Juvenile-Mature Correlations in Selected Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] Provenances and Progenies

by

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ABSTRACT

Growth and branch characteristics of thirteen year old Douglas-fir trees were analysed with the objectives of partitioning the variance into additive and non-additive, estimating heritabilities, and estimating juvenile-mature genetic correlations. High correlations could be used in early selection to reduce the progeny testing periods with possible advantage of increasing selection differential and hence genetic gains.

Most of the traits rendered non-significant additive variance, consequently non-significant heritabilities. Among the juvenile traits, embryo class and dormancy period revealed significant genetic correlations with the thirteen year old root collar diameter (0.73 and 0.32 respectively). This highlights the possible predictability of root collar diameter correlated response as a result of early selection based on embryo class or dormancy time.

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DEDICATION

I dedicate this thesis to my late mother, Ephrance, whose love and dedication to motherhood will always be cherished and remain a source of inspiration.

1. INTRODUCTION

Forest genetics is a study of hereditary variation in forest trees (Wright, 1976). These hereditary differences are caused by genes and/or cytoplasm within the tree. They are predetermined at the time the ovule is fertilized and in that sense are opposed to differences which are caused by the external environment. As the world's population grows, the land available to forestry shrinks because of the agricultural demands, expansion of cities, and road development. Through implementing intensive forest management, forest genetics intends to improve the quality and amount of wood produced per unit area during the shortest possible time most economically.

Progeny testing is one of the earliest methods developed and is the main procedure for evaluating the genetic values of an individual (Shelbourne, 1969 and Sziklai, 1974) in forest tree breeding. Progeny testing usually produces reliable observations on yield at approximately half the rotation age, while other characteristics such as frost, disease and insect resistance could be evaluated at earlier years. For example, in case of Coastal and Interior Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] (whose rotation ages are about 80 and 120 years respectively); it may take 40-60 years before yield could be evaluated with a high degree of certainty. The long testing period in that case is inconvenient, expensive and hampers tree improvement programs. For this reason attempts are made by scientists to obtain valid early testing methods which give a definite advantage in terms of efficiency, easiness and rapidity leading to greatly increased return on capital investment (Wyk, 1976b).

To increase the rate of genetic gain; early selection is needed in most tree breeding programs (Nanson, 1967, 1968, 1970). Selection therefore is an important step in tree improvement programs because this is where the best provenances, families or individuals are chosen to establish base population for future work. Measurements made in the nursery phases of provenance or progeny tests provide the first opportunity to estimate performance of the same provenances and progenies grown in plantations to various ages. Thus, the concept of juvenile-mature correlation becomes useful.

The juvenile-mature correlation concept was initiated by Schmidt (1964) to select provenances and progenies mainly in Scots pine (Pinus silvestris L.). He suggested that future research on juvenile-mature correlations should include investigations related to chemistry of the seed and physiology of the seedlings. Prior knowledge of genetic variation, mode of inheritance and heritabilities of different traits is recommended (Sziklai, 1974) before their future performance can be assessed with a high degree of certainty. Therefore, juvenile-mature correlation expresses the relationship between qualitative and quantitative data collected at different intervals during the life cycle and depends on the strength of the genetic control. The between family correlations indicate the reliability of early selection on families, within family correlations relate to early selection of individuals within families, while total/overall correlations indicate the reliability of early mass selection (Squillace and Gansel, 1974).

Besides height, diameter at breast height (dbh), volume, stem form, and root collar diameter, crown width is an important characteristic for selection in progeny testing. Denison (1967), Dyson (1969), and Wyk (1977) pointed out that trees with smaller crowns are preferred in selection as more trees of high wood production and higher timber quality would fit on a unit area. The crown is made of branches which for selection purposes must satisfy certain conditions. Large numbers and sizes of the branches are not desired as they leave a large proportion of knotwood in logs which in turn degrades the quality of sawn timber and pulpwood. Branch characteristics respond less to genetic manipulation than stem form. In spite of this, there is a tendency to get generally finer more horizontal branches from the improved trees as compared to the plantation stock.

In light of the foregoing statements, this study was initiated to attempt to meet the following objectives:

1. To investigate variation in Douglas-fir populations and partition it into additive versus all the rest (the rest being non-additive genetic and environmental) using the following traits:
   (a) height
   (b) diameter at breast height
   (c) root collar diameter
   (d) volume
   (e) taper
   (f) crown width

(g) growing space

(h) yearly growth

(i) diameter of yearly growth

(j) number of branches in a whorl

(k) number of interwhorl branches

(l) length of branches in a whorl

(m) diameter of branches in a whorl

(n) angle of branches in a whorl

(o) length of interwhorl branches, and

(p) diameter of interwhorl branches

2. to estimate heritabilities of the above-mentioned traits, and

3. to study juvenile-mature genetic correlations in relation to their possible use to reduce the progeny testing period by early selection with possible advantage of increasing selection differential and hence genetic gains.

2. LITERATURE REVIEW

2.1 Variation

Prior to selecting individuals for a tree breeding program, the genetic variation within the base population should be known. The existence of a wide range of variation among the breeding individuals provides a basis for genetic manipulation.

Amount of variation in a trait is measured and expressed as the variance. The total variation known as the phenotypic variation (σ_P^2) is composed of genotypic (σ_G^2) and environmental variances (σ_E^2) (Falconer, 1960). The genotypic and environmental components generally cannot be estimated directly from observations on the population, though Sakai and Hatakeyama (1963) estimated them. They obtained the values from the line of best fit between observed and expected plot means using least squares. The most frequent estimates of these components are obtained from experimental populations. The relative magnitude of these components determines the genetic properties of the population, in particular the degree of resemblance between relatives.

The genetic variance is subdivided into additive, dominance and interaction variances (Falconer, 1960):

$$\underset{\text{(genetic)}}{\sigma_G^2} = \underset{\text{(additive)}}{\sigma_A^2} + \underset{\text{(dominance)}}{\sigma_D^2} + \underset{\text{(interaction)}}{\sigma_I^2}$$

The additive variance is the variance of breeding values, the most important component since it is the chief cause of resemblance between relatives and therefore the chief determinant of the observable genetic properties of the population and the response of the

population to selection (Falconer, 1960). It is the only component that can be readily estimated from observations made on the population. Therefore the important partition is into additive genetic variance versus all the rest (the rest being non-additive genetic and environmental variance).

The interaction variance is also subdivided according to whether it involves breeding values or dominance deviations (Falconer, 1960). Considering two loci, there would be three sorts of two-factor interactions. Interaction between two breeding values gives rise to additive x additive variance (σ^2_{AA}); interaction between breeding value of one locus and dominance deviation of the other gives rise to additive x dominance variance (σ^2_{AD}); and interaction between two dominance deviations gives rise to dominance x dominance variance (σ^2_{DD}). Therefore the interaction variance is expressed as $\sigma^2_I = \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD}$ + etc, where the terms designated "etc." are similar to components arising from interactions between more than two loci. The amount of variance contributed by interactions is usually very small, especially involving large numbers of loci so that they are ignored in most cases without leading to serious errors (Falconer, 1960). However, σ^2_D and σ^2_I are collectively known as non-additive variances.

Using observations of resemblance between relatives, the additive variance is estimated, enabling the partition of σ^2_A: $(\sigma^2_D + \sigma^2_I + \sigma^2_E)$. If the inbred lines are available, the environment component can be estimated, providing a partition of σ^2_G:σ^2_E. A combination of the two partitions provides estimates of the three

different parts of the phenotypic variance thus:

$$\sigma_P^2 = \sigma_A^2 : (\sigma_D^2 + \sigma_I^2) : \sigma_E^2$$

(phenotypic) (additive) (non-additive) (environmental)

Environmental variance is composed of all non-additive variance, and much of this is beyond experimental control (Falconer, 1960). Therefore, it can mainly be estimated from highly inbred lines which possess no genetic variance.

Natural populations of trees contain large amounts of variability for both quantitative and qualitative traits. Generally, genetic and environmental factors affect the quantitative traits, whereas, the qualitative ones are almost exclusively determined by genetic factors (El-Kassaby, 1980). The extent of genetic variability in natural populations has been extensively studied with respect to quantitative traits using mainly quantitative genetic methods. Some of the work that has been done on qualitative and quantitative traits is presented in the following sections.

