterns of interior populations, a provenance study was established with 128 provenances from the U.S. and Canada. Both east-west and north-south trends in geographic variation were noticed. The lack of elevational trends were explained by continued intermigration which opposed the tendency for genetic differentiation of low- and high-elevation races.

Callaham (1964) drew attention to short term studies, emphasizing the value of thorough, biosystematic studies as a prelude to the more expensive field performance trials at the Food and Agriculture

Organization (FAO) / IUFRO meeting on Forest Genetics. Short term nursery studies and field experiments were to be developed parallel to the long-term provenance experiments. Some of those early experiments on the physiology of Douglas-fir are worth mentioning. Herman and Lavender (1965) investigated the dormancy period of Douglas-fir and reported that both light intensity and photoperiod affected meristematic activity in shoots and roots until the chilling requirements were satisfied . In another report, they studied the early growth of seedlings from 14 different seedlots from various altitudes and aspects in two different nursery beds as well as in growth rooms. The study provided information on the existence of "aspect races". Greater variation of height growth within seed sources than between seed sources was found and this was attributed to the heterogeneity of the nursery beds (Herman and Lavender, 1967).

Irgens-Moller studied the responses of various origins which come from different elevations to temperature and photoperiod under controlled environments and demonstrated the important effect of climate of origin on photoperiod sensitivity as reflected by the date of cessation of height growth (Irgens-Moller, 1957). He also tried to relate the observed differences in growth behaviour under a number of controlled environmental, as well as field, conditions to the differences in environmental conditions of the native habitat. For example, the late onset of dormancy in the seedlings from Vancouver Island was related to the relatively long period favourable for growth in their native habitat. Similarly, the low summer precipitation and short, frost-free season in the northern Rocky Mountains were

responsible for the early onset of dormancy in seedlings from this area (Irgens-Moller, 1968)

Allen has developed a method to distinguish between coast and interior origins based on seed morphology and germination energy (Allen, 1960).

At the beginning of the 1960's with the increasing size of reforestation programs , the supply of sufficient quantities of local seed became a major problem in North America. The only answer to this dilemma was the movement of seed between localities. Haddock (1965) documented the information available for other western species that might have sufficient generality to be applied to the Douglas-fir seed movement problem. Consequently seed collection zones for Douglas-fir in Canada were delineated based on climatic data and the distribution of associated species as well as vegetation maps of the area as a temporary solution to this problem (Haddock and Sziklai, 1966).

In 1966, IUFRO started seed collection expeditions following a survey of the requirements of various member countries and institutes (Fletcher and Barner, 1978). This was the turning point in provenance research in northwest America and Europe. For Douglas-fir by 1970, 326 kilograms of seed comprised of 182 sources were collected and distributed to 59 institutes in 36 countries. This was the first range-wide collection of seed in Douglas-fir. In 1967 Canada participated in the Organization for Economic Co-operation and Development (O.E.C.D). scheme for control of forest reproductive material in international trade and the Canadian Forest Service (C.F.S.) undertook certification of the 1970 seed crop in British Columbia.

From August 21 to September 9, 1978, four IUFRO working parties held a joint meeting in Vancouver, B.C. to bring others up to date with the latest results of provenance tests carried out on Douglas-fir, lodgepole pine, Sitka spruce, and *Abies* provenances. Two volumes of valuable information were gathered. In the first volume, the environmental characteristics of western North America, distribution, genetics and silvical characteristics of the four species, seed procurement problems, and implementation of results from provenance research and field experiments were reported by various authors from North America and Europe. The performance of the Douglas-fir provenances in various countries, variations in growth characteristics between provenances, correlations to various degrees between growth characteristics and the geographic variables associated with the origin of the provenances were reported and future breeding activities including seed orchard establishment were discussed. Birot proposed a computer based data bank to pool the available data from the experiments established in various countries all over the world (Birot, 1978). Campbell reported that source-related variation of Douglas-fir in western Oregon and Washington was mainly clinal (Campbell, 1978). One common feature of these trials was that the majority of the tests were established from the bulked seed of provenances, therefore intraspecific variation associated with families within provenances remained unknown. Only the French Research Organization and UBC maintained the identity of individual families within provenances.

When growing seedlings from 40 northwestern populations of Douglas-fir in eight nursery-bed treatments which contrasted air and

soil temperatures and nutrition, depending on the trait and the environment in which the test was conducted, it was found that 20 to 75 % of the source related variance was clinally associated with latitude, elevation and distance from the ocean of parent trees. Population samples interacted significantly with soil temperature for growth traits, and with soil and air temperatures combined for phenological traits. It was concluded that there is more risk within the northwestern U.S. in moving provenances east-west than north-south, that this risk increases with elevation of provenances and that north-south transfers are more critical near the coast than inland (Campbell and Sorensen, 1978).

The genetic variation associated with 193 parent trees for 16 traits, sampling 115 locations in a 6100 hectare watershed was reported (Campbell, 1979). For most traits the pattern of variation was found to be clinal. The clinal gradient depended upon position within the watershed, and was steeper on the north-facing slope. Also, estimated genotypic values of parent trees differed at identical elevations depending on position in the watershed.

The development of electrophoretic techniques during the last two decades provided an alternative to common garden techniques for estimating levels of genetic variation in natural populations (Lewontin, 1974) There are numerous isozymes studies in Douglas-fir (Rudin, 1976; Yeh, 1981, Yeh and O'Malloy, 1980; el-Kasaby, 1980). In isozymes studies the amount of genetic variation, whether considering an entire species or a small group of trees, is measured by the average heterozygosity of numerous loci. One feature of conifers, that mature seeds contain a

haploid gametophyte and a diploid embryo, increases their value in isozyme studies.

Enzyme variations at up to 21 loci in natural populations of coastal and interior Douglas-fir from B.C. were studied and results showed that 97% of the total gene diversity resided within populations (Yeh, 1981; Yeh and O'Malley, 1980). However, the study also revealed a high degree of inter-loci variation in heterozygosities within populations. It was concluded that the isozymes surveyed do not seem to be equivalent in their contribution to the overall mean heterozygosity of the populations; therefore many isozyme loci should be surveyed to reliably estimate genetic variation patterns in Douglas-fir.

Association between heterozygosity and radial growth rate variables were studied (Mitton, 1981). It was found that the level of heterozygosity was associated with growth variability, but the direction of the relationship found in lodgepole pine was opposite to those in ponderosa pine and aspen. In lodgepole pine, high heterozygosity was associated with low variability in growth rate. Although they failed to find an association between mean growth rate and heterozygosity in either ponderosa pine or lodgepole pine, the mean growth rate of highly heterozygous clones of aspen were higher than those of predominantly homozygous clones.

MATERIALS AND METHODS

In this study, 464 open-pollinated progeny of 58 provenances were analyzed in one set of growing conditions. The cones were collected from the natural range of Douglas-fir from British Columbia to California (Figure 1). The test was established as a randomized complete block design using three blocks in the University of British Columbia (U.B.C.) Research Forest in Haney in 1971 (Kvestich, 1976).

Provenances were represented by eight families including five seedlings per family in a row plot. The spacing was three feet between seedlings in a row with 12 feet between rows. 1 + 0 plugs were used as planting stock. The planting site had a gentle slope, south facing aspect, was burned before planting and had a site index of 35 m for a reference age of 50 years measured at breast height (Kvestich, 1976) (Figures 2 and 3).

Up to 1979 there were no thinnings and mortality was very low, averaging about 9.8% (Fashler, 1979). The first thinnings were carried out by Haddock in 1979, by removal of suppressed, misshaped and damaged trees, considering spontaneous mortality and endeavouring to obtain the most even distribution possible of the remaining trees (personal communication, Sziklai).

Statistical analyses were carried out for provenances arranged in groups according to four seed zones (three coastal and one interior). Provenance means were compared using Duncan's multiple range test for each zone.

The data were unbalanced with up to three trees per family. Therefore, the analysis of variance for each of three growth variables,

FIGURE 1 Location of Douglas-fir Provenances

Note: Zones 4, 5, 6, 7 and 8 are pooled as interior zone

FIGURE 2   IUFRO Plantation, U.B.C. Research Forest

I.U.F.R.O. Plantation, U.B.C. Research Forest, Haney.

TIMBER

ROAD M

BLOCK 3

89	99
57	104
67	86
11	46
91	77
98	28
72	29
83	18
73	116
96	58
117	39
110	40
27	12
6	97
124	108
25	88
52	53

Right column: 90, 51, 32, 55, 66, 10, 61, 76, 23, 92, 56, 60, 43

TIMB

BLOCK 2

83	79	53		
73	10	109	114	44
25	46	66	9	111
108	67	28	99	51
91	97	11	6	109
72	116	80	61	42
89	64	45	105	95
34	41	103	58	123
70	88	75	123	87
36	18	8	84	106
117	63	124	87	93
37	55	29	56	80
86	12	76	39	79
104	95	60	40	111
26	32	52	93	64
96	110	38	42	
43	4	27	77	
23	92	90	106	
21	13	98	57	

| 1 |
98	28
40	32
61	52
91	83
45	92
10	51	108

BLOCK 1

63	124	111	87	29	20	53	15
95	34	41	23	93	50	26	9
31	11	21	38	96	84	8	102
123	4	5	6	100	74	37	72
85	110	18	97	44	78	36	76
12	106	90	58	27	99	54	109
60	33	103	104	25	117	67	56
13	46	49	73	77	43	17	14
86	64	114	19	42	70	79	75
105	80	55	22	88	107	89	116
57	69	48	115	82	66	16	39

N

ROW   1   2   3   4   5   6   7   8   9   10   11   12   13   14   15   16

ROAD G

ROAD G

FIGURE 3   Experimental Layout of the five Seedlings (1 to 5)
            of the Eight Families Representing a Provenance

diameter at breast height (dbh), total height and volume by seed zone was performed using a computer program called GENLIN, according to the following linear model:

$$Y_{ijkm} = \mu + P_i + B_j + (P*B)_{ij} + F/P_{k(i)} + (B*F/P)_{jk(i)} + E_{m(ijk)}$$

where Y_{ijkm} = the measurement of the mth tree in the kth family in the jth block in the ith provenance

μ = mean of all trees over all families, blocks and provenances

P_i = provenance effect

B_j = block effect

$(PB)_{ij}$ = provenance and block interaction

$F/P_{k(i)}$ = family within provenance effect

$(B*F/P)_{jk(i)}$ = block and family within provenance interaction

$E_{m(ijk)}$ = sampling error

All expected mean squares were derived using a random effects model, using SAS, a computer package available from the UBC Computing Centre (Table 1).

Assumptions for the analysis of variance, namely homogeneous variances and normal distribution of observations, were checked with a computer package called MIDAS. The normality of distribution of observations was met. Variances were within an acceptable range and therefore assumed homogeneous.

Height measurements were taken to the nearest centimeter, and dbh measurements were taken to the nearest tenth of a centimeter, in 1986.

The highest order interaction (B*F/P) was found to be significant at 0.01 confidence level. Therefore sampling error, $E_{m(ijk)}$, and

TABLE 1

ANALYSIS OF VARIANCE AND EXPECTED MEAN SQUARES FOR ANALYSIS OF
BETWEEN PROVENANCE VARIATION

Source	D.F.	Expected Mean Squares
Provenance	$p-1$	$V_E + tV_{BF/P} + btV_{F/P} + ftV_{PB} + bftV_P$
Block	$b-1$	$V_E + tV_{BF/P} + \quad\quad\quad ftV_{PB} + pftV_B$
Prov*Block	$(p-1)(b-1)$	$V_E + tV_{BF/P} + \quad\quad\quad ftV_{PB}$
Fam(Prov)	$p(f-1)$	$V_E + tV_{BF/P} + btV_{F/P}$
Block*F(Prov)	$p(b-1)(f-1)$	$V_E + tV_{BF/P}$
Residual	$bp\sum\limits_{k=1}^{f\,1}(t_{ijk}-1)$	V_E

where

    p = number of provenances

    b = number of blocks

    f = number of families nested in provenance

    t = number of trees per family

    V_P = variance between provenances

    V_B = variance between blocks

    V_{PB} = variance due to block * provenance interaction

    $V_{F/B}$ = variance between families within provenances

    $V_{BF/P}$ = variance due to block * family within prov. interaction

    V_E = residual error

experimental error, $(B * F/P)_{jk(i)}$, were kept separate.

    Additive genetic variances (V_A) for each seed zone were calculated from the following formula: $V_A = 4 V_{F/P}$, since variance among outcrossed half-sib family means, $(V_{F/P})$ is the covariance of half-sibs

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and estimates one fourth of V_A (Becker, 1984).

Narrow sense heritabilities were estimated from the components of variance for each seed zone as follows:

$$h^2 = \frac{4\ V_{F/P}}{V_{F/P} + V_{B*F/P} + V_E} \qquad \text{(Falconer, 1960)}$$

The response to selection at the Haney site was estimated from the following formula:

$$R = i * \sigma_P * h^2 \qquad \text{(Falconer, 1960)}$$

where:

i is the intensity of selection expressed in standard deviations above the mean of a normal distribution (in our case a selection intensity of only 1 in 5 individuals from each provenance was chosen; therefore the value for i was taken as 1.4)

σ_P is the phenotypic standard deviation for the traits studied and is calculated as the square root of the denominator of the formula for h^2

h^2 is the narrow sense heritability

The effects of family by block interactions on heritability and genetic gain estimates were evaluated by using the concept discussed by Matheson and Raymond (1986). For this purpose heritabilities and gains for each zone grouping were calculated considering the presence and absence of these interactions. Therefore the difference is the potential loss of genetic gain if any of these provenances in the experiment is to be used for reforestation in Haney or similar coastal Douglas-fir

ecosystems in the Lower Mainland.