2.1.1 Quantitative Genetic Methods

Douglas-fir cones were analysed by Willett (1963) who found their lengths ranging from 5.1 - 7.7 cm with an average of 6.0 cm. The widths ranged from 1.8 - 2.4 cm with an average of 2.1 cm. Out of the total variation observed within and between provenances for cone length only 9.8% was attributed to longitude, latitude, height, diameter at breast height (dbh), crown width, and age of parent trees. The same traits explained 13.2% of the total variation in cone width. These results postulated that other variables, genetical and

environmental; might account for the remaining part of variation.

Douglas-fir seed traits were studied and analysed by Robinson (1963) and Dunlap (1964). Their results in conjunction with Willett's (1963), confirmed Allen's (1960) findings that seed shape, colour and markings could differentiate with certainty Coast and Interior provenances.

Kiss (1971) described Douglas-fir seeds and their germinants recording these traits, endosperm and embryo class; germination, dormancy and growing periods; and height, root collar diameter (RCD) and number of branches of the 1+0 seedlings. The analyses revealed significant variation within and between provenances. The embryo class alone accounted for 97% variation in the endosperm-embryo class, indicating that the embryo can be used alone in seed classification. Latitude and elevation accounted for the largest part of variation in height, while longitude, latitude and germination period explained a large part of variation in RCD. The largest amount of variation in number of branches was attributed to longitude, latitude and dormancy period. It is worth mentioning at this point that the foregoing studies of Robinson (1963), Willett (1963), Dunlap (1964) and Kiss (1971) all dealt with earlier materials which gave rise to trees that provided data for this study.

The study of intraspecific variation in deoxyribose nucleic acids (DNA) contents of Douglas-fir by El-Lakany and Sziklai (1973) revealed intraphase nuclear volume (INV) and relative amounts of DNA to be correlated with latitude of seed source. The trend of variation in INV and DNA content appeared to be clinal with an increase from

South to North along the range of species. The coastal provenances were found to have higher amounts of DNA than the interior ones.

Whiteside et al. (1977) measured timber stiffness in Douglas-fir. They found 80% of the variation to be due to branch size and wood density.

Most of the genetic variation in height growth of juvenile Douglas-fir trees in one of the International Union of Forest Research Organization (IUFRO) provenance-progeny tests was reported by Fashler (1979) to be attributed to within provenance effects for two seed zones. However, the trend in the other two seed cones was observed in the opposite direction. The apparent contradiction may be explained by different adaptation responses of the different provenances to the progeny test site. She also obtained significant (0.01 probability level) additive variances for all the years from age two to eight. There was a slight drop in the proportion contributed by the additive variance towards the phenotypic variance as the seedlings advanced in age.

2.1.2 Qualitative Genetic Methods

Qualitative genetic methods are made possible through use of starch gel electrophoresis by which genetic heterogeneity of proteins and isozymes can easily be detected. Qualitative analysis provides information on the distribution of allelic variation in natural populations since the enzymes are composed of polypeptides and synthesized by the action of one or more structural genes. The

electrophoretic variation of enzymes can be directly related to changes in gene structure or codon sequence and always follow Mendelian segregation in ideal populations (Yang et al., 1977).

Genetic variability in natural populations of Douglas-fir was studied at the enzymatic level by Yang et al. (1977). He observed significant allelic frequency differences among the provenances examined and the genetic differences in terms of genetic identity and distance between the provenances was more or less similar to the geographic distance. Heterogeneity in general was found to decrease with increase in altitude and, to a lesser extent, latitude.

Several species showed close agreement between their electrophoretic and quantitative data in partitioning the total variation between and within population level. Among those is Douglas-fir, Yeh and O'Malley (1980) found 3% of genic variation in Coastal populations to be due to between population gene differences. They also applied the analysis of gene diversity to the work of Yang et al. (1977) and the results were strikingly similar. El-Kassaby (1980) investigated genetic variation at 27 allozyme loci and seven different seedling traits in a Coastal stand of Douglas-fir with respect to different elevational classes. The traits were number of cotyledons and needles, length of hypocotyl and epicotyl, total height and, shoot and root dry weight. He found 7% of total genetic variation attributed to differences between while 93% was due to differences within elevational classes.

In the International Union of Forest Organization (IUFRO) provenances of Sitka spruce [Picea sitchensis (Bong.) Carr], Illingworth (1978) reported that 11% of total variation for 3-year height growth of seedlings, was due to differences between the populations. Yeh and El-Kassaby (1980) used the same provenances and found that only 8% of total genetic variation was also explained by differences between the populations.

In lodgepole pine (Pinus contorta spp latifolia) Yeh and Layton (1979) pointed out that 4% and 96% of the total genetic variation was due to interpopulation and intra-population gene differences respectively. The high level of within population variation was consistent with the observations on general physiological functions (Perry and Lotan, 1977). O'Malley et al. (1979) estimated 12% of the detected genetic variation in ponderosa pine (Pinus ponderosa) to be attributed to differences between the stands.

The above studies indicate possible use of electrophoresis techniques to supplement traditional studies in assessing the amount and extent of genetic variability in forest tree species.

2.2 Heritability

Individual genes cannot ordinarily be identified in quantitative inheritance and therefore studies of quantitative traits focus on the study of phenotypic variance (σ_P^2). A proportion of the observed σ_P^2, which is due to the genetic variance (σ_G^2) is known as heritability (h^2). Heritability then determines the degree of resemblance

between relatives. Estimates of h^2s are necessary to express the reliability with which the phenotypic traits might be expected to appear in the next generation.

Warner (1952), Lerner (1958), Falconer (1960) and Hattemer (1963) list various ways of estimating heritabilities. Firstly, by the use of offspring-parent regression. Secondly, by the use of correlation between full and half-sibs. Thirdly, by using approximation of non-heritable variance from genetically uniform populations. Fourthly, by comparing phenotypic traits displayed by monozygotic as against dizygotic twins. And lastly by the use of clonal analysis which estimates h^2 in the broad sense.

Besides the above methods of estimating heritability, Sakai and Hatakeyama (1963) estimated heritabilities in Populus euramericana and Abies sachalinensis without raising progenies. They used Shirikhande's (1957) method which is based on the assumption that variation between plot means consists of one N-th of the genetic variance and one N^b-th of the environmental variance. The number of individuals in each plot is represented by N while b is a constant depending on the variation pattern of environmental conditions. The expression then is:

$$\sigma_N^2 = \frac{\sigma_G^2}{N} + \frac{\sigma_E^2}{N^b}$$

where σ_N^2 = plot variance

σ_G^2 = genotypic variance

σ_E^2 = environmental variance

b = constant whose value is between zero and one.

From these components of variance values of a number of plots, they obtained genotypic (σ^2_{Go}) and environmental (σ^2_{Eo}) variances. The and σ^2_{Eo} referred to the values of best fit between observed and expected plot means using least squares. Using this formula, $h^2 = \frac{\sigma^2_{Go}}{\sigma^2_{Go} + \sigma^2_{Eo}}$, estimates of h^2s were then obtained. The method is recommended for a population with trees of about the same age, fairly uniform spacing and without any damage or heavy thinning.

There are two types of heritabilities, the narrow sense (h^2n) and the broad sense (h^2b) (Lush, 1949; Toda, 1958; Warwick and Legates, 1979). The h^2n is the proportion of the observed phenotypic variance which is additively genetic or which is associated with differences in average breeding values. Heritability in the broad sense is considered as the sum of the additively genetic, the dominance and the interaction (known as epistasis) variances expressed as a proportion of the phenotypic variance. Expressions of the two types of h^2s are as follows:

$$h^2n = \frac{\sigma^2_A}{\sigma^2_P} = \frac{\sigma^2_A}{\sigma^2_A + \sigma^2_E}$$

$$h^2b = \frac{\sigma^2_G}{\sigma^2_P} = \frac{\sigma^2_A + \sigma^2_D + \sigma^2_I}{\sigma^2_A + \sigma^2_D + \sigma^2_I + \sigma^2_E}$$

The higher the heritability value, the stronger the trait expression is controlled by the genetic make up of the individual. On the contrary, a small h^2 value would mean that the environment is contributing more to the variation relative to the genetic factors. Hence depending on the heritability value, a breeder should be able to tell the major source of variation for the trait in question.

The most important use of h^2 is in predicting the amount of genetic improvement (gains) that might be attained under various breeding Schemes (Squillace et al., 1966). Prior knowledge of heritability assists in selecting the best breeding approach, suggests the amount of money that can justifiably be spent, indicates the amount of effort to put on a trait which is to be improved, indicates the number of trees to be selected and progeny tested, and also indicates the intensity of each phase of the breeding program. The genetic gain (ΔG) is given by the following formula $\Delta G = ih^2$ where i is the selection differential. This would be the difference between the population mean before selection and that of the selected population (Falconer, 1960; Wright, 1976).