The standard error of heritability estimates derived from the interclass correlations was computed as follows (Falconer, 1960; Wright, 1976):

$$S.E.h^2 = \frac{(1 - d)(1 + tbd)}{\sqrt{(tb)(f - 1)/2}}$$

where
$d = 1/4\ h^2$
t = number of trees within families
b = number of blocks, and
f = number of families

To investigate within-provenance variation for height, analyses of variance were performed for each provenance according to the following model:

$$Y_{ijk} = \mu + B_i + F_j + (BF)_{ij} + E_{k(ij)}$$

where:

Y_{ijk} = the mean measurement of the kth tree in the jth family in the ith block

μ = mean of all families over all blocks

B_i = block effect

F_j = family effect

$(BF)_{ij}$ = block * family interaction

$E_{k(ij)}$ = experimental error

Table 2 shows the expected mean squares considering random effects.

The main objective of the analysis of variance at the provenance level was to generate a variable which would show the variability between families in provenances and relate this variability to

geographical variables. For this purpose mean squares of families for each provenance were chosen and regressed to the geographical variables.

TABLE 2

ANALYSIS OF VARIANCE AND EXPECTED MEAN SQUARES FOR ANALYSIS OF WITHIN PROVENANCE VARIATION

Source of Variation	Degrees of Freedom (D.F.)	Expected Mean Squares (E.M.S.)
Block	$b - 1$	
Family	$f - 1$	$V_E + tV_{BF} + btV_F$
Block * Family	$(b-1)(f-1)$	$V_E + tV_{BF}$
Error	$bf(t-1)$	V_E

where: V_F = variance between families

V_{BF} = variance due to block * family interaction

V_E = residual

b = number of blocks

f = number of families nested in provenance

t = number of trees per family

The zone effect was not included in the model used for analysis of variance; therefore "t" tests were carried out to test the significance of the seed zone means. For hypothesis testing, the following formulas were used (Walpole, 1982):

$$t_r = \frac{(\bar{x}_1 - \bar{x}_2) - (\mu_1 - \mu_2)}{s_{\bar{x}_1 - \bar{x}_2}}$$

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where:

$$s_{\bar{x}_1 - \bar{x}_2} = s_p \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}$$

and

$$s_p = \sqrt{\frac{s_1^2 (n_1 - 1) + s_2^2 (n_2 - 1)}{n_1 + n_2 - 2}}$$

This applies under the following conditions:

n_1 and $n_2 < 30$, and population variances $\sigma_1^2 = \sigma_2^2$.

$v = n_1 + n_2 - 2$ (degrees of freedom)

x_1 and x_2 are the means for the zones which were compared

μ_1 and μ_2 are unknown population means

$s_{\bar{x}_1 - \bar{x}_2}$ is the standard error of differences of two means

n_1 and n_2 are ther number of provenances in each zone

s_1^2 and s_2^2 are sample variances

s_p is the pooled standard deviation

Volume calculations were carried out using Fortran programming language for all individual trees in the experiment using volume equations from both the B.C. Forest Service for immature Douglas-fir and from Kovats (1977) particularly developed for provenance and progeny tests. However, the volume equation from the B.C. Forest Service which uses dbh and height, was adopted, because of the limitations of height ranges of Kovats' equation.

The estimation of juvenile by mature correlation was done by simple correlations between total heights at various ages using MIDAS. For this purpose, yearly total height measurements of 100 individual trees,

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representing one tree from five randomly chosen families of 20 randomly selected provenances, were obtained from previously analyzed data by Fashler (Kvestich, 1976; Fashler, 1979).

To investigate the effect of original provenance location on growth performance of provenances in Haney, mean values of provenance height, dbh, and volume were related to each of the geographical variables by simple linear regression. Multiple regression analysis by all combinations method was used to select the equation that would best describe the growth variables (dbh, height and volume) using the four independent geographical variables (elevation, latitude, longitude, and ecophysiological latitude) by zone and by pooling provenances for all zones. Ecophysiological latitude was calculated according to the formula:

$$E = L + \frac{H}{100}$$

where: E = ecophysiological latitude
       L = latitude
       H = altitude in meters

To fulfill the final objective of this study which is to select the best performing provenances for the Haney planting site, a statistical technique was used to compare the adaptability of provenances on the basis of the performance of their total height growth.

The major difficulty when assessing the adaptability of populations or individuals is how to formulate the environment mathematically. If a physical measure of the environment could be found and considered as fixed then the genotypic means at each site could be regressed against the mean value of the environmental effect. Unfortunately the critical factors causing the interactions are very complex and rarely known in

forest ecosystems. It has been suggested that the most relevant measure of the environment over the duration of an experiment is the performance of the experiment itself (Matheson and Raymond, 1986; Finlay and Wilkinson, 1963). Finlay and Wilkinson (1963) developed a regression approach based on the plantation performance to compare the adaptability of barley varieties grown at several sites for several seasons.

Since our experiment is not repeated in several sites, the above mentioned technique was adapted with some modifications, namely provenance by site interactions were omitted. Even in a uniform edaphic environment a considerable degree of general adaptability will be important, because of the marked fluctuation of climatic conditions from year to year. There were also changes in the experiment over time in terms of spacing after thinnings. Therefore the technique developed in this study may show the responses of the phenotypes to the year to year climatic fluctuation and the changing conditions after thinnings. For this purpose the mean heights of all provenances at each year provided a numerical grading of years and were used for the evaluation of the environment; in the results section of this study, it will be referred to as the "plantation line." For each provenance a linear regression of mean total height on the mean total height of all provenances for each year was computed. The slopes of each regression line provided a fairly good measure of provenance performance over the years. From the interpretation of slopes, it was possible to classify the provenances as stable inferior, unstable or progressive.

All graphs in this study were done with the Tell-A-Graf graphics program.

RESULTS AND DISCUSSION

Analysis of the variance for total height, dbh and volume for all seed zones is summarized in Table 3. Within zone (between provenance) variation was significant at 0.01 confidence level for all of the traits studied. The large range in provenance means indicates considerable genetic variation. This high variability in height, DBH and volume suggests that substantial gains can be made by selecting the most desirable provenances (Table 4).

Block differences were not significant for Zone 1 and the interior groupings but significant for Zone 2 and Zone 3 groupings at 0.05 confidence level. When we look at the adaptability values of those provenances which showed no block differences, the majority of them had values lower than 1.00 which are classified as stable inferior growing provenances. Their height growth was under the plantation average; apparently they did not respond to the Haney planting conditions very well. A possible interpretation may be that provenances from Zone 1 and the interior were stable growing in different environments but they were inferior in their height growth, therefore did not respond to the blocking in the experiment, nor did they to the Haney planting site.

In contrast to the above situation, provenances from Zone 2 and Zone 3 responded well to the Haney planting conditions. Their adaptability values were greater than 1.00. Their height growth was above the plantation average and most of them were classified as progressive provenances according to their adaptability values for height. Block differences for dbh and volume were not significant at 0.05 confidence level for those provenances which originated in Zone 2

TABLE 3

LEAST-SQUARES ANALYSIS OF VARIANCE

F VALUES

Source of Variation	DF	Height	DBH	Volume	Test Term
			SEED ZONE 1		
Provenance	16	4.39^{**}	3.11^{**}	3.18^{**}	MS^a
Block	2	1.18^{NS}	0.26^{NS}	0.006^{NS}	Block * Prov.
Block*Prov	32	4.90^{**}	3.75^{**}	4.42^{**}	Block*Fam(Prov)
Family/Prov	119	1.27^{NS}	1.29^{NS}	1.23^{NS}	Block*Fam(Prov)
B * F/Prov	220	2.50^{**}	1.55^{**}	1.78^{**}	Residual
			SEED ZONE 2		
Provenance	11	6.69^{**}	4.40^{**}	3.72^{**}	MS^a
Block	2	4.21^{*}	1.91^{NS}	2.82^{NS}	Block * Prov.
Block*Prov	22	5.62^{**}	3.94^{**}	4.83^{**}	Block*Fam(Prov)
Family/Prov	84	1.42^{*}	1.16^{NS}	1.18^{NS}	Block*Fam(Prov)
B * F/Prov	167	2.35^{**}	1.51^{**}	1.68^{**}	Residual
			SEED ZONE 3		
Provenance	18	2.41^{*}	2.07^{*}	2.32^{*}	MS^a
Block	2	4.37^{*}	1.43^{NS}	1.41^{NS}	Block * Prov.
Block*Prov	36	5.99^{**}	5.64^{**}	5.20^{**}	Block*Fam(Prov)
Family/Prov	133	1.34^{*}	1.37^{*}	1.23^{NS}	Block*Fam(Prov)
B * F/Prov	263	2.61^{**}	1.70^{**}	1.91^{**}	Residual
			INTERIOR ZONES		
Provenance	9	8.52^{**}	6.96^{**}	7.53^{**}	MS^a
Block	2	1.74^{NS}	0.09^{NS}	0.29^{NS}	Block * Prov.
Block*Prov	18	5.27^{**}	5.12^{**}	4.36^{**}	Block*Fam(Prov)
Family/Prov	70	1.09^{NS}	1.04^{NS}	0.77^{NS}	Block*Fam(Prov)
B * F/Prov	139	1.81^{**}	1.27^{NS}	1.31^{*}	Residual

* $P \leq 0.05$

** $P \leq 0.01$

NS not significant

[a] $MS_P + MS_{B*F/P} / MS_{BP} + MS_{F/P}$ (Zar, 1974)

TABLE 4

MEANS AND STANDARD DEVIATIONS OF 1986
TOTAL HEIGHT, DBH AND VOLUME IN ALL SEED ZONES

Seed Zone	Prov. No.	Mean Total Height(cm)	Mean DBH (cm)	Mean Volume (m^3)	Std. dev. Height	Std. dev. DBH	Std. dev. Volume
	23	1019.0	11.79	0.0532	177.6	3.13	0.0344
	32	1157.6	12.48	0.0645	137.7	2.94	0.0346
	55	1088.4	13.66	0.0699	145.0	3.03	0.0318
	90	1047.8	13.43	0.0672	198.4	3.07	0.0337
	95	865.3	10.01	0.0341	203.3	2.73	0.0213
	96	720.8	8.35	0.0219	215.9	2.89	0.0194
1	99	812.3	8.98	0.0268	194.4	2.74	0.0187
	104	824.6	9.52	0.0300	188.6	2.72	0.0204
	106	828.1	10.67	0.0372	220.9	3.42	0.0259
	108	943.1	11.16	0.0446	187.4	2.98	0.0273
	109	1011.5	11.79	0.0506	158.3	2.58	0.0261
	110	861.7	12.00	0.0482	195.0	4.04	0.0338
	111	843.6	10.72	0.0400	245.8	3.67	0.0279
	116	1213.6	13.41	0.0767	223.0	2.69	0.0349
	117	1090.1	12.84	0.0646	185.7	2.88	0.0345
	123	740.8	8.75	0.0247	196.4	2.94	0.0228
	124	779.4	9.89	0.0295	116.0	2.58	0.0186
Overall mean		937.96	11.19	0.0467	241.18	3.43	0.0328
	12	1150.0	12.13	0.0592	128.9	2.17	0.0230
	51	1125.3	11.79	0.0556	163.2	2.20	0.0255
	52	1252.5	14.30	0.0876	136.6	2.94	0.0377
	53	1256.5	14.80	0.0954	147.1	3.32	0.0466
	67	1197.9	13.50	0.0767	210.5	3.18	0.0392
2	79	1045.2	13.34	0.0659	174.6	2.87	0.0348
	83	1130.9	13.40	0.0703	181.8	2.39	0.0320
	87	1155.0	13.57	0.0741	174.2	2.60	0.0335
	89	1175.2	14.73	0.0907	201.5	3.92	0.0508
	91	1092.2	12.46	0.0579	121.9	1.72	0.0192
	92	808.16	9.66	0.0296	157.3	2.66	0.0200
	93	712.38	8.58	0.0213	187.4	2.17	0.0143
Overall Mean		1096.2	12.74	0.0659	227.9	3.26	0.0393
	25	1197.5	13.49	0.0762	153.9	2.81	0.0346
	27	1131.1	12.71	0.0638	127.97	2.60	0.0271
	29	1067.0	11.48	0.0496	143.7	1.98	0.0194
	39	1023.8	11.54	0.0506	167.5	2.89	0.0301
	40	1037.0	11.15	0.0459	169.2	2.03	0.0200
	42	1188.8	14.68	0.0861	135.9	3.07	0.0356
	43	1272.0	15.57	0.1033	138.7	3.04	0.0396
3	56	1194.5	12.32	0.0649	147.2	2.75	0.0300
	57	1059.2	13.64	0.0680	162.5	2.76	0.0313

TABLE 4
(continued)

Seed Zone	Prov. No.	Mean Total Height(cm)	Mean DBH (cm)	Mean Volume (m³)	Std. dev. Height	Std. dev. DBH	Std. dev. Volume
	58	1141.7	12.88	0.0674	209.7	2.64	0.0332
	60	1135.7	12.05	0.0598	206.4	2.65	0.0301
	61	1072.8	11.74	0.0529	163.3	2.52	0.0256
	72	1185.7	12.93	0.0687	168.3	2.05	0.0263
	73	1086.5	12.97	0.0632	197.6	2.37	0.0260
3	76	963.6	10.73	0.0400	189.7	2.23	0.0200
	86	802.8	9.26	0.0280	193.3	2.68	0.0188
	88	1071.5	13.32	0.0677	177.3	3.08	0.0344
	97	980.7	11.42	0.0522	282.4	3.63	0.0392
	98	996.1	12.92	0.0624	222.5	3.70	0.0624
Overall Mean		1086.0	12.466	0.0617	206.7	3.05	0.0341
	6	911.3	9.84	0.0357	240.3	2.70	0.0233
	10	655.3	7.17	0.0139	162.4	1.81	0.0088
	11	503.9	5.53	0.0076	150.8	2.04	0.0103
	18	648.1	7.02	0.0135	171.3	2.00	0.0105
Interior	28	710.1	7.24	0.0156	173.2	2.09	0.0113
	46	563.7	6.29	0.0099	139.5	2.06	0.0079
	64	954.8	11.50	0.0476	178.5	3.26	0.0283
	66	630.7	7.94	0.0162	124.4	2.34	0.0120
	77	1032.5	11.76	0.0551	200.4	3.54	0.0347
	88	950.8	11.22	0.0445	173.4	2.66	0.0250
Overall Mean		759.8	8.59	0.0262	248.1	3.32	0.0257

and Zone 3. This was due to the higher provenance by block interactions for dbh and volume for those provenances.