Some of the work that has been done on h^2 estimates in forest trees is presented by Birot (1976). He worked on IUFRO Douglas-fir half-sibs from which the following h^2 estimates were reported; 0.52 for cotyledon number, 0.32 for growth cessation, 0.84 for flushing, 0.60 for height in year one and 0.46 for height in the second year. The decrease in height heritability was attributed to the possible disappearance of maternal effects or may be related to increase of competition effects.

Fashler (1979) estimated height heritabilities of juvenile Douglas-fir trees in one of IUFRO provenance-progeny tests. The h^2s ranged from 0.28 - 0.52 with an average of 0.38. The relatively high h^2 values indicated opportunities for significant improvement by selection in Douglas-fir provenances and progenies.

The trees that provided data for this study were worked on at the age of one year by Kiss (1971). He estimated heritabilities of 0.13 for endosperm embryo class, 0.08 for dormancy period, 0.11 for the growing season, 0.14 for height, 0.17 for root collar diameter, and 0.15 for the number of branches.

Heritabilities, however, have their own limitations, in that they vary within a species and between locations. In general the more uniform the environment, the higher the h^2 values. Therefore, whenever a h^2 value is given, it must refer to a particular population under particular conditions (Falconer, 1960; Zobel, 1961; Warwick and Legates, 1979). In addition h^2 is a population concept which measures the genetic variation within a population, but not the contributions of the genotype and the environment to the phenotype of the individual (Suzuki and Griffiths, 1976). Heritabilities are subject to large standard errors as a result of very large standard errors of the variances (Falkenhagen, 1972). In an attempt to improve the accuracy of the variances, the number of observations can easily become impractical.

2.3 Juvenile-Mature Correlations

The conventional methods of progeny testing in tree breeding lasts for long periods of time. For example, Coastal and Interior Douglas-fir have rotation ages of 80 and 120 years respectively and their progeny test periods usually last for 40 and 60 years respectively. Since man is impatient, seeks to accomplish in a few years

what nature may be content to wrestle with for centuries, Schmidt (1964) initiated the juvenile-mature correlation concept. This is a measure of the association between the juvenile and mature traits. If they are closely related, the performance of the mature trait can be accurately predicted from the juvenile trait. However, it is important to resist the temptation of overestimating the value of early tests.

There are three types of correlations, environmental (r_E), genetic (r_A) and phenotypic (r_p). The r_E is the one between the environmental deviations of the two traits while the r_A is the one between the genotypic values. In principle it is not easy to partition variance into non-additive components and therefore strictly speaking the r_E consists of correlation of environmental deviations together with non-additive genetic deviations (Falconer, 1960). Hence r_A is the correlation of additive genetic deviations. A combination of r_A and r_E gives rise to the observable phenotypic correlation (r_p). The relationship is expressed as $r_p = h_x h_y r_A + e_x e_y r_E$

where x = the juvenile trait

y = the mature trait

h = the square root of the heritability

$e = \sqrt{1-h^2}$

If both traits have low h^2s then the phenotypic correlation is determined mainly by the r_E. In case of high h^2s the r_A is the most important.

Genetic and environmental source of variation affect the trait through different physiological mechanisms thus causing the two correlations to be different in magnitude and sometimes different in sign. Hence the magnitude and sign of the r_A cannot be determined from the phenotypic correlation alone. Genetic correlations can be estimated in 3 different ways (Falconer, 1960). Firstly, by use of resemblance between relatives thus:

$$r_A = \frac{Cov_{xy}}{\sqrt{\sigma^2_x \, \sigma^2_y}}$$

where Cov = covariance component

σ^2 = variance component

Secondly, by the use of offspring-parent relationship thus:

$$r_A = \frac{Cov_{xy}}{\sqrt{Cov_{xx} \, Cov_{yy}}}$$

where Cov_{xy} = Cross-covariance component

Cov_{xx} and Cov_{yy} = the offspring-parent covariances of each trait separately.

And thirdly by using response to selection thus:

$$r_A = \sqrt{\frac{CR_x}{R_x} \cdot \frac{CR_y}{R_y}}$$

where CR = correlated response (one in which selection is primarily for one trait, but due to a strong genetic correlation a change occurs in a second trait).

R = response of a trait when selected directly.

The basic problem in tree breeding is to determine the extent to which early selection is effective at the utilization stage and when it must be carried out to achieve sufficient correlated gains (Nanson, 1976). The existing experimental plots established in the past which are almost a unique source of information on juvenile-mature relationship have been concerned primarily with provenances and have lacked proper replication and randomization. Therefore, correlation estimates were based on means of individuals of one plot resulting in high environmental effects and overestimation of genetic gains. However, experimental plots established more recently have the advantage (over old ones) that they incorporate sufficient replication and randomization, resulting in less environmental effects and better estimate genetic gains.

Most of the juvenile-mature correlation work in tree breeding has been primarily concerned with phenotypic correlations. The work that has been done in Douglas-fir (species) includes that of Sziklai (1964). Heights of 132-day-old full-sib progenies were correlated with their heights at 4 years of age obtaining a very high correlation of 0.89. Results indicated that performance of these trees at age 4 could have been predicted at the age of 132 days.

Kiss (1971) correlated a number of variables with one year old seedling traits. The variables were those related to location of parent trees, parent tree, cone, seed and germinant's traits. Seedling traits included height, root collar diameter and number of branches. Strong correlations were observed between seed weight,

endosperm-embryo class and seedling height. Heavier seeds have been observed to give rise to faster growing seedlings which do not necessarily become potential winners (Sluder, 1979). Therefore, selection is not recommended to be based on seed weight as it might result in seedlings with a survival and growth disadvantage.

Height correlations for the ages 5, 10, 12, 15, 18, 23, 28, 33, 40 and 53 years were estimated (Namkoong et al., 1972) in one of the Douglas-fir plantations. The correlations declined for any given age when correlated with successively older ages. The results pointed to the possibility of selecting at age 28 for height performance at age 53 ($r = 0.82$). Since age 53 is in the range of half the rotation age (40-60 years), then selection based on height performance at age 28 might be a good predictor of height performance at the end of the rotation age.

Haddock et al. (1976) obtained very high correlations (close to one) between average total heights of 2-year-old seedlings and their heights at 5, 6, 7, 8 and 11 years of age. Hence height performance at all these ages could have been predicted at age two. However, caution should be taken since it is well known that during early stages, the genetic traits change quite often (Namkoong et al., 1972; Squillace and Gansel, 1974; Sziklai, 1974).

Autocorrelations of heights at the ages of 4, 5, 6 and 7 were estimated in one of IUFRO's Douglas-fir provenance-progeny test by Fashler (1979). The trend of the results was similar to that of Namkoong et al. (1972). Continuation of the research was recommended

to determine whether these high correlations would persist in later ages. Persistance of the high correlations would indicate preference of early selection as a predictor of late performance with minimal risks of losing potential winners.

Similar type of work (juvenile-mature phenotypic correlations) has been done in Pinaceae (Wakeley, 1971). His study involved slash pine (Pinus elliottii, Engelm), loblolly pine (Pinus taeda L.), longleaf pine (Pinus echinata Mill). The correlations were of total heights (at 3, 4, 5, 8, 10, 15 and 20 years) and diameter at breast height (at 10, 15 and 20 years) with corresponding measurements at age 30. The correlation coefficients obtained were relatively higher for diameters compared to heights. They were increasing with age, similar to Namkoong et al's (1972) and Fashler's (1979) results.

Squillace and Gansel (1974) correlated growth traits (height, diameter at breast height, and volume) and oleoresin yield recorded measurements of slash pine at age 25 with those of earlier years 3, 8, 14 and 18. Growth trait correlations increased with age while those of oleoresin yield were moderate ($r = 0.61$). Depending on the age of selection, the highest genetic height gains were realised around 9 and 10 years which led to the conclusion that less than mature trees can be selected for mature performance. Therefore, a breeder is advised to consider the additional cost of short generation intervals when making a final decision. However, the extra developmental costs could be outweighed by the increased genetic gains per year.

Juvenile-mature correlation coefficients were presented relating heights and diameters of ponderosa pine (Pinus ponderosa Laos.) and western white pine (Pinus monticola Dougl.) of early ages to heights and diameters at ages ranging up 50 years (Steinhoff, 1974). It is recommended that in both species evaluation of provenance trials or progeny tests would not be very reliable at ages less than 15-20 years though limited selection for culling the poorest provenances or families could begin at about 10 years of age.