Block by provenance interactions were significant at 0.01 confidence level for all traits in all zone groupings (Figure 4). Therefore it can be said that provenances behave differently in different blocks. The highest interactions for height were obtained for Zone 1 and Zone 3 (transitional coastal zones) and the lowest for Zone 2 (coastal zone which is most adjacent to the coast). Zone 2 provenances showed higher provenance by block interactions for dbh and volume. Therefore their heritabilities decreased substantially for these traits.

FIGURE 4

Block * Provenance Interaction for Height for All Provenances

MEAN PROVENANCE HEIGHTS

We know that radial growth is more affected by density relative to height; apparently these coastal provenances have a good built in superiority for height growth compared to interior and transitional groupings but not for dbh and volume. Further regression analysis revealed that for those provenances, correlations between height and dbh were lower compared to the others. If we relate these findings to natural selection in the evolutionary process, in the coast natural selection probably operated on those genotypes which do not have good competing ability for light since growth period and water were not the limiting factors.

Block by family within provenance interactions were also significant (P ≤ 0.01) for all traits in all zone groupings, and families too showed a trend similar to provenances in their response to blocking.

Genotype environment (GE) interaction receives substantial attention from tree breeders because it affects tree improvement strategy (Campbell and Shelbourne, 1976; Burdon, 1977; Campbell, 1973; Matheson and Raymond 1986). Campbell (1973) reported that genotype environment interactions in Douglas-fir usually occur in spacing trials that include greatly different plot densities or widely divergent genotypes. In a subsequent paper they discussed how these interactions affected the breeding strategy (Shelbourne and Campbell, 1976). They suggested that, firstly environments must be grouped into breeding zones within which there are minimal interactions with sites both at the provenance and family level; secondly, well adapted populations and genotypes must be selected for high and stable performance in the case of these GE interactions.

Burdon (1977) introduced the concept of making use of type A and type B genetic correlations, the former being when both traits have been measured on the same individuals and the latter where the two traits are measured on different individuals within genetic groups, to evaluate GE interactions. He suggested that it would be much easier to evaluate each genotype in just a few environments which are already characterized so as to permit satisfactory extrapolation of performance to the remaining environments rather than test all those genotypes over a comprehensive range of environments.

Matheson and Raymond (1986) working with tropical species reported that statistical significance of GE interactions is not enough to make any decision in breeding strategy. These interactions should be evaluated on the basis of their effect on genetic gain. They suggested that the loss of potential genetic gain caused by the interactions would be a more appropriate measure. However they found that the loss of potential gain was less than 5% for most characters in most species surveyed.

In the Haney plantation, there was a grass invasion in the early years of the experiment (Kvestich, 1976) and also thinnings made the spacing irregular within plots. In addition, the genetic material used was very divergent. Hopefully these observed interactions were caused by these factors or are the expression of changes in variance among genotypes at different spacings. Otherwise, up to 1.9%, 1.5% and 2.5% potential genetic losses (reduction from the gain) would be expected for height, dbh and volume respectively (Table 5).

Table 6 and Figure 5 show the additive genetic variances and narrow

TABLE 5

POTENTIAL GENETIC LOSS
(REDUCTION FROM GENETIC GAIN DUE TO INTERACTIONS)

Zone	Variable	Assuming No Interaction			Considering Interaction			Potential Genetic
		h^2	Gain[a]	% Gain[b]	h^2	Gain[a]	% Gain[b]	% Loss
1	Height	0.42	78.7	8.4	0.25	60.9	6.5	1.9
1	DBH	0.29	1.03	9.2	0.23	0.92	8.2	1.0
1	Volume	0.26	0.0081	17.4	0.19	0.0070	14.9	2.5
2	Height	0.57	92.2	8.4	0.36	73.4	6.7	1.7
2	DBH	0.16	0.51	4.0	0.13	0.50	3.7	0.3
2	Volume	0.19	0.0069	10.5	0.14	0.0059	9.0	1.5
3	Height	0.51	85.3	7.9	0.30	65.6	6.0	1.9
3	DBH	0.39	1.18	9.5	0.29	1.01	8.0	1.5
3	Volume	0.27	0.0087	14.1	0.19	0.0073	11.9	2.2
Int	Height	0.10	18.4	2.4	0.07	15.3	2.0	0.4
Int	DBH	0.03	0.30	3.5	0.03	0.10	1.1	0
Int	Volume	0	0	0	0	0	0	0

[a] in units of variable, cm, cm and m^3 for height, dbh and volume respectively
[b] gain as % of population (zone) mean

sense heritabilities calculated for all traits for each zone grouping. Among the coastal zones, the highest values for additive genetic variances were attained by Zone 1 and Zone 3 for dbh and volume, and Zone 2 and Zone 3 for height. Franklin (1979) reported that inter-tree competition may be a major causal factor in the behaviour of additive genetic variance with stand development. MS_E and $MS_{B*F/P}$ for height were lower for for Zone 2 provenances (Table 7). Therefore, these provenance had higher heritability for height compared to the other coastal zones. MS_E (sampling error) shows the variation within plot and

TABLE 6

ADDITIVE GENETIC VARIANCES (V_A) AND V_A AS A PERCENT OF TOTAL VARIANCE (V_A / V_T) AND NARROW SENSE HERIABILITY FOR THE TRAITS

Zone	Trait	$V_A = 4V_{F/P}$	V_A / V_T	h^2	SE (h^2)
1	Height	7589.24	12.76	0.25	0.50
1	DBH	1.87	15.60	0.23	0.50
1	Volume	0.000131	11.88	0.19	0.50
2	Height	7604.00	13.80	0.36	0.49
2	DBH	0.82	7.44	0.13	0.47
2	Volume	0.000127	7.92	0.14	0.47
3	Height	7255.88	16.48	0.30	0.48
3	DBH	1.80	19.04	0.29	0.48
3	Volume	0.000142	12.08	0.19	0.47
Interior	Height	1651.68	2.52	0.07	0.47
Interior	DBH	0.14	1.20	0.03	0.47
Interior	Volume	0.0001	0	0	

TABLE 7

COMPARISONS OF MEAN SQUARES AMONG ZONES
FOR ALL GROWTH VARIABLES

Variable	Zone	MS_{B*P}	$MS_{B*F/P}$	$MS_{F/P}$	MS_E
Height	1	196570	40114.8	51023.1	16023.8
Height	2	151590	26965.3	38377.4	11469.1
Height	3	194890	32502.5	43394.0	12451.4
Height	Int	160760	30491.0	33245.2	16848.8
DBH	1	34.53	9.21	11.85	5.95
DBH	2	29.93	7.59	8.83	5.02
DBH	3	40.46	7.18	9.86	4.22
DBH	Int	30.38	5.93	6.17	4.65
Volume	1	0.0037	0.0008	0.0010	0.0003
Volume	2	0.0053	0.0011	0.0013	0.0007
Volume	3	0.0049	0.0009	0.0012	0.0005
Volume	Int	0.0017	0.0004	0.0003	0.0003

FIGURE 5

Narrow Sense Heritabilities (Above)and Additive Genetic Variances(Below)

harbours the effect of environment and 3/4 of additive genetic variance according to the half-sib genetic assumption. $MS_{B*F/P}$ is type b experimental error which shows the responses of families to blocking, and therefore the responses of genotypes to the site. Apparently, these Zone 2 provenances had very well established genetic superiority for height growth at the population level, and therefore had the highest heritability for this trait among the coastal groupings. The responses of the families of Zone 2 provenances to different blocks were unpredictable in terms of their dbh and volume. This may be due to greater competition among the families within plots for radial growth. As a consequence, they had lower heritabilities and additive genetic variances for dbh and volume.

These results suggest that any selection among these provenances solely on the merit of their height growth could be misleading. Therefore, a selection criterion which incorporates radial growth would be a better approach.

Family-within-provenance variation was significant for height in Zone 2 and Zone 3 and for dbh in Zone 3. B * F/P interactions camouflage the differences between families. From examination of Table 7, it can be seen that although the Zone 1 grouping had the highest $MS_{F/P}$, these provenances did not show significant family variability due to very high $MS_{B*F/P}$ interactions.

Table 8 and Figure 6 show all the components of variance for all the hypothesized sources of variation. The largest variation was due to provenance differences for height, except in Zone 3. In Zone 3, the largest variation was due to sampling error (V_E). For dbh and volume,

TABLE 8

COMPONENTS OF VARIANCE

	Height		DBH		Volume	
		%		%		%
SEED ZONE 1						
V_P	18621.9	31.30	2.1633	18.07	0.000225	20.40
V_B	100.3	0.17	0	0	0	0
V_{P*B}	10461.5	17.58	1.7118	14.30	0.000194	17.52
$V_{F/P}$	1897.3	3.19	0.4667	3.89	0.000033	2.97
$V_{BF/P}$	12395.9	20.83	1.6745	13.90	0.000188	16.99
V_e	16023.8	26.93	5.9538	49.74	0.000466	42.13
SEED ZONE 2						
V_P	22805.6	41.44	2.8753	26.19	0.000169	23.61
V_B	2955.2	5.37	0.1604	1.46	0.000055	3.44
V_{P*B}	8033.5	14.60	1.4130	12.87	0.000262	16.33
$V_{F/P}$	1901.0	3.45	0.2043	1.86	0.000032	1.98
$V_{BF/P}$	7870.9	14.30	1.3058	11.89	0.000226	14.05
V_e	11469.1	20.84	5.0215	45.73	0.000651	40.59
SEED ZONE 3						
V_P	7064.0	16.05	1.1371	12.04	0.000169	14.33
V_B	2212.3	5.03	0.0511	0.54	0.000007	0.56
V_{P*B}	10348.7	23.50	2.0945	22.18	0.000248	21.06
$V_{F/P}$	1814.0	4.12	0.4495	4.76	0.000036	3.02
$V_{BF/P}$	10129.5	23.01	1.4935	15.81	0.000226	19.18
V_e	12451.4	28.29	4.2195	44.67	0.000494	41.87

TABLE 8
(continued)

	Height		DBH		Volume	
		%		%		%
			INTERIOR ZONES			
V_P	31273.5	47.95	4.6583	39.95	0.000282	39.53
V_B	859.8	1.31	0	0	0	0
V_{P*B}	8735.7	13.39	1.6480	14.13	0.000086	11.98
$V_{F/P}$	412.9	0.63	0.0357	0.30	0	0
$V_{BF/P}$	7096.3	10.88	0.6670	5.72	0.000049	6.80
V_e	16848.8	25.83	4.6505	39.89	0.000298	41.73

the largest variation was due to sampling error (V_E) for all zones. As noted before, sampling error shows the within-plot variation (variation between individuals of a family). This within-plot variability is attributable to the environmental effect, 3/4 of additive genetic variation and the dominant genetic variation in the half-sib progeny experiments. This value did not vary substantially for dbh and volume among the seed zones, but it was low for height for Zone 2 and Zone 3 provenances. As is known, height is a good measure of fitness compared to dbh since it is less affected by the density. Zone 2 and Zone 3 provenances come from coastal ecosystems similar to Haney; therefore in the evolutionary process, they are better adapted to these ecosystems. Consequently, their height growth is less affected by the environment of the Haney planting site as compared to the other zone groupings.