Mean heights of slash pine and loblolly pine progenies in the nursery were correlated with mean heights of the same families in 5 year old plantations (La Farge, 1975). Only 12% of the correlations were significant indicating that future performance should not be predicted at the nursery stage. Therefore, field plantations should be established regardless of nursery performance.

Nanson (1976), working with Scots pine (Pinus silvestris), Norway spruce (Picea abies) and Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco], found that heights in the nursery, but more importantly in the field between ages 5 and 10 were good indicators of wood production at the end of the rotation age. Selection for height growth was then suggested to be suitable between ages 5 and 10 while 10 and 20 could be optimal for form and branching characteristics, and perhaps still later for disease peculiar to the mature ages.

Meier and Goggans (1977a,b) observed low significant correlations between the cortical monoterpenes of the eight year old Virginia pine (Pinus virginiana Mill.) and commercially important characteristics

namely height and diameter. Therefore, monoterpenes would probably not be valuable as an indirect selection tool.

Besides juvenile-mature correlation work in Douglas-fir and Pinaceae, other species have also been dealt with. Wyk (1976a,b) examined a complete dialled cross of Eucalyptus grandis. He correlated data relating to total height, root collar diameter, dbh, volume seedling dry weight, rate of growth, and number, length and diameter of branches. The results revealed strong relationships between these traits, but greenhouse results showed a generally poor relationship with nursery results. However, the data revealed maternal effects to be significant at two months and seemed to disappear in older trees indicating possible effects of embryo-endosperm viability. Maternal effects are most often considered of little importance in tree improvement programs. Barnes (1973) has confirmed this by showing that these effects are negligible in most traits studied in Pinus patula especially in long term studies.

Height, diameter and volume of the 8-year-old clones of eastern cottonwood (Populus deltoides Bartr.) were correlated with those of the earlier ages (Randall, 1977). Phenotypic and genotypic correlations obtained increased with increase in age.

Nepevue et al. (1978) correlated wood density of one year old stems of Populus nigra and Populus euramericana clones. The correlations were high indicating that early selection of clones with high wood density is possible without endangering yield. However, no significant correlation was observed between density and girth

increment. Similar results had been reported by Reck and Sziklai (1970) from their studies of wood quality (ring width, wood density and dry matter content) in Douglas-fir. Results implied that future wood quality can be assessed using wood samples from increment cores with the exception of the latest five rings. Therefore, progeny tests for estimating these genetic parameters should commence with trees old enough (at least 8 years) to provide wood samples with more than five annual rings.

Ring width and wood density in a 30-year-old stand of Norway spruce was correlated with the juvenile measurements. The correlations revealed the possible predictability of mature wood density from early juvenile stages.

Work supporting the above-mentioned studies of the feasibility of early selection of superior progenies is presented by Ying and Morgenstern (1979). They obtained high height correlations at ages 8 and 22 in white spruce [Picea glauca (Moench) Voss].

Lambeth (1980) reviewed and analysed juvenile-mature phenotypic correlations from the literature and found it more predictable than what could have appeared to be the case in the first place. Age - age correlations were estimated with reasonable accuracy, with the exception of very young ages (1-3 years), by a single regression equation which applied to several species and studies. Optimum selection ages recommended were 5, 6, 6, 7, 7, 8 and 8 years for 20, 25, 30, 35, 40, 45 and 50 years of economic rotations in that order.

Besides work done on juvenile-mature correlations in trees, similar studies have been attempted in other fields. Only to mention

a few, poultry breeders found a correlation between the weight of the egg and that of the chick at later ages. Funk et al. (1930) indicated that chicks were very highly variable individuals while Jaap and Morris (1937) pointed out that growth to 8 weeks of age appeared to be separate and not necessarily related to adult weight.

Human geneticists have also found that trends evident in early stages may not be correlated to those of other ages. Bock et al. (1973) developed a model to describe human growth that includes two logistic functions, the first accounting for a component for prepubertial growth, which continues in reduced degree until maturity, while the second accounts for the contribution of the adolescent spurt.

Considering Schmidt's (1927, 1930, 1935, 1936 and 1964) suggestion cited earlier, and Sziklai's (1974) observation concerning prior knowledge of the pattern of genetic variation, mode of inheritance, and heritabilities of the different traits, future performance can be assessed with a high degree of certainty. Repetitive experiments using various species taking into account a number of economically important traits will make it possible to draw valid conclusions for each species. Use of juvenile-mature correlations will lead to short generation interval permitting the testing of more families and more individuals which would in turn permit greater selection intensity and realization of greater genetic gains (Nanson, 1970).

3. MATERIALS AND METHODS

The trees that provided data for this study represent open pollinated progenies of 7 Douglas-fir provenances from British Columbia. Details of location of these provenances are presented in Figure 1 and Table 1. Historical information on these trees is given by Kiss (1971).

Originally there were 29 Douglas-fir provenances from British Columbia and one in Alberta from which dominant trees were selected. The cones and seeds from these trees were studied and the information is available from Robinson (1963), Willett (1963) and Dunlap (1964). In 1966, seedlings from 21 provenances consisting of five dominant trees each, were raised in the nursery at the University of British Columbia. All the information concerning provenance location, plus tree, cone, seed, germinant and seedling traits was compiled by Kiss (1971).

Seedlings were then transplanted into large containers of about 210 cm^3 in volume. The containers are known as "French Jiffy Pots" made of compressed peat. In 1967, they were planted out in three different permanent locations, as 1+0 seedlings with the containers in situ. The three locations are Lens Creek on Vancouver Island, the University Research Forest in Haney, and at the South Campus Research nursery of the University of British Columbia (UBC). The layout of provenances planted on South Campus at UBC is shown in Appendix 1, and samples for this study were obtained from this location. The

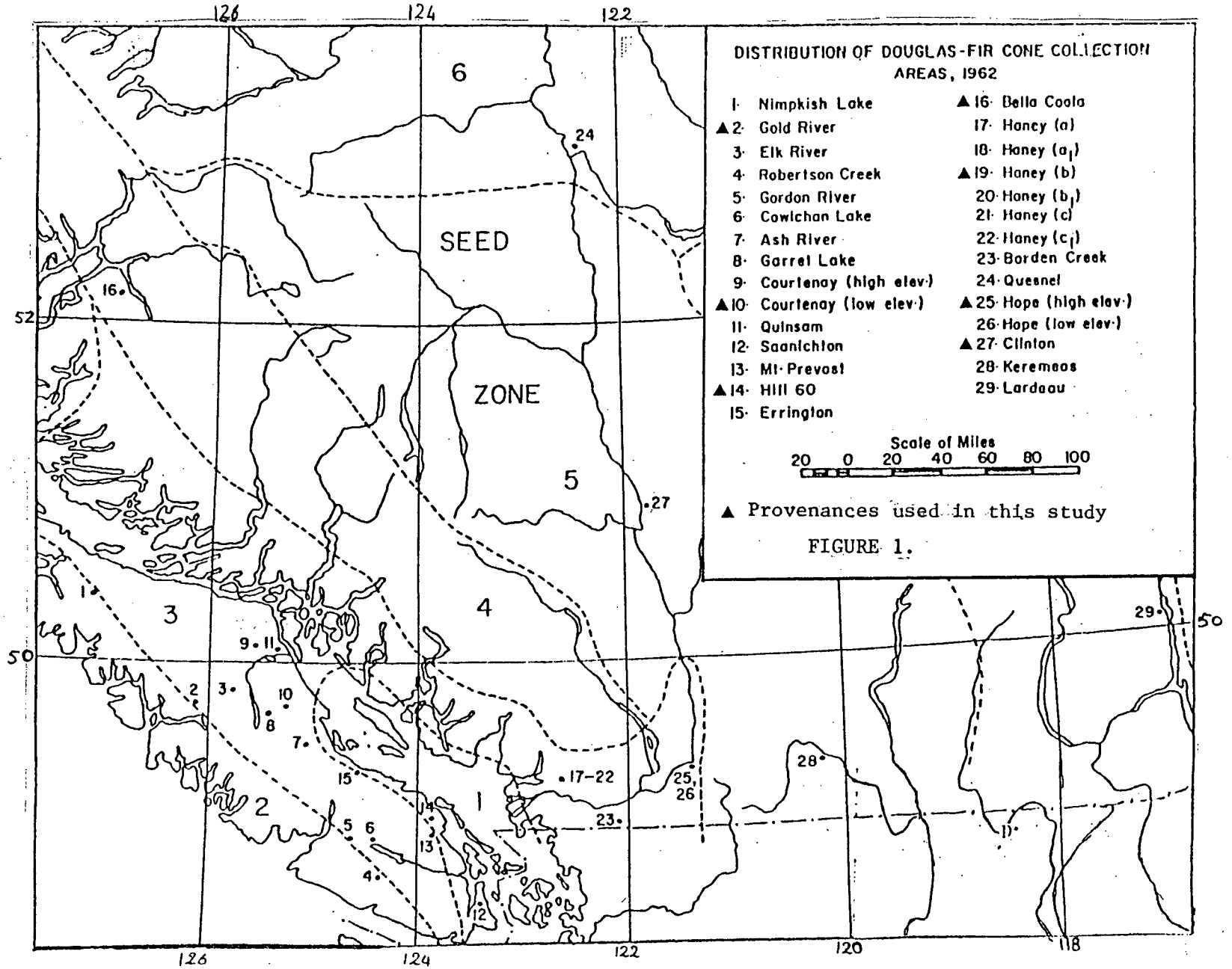
126
124
122
120
118
52
50
6
SEED
ZONE
5
4
3
2
1
DISTRIBUTION OF DOUGLAS-FIR CONE COLLECTION AREAS, 1962
1. Nimpkish Lake
▲2. Gold River
3. Elk River
4. Robertson Creek
5. Gordon River
6. Cowichan Lake
7. Ash River
8. Garrel Lake
9. Courtenay (high elev.)
▲10. Courtenay (low elev.)
11. Quinsam
12. Saanichton
13. Mt. Prevost
▲14. Hill 60
15. Errington
▲16. Bella Coola
17. Haney (a)
18. Haney (a_1)
▲19. Haney (b)
20. Haney (b_1)
21. Haney (c)
22. Haney (c_1)
23. Borden Creek
24. Quesnel
▲25. Hope (high elev.)
26. Hope (low elev.)
▲27. Clinton
28. Keremeos
29. Lardeau
Scale of Miles
20 0 20 40 60 80 100
▲ Provenances used in this study