The largest value of variation, in the case of dbh, was attributable to V_E in all coastal zones. In contrast, variance

FIGURE 6

Components of Variance as % of Total Variance for all Seed Zones

and For All Traits Studied

attributable to provenance differences were higher than V_E for interior provenances. For these provenances, block by family interactions were very low compared to the coastal provenances; in addition, they did not respond to blocking in the experiment. A possible interpretation is that they were forced to grow in conditions quite different from their natural habitats; therefore small changes in the environment of the experiment probably did not affect their ability to express family differences. If the design of the experiment had been single tree plots (which would reveal inter-tree competition better), then these interior provenances would probably have been eliminated long ago as a result of competition for light. Under the circumstances of the experiment, the design, where each provenance is represented by 40 individuals, allowed their survival since they did not have to compete with coastal provenances on an individual basis.

Zone differences:

Table 9 shows the differences between zone means for all traits. The "t" test results showed that the means of Zone 1, 2, and 3 were not significantly different at 0.05 confidence level. The interior zone mean was significantly different from the means of Zone 2 and Zone 3, but not different from Zone 1 at 0.05 confidence level. This shows that interior provenances did not adapt well to the Haney planting site. Provenances from Zone 1 produced the lowest height, dbh and volume of all the coastal provenances.

Provenance differences (within zone differences):

Significant differences ($p \leq 0.01$) were found within each zone between provenances. Table 4 and Figures 7, 8 and 9 show the

TABLE 9

TOTAL 1986 HEIGHT, DBH AND VOLUME DIFFERENCES BETWEEN SEED ZONES

Seed Zone	Variable	Mean	Std. dev.
1	Height	937.96 cm.	241.18 cm.
	DBH	11.12 cm.	3.43 cm.
	Volume	0.0467 m^3	0.0328 m^3
2	Height	1096.2 cm.	227.92 cm.
	DBH	12.74 cm.	3.26 cm.
	Volume	0.0650 m^3	0.0393 m^3
3	Height	1086.0 cm.	206.70 cm.
	DBH	12.46 cm.	3.05 cm.
	Volume	0.06168 m^3	0.0341 m^3
Interior	Height	759.8 cm.	248.14 cm.
	DBH	8.59 cm.	3.32 cm.
	Volume	0.02624 m^3	0.02474 m^3

differences between provenances within each zone for all traits studied. Standard deviations are not shown in the figures since they are presented in the table. Provenance means were compared using Duncan's test (Table 10). As seen in the table, within each seed zone there is still substantial heterogeneity in terms of the differences between provenances for all traits studied. This heterogeneity is higher for Zone 1 and Zone 3 but low for Zone 2 and the interior grouping. Family variability was also found to be higher for Zone 1 and Zone 3 in the variance analysis at the provenance level. This variability will be discussed later, in terms of its relationship with the geography of variables, in the section dealing with regression.

For height, three provenances from Washington (43, 52 and 53) surpassed the overall plantation mean by at least 25%. Six provenances surpassed the overall plantation mean by at least 20%; of these, one was from B.C. (25), one from California (116), and four from Washington (42, 56, 67 and 72).

41

FIGURE 7

Mean Total Height Differences among Provenances
for all the Seed Zone Groupings

MEAN HEIGHTS

MEAN HEIGHTS OF 17 PROVENANCES FROM ZONE 1

MEAN HEIGHTS OF 12 PROVENANCES FROM ZONE 2

MEAN HEIGHTS OF 19 COASTAL PROVENANCES FROM ZONE 3

MEAN HEIGHTS OF 10 INTERIOR PROVENANCES

MEAN HEIGHT(CM)

PROVENANCE NUMBER

42

FIGURE 8

Mean DBH Differences among Provenaces
for all the Seed Zone Groupings

MEAN DBH

MEAN DBH OF 17 COASTAL PROVENANCES FROM ZONE 1

MEAN DBH OF 12 COASTAL PROVENANCES FROM ZONE 2

MEAN DBH OF 19 COASTAL PROVENANCES FROM ZONE 3

MEAN DBH OF 10 INTERIOR PROVENANCES

MEAN DBH(CM)

PROVENANCE NUMBER

FIGURE 9

Mean Volume Differences among Provenances
for all the Seed Zone Groupings

MEAN VOLUME

TABLE 10

COMPARISON OF PROVENANCE MEANS IN EACH ZONE WITH
DUNCAN'S MULTIPLE RANGE TEST

Seed Zone	Variable	Number of Provenances Studied	Number of Homogeneous Subsets $P \leq 0.05$
1	Height	17	9
	DBH	17	10
	Volume	17	8
2	Height	12	7
	DBH	12	6
	Volume	12	4
3	Height	19	10
	DBH	19	8
	Volume	19	8
Interior	Height	10	6
	DBH	10	5
	Volume	10	5

Table 11 illustrates the differences between the best and the poorest provenances from each zone. To show the percent differences between the best and the poorest provenances, the following equation was used:

$$\% \text{ difference} = \frac{\text{differences between the best and the poorest}}{\text{poorest}} \text{ X } 100$$

Family Differences:

Significant family within provenance variation gives the opportunity for selection of the best families in the best provenance. Table 12 shows the differences between the mean of the best family in the best provenance and poorest family in the poorest provenance. Figures 10, 11, 12 and 13 show the differences between families of the

TABLE 11

DIFFERENCES BETWEEN THE MEANS OF THE BEST AND THE POOREST PROVENANCES OF ALL SEED ZONES FOR ALL TRAITS STUDIED

Seed Zone	Variable	Mean of Best Provenance		Mean of Poorest Prov.		Difference	
		Prov No.	(cm)	Prov No.	(cm)	(cm)	%
	Height	116	1213.6	96	720.8	492.8	68
1	DBH	55	13.66	96	8.35	5.31	64
	Volume	116	0.0767[1]	96	0.0219[1]	0.054[1]	250
	Height	53	1256.5	93	712.4	544.1	76
2	DBH	53	14.80	93	8.58	6.22	73
	Volume	53	0.0954[1]	93	0.0213[1]	0.0741[1]	348
	Height	43	1272.0	86	802.8	469.2	58
3	DBH	43	15.57	86	9.26	6.31	68
	Volume	43	0.1033[1]	86	0.0280[1]	0.0753[1]	269
	Height	77	1032.5	11	503.9	528.6	105
Interior	DBH	77	11.76	11	5.53	6.23	113
	Volume	77	0.0550[1]	11	0.00764[1]	0.0474[1]	620

[1]cubic meters

best and the poorest provenances for each seed zone. Percent differences were calculated using the same equation as noted before. Differences between families are the most marked with volume, then dbh and height, respectively. Graphic representation of this situation is shown in Figure 14.

Assuming, for instance, the selection criterion is to choose those families which surpass the overall provenance mean by 10%. For height, no family surpassed the overall provenance mean by 10%; for dbh only one of the eight families (No. 8), and for volume, two of the eight families exceeded the overall provenance mean by at least 10%. Similar results

TABLE 12

DIFFERENCES BETWEEN MEANS OF BEST FAMILY IN BEST PROVENANCE
AND POOREST FAMILY IN POOREST PROVENANCE FOR ALL TRAITS STUDIED

Seed Zone	Variable	Mean of Best Family of Best Provenance			Mean of Poorest Family in Poorest Provenance			Difference	
		Prov. No.	Fam. No.	Mean (cm)	Prov. No.	Fam. No.	Mean (cm)	(cm)	%
1	Height	116	3	1300.3	96	4	561.0	739.3	132
	DBH	55	1	15.58	96	4	5.67	9.91	175
	Volume	116	7	0.1063[1]	96	4	0.0084[1]	0.0979[1]	1165
2	Height	53	2	1355.8	93	3	592.5	763.3	129
	DBH	53	4	16.67	93	3	6.85	9.82	143
	Volume	53	6	0.1145[1]	93	3	0.0116[1]	0.1029[1]	887
3	Height	43	5	1366.5	86	8	514.3	852.2	166
	DBH	43	8	18.48	86	8	5.65	12.83	227
	Volume	43	8	0.1413[1]	86	8	0.0069[1]	0.1344[1]	1948
Int.	Height	77	3	1076.8	11	4	441.0	635.8	144
	DBH	77	3	12.88	11	5	4.38	8.50	194
	Volume	77	4	0.0704[1]	11	5	0.00422[1]	0.0662[1]	1568

[1] Cubic Meters

were observed at the zone level. Therefore, correlations between height and dbh affected the volume performance of the genotypes. It could be said that good height performance does not necessarily mean good volume performance which depends upon the ability of provenance for radial growth.

Finally, the differences between zones, provenances within zones and families within provenances suggest that a substantial increase in yield could be achieved with selection. Figure 15 illustrates the difference in yield/ha when selecting the best family in the best provenance from the appropriate seed zone at age 15.

FIGURE 10

Mean Total Height and Volume Differences
Between Families of the Best (116) and the Poorest (96) Provenances
From Seed Zone 1

MEAN FAMILY HEIGHTS OF PROVENANCE 116

MEAN VOLUME OF FAMILIES IN PROVENANCE 116

MEAN FAMILY HEIGHTS OF PROVENANCE 96

MEAN VOLUME OF FAMILIES IN PROVENANCE 96

MEAN HEIGHT(CM)

MEAN VOLUME (CUBIC METER)

NUMBERS OF FAMILIES

FIGURE 11

Mean Total Height and Volume Differences
Between Families of the Best (53) and the Poorest (93) Provenances
From Seed Zone 2

MEAN FAMILY HEIGHTS OF PROVENANCE 53

MEAN VOLUME OF FAMILIES IN PROVENANCE 53

MEAN FAMILY HEIGHTS OF PROVENANCE 93

MEAN VOLUME OF FAMILIES IN PROVENANCE 93

MEAN HEIGHT(CM)

MEAN VOLUME (CUBIC METER)

NUMBERS OF FAMILIES

FIGURE 12

Mean Total Height and Volume Differences
Between Families of the Best (43) and the Poorest (86) Provenances
From Seed Zone 3

MEAN FAMILY HEIGHTS OF PROVENANCE 43

MEAN VOLUME OF FAMILIES IN PROVENANCE 43

MEAN FAMILY HEIGHTS OF PROVENANCE 86

MEAN VOLUME OF FAMILIES IN PROVENANCE 86

MEAN HEIGHT(CM)

MEAN VOLUME (CUBIC METER)

NUMBERS OF FAMILIES

FIGURE 13

Mean Total Height and Volume Differences
Between Families of the Best (77) and Poorest Provenances
From the Interior Seed Zone

FIGURE 14

Family Differences of the Best Performing Provenance (43)
for All Traits Studied

MEAN FAMILY HEIGHTS OF PROVENANCE 43

MEAN DBH OF FAMILIES IN PROVENANCE 43

MEAN VOLUME OF FAMILIES IN PROVENANCE 43

Please note that for selection purposes, volume is the most important trait.

FIGURE 15
Expected Yield (Volume - m³/ha) at Age 16

One cube represents 20 m³ of volume. This figure represents, from left to right, the
expected yield at age 16, A - given by the managed yield tables for Douglas-fir at this
age, and when selecting seed from, B -the proper seed zone (ie- vicinity of Haney), C -
the best provenance or, D - the best family, all at age 16.

Regression Analysis:

Influence of geography of origin on provenance performance

Tables 13, 14 and 15 show the influence of geographical variables on the variability of mean height, mean dbh and mean volume of provenances. While 54% of height variability between provenances can be explained by four geographical variables, 47% of this variability in height can be explained by longitude alone (Table 13).

49% of variability in dbh can be explained by the four geographical variables; 44% of this variability was attributable to ecophysiological latitude (incorporation of elevation with latitude) and longitude, the latter being more influential (Table 14).

Table 15 shows 44% of variability in volume differences between provenances can be explained by the four geographical variables. Longitude and ecophysiological latitude, the former being more important, accounted for 38% of this volume variability among provenances.

These results suggest that longitude is the most important factor in the growth variability among provenances. The results of the provenance experiment of Association-Foret-Cellulose (Michaud, 1985) which used the same IUFRO material showed, that the provenances east of longitude 121 had weak growth. However, further investigation of the effect of geographical variables on height growth variability for each zone revealed that each zone grouping exhibited a different spectrum of variability according to their natural habitat of origin.

Provenances belonging to Zone 1 and interior groupings exhibited different results than those belonging to Zone 2 and 3 groupings. 87%

TABLE 13

MULTIPLE LINEAR REGRESSION ANALYSIS FOR HEIGHT
BY ALL COMBINATIONS METHOD
AND CONSIDERING ALL PROVENANCES

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
Height	$X_1 X_2 X_3 X_4$	.3178	.3345	.5612	-.3426	.5381	144.80	40
	$X_1 X_2 X_3$	-.1279	-.0086	.5629		.4767	151.97	40
	$X_1 X_2 X_4$	.2747	.2908		-.3461	.3258	172.50	40
	$X_1 X_3 X_4$	-.0578		.5421	-.0792	.4800	151.50	40
	$X_2 X_3 X_4$		.1239	.5436	-.1851	.4862	150.59	40
	$X_1 X_2$	-.4636	-.2885			.2340	181.37	40
	$X_1 X_3$	-.1383		.6113		.4767	149.91	40
	$X_1 X_4$	-.0566			-.3443	.2635	177.84	40
	$X_2 X_3$		.0537	.6744		.4680	151.15	40
	$X_2 X_4$		.1140		-.5026	.2707	176.96	40
	$X_3 X_4$			.5420	-.1484	.4782	149.69	40
	X_1	-.4056				.1645	186.91	40
	X_2		-.1558			.0243	201.98	40
	X_3			.6830		.4665	149.36	40
	X_4				-.5110	.2611	175.77	40

R^2 = multiple coefficient of determination

X_1 = elevation

X_2 = latitude

X_3 = longitude

X_4 = ecophysiological latitude (latitude + altitude in hm.)