FIGURE 1.

TABLE 1. Locations of Douglas-fir cone collection areas

Code	Provenance area	Longitude degrees	Latitude degrees	Elevation degrees	Collection agency
1	Nimpkish Lake	127.0	50.4	180	Can.For. Pro.
2	Gold River*	126.1	49.9	900	Tahsis Co.
3	Elk River	125.9	49.9	1000	B.C.F.S.
4	Robertson°	124.2	48.7	-	B.C.F.S.
5	Gordon River°	124.5	48.9	-	B.C.F.S.
6	Cowichan Lake	124.5	48.8	1750	B.C.F.P.
7	Ash River	125.1	49.5	1150	MB & PR Co.
8	Garret Lake	125.6	50.1	1000	B.C.F.S.
9	Courtney (high elev.)	125.2	49.6	2050	Crown Zell.
10	Courtney (low elev.)*	125.3	50.0	400	Crown Zell.
11	Quinsam	125.3	50.0	300	B.C.F.S.
12	Saanichton	123.4	48.5	250	B.C.F.S.
13	Mt. Prevost	123.7	48.9	1400	B.C.F.S.
14	Hill-60*	123.4	49.4	700	B.C.F.S.
15	Errington	124.5	49.4	450	U.B.C.
16	Bella Coola*	127.0	52.2	20	B.C.F.S.
17	U.B.C. Forest A°	122.6	49.3	-	U.B.C.
18	U.B.C. Forest Check A°	122.6	49.3	-	U.B.C.
19	U.B.C. Forest B*	122.6	49.3	1600	U.B.C.
20	U.B.C. Forest Check B Δ	122.6	49.3	1300	U.B.C.
21	U.B.C. Forest C	122.6	49.3	650	U.B.C.
22	U.B.C. Forest Check C°	122.6	49.3	-	U.B.C.
23	Borden Creek	121.7	49.0	800	B.C.F.S.
24	Quesnel Area Δ	122.7	53.3	2000	U.B.C.
24b	Quesnel Area 2°	122.7	53.3	-	U.B.C.
25	Hope (high elev.)*	121.4	49.4	750	U.B.C.
26	Hope (low elev.) Δ	121.4	49.4	250	U.B.C.
27	Clinton*	121.3	51.2	3200	U.B.C.
28	Keremeos°	120.3	49.4	-	U.B.C.
29	Lardeau	117.0	50.2	1800	Koot. F.P.
30	Kananaskis	115.0	51.0	5050	Kan. F.E.S.

* Provenances selected for this study.

Δ Provenances that did not provide enough seed to replicate the experiment.

° Provenances that did not provide enough seed to warrant their incorporation in the experiment.

plantation site at South Campus of UBC is of about site index one, with 1550 mm average rainfall, minimum and maximum daily temperatures of -12° and 38°C respectively.

The experiment at South Campus Research Nursery of UBC was laid down in a randomized complete block design with five treatments and eight replications for each treatment. The blocks refer to provenances, while the treatments refer to dominant trees from each provenance. Replications represent seedlings from each dominant tree. In this study seedlings from a dominant tree are called a family and the individual seedlings are referred to as trees.

At the time of data collection for this study (May 1980), trees were 14-year-old with a survival percentage of 41.25. From the remaining provenances, seven (2, 10, 14, 16, 19, 25 and 27) could provide at least four families each and three trees from each family and therefore, were selected. The families and the trees within each family were randomly selected after eliminating trees that were dying, stunted, crooked and forked. Hence observations were taken on a total of 84 trees. A summary of the traits recorded on each tree is presented in Table 2. It is worth noting that, all measurements did not include the growth of 1980 (the 14th year). Therefore throughout the discussion of this study, trees will be referred to as "13-year-old trees".

Using Huber's formula (Husch et al., 1972), individual measurements of yearly growth and diameter of yearly growth, the volume was computed section by section and then summed to obtain volume for a whole tree. Huber's formula states that $V = hA_m$ where

TABLE 2. Traits recorded on the 13-year-old Douglas-fir trees

No.	Trait	Unit	Remarks
1	Total height	m	up to 1979's growth
2	DBH	cm	at 1.3 m high
3	Root collar diameter	cm	at ground level
4	Volume	m^3	-
5	Taper	-	-
6	Crown width	m	-
7	Growing space	m^2	-
8	Yearly growth	m	-
9	Yearly growth diameter	cm	-
10	No. of branches in a whorl	-	-
11	Length of branches in a whorl	m	of the three longest branches in each whorl
12	Diameter of branches in a whorl	cm	
13	Angle of branches in a whorl	degrees	
14	No. of interwhorl branches	-	-
15	Length of interwhorl branches	m	of the three longest branches in each interwhorl
16	Diameter of interwhorl branches	cm	

V = volume

h = height or length of the section

A_m = middle cross-sectional area of the section.

The taper was calculated as an index using the following formula (Kozak, 1980)

$$\text{Taper} = \frac{\text{dbh} - \text{last diameter}}{\text{length}}$$

where last diameter refers to mid diameter of the youngest whorl and length being the distance between the two diameters.

Crown width was measured as the sum of the lengths of the two longest branches on opposite sides (Denison, 1967; Dyson, 1969; Wyk, 1977). In addition, growing space available for each tree was computed because of the non-uniform tree spacing (Appendix 1).

The branch lengths, diameters and angles measured were restricted to the three longest branches in each whorl and interwhorl. The diameters were taken very close to the main stem. The angles were recorded only on the whorl branches since the interwhorls do not last long before they are shed.

3.1 Variation

The data was analysed using the ANOVAR, a computer package available from the University of British Columbia Computing Center. ANOVAR performs analysis of variance and covariance for a wide variety of problems both with equal and unequal number of observations. In this study it was used to perform both analysis of variance (ANOVA) and covariance (ANACOVA) for a 2-way nested design.

To begin with, the provenances were subdivided into four groups according to their locations. Provenance 2 and 16 represented the Wet Coastal Region, while 10 and 14 represented the Dry Coastal Region; 19 and 25 representing the Wet Mainland and finally, 27 representing the Interior Mainland. Analysis of variance carried out on the first three locations, (since they were balanced) revealed non-significant differences among locations. Therefore, they were all pooled together and analysed as the seven provenances.