$SE = \sqrt{MS_{Error}}$

TABLE 14

MULTIPLE LINEAR REGRESSION ANALYSIS FOR DBH
BY ALL COMBINATIONS METHOD
AND CONSIDERING ALL PROVENANCES

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
DBH	$X_1X_2X_3X_4$	.3026	.2872	.4852	-.3272	.4932	1.85	40
	$X_1X_2X_3$	-.1266	-.1754	.4925		.4324	1.93	40
	$X_1X_2X_4$	.2738	.2615		-.3396	.3370	2.09	40
	$X_1X_3X_4$	.1124		.4730	-.2381	.4476	1.91	40
	$X_2X_3X_4$		-.0525	.4706	-.1810	.4421	1.92	40
	X_1X_2	-.4323	-.3961			.2506	2.19	40
	X_1X_3	-.0533		.5841		.4144	1.94	40
	X_1X_4	.0922			-.4465	.2884	2.14	40
	X_2X_3		-.1333	.6117		.4232	1.92	40
	X_2X_4		-.0378		-.4716	.2833	2.14	40
	X_3X_4			.4696	-.2176	.4405	1.89	40
	X_1	-.3334				.1112	2.36	40
	X_2		-.2799			.0783	2.40	40
	X_3			.6424		.4127	1.92	40
	X_4				-.5313	.2823	2.12	40

R^2 = multiple coefficient of determination

X_1 = elevation

X_2 = latitude

X_3 = longitude

X_4 = ecophysiological latitude (latitude + altitude in hm.)

$SE = \sqrt{MS_{Error}}$

TABLE 15

MULTIPLE LINEAR REGRESSION ANALYSIS FOR VOLUME
BY ALL COMBINATIONS METHOD

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
VOLUME	$X_1X_2X_3X_4$	.2842	.2857	.4421	-.3109	.4352	.01890	40
	$X_1X_2X_3$	-.1387	-.1000	.4527		.3748	.01961	40
	$X_1X_2X_4$	.2628	.2655		-.3274	.2980	.02078	40
	$X_1X_3X_4$	.0209		.4309	-.1617	.3850	.01945	40
	$X_2X_3X_4$		.0370	.4303	-.1901	.3856	.01944	40
	X_1X_2	-.4243	-.3192			.2137	.02169	40
	X_1X_3	-.1054		.5279		.3685	.01944	40
	X_1X_4	.0125			-.3707	.2448	.02126	40
	X_2X_3		-.0424	.5790		.3625	.01953	40
	X_2X_4		.0413		-.4622	.2459	.02124	40
	X_3X_4			.4307	-.1913	.3847	.01919	40
	X_1	-.3528				.1245	.02259	40
	X_2		-.2027			.0411	.02364	40
	X_3			.6012		.3614	.01929	40
	X_4				-.4946	.2447	.02098	40

R^2 = multiple coefficient of determination
X_1 = elevation
X_2 = latitude
X_3 = longitude
X_4 = ecophysiological latitude (latitude + altitude in hm.)
$SE = \sqrt{MS_{Error}}$

and 71% of height variability among provenances for interior and Zone 1 groupings, respectively, were explained by the four geographical variables. For the interior zone 74% of height variability was explained by ecophysiological latitude alone (Table 16, Figure 16). Longitude and ecophysiological latitude, the former being more influential accounted for 67% of variability in height growth in Zone 1 (Table 17).

Zone 2 and 3 provenances exhibited different spectra of variability in their height growth than Zone 1 and interior zone groupings. 65% and 30% of height variability among provenances of Zone 3 and Zone 2 were explained by the four geographical variables, with 58% and 11% of variability between provenances attributable to the effect of latitude for Zones 3 and 2, respectively (Tables 18 and 19). Longitude had very little (5% for Zone 3) or no (0.5% for Zone 2) effect on height growth variability for these provenances.

These results suggest that for Zone 1 and interior provenances longitude of origin had a pronounced influence on height growth performance. Longitude together with ecophysiological latitude was able to explain, on average, 71% of variation in total height between these provenances. For Zone 2 and Zone 3 provenances, the latitude of origin was the major source of variability; however for Zone 2 these four geographical variables were able to explain only 30% of variability in height growth. This amount is very low compared to the three other zones. Apparently, elevation of origin had very little effect on height variability of these Zone 2 provenances. For example, the total height growth difference between high elevation (provenance 52) and low

TABLE 16

MULTIPLE LINEAR REGRESSION ANALYSIS FOR HEIGHT
BY ALL COMBINATIONS METHOD
INTERIOR ZONE

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
Height	$X_1X_2X_3X_4$	.6695	.6555	.4118	−.6884	.8734	89.74	10
	$X_1X_2X_3$	−.3568	−.7321	.3363		.7595	112.94	10
	$X_1X_2X_4$	.6293	.6245		−.6619	.8476	89.90	10
	$X_1X_3X_4$	.3211		.3345	−.7562	.7781	108.48	10
	$X_2X_3X_4$		−.2702	.3017	−.4097	.7706	110.28	10
	X_1X_2	−.7667	−.7806			.7288	111.03	10
	X_1X_3	.0274		.5032		.4817	153.49	10
	X_1X_4	.1421			−.8000	.7501	106.57	10
	X_2X_3		−.6846	.7623		.7244	111.93	10
	X_2X_4		−.1028		−.7852	.7477	107.09	10
	X_3X_4			.1726	−.7232	.7526	106.04	10
	X_1					.3059		10
	X_2					.3421		10
	X_3					.4812		10
	X_4					.7449		10

R^2 = multiple coefficient of determination
X_1 = elevation
X_2 = latitude
X_3 = longitude
X_4 = ecophysiological latitude (latitude + altitude in hm.)
SE = $\sqrt{MS_{Error}}$

FIGURE 16

The Relationship Between Mean Provenance Heights and
the Ecophysiological Latitude for Interior Provenances

TABLE 17

MULTIPLE LINEAR REGRESSION ANALYSIS FOR HEIGHT
BY ALL COMBINATIONS METHOD
ZONE 1

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
	$X_1 X_2 X_3 X_4$	.3538	.3601	.7198	-.3331	.7175	106.79	10
	$X_1 X_2 X_3$	.6085	.4988	.7570		.6822	103.39	10
	$X_1 X_2 X_4$	.4687	.4854		-.4608	.4137	140.43	10
	$X_1 X_3 X_4$	-.1525		.7594	.4823	.6754	104.50	10
	$X_2 X_3 X_4$		.1681	.7551	.6000	.6770	104.23	10
	$X_1 X_2$	.3082	.5004			.2556	146.50	10
	$X_1 X_3$	.4182		.7576		.5769	110.44	10
Height	$X_1 X_4$	-.4504			.4771	.2330	148.71	10
	$X_2 X_3$		.1250	.6216		.4953	120.63	10
	$X_2 X_4$		.4680		.2941	.2487	147.18	10
	$X_3 X_4$			.8090	.5931	.6676	97.89	10
	X_1					.0071		10
	X_2					.1775		10
	X_3					.4873		10
	X_4					.0379		10

R^2 = multiple coefficient of determination

X_1 = elevation

X_2 = latitude

X_3 = longitude

X_4 = ecophysiological latitude (latitude + altitude in hm.)
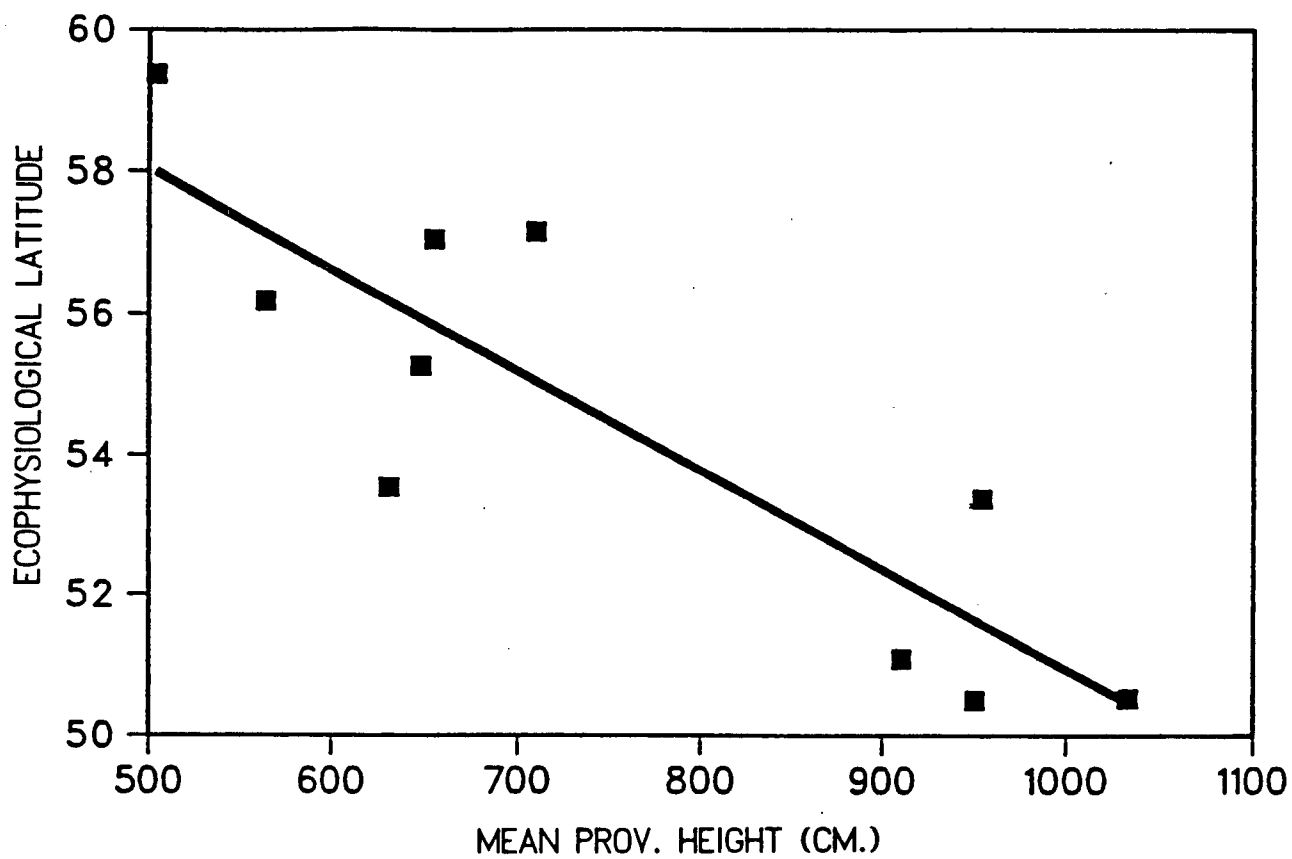
$SE = \sqrt{MS_{Error}}$

TABLE 18

MULTIPLE LINEAR REGRESSION ANALYSIS FOR HEIGHT
BY ALL COMBINATIONS METHOD
ZONE 3

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
Height	$X_1 X_2 X_3 X_4$	-.3523	.4209	-.2747	.3604	.6433	93.47	10
	$X_1 X_2 X_3$	-.0116	.7411	-.1292		.5901	91.47	10
	$X_1 X_2 X_4$	-.2948	.4153		.3145	.6244	87.57	10
	$X_1 X_3 X_4$	-.7307		-.2123	.7234	.5666	94.07	10
	$X_2 X_3 X_4$		.7498	-.1001	.0819	.5928	91.17	10
	$X_1 X_2$	.0462	.7402			.5832	85.40	10
	$X_1 X_3$	-.1869		.1182		.0908	126.13	10
	$X_1 X_4$	-.7389			.7126	.5461	89.12	10
	$X_2 X_3$		.7516	-.1366		.5901	84.69	10
	$X_2 X_4$		.7671		.1233	.5886	84.84	10
	$X_3 X_4$			.2640	.1137	.0701	127.56	10
	X_1					.0779		10
	X_2					.5823		10
	X_3					.0579		10
	X_4					.0004		10

R^2 = multiple coefficient of determination
X_1 = elevation
X_2 = latitude
X_3 = longitude
X_4 = ecophysiological latitude (latitude + altitude in hm.)
$SE = \sqrt{MS_{Error}}$

TABLE 19

MULTIPLE LINEAR REGRESSION ANALYSIS FOR HEIGHT
BY ALL COMBINATIONS METHOD
ZONE 2

Depend. Var.	Independent Variables	Partial Correlation Coefficients				R^2	SE	N
		1	2	3	4			
Height	$X_1X_2X_3X_4$	.3560	.3985	-.1471	-.3776	.3047	74.07	10
	$X_1X_2X_3$	-.2881	.3862	-.1881		.1891	73.02	10
	$X_1X_2X_4$	.3765	.4091		-.3933	.2894	68.36	10
	$X_1X_3X_4$	-.3978		-.1779	.3644	.1735	73.71	10
	$X_2X_3X_4$		.4349	-.1961	-.3157	.2038	72.35	10
	X_1X_2	-.2391	.3435			.1594	68.83	10
	X_1X_3	-.2048		.0102		.0470	73.29	10
	X_1X_4	-.3644			.3234	.1465	69.35	10
	X_2X_3		.3332	-.0907		.1160	70.60	10
	X_2X_4		.3983		-.2672	.1720	68.31	10
	X_3X_4			.0481	.1139	.0181	74.39	10
	X_1					.0469		10
	X_2					.1084		10
	X_3					.0052		10
	X_4					.0159		10

R^2 = multiple coefficient of determination

X_1 = elevation

X_2 = latitude

X_3 = longitude

X_4 = ecophysiological latitude (latitude + altitude in hm.)

$SE = \sqrt{MS_{Error}}$

elevation (53) provenances, both of Matlock, Washington, was only 4 cm.,
whereas the elevational difference was 1250 feet. It would, of course,
be very interesting to know the aspect of the origin of these
provenances. As noted in the literature review, earlier studies
revealed that aspect is an important factor in the behaviour of
provenance growth (Herman and Lavender, 1965).

The lack of an elevational trend in variability in interior
populations was explained by continued intermigration (Wright *et al.*,
1971). In this study, the influence of elevation on mean height growth
was not significant at 0.05 confidence level for all zones (Table 20).
However the influence of elevation on height growth was more pronounced
for interior provenances compared to coastal provenances. This
influence increased especially when elevation was incorporated into
latitude . As a result, the correlation between ecophysiological
latitude and mean height was highly significant (r = -0.86) for interior
provenances (Figure 16).

The fact that four geographical variables were able to explain only
30% of variation in height growth of Zone 2 provenances suggests that
internal control of height growth is stronger compared to external
control. Also, the high heritability estimate for height of these
provenances seems to support this explanation. However the relationship
between environmental influence and the radial growth for these
provenances was more complicated. The correlation between height and
dbh for these provenances was found to be very low compared to the other
zones. In contrast to the findings of Yeh and Heaman (1982) in which a
large positive genetic correlation between height performance and

TABLE 20

SIMPLE LINEAR CORRELATIONS AMONG GROWTH AND GEOGRAPHICAL VARIABLES
(R VALUES)

Zone	Variables	Elevation	Longitude	Latitude	Ecophysical Latitude	N
	Height	-0.0840	0.6981*	0.4213	0.1947	10
	dbh	0.0148	0.5597	0.2869	0.2189	10
1	Volume	-0.0242	0.5886	0.3286	0.1996	10
	MS_{fam}	0.2508	-0.2787	-0.4122	0.0145	10
	TSW	0.6791*	-0.8099**	-0.5127	0.3032	10
	Height	-0.2165	0.0723	0.3292	0.1259	10
	dbh	-0.0212	-0.4058	-0.2300	-0.2030	10
2	Volume	-0.1162	-0.2920	-0.0761	-0.1378	10
	MS_{fam}	-0.2445	-0.2319	-0.0618	-0.2061	10
	TSW	0.4269	-0.2198	-0.4763	-0.1379	10
	Height	-0.2791	0.2406	0.7631*	0.0207	10
	dbh	-0.0975	0.1315	0.5764	0.1702	10
3	Volume	-0.1125	0.1280	0.6081	0.1650	10
	MS_{fam}	0.2954	-0.3177	-0.8844**	-0.0173	10
	TSW	0.0574	-0.0015	-0.5326	-0.1088	10
	Height	-0.5531	0.6937*	-0.5849	-0.8631**	10
	dbh	-0.4942	0.6386*	-0.6840*	-0.8864**	10
Int	Volume	-0.4674	0.6487	-0.6590*	-0.8512**	10
	MS_{fam}	0.3023	-0.0064	-0.2925	0.0396	10
	TSW	-0.0719	0.4674	-0.7045*	-0.5652	10
	Height	-0.4055**	0.6830**	-0.1558	-0.5110**	40
	dbh	-0.3334*	0.6424**	-0.2799	-0.5313**	40
Gen[1]	Volume	-0.3528*	0.6012**	-0.2027	-0.4946**	40
	MS_{fam}	0.1950	-0.0245	-0.355*	-0.0512	40
	TSW	0.3517*	0.1573	-0.6487**	-0.1078	40

* $p \leq 0.05$

** $p \leq 0.01$

[1] considering all provenances regardless of originating zone

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diameter was found, and selection based on height to simultaneously improve both traits was proposed, this present study suggests that these correlations between height and dbh are very much dependent upon the natural habitat of origin.

As well as primary growth variables such height and dbh, much interest has been shown in using photosynthetic capacity as an index of growth potential of trees. High rates have been confirmed for *Eucalyptus*, *Populus* and *Pseudotsuga*. However, rates vary appreciably among species as well as among varieties, clones and provenances. The rate of photosynthesis of several *Pinus banksiana* provenances changed with time (Kozlowski, 1979). One provenance with a very high rate in July had one of the lowest rates in November. Provenances with high rates in October and November also had the highest growth rates. In addition, the amount of seed crop is negatively correlated with vegetative growth. This, of course, complicated the relation between photosynthesis rate and wood production.

Two different pathways of photosynthesis have also been identified. Most higher plants and almost all trees, except some mangroves and a few others, are classified as C_3 plants which follow the Calvin Cycle. C_3 plants are less well adapted to undergo environmental stress compared to C_4 (crop) plants. Another disadvantage for C_3 plants is that they use atmospheric CO_2 less efficiently than C_4 plants, due to the inhibition of RuBP carboxylase by photorespiration (Kozlowski, 1979). It would be very interesting to investigate the relationship between photosynthetic rate and the stomatal conductance at the provenance level and relate the findings to the vegetative growth performance of the

provenances on the same experiment. Furthermore, electrophoretic methods when trees reproduce could also be used for further investigation of the genetic variation at the DNA level and the results could be correlated to physiological and phenotypical variables.

Relationships among Growth Variables:

Investigation of correlations between height and dbh revealed different results when all provenances are considered as opposed to individual zone groupings. When all provenances are considered in the analysis, the correlation between height and dbh was very significant (r = 0.9615) (Table 21). However, as seen in the table, investigation of the situation of individual zone groupings showed different results. The highest correlation between height and dbh was obtained for the interior zone grouping (r = 0.9767) and the lowest for Zone 2 (r = 0.6164) (Table 21). The transitional zone groupings (Zone 1 and Zone 3) averaged a value in between (r = 0.92). Zone 2 provenances were the best performing provenances in Haney planting conditions in terms of height growth. This shows once more that selection based on height performance could be misleading.

Correlations between TSW and the growth variables (height, dbh and volume) were not significant (p ≤ 0.05), but there was a positive correlation between TSW and the variability between families within provenances (MS_F) for Zones 1 and 3, which are the transitional zones between coastal Zone 2 and the interior. As noted in the Materials and Methods section, MS_F shows the variability among families within a provenance and was generated as a result of 58 separate analysis of variance runs for each provenance, so that within provenance variation

TABLE 21

SIMPLE LINEAR CORRELATIONS AMONG GROWTH VARIABLES
(R VALUES)

Zone	Variable	Height	DBH	Volume	MS_{fam}	TSW	N
	Height	1.0000	0.9329**	0.9623**	-0.2016	-0.3723	10
	DBH		1.0000	0.9926**	-0.0751	-0.2448	10
1	Volume			1.0000	-0.1101	-0.2949	10
	MS_{fam}				1.0000	0.6803	10
	TSW					1.0000	10
	Height	1.0000	0.6164	0.7765*	-0.2151	-0.5135	10
	DBH		1.0000	0.9703**	0.0600	0.0149	10
2	Volume			1.0000	0.0476	-0.1762	10
	MS_{fam}				1.0000	-0.0272	10
	TSW					1.0000	10
	Height	1.0000	0.9146**	0.9211**	-0.8694**	-0.5942	10
	DBH		1.0000	0.9911**	-0.7269*	-0.3458	10
3	Volume			1.0000	-0.7034*	-0.3422	10
	MS_{fam}				1.0000	0.6896*	10
	TSW					1.0000	10
	Height	1.0000	0.9767**	0.9775**	0.1378	0.4748	10
	DBH		1.0000	0.9862**	0.1062	0.4965	10
Int	Volume			1.0000	0.0498	0.5482	10
	MS_{fam}				1.0000	0.0963	10
	TSW					1.0000	10
	Height	1.0000	0.9615**	0.9530**	-0.1077	-0.1600	40
	DBH		1.0000	0.9817**	-0.0649	-0.0426	40
All	Volume			1.0000	-0.1168	-0.1012	40
Prov.	MS_{fam}				1.0000	0.4393*	40
	TSW					1.0000	40

* $p \le 0.05$

** $p \le 0.01$

can be investigated as independent from the block by family interactions which camouflaged family variability.
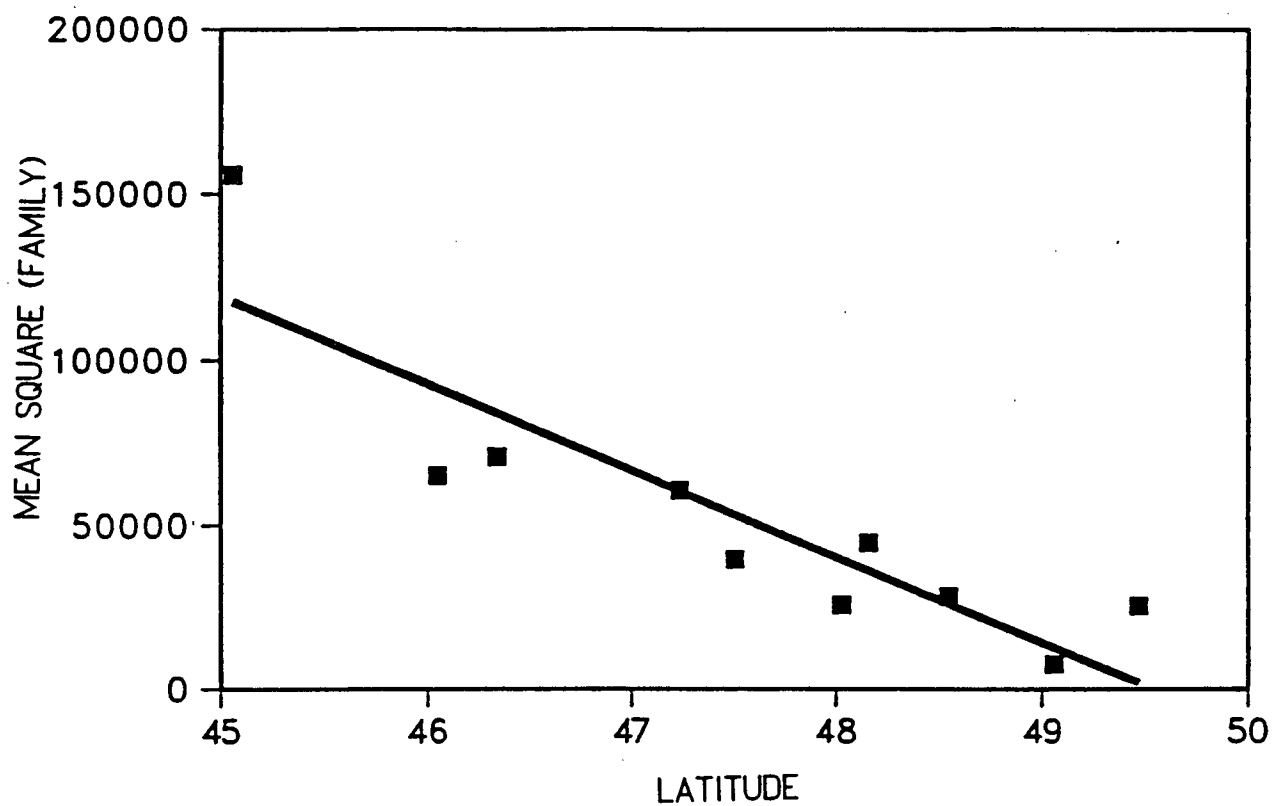
When family variability among provenances was correlated to geographical variables, the results were interesting from the view point of evolutionary biology.

The simple linear correlation between MS_F and latitude was very high (r = -0.8844), (Figure 17, Table 20) for those provenances which originated from the zone transitional (Zone 3) between the interior and the coast (Zone 2). This relationship was weaker for Zone 1 (r = -0.4213) and the interior zone (r = -0.2925) but almost non-existent for Zone 2 (r = -0.0618). Ledig, in his talk, "Gene Conservation" given at UBC in the fall of 1988, mentioned that diversity within a species decreases when one goes towards the north from the equator. The correlation found in this study between latitude and MS_F is in agreement with this statement. However, the lack of this trend for Zone 2 provenances could be explained by natural selection for high diversity due to favourable climate in the evolutionary process.