Due to the large number of traits (Table 2) involved in this study and different sources of variation, the analyses were done in three subsets. The first subset involved ANACOVA on height, diameter at breast height (dbh), root collar diameter (RCD), volume, taper and crown width using growing space as a covariate. The ANACOVA table and the expected mean squares (EMS) based on the following random effects linear model:

$$Y_{ijk} = \mu + \tau_i + \beta_{j(i)} + \varepsilon_{k(ij)}$$

where

Y_{ijk} = measurement of the k^{th} tree in the j^{th} family of the i^{th} provenance

μ = overall mean

τ_i = effect due to provenances

$\beta_{j(i)}$ = effect due to families nested within provenances

$\varepsilon_{k(ij)}$ = residual variation $(0, \sigma_E)$

i = number of provenances $i = 1,.....,p$

j = number of families nested within provenances $j=1,.....,f$

k = number of trees nested within families and provenances

$$k = 1,\ldots\ldots,t$$

are presented in Table 3.

The second subset involved ANOVA on number of branches in a whorl and an interwhorl, yearly growth and diameter of yearly growth. The ANOVA table and EMS based on the following random effects linear model:

$$Y_{ijkl} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \varepsilon_{l(ijk)}$$

where

Y_{ijkl} = measurement of the l^{th} whorl on the k^{th} tree of the j^{th} family in the i^{th} provenance

τ_i = effect due to provenances

$\beta_{j(i)}$ = effect due to families nested within provenance

$\gamma_{k(ij)}$ = effect due to trees nested within family within provenance

$\varepsilon_{l(ijk)}$ = residual variation $(0, \sigma_E^2)$

i = number of provenances i = 1,.....,p

j = number of familes nested within provenances j = 1,.....,f

k = number of trees nested within families and provenances k = 1,.....,t

l = number of whorls nested within trees, families and provenances l = 1,....,w

are presented in Table 4. The four uppermost whorls (except for that of 1979) uniform for all trees, were selected for this study. All of these whorls were still young, had all the interwhorl branches intact, and they were counted despite the fact that some would drop off soon afterwards.

TABLE 3. Analysis of covariance and expected mean squares (EMS) for height, dbh, RCD, volume, taper and crown width

Source of variation	df	MS	EMS
Provenance	p-1	MS_I	$\sigma_E^2 + t\sigma_F^2 + ft\sigma_p^2$
Families within provenance	p(f-1)	MS_{II}	$\sigma_E^2 + t\sigma_F^2$
Residual	pf(t-1)	MS_{III}	σ_E^2
Total	pft-1		

where: σ_p^2 = variance among provenances

$$= \frac{MS_I - MS_{II}}{ft}$$

σ_F^2 = variance among families nested within provenances

$$= \frac{MS_{II} - MS_{III}}{t}$$

σ_E^2 = residual component of variation

$$= MS_{III}$$

TABLE 4. Analysis of variance and expected mean square (EMS) on a number of branches in a whorl and an interwhorl, yearly growth and diameter of yearly growth

Source of variation	df	MS	EMS
Provenance	p-1	MS_I	$\sigma_E^2 + w\sigma_T^2 + tw\sigma_F^2 + ftw\sigma_p^2$
Families within provenance	p(f-1)	MS_{II}	$\sigma_E^2 + w\sigma_T^2 + tw\sigma_F^2$
Trees with family, within provenance	pf(t-1)	MS_{III}	$\sigma_E^2 + w\sigma_T^2$
Residual	pft(w-1)	MS_{IV}	σ_E^2
Total	pftw-1		

where: σ_p^2 = variance among provenances

$$= \frac{MS_I - MS_{II}}{ftw}$$

σ_F^2 = variance among families nested within provenances

$$= \frac{MS_{II} - MS_{III}}{tw}$$

σ_T^2 = variance among trees nested within families within provenances

$$= \frac{MS_{III} - MS_{IV}}{w}$$

σ_E^2 = residual component of variation

$$= MS_{IV}$$

The third subset of analyses consisted of ANOVA on whorl and interwhorl branch lengths, diameters and angles. The ANOVA table and EMS based on the following mixed effects linear model:

$$Y_{ijklm} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \alpha_{l(ijk)} + \varepsilon_{m(ijkl)}$$

where

Y_{ijklm} = measurement of the m^{th} branch of the 1^{th} whorl on the k^{th} tree of the j^{th} family in the i^{th} provenance.

τ_i = effect due to provenance

$\beta_{j(i)}$ = effect due to families nested within provenances

$\gamma_{k(ij)}$ = effect due to trees nested within families within provenances

$\alpha_{l(ijk)}$ = effect due to whorls nested within trees, families and provenances

$\varepsilon_{m(ijkl)}$ = residual variation $(0, \sigma_E^2)$

i = number of provenances i = 1,.....,p

j = number of families nested within provenances j = 1,.....,f

k = number of trees nested within families and provenances k = 1,....,t

l = number of whorls nested within trees, families and provenances l = 1,.....,w

m = number of branches nested within whorls, trees, families and provenances m = 1,.....,b

are given in Table 5.

TABLE 5. Analysis of variance and expected mean squares (EMS) on whorl and interwhorl branch lengths, diameters and angles

Source of variation	df	MS	EMS
Provenance	p-1	MS_I	$\sigma_E^2 + bw\sigma_T^2 + bwt\sigma_F^2 + bwtf\sigma_p^2$
Families within provenance	p(f-1)	MS_{II}	$\sigma_E^2 + bw\sigma_T^2 + bwt\sigma_F^2$
Trees within families, within provenances	pf(t-1)	MS_{III}	$\sigma_E^2 + bw\sigma_T^2$
Whorls within trees, families and provenances	pft(w-1)	MS_{IV}	$\sigma_E^2 + b\theta_w$
Residual	pftw(b-1)	MS_V	σ_E^2
Total	pftwb-1		

where: σ_p^2 = variance among provenances

$$= \frac{MS_I - MS_{II}}{bwtf}$$

σ_F^2 = variance among families nested within provenances

$$= \frac{MS_{II} - MS_{III}}{bwt}$$

σ_T^2 = variance among trees nested within families within provenances

$$= \frac{MS_{III} - MS_{IV}}{bw}$$

θ_w = variance among whorls within trees within families within provenances

$$= \frac{MS_{IV} - MS_V}{b}$$

θ = variance of a fixed term (Anderson and Bancroft 1952)

σ_E^2 = residual component of variation

$= MS_V$

3.2 Heritability

Heritability calculations were based on the assumption that open pollinated progenies within families were half-sibs. Therefore σ_F^2 is an estimate of a quarter of additive genetic variation (σ_A^2) so that $\sigma_A^2 = 4\sigma_F^2$ (Falconer, 1960). The assumption regarding the half-sib is partially incorrect as it is difficult to admit that there are so many pollen sources contributing to a progeny as the number of individuals within the progeny test (Birot, 1976). However, the probability is high for an individual to be pollinated by immediate neighbours. Therefore, a certain rate of full-sibs exists within a provenance and this may overestimate the heritabilities. Pollination between related trees may occur but since the rate of self pollination is low (Sorenson 1971, 1973 and El-Kassaby, 1980), this factor can be ignored. Based on the above discussion, heritabilities estimated in this study are the maximum possible values. The narrow sence heritabilities for height, dbh, root collar diameter, volume, taper and crown width were given by the following formula

$$h^2 = \frac{4\sigma_F^2}{\sigma_P^2 + \sigma_F^2 + \sigma_E^2}$$

(from Table 3). Those of whorl and interwhorl branches, yearly growths and their diameters were given by

$$h^2 = \frac{4\sigma_F^2}{\sigma_P^2 + \sigma_F^2 + \sigma_T^2 + \sigma_E^2}$$

(from Table 4). Heritabilities for whorl and interwhorl branches, lengths, diameters and angles were obtained using the following formula

$$h^2 = \frac{4\sigma_F^2}{\sigma_P^2 + \sigma_F^2 + \sigma_T^2 + \sigma_E^2}$$

(from Table 5).

3.3 Juvenile-mature Correlations

A tree breeder's major concern in juvenile-mature correlation work, is the response of a trait at later ages or at maturity as a result of selection on the juvenile trait. This is known as a correlated response (CR) to selection. The response of the correlated character can be predicted from the following formula $CR = ih_x h_y r_A \sigma_{py}$ if the genetic correlation and the heritabilities of the two traits are known (Falconer, 1960).

Where i = selection intensity of the juvenile trait

h = square root of the heritability

x = juvenile trait

y = trait at later ages or at maturity

r_A = genetic correlations between traits x and y

σpy = phenotypic standard deviation of trait y.

A more detailed discussion of genetic correlations is given on pages 16 and 17 of the literature review. Therefore, this study aimed at estimating genetic correlations between all the earlier and later recorded traits. The earlier ones consisted of characteristics of

cones, seeds, germinants and 1+0 seedlings and these were available from Kiss' (1971) work. Traits concerning parent tree locations and their characteristics were left out because they do not bear any genetic relationship for additive variance estimation. The later traits are those recorded from the 13-year-old trees by the author in May 1980. A listing of the early, juvenile and 13-year-old tree traits, is presented in Table 6.