Apparently plants have different strategies for adaptation, and their strategies depend on the environment they are in. According to the theory of "r" and "k" selection, genotypes which allocate a large fraction of their energy resources to reproductive activities ("r" strategists) will be favoured in environments characterized by high density independent mortality. Conversely, populations subjected to high density dependent mortality ("k" types)will be characterized by genotypes which devoted a larger proportion of resources to vegetative rather than reproductive structures. The "k" selected populations,

FIGURE 17

The Relationship Between Latitude and Family Variability
of Each Provenance for Zone 3

will, therefore, be successful competitively but at the expense of rapid population growth (King and Anderson, 1971; Clegg *et al.*,1978). The "k" selection therefore, favours those genotypes best able to buffer the effects of high population density. It is known that Douglas-fir colonized northwestern America from south to north after the glaciers retreated. Probably afterwards individuals adapted to lower elevation coastal Douglas-fir ecosystems and populational differences emerged as a result of natural selection, probably "k" selection. Most probably selection operated against those which did not have good competing ability for light since the growth period and water were not the limiting factors.

If the above mentioned hypothesis is true, isozyme studies should also reveal these genetic variation at the DNA level, but, as noted before, isozyme studies in Douglas-fir revealed that only 3% of variation in Douglas-fir was attributable to the populational differences. However, electrophoretic data obtained from two different species, *Drosophila silvestris* and *D. heteroneura* from the geologically new island of Hawaii was remarkably close, yet the two species were morphologically and cytologically very distinct. (Lewontin, 1974).

Significant negative correlations were also found between TSW and MS_F for the transitional zone groupings (for Zone 1, r = -0.6803 and for Zone 3, r = -0.6896) (Table 21). This relationship did not exist for interior and Zone 2 groupings. When all provenances are considered (Table 20), a negative correlation exists between TSW and latitude (r = -0.6487, $p \leq 0.01$). The simple linear correlation between TSW and elevation (r = 0.35, $p \leq 0.05$) was significant. This relationship was

stronger in Zone 1, which is the second transitional zone ($r = 0.6791$, $p \leq 0.05$). The relationships among elevation, latitude and TSW found in this study is in confirmation with Yao's previous work on the same material (Yao, 1971).

These results suggest that are well defined relationships among TSW, latitude, elevation and MS_F. Family variability within provenances for height increased with increasing TSW and decreased with increasing latitude.

Age to Age Correlations and Ontogenic Considerations:

Many species have useful juvenile characteristics, which disappear with increasing age, which allow them to withstand negative impacts of the environment. For example, shade tolerance in juvenile stages enables young plants to stay alive under a dense forest canopy. The fact that the entire lower trunk portion of an old beech tree carries leaves, while upper leaves are dropped in winter (leaf retention is a juvenile characteristic of a beech which protects the seedling against cold injury) is the demonstration of disappearance of a juvenile character with age in the same tree.

In a beech (*Fagus silvatica*) experimental scions from the upper and lower branches were grafted onto rootstock of identical origin, growing under similar conditions in two adjacent rows. The juvenile scions, which were taken from basal epicormic branches, flushed earlier. This demonstrates the control that age has on phenological characteristics of trees.

In very heavy shade, young beeches become leaf-shedding, *i.e.*, environment causes the disappearance of their juvenile character, leaf

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retention. In order to study the extent to which shade influences leaf retention, 14 leafless seedlings growing under a 120-year-old beech stand were selected and transplanted with wide spacing to favourable shade conditions (25% of full light). The results anticipated was that they had left the juvenile leafy stage and therefore they would continue leaf-shedding. However, during the period form 1952 to 1958 all surviving plants gradually became leaf-retaining. This was interpreted as a demonstration of the ability of shade to prolong the juvenile stage (Schaffalitzky de Muckadell, 1962).

Since internal and external controls over ontogenic changes in trees have been demonstrated, tree breeders are interested in knowing the correlations among quantitative and/or qualitative traits in these different stages for early selection purposes.

Age to age correlations for height among various years are given in Table 22. As seen, correlations decreased with increasing age. The simple linear correlation coefficient between 1972 and 1986 total height is 0.47. In other words, only 22% of variation in total height performance at age 16 could be explained by the total height at age 2. This figure increases to 37% at age 5 and to 85% at age 9. Age - to - age correlations are given by Fashler (1979) on the same material for each seed zone between ages 1 and 8. Correlations were very similar in all zone groupings. Therefore, in this study, investigation of correlations has been done considering all provinces. The r^2 value between total height in 1975 and 1978 is 0.75 (Fashler, 1979). These results therefore suggest waiting at least until age 7 before making any selection on the basis of height performance. Fashler (1979) ,

TABLE 22

JUVENILE BY MATURE CORRELATIONS OF TOTAL HEIGHTS
AT DIFFERENT YEARS
r VALUES

Year	1973	1975	1980	1981	1982	1983	1984	1985	1986
1973	1.00								
1975	0.86	1.00							
1980	0.60	0.75	1.00						
1981	0.58	0.73	0.99	1.00					
1982	0.56	0.71	0.97	0.99	1.00				
1983	0.52	0.66	0.95	0.98	0.99	1.00			
1984	0.49	0.64	0.94	0.96	0.98	0.99	1.00		
1985	0.48	0.62	0.93	0.95	0.97	0.98	0.99	1.00	
1986	0.47	0.61	0.92	0.94	0.96	0.98	0.99	0.99	1.00

All of the simple correlations are significant at the 0.01 confidence
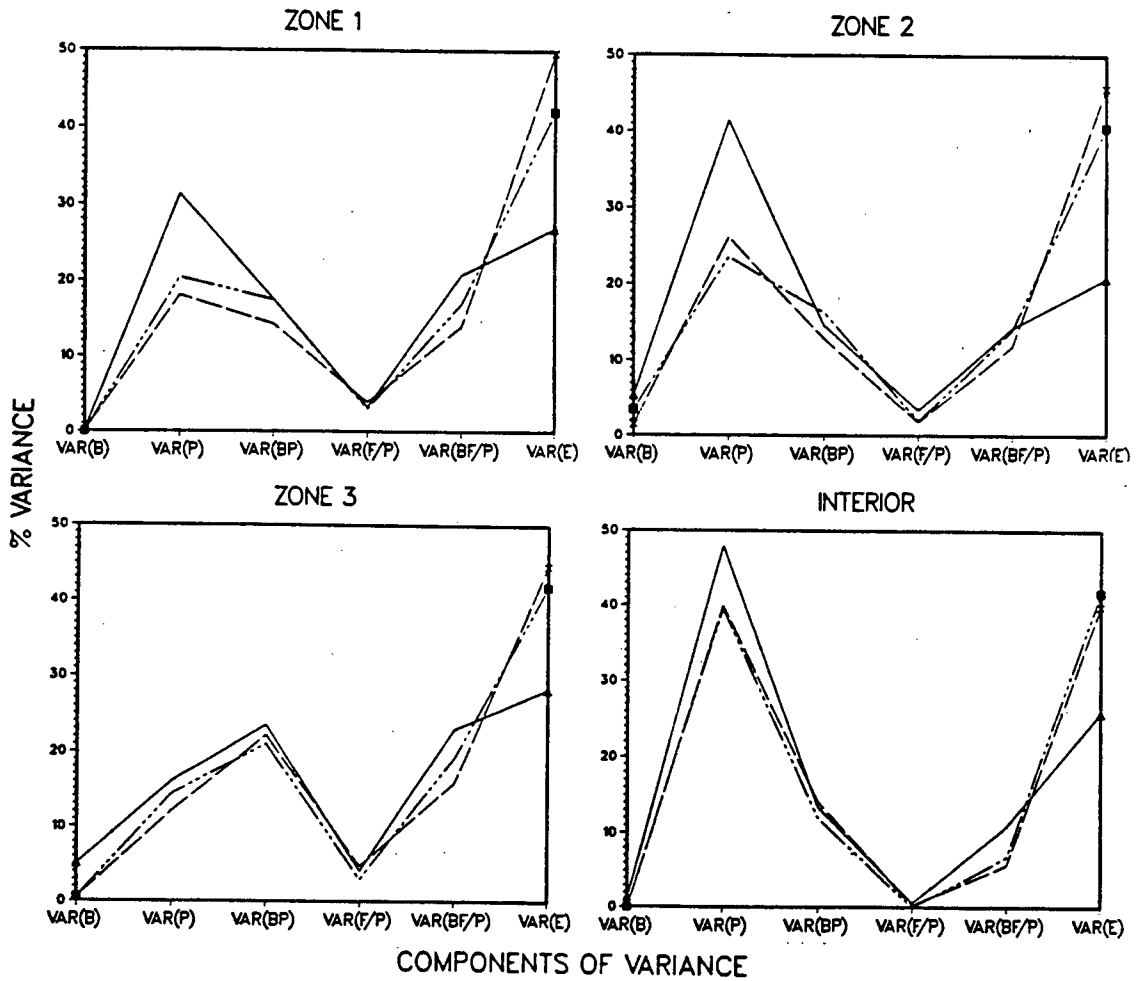level (DF = 98)

analyzing the data up to age 8, found that for selection purposes,
waiting until age 5 would be appropriate. It seems that the age for
selection increases as the experiment continues.

In this study, investigation of the development of genetic
variances in height growth over time revealed that genetic parameter V_p
and $V_{F/P}$ changed with the aging of the experiment (Figure 18). The
magnitude of these changes varied according to zone groupings. In the
early years of the experiment, V_p was greater than $V_{F/P}$ for Zone 1 and
the interior zone. There was a reversed relationship between V_p and
$V_{F/P}$ for Zone 2, $V_{F/P}$ being greater than V_p. The difference between V_p
and $V_{F/P}$ was not very well defined for the Zone 3 grouping (Fashler,
1979). Over the years $V_{F/P}$ decreased for all zone groupings. This
decrease was very pronounced for the interior grouping compared to

FIGURE 18

Trends in Components of Variance
Over the Years for Height

COMPONENTS OF VARIANCE AS % OF TOTAL VARIANCE

other zones. As a parallel to this decrease in the family component $(V_{F/P})$ of variance, additive genetic variances and narrow sense heritabilities also decreased (Table 23) and the magnitude of this decrease was more pronounced for Zone 2 and the interior zone. The decrease of V_E was also noticed for all zones over the years. The magnitude of this decrease again was more pronounced for the interior and Zone 2 groupings.

Changes in genetic parameters for height growth over time was also noted by Namkoong *et al.* (1972) in a 53 year old experiment. As Franklin (1979) said, "We can ill-afford to wait for the mature

TABLE 23

ADDITIVE GENETIC VARIANCE (V_A) AND V_A AS A PERCENT
OF TOTAL PHENOTYPIC VARIANCE (V_A/V_T) FOR TOTAL HEIGHT
OVER THE YEARS

Seed Zone	Year	$V_A = 4V_{F/P}$	V_A/V_T (%)	h^2 (narrow)
1	1972	41.12	23.64	0.36
	1975	594.67	25.44	0.42
	1978	1911.97	19.12	0.33
	1986	7589.24	12.78	0.25
2	1972	94.86	43.40	0.52
	1975	694.04	28.52	0.35
	1978	2854.15	28.40	0.37
	1986	7604.00	14.60	0.36
3	1972	52.30	26.76	0.42
	1975	470.87	20.92	0.33
	1978	2209.26	25.12	0.39
	1986	7255.88	17.36	0.30
Interior	1972	23.31	25.24	0.39
	1975	392.19	24.32	0.38
	1978	1308.30	17.52	0.28
	1986	1651.68	2.57	0.07

genotype phase to obtain progeny test results to make selections. The need is to hasten the onset of the mature genotypic phase by inducing fast growth at close spacing and perhaps by manipulating other environmental factors."

Campbell *et al.* (1986) investigated the effect of spacing (square spacing ranging from 30 to 90 cm.) on the variance structure in a population of unselected Douglas-fir over a 9 year period and found that close spacing did not shift the genetic variance structure from the juvenile to the mature phase. However, components of variance for female by spacing effect decreased and male by spacing effect increased with the measurement age. Another study in loblolly pine (*Pinus taeda L.*), in a 20 year old open-pollinated progeny test, suggested that genetic parameter changes expressed by families were not in direct response to the onset of competition. The same study also revealed significant differences in the competitive abilities and competitive influences among the seedlings of tested families (Tuskan and Buijtenen, 1985).

In our study, estimates of the male effect, the dominant effect, the epistatic effect and the interactions between these effects and the blocks are unattainable. These effects are pooled in V_E. However, 1979 thinnings increased V_{P*B} interactions in Zone 1, Zone 3 and the interior zone (Figure 18). For Zone 2 provenances, provenance * block interactions did not fluctuate appreciably over the years.

Block by family / provenance interactions were not significant up to 1978 (Fashler, 1979), but significant increases were noticed in the 1986 analysis. Thinnings and natural mortality removed 40% of the trees

from the experiment up to 1979; Fashler (1979) estimated the natural mortality at 8.9%. Therefore part of the reason for the increase in B*F/P interactions could be explained by the 1978 thinnings which unregulated the spacing in the experiment. However, physiological experiments in forestry and agriculture suggest the existence of developmental changes or meristematic aging in trees and the interplay between this phenomenon and the environment. For example, gibberellic acid can cause an adult ivy plant (*Hedera helix*) to revert to the juvenile form. The adult ivy has elliptic leaves and upright shoots as compared to the juvenile characters of climbing shoots and palmately lobed leaves. Marked changes in the concentration of RNA and DNA as the plant matures and increases in the RNA/DNA ratio when a plant reproduces are also reported. Flowering of olive trees and grape vines can be promoted by spraying the plants with uracil, xanthine or caffeine. There is a direct correlation between RNA content and protein synthesis (Schaffalitzky de Muckadell, 1979). These studies suggest that there are biochemical changes triggered by internal and external factors during the changes from the juvenile to the adult stage. An understanding of the ontogenic changes in tree species and their biochemical control would be of great value in forestry especially in nursery activities in order to shorten the time needed in an improvement program.

Investigation of the development of variance components according to the different zone groupings suggests that native habitat of provenances has an influence. The different environmental triggers of natural habitats of provenances seem to have a differential conditioning

effect depending upon the different regions. Therefore, the juvenile
and mature relationships might be different according to the natural
habitat of the provenance.

Adaptability to Haney Conditions

A selection based on the 1986 total height performance would not be
able to reflect the responses of these provenances to the year to year
fluctuating climate. Therefore the selection technique used in this
study will consider the performance of the provenances over the years.
As seen in Table 24, provenance 91 was the first ranking provenance in
1973 but gradually decreased its ranking to 14th position in 1986. A
selection based on 1986 height would choose this provenance as 14th
choice, whereas according to the slope of regression it would be the
17th choice, considering its performance for the entire course of the
experiment. Conversely, provenance 25, from Squamish, gradually
increased its total height ranking from 14th in 1973 to 4th in 1986, and
therefore would be our third choice.

Figure 19 illustrates provenance performance over the years.
Height performance of almost all interior provenances was significantly
under the average plantation performance; they are therefore classified
as stable inferior growing provenances. Provenance 11 is a typical
example of such a stable inferior provenance (Table 24, Figure 19).
Some provenances, although their height performance is normally under
the plantation performance, showed an unusual increase in their ranking
in a particular year. Such provenances are classified as unstable
provenances. Provenances which attained a cefficient value
substantially greater than 1 are classified as progressive provenances;

TABLE 24

MEAN TOTAL PROVENANCE HEIGHTS OVER THE YEARS
AND RANKING OF PROVENANCES

Prov No.	1973 Ht.	Rank	1975 Ht.	Rank	1978 Ht.	Rank	1986 Ht.	Rank	Reg.[a] (b)	Rank[b]
				Zone 1						
23	59.64	24	138.0	25	288.6	26	1019.0	24	1.0428	24
32	59.90	23	153.0	19	345.3	12	1157.6	7	1.1901	6
55	57.32	26	140.4	24	319.5	20	1088.4	16	1.1901	15
90	54.48	27	131.8	26	297.8	25	1047.8	20	1.0819	20
95	44.49	32	111.0	33	327.7	17	865.3	30	0.8822	30
96	45.94	30	99.5	35	372.1	7	720.8	35	0.7136	35
99	44.38	33	110.0	34	281.8	28	812.3	33	0.8274	33
104	46.20	29	111.1	32	211.3	36	824.6	32	0.8493	32
111	40.22	35	99.5	36	227.2	34	843.6	31	0.8778	31
117	61.31	21	144.5	21	211.8	35	1090.1	15	1.1325	14
				Zone 2						
12	65.78	18	154.9	16	313.0	22	1150.0	9	1.1813	8
51	75.09	6	165.7	11	335.7	14	1125.3	13	1.1396	12
52	65.77	19	173.9	4	380.4	5	1252.5	2	1.2826	2
53	69.47	12	170.1	8	387.7	1	1256.5	1	1.2857	1
67	78.88	2	180.9	1	377.6	6	1197.9	3	1.2091	4
79	74.34	7	155.3	15	323.1	19	1045.2	21	1.0537	22
83	77.96	4	173.0	6	358.2	11	1130.9	12	1.1374	13
87	71.05	10	166.3	10	363.7	10	1155.0	8	1.1723	10
89	72.79	9	179.3	2	383.4	3	1175.2	6	1.1864	7
91	81.96	1	177.6	3	370.8	8	1092.2	14	1.0875	17
				Zone 3						
25	68.81	14	171.8	7	384.3	4	1197.5	4	1.2177	3
27	74.04	8	168.3	9	369.3	9	1131.1	11	1.1414	11
29	69.26	13	154.1	17	324.3	18	1067.0	19	1.0822	19
40	75.80	5	158.3	3	307.9	23	1037.0	22	1.0440	23

TABLE 24

(continued)

Prov No.	1973 Ht.	Rank	1975 Ht.	Rank	1978 Ht.	Rank	1986 Ht.	Rank	Reg.[a] (b)	Rank[b]
					Zone 3					
42	68.67	15	173.2	5	384.3	2	1188.8	5	1.2071	5
60	60.63	22	142.1	22	299.2	24	1135.7	10	1.1752	9
61	78.36	3	162.2	12	341.9	13	1072.8	18	1.0777	21
73	70.17	11	156.7	14	330.0	16	1086.5	17	1.1023	16
76	68.08	16	150.6	20	315.5	21	963.6	26	0.9661	28
86	42.84	34	111.6	30	237.4	33	802.8	34	0.8225	34
97	65.11	20	153.4	18	331.9	15	980.7	25	0.9843	26
					Interior					
6	66.62	17	140.5	23	273.9	29	911.3	29	0.9164	29
46	37.37	38	89.5	38	192.9	37	563.7	40	0.5649	40
64	44.63	31	114.2	29	263.0	31	954.8	27	0.9925	25
77	39.61	37	111.3	31	269.1	30	1032.5	23	1.0857	18
80	58.10	25	128.6	27	287.2	27	950.8	28	0.9705	27
10	40.02	36	96.4	37	192.0	38	655.3	38	0.6663	37
18	36.96	39	88.7	39	183.6	40	648.1	37	0.6642	38
28	46.74	28	114.3	28	237.7	32	710.1	36	0.7119	36
66	31.63	41	80.7	41	185.3	39	630.1	39	0.6499	39
11	34.21	40	82.4	40	164.7	41	503.9	41	0.5045	41
Av.[c]	59.1		138.9		301.2		982.3			

[a] regression coefficient (slope) (b)

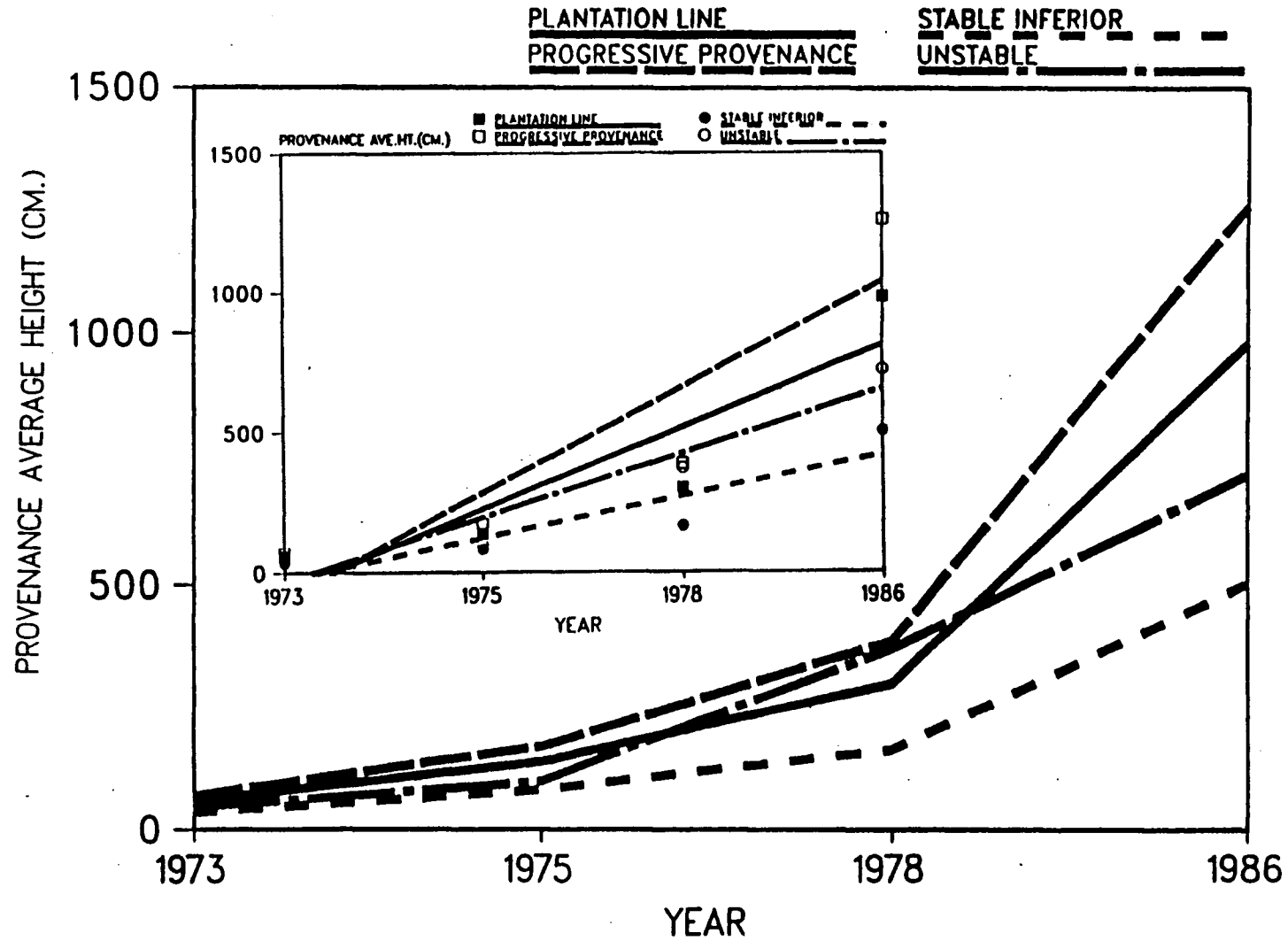[b] priority for reforestation

[c] mean total plantation height

provenance 53 is such a provenance.

The simple linear regression coefficient (slope) for the plantation line is 1.00, because the same values (mean total plantation heights in different years, Table 24, last row) were regressed to each other.

Provenance 43, from Marblemount, Washington, a low elevation provenance, which was the best performing provenance according to its height and dbh ranking, is not included in the analysis due to the lack of height data in previous years.

Provenances 53 and 52 from Matlock, Washington would be selected as first and second choice according to this analysis. However, local provenances such as provenance 25 from Squamish increased their height rankings over the years. As noted in the literature review, mild climate and sheltered sites may mask the performance of local provenances. Fifty-three year results of an experiment (Silen, 1965) showed that at the most severe site both survival and growth rate began to strongly favour the adapted local race by the end of the second decade. Moving southern provenances northward results in faster growth as a result of a longer growth period, but the trees may then bemore susceptible to fall frost damage because they undergo dormancy later. Therefore, to be on the safe side, before making any decision on selection, it would be appropriate to wait for further results on the same material.

FIGURE 19   ADAPTATION OF PROVENANCES

SUMMARY AND CONCLUSIONS

Sixteen-year results are reported for 58 provenances and 464 families of Douglas-fir growing in Haney planting conditions. Results of this analysis confirm those of previous analyses that interior and Zone 1 provenances have slower growth than do the provenances of other zones at Haney conditions.

Simple and multiple linear regression analyses conducted by individual zone groupings indicated that different clinal expressions may be exhibited by provenances depending upon the region, or zone grouping, they came from in terms of the effect of geography of origin on provenance performance.

Correlations among growth variables (height, dbh, volume, TSW, MS_F) also varied according to zone groupings. Correlations between height and dbh were lower for Zone 2 provenances, which were the best performing provenances in Haney conditions, compared to the others. Therefore selection based on height alone might be misleading.

Ontogenetical changes in gene expression are evident by the changes of variance components over time. Family by block (B*F/P) interactions intensified, while error variance (V_E) decreased over the years. Family within provenance variability ($V_{F/P}$) decreased and differences between provenances (V_P) increased. The magnitude of these changes seems to vary according to zone groupings. However, age − to − age correlations for height indicated significant correspondence over time. Results suggest that early selection is possible after age 7. Because this value was 5 for the previous analysis, therefore it seems that the age for selection increases as the experiment continues.

Regression analyses for height suggest that within provenance variability is not random and probably has an adaptive significance. There are well defined relationships among TSW, latitude, elevation and within provenance variability. Family variability within provenances for height increased with increasing TSW and decreased with increasing latitude.

At present, at age 16 the best performing provenances in the experiment are non-local provenances from Washington. However local provenances have greatly increased their height rankings over time. Perhaps, a strong adaptation of Douglas-fir populations to the local environment in which they evolved will become more evident as the experiment approaches the rotation age if the present trend continues.

The statistical power of many of the hypotheses tested was probably reduced due to the additional contributions to experimental error(s) by varying family-plot size and early brush invasion in the experiment. The thinnings conducted in 1979 truncated the distribution of trees remaining on a given measurement plot and unregulated the spacing in the experiment. This, therefore may have affected the interactions between families and blocks. Because both spacing and tree size were used as thinning criteria, different plot volumes may have been removed thus reducing differences among families and increasing the differences among provenances.

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