Analysis of variance using the ANOVAR package program was carried out on all the earlier traits besides the later ones. It was only that trait whose family source of variation showed significant differences, that was considered for genetic correlations (Peterson, 1981). The significance of the additive variance depended on the significance of the F value of the corresponding family component. The argument was based on the nature of derivation of the correlated response (page 38). Non-significant additive variance give rise to non-significant genetic correlation which in turn renders the correlated response meaningless. In addition non-siginificant additive variance give rise to non-significant heritabilities which also renders the correlated response meaningless. With the assumption of half-sibs, the significant estimated family component (σ^2_F) was multiplied by four (since it estimates a quarter of the additive variance) to obtain the estimated additive variance (σ^2_A). Individual observations of the pair to be correlated were then added and analysed to estimate the variance of the two traits (σ^2_{x+y}). This variance was used in the following formula to obtain a covariance of the two traits (Cov_{xy})

$$\sigma^2_{x+y} = \sigma^2_x + \sigma^2_y + 2Cov_{xy}$$

TABLE 6: Early, juvenile and 13-year-old tree traits used in the juvenile-mature genetic correlations

No.	Traits	Units
	Cone and seed measurements	
1	Length of cone	mm
2	Width of cone	mm
3	Length of seed	mm
4	Width of seed	mm
5	Length of seed wing	mm
6	Width of seed wing	mm
7	A thousand seed weight	mg
8	No. seeds per cone	-
9	No. filled seed per cone	-
10	Endosperm class	-
11	Embryo class	-
12	Endosperm-embryo	-
	Germinants	
13	Germination period	weeks
14	Dormancy time	weeks
15	Growing season	weeks
	1+0 seedling measurements	
16	Height	m
17	Root collar diameter	cm
18	No branches	-
	Measurements at age 13	
19	Height	m
20	DBH	cm
21	Root collar diameter	cm
22	Volume	m^3
23	Taper	-
24	Crown width	m
25	Yearly growth	m
26	Yearly growth diameter	cm
27	No. of branches in a whorl	-
28	No. of interwhorl branches	-
29	Length of branches in a whorl	m
30	Diameter of branches in a whorl	cm
31	Angle of branches in a whorl	degrees
32	Length of interwhorl branches	m
33	Diameter of interwhorl branches	cm

where σ^2_x and σ^2_x are the individual estimated additive variances. The above estimated variances and covariance were then used in the following formula to obtain the genetic correlations (r_A).

$$r_A = r_{xy} = \frac{Cov_{xy}}{\sqrt{\sigma^2_x . \sigma^2_y}}$$

4. RESULTS AND DISCUSSION

4.1 Variation and Heritability

Analysis of covariance on height, diameter at breast height (dbh), root collar diameter (RCD), volume, taper and crown width resulted in significant variation only among provenances except for RCD and crown width (Table 7). Considering the total phenotypic variation in height, 7.0% was attributed to differences among families within provenances (σ^2_F) which is an estimate of a quarter of the additive genetic variance (Table 8). Approximately 39.0% of the variation was due to differences among provenances, while the rest of it 54.0% was due to residual component (Table 8). Besides the variation contributed by the family component, the rest is considered to be due to the remaining three quarters of the additive effects, non-additive effects and environmental effects, where non-additive effects consists of dominance and epistatic (interaction between non-allelic genes) effects. However, there was an attempt of minimizing the environmental component in the experimental design by randomizing provenances and families within provenances on the experimental site.

Analysis of heights of the same trees at age one (Kiss, 1971) revealed significant variation among both provenances and families. In comparison with other studies also conducted in other Douglas-fir provenances, Birot (1976), Christophe and Birot (1979) and Fashler (1979) observed significant variation among provenances and families. El-Kassaby (1980) determined the significance mainly among families.

TABLE 7. Heritability estimates and F ratios (for all sources of variation) from the analyses of covariance (traits 1-6) and variance (traits 7-15) for the 15 measured traits of the 13-year-old Douglas-fir trees

Traits	Heritability (h^2)	Source of variation			
		Provenance σ^2_P	Families σ^2_F	Trees σ^2_T	Whorls σ^2_W
1. Height	0.28	7.29 **	1.39 ns	-	-
2. Diameter at breast height	0.41	3.02 *	1.43 ns	-	-
3. Root collar diameter	0.72	4.61 **	2.06 *	-	-
4. Volume	0.52	3.47 *	1.60 ns	-	-
5. Taper	0.36	3.56 *	1.39 ns	-	-
6. Crown width	0.66	2.47 ns	1.70 ns	-	-
7. Yearly growth (YRG)	0.01	7.00 **	1.35 ns	0.26 ns	-
8. YRG diameter	0.03	3.19 *	1.43 ns	0.93 ns	-
9. No. of branches in a whorl	0.08	0.98 ns	1.15 ns	2.13 *	-
10. No. of interwhorl branches	0.17	1.17 ns	1.30 ns	2.51 *	-
11. Length of branches in a whorl	0.02	3.04 *	1.15 ns	18.63 **	44.27 **
12. Diameter of branches in a whorl	0.00	6.29 *	0.49 ns	8.59 *	5.14 *
13. Angle of branches in a whorl	0.30	1.86 ns	2.15 *	4.60 **	2.42 **
14. Length of interwhorl branches	0.00	2.34 ns	0.82 ns	11.36 **	15.68 **
15. Diameter of interwhorl branches	0.10	2.40 ns	1.39 ns	11.32 **	9.59 **

* Significant at 0.05 probability level.
** Significant at 0.01 probability level.
ns Not significant.

TABLE 8. Heritability estimates and percentages of various variance components making up the total phenotypic variation. σ^2_F = a family component estimating 1/4 of additive variance. σ^2_P, σ^2_T, and σ^2_E = provenance, tree and residual components respectively, estimating the rest of the genetic variance together with the environmental variance.

	Traits	Heritability (h^2)	% contribution of each component towards total phenotypic variation			
			σ^2_P	σ^2_F	σ^2_T	σ^2_E
1.	Height	0.28	39.0	7.0	-	54.0
2.	Diameter at breast height	0.41	17.4	10.4	-	72.2
3.	Root collar diameter	0.72	31.4	17.9	-	50.7
4.	Volume	0.52	21.5	13.1	-	65.4
5.	Taper	0.36	20.8	9.1	-	70.1
6.	Crown width	0.66	14.5	16.6	-	68.9
7.	Yearly growth (YRG)	0.01	1.3	0.2	0.0	98.5
8.	YRG diameter	0.03	1.8	0.8	0.0	97.4
9.	No. of branches in a whorl	0.08	0.0	2.0	21.5	76.5
10.	No. of interwhorl branches	0.17	0.8	4.3	26.1	68.8
11.	Length of branches in a whorl	0.02	10.6	2.6	51.6	35.2
12.	Diameter of branches in a whorl	0.00	8.7	0.0	35.4	56.9
13.	Angle of branches in a whorl	0.30	3.9	9.7	19.9	66.5
14.	Length of interwhorl branches	0.00	7.9	0.0	0.0	92.1
15.	Diameter of interwhorl branches	0.10	7.2	5.7	40.2	46.9

There is a fairly weak genetic control on height because of the relatively low heritability value of 0.28 (Table 7). The same heritability estimated by Kiss (1971) at the age of one year, was only 0.14. It is rather inappropriate to compare the two values since Kiss' sample was far larger than that of the present study. However, results from the literature suggest higher heritability values during the nursery phases and/or the early years of outplanting. This is due to the influence of maternal effects and uniformly favourable environment (Barnes, 1973). Birot (1976) together with Christophe and Birot (1979), for instance reported heritability values of 0.60, 0.46, 0.30 and 0.26 for heights of Douglas-fir trees at ages 1, 2, 3 and 4 in that order. The decrease in heritabilities was attributed to the disappearance of maternal effects and possibly onset of competition. Furthermore, in the same species, Fashler (1979) reported average heritability values of 0.42 and 0.34 for ages 1 and 7 respectively.

The family component contributed 10.4% towards the total phenotypic variation in dbh (Table 8). Differences among provenances accounted for 17.4% of the variation while residual component accounted for 72.2%. Selection of best individuals within the best provenances for dbh is likely to yield reasonable genetic gains because of the strong genetic control ($h^2 = 0.41$).

The root collar diameter showed significant variation in both among provenances and families (Table 7). Out of the total phenotypic variation, 17.9% is attributed to the family component, while 31.4% is due to differences among provenances and 50.7% due to residual component

(Table 8). A lot more genetic gains would be expected from RCD selection of the best individuals within the best families, because of the high heritability value (0.72) as compared to dbh (0.41). A similar analysis (by Kiss, 1971) on RCD of the same trees at age one revealed the same variation as obtained in this study with a heritability of 0.17 except that his sample was much larger than the one used in this study.

Both volume and taper showed significant variation only among provenances (Table 7). The volume showed 21.5% provenance contribution towards the total phenotypic variation (Table 8). The family component contributed 13.1% while 65.4% was due to residual. The heritability estimate (0.52) showed a fairly strong genetic control. The taper showed 20.8% of the phenotypic variation to come from the differences among provenances. The family component contributed 9.1% while 70.1% was due to residual. The heritability estimated was 0.36. However, when making a decision concerning volume and taper, caution should be taken in view of the probable influence of other factors on these traits. For example, the two traits are functions of height and diameter, influenced by spacing in the field, site quality geographical location and climate.

Crown width showed no significant variation among provenances and families whose contributions were 14.5% and 16.6% respectively towards the total phenotypic variation. The remaining 68.9% was due to the residual. There is a strong genetic control ($h^2 = 0.66$) on crown width despite the fact that no significant variation exists among the

partitioned sources. According to the results selection concerning crown width should be based on individual trees within families within provenances.

For yearly growth and diameter of yearly growth analysis of variance revealed significant variation only among provenances (Table 7). Contributions towards total phenotypic variation by the family components are very small 0.2% and 0.8% for yearly growth and diameter of yearly growth respectively (Table 8). Low additive genetic variances resulted in low estimates of heritabilities of 0.01 and 0.03 in the same order, suggesting the possibility of eliminating these traits from consideration for selection as breeding traits.

Significant variation for number of branches in a whorl and number of interwhorl branches was observed only among trees (Table 7). There was a very small contribution towards the total phenotypic variation by the family component resulting in very low heritability estimates. The h^2s were 0.08 and 0.17 for number of branches in a whorl and interwhorl branches respectively. Again these two traits would be precluded from consideration for selection as breeding traits.

The length and diameter of branches in a whorl showed significant variation among provenances, trees and whorls (Table 7). Only 2.6% of the total phenotypic variation in length of branches in a whorl was due to differences among families, giving rise to a low heritability estimate of 0.02 (Table 8). The diameter did not show any additive effects towards the phenotypic variation hence resulting in zero heritability estimate (Table 8). Once again it would be advisable to

preclude these two traits from consideration for selection as breeding traits.

The analysis of angles of branches in a whorl revealed significant variation among families, trees and whorls (Table 7). There was a fair contribution of the family component towards the total phenotypic variation (9.7%) and a significant heritability estimate of 0.3 (Table 8). Hence selection for branch angles based on good trees among the best families is likely to give a reasonable response in terms of genetic gains.

Significant variation for length and diameter of interwhorl branches was observed among trees and whorls only (Table 7). Similar to many branch characteristics, contributions towards the total phenotypic variation by the family components are low, 0% for the lengths and 5.7% for the diameters (Table 8). This resulted in low estimates of heritabilities, 0.0 for the lengths and 0.1 for the diameters. Because of low heritabilities, these traits are also recommended to be precluded from consideration for selection as breeding traits in these particular provenances.

Collectively, branch characteristics except for the angles, have shown low heritability estimates, which is in agreement with Dyson's (1969) findings. Because of the low heritability estimates, branch characteristics are not normally used as a basis for selection as breeding traits. However, there is a tendency for improved trees to carry fine horizontal branches.

4.3 Juvenile-mature Correlations

Partitioning of the variance into additive and the rest (the rest being non-additive and environmental) revealed that most of the additive variances were not significant except for the RCD and the angle of whorl branches (Table 7). It is possible that most of these traits showed non-significant additive variances because of the relatively small sample size of only 7 provenances, 4 families per provenance and 3 trees per family. As recommended by Peterson (1981), it was only RCD and branch angles that were considered for genetic correlations since they showed significant additive variances.

Analyses of variance of all the earlier traits revealed only embryo class and dormancy time to have significant additive variances. Therefore, these were the ones considered for genetic correlations. Results from the analyses of variance and the corresponding heritabilities are presented in Table 9. Embryos were classified into four categories according to their visibility on X-ray photographs in relation to seed sizes (Sziklai, 1964). Class one consisted of absent embryos while class two embryo was less than 50% of the seed length. Classes three and four consisted of embryos 50-70% and over 75% of the seed length respectively. Out of the 84 trees used in this study 10% were in embryo class two, 19% in class three and 71% in class four. The dormancy time was determined by calculating number of days between dates of sowing and seedling entering dormancy. The heritability estimates for embryo class was 0.5 while 1.21 was for the dormancy time. The overestimate of dormancy time heritability could be due to

TABLE 9. Heritability estimates and F ratios (for each source of variation) from the analyses of variance of the 18 early and juvenile traits of the sample used in this study

Trait	Heritability	Source of variation: provenance σ^2_P	Source of variation: family σ^2_F
1. Length of cone	Analyses were impossible because only mean values were given per family		
2. Width of cone			
3. Length of seed			
4. Width of seed			
5. Length of seed wing			
6. Width of seed wing			
7. A thousand seed weight			
8. No. seeds per cone			
9. No. filled seeds per cone			
10. Endosperm class	0.0	3.00 *	0.67 ns
11. Embryo class	0.5	6.22 **	1.75 *
12. Endosperm-embryo class	0.32	6.74 *	1.44 ns
13. Germination period	0.35	4.71 *	1.41 ns
14. Dormancy time	1.21	2.47 ns	2.74 *
15. Growing season	0.0	14.42 *	0.76 ns
16. Height	0.0	10.54 **	0.97 ns
17. Root collar diameter	0.0	9.11 **	0.84 ns
18. No. branches	0.31	5.78 *	1.39 ns

* Significant at 0.05 probability level.
** Significant at 0.01 probability level.
ns Not significant.

the assumption of half-sibs when it could have been full-sibs and also could be due to sampling errors. Allen and Owens (1972) observed pollen grains in Douglas-fir, to be dispersed by wind, larger than most other conifers, and lacks wings or bladders. As a result, they have relatively short dispersal distance. A small fraction of pollen is dispersed a distance further than 5-10 times the tree height. Because of the above reasons the chances of full-sibs increase. The sample size also could have had an effect.

The estimated genetic correlation coefficient between the embryo class and the RCD was relatively high and positive (0.73). The high correlation suggests higher chances of accurate prediction of the correlated response of RCD at age 13 from the size of the seed embryo. The bigger the embryo, the bigger the RCD is likely to be. These results suggest the possibility of carrying out selection at the seed stage. Obviously this would be a great relief to tree breeders in terms of reducing the progeny testing periods. Since the majority of trees used in this study (71%) belonged to the highest embryo class (4), it is advisable to select if possible only those seeds with embryo class four. Such early selection would mean increasing selection intensity which in conjunction with high heritabilities yields high genetic gains. It is well known that RCD is highly and positively correlated with dbh and height, so that any selection imposed on RCD, indirectly result in a similar response in dbh and height. It is worth mentioning at this point that this is the first time, embryo

class is being used in juvenile-mature correlation studies. The author consider it an important finding worth pursuing in future.

The genetic correlation coefficient estimated between dormancy time and RCD was 0.32, suggesting again that correlated response of RCD at age 13 can be predicted using the dormancy time. Results imply that the longer the growing period, the larger the RCD would be at age 13. Selection at this very early seedling stage would also facilitate the tree breeding program in the same way as selection at the seed stage. However, selection at the seed stage is bound to be less costly in terms of money and time as compared to selection at the seedling stage. According to the results it is obvious that the accuracy of prediction from dormancy time will not be as precise as that from the embryo class. Therefore, it is better to use embryo class if it could be obtained. Similar to embryo class dormancy time also is being used for the first time in connection with juvenile-mature correlation studies.

The angles of whorl branches also showed significant additive variance, but they were not correlated with the embryo class, dormancy time and RCD. This is because the angles were analysed on a bigger model to which the others could not be expanded. However, there is almost a perfect relationship ($r = 1.06$) between the embryo class and dormancy time. The overestimate could be due to the assumption of half-sibs when it could have been full-sibs, possibly the small sample size and may be the sampling errors. Significant and high genetic correlation coefficients obtained from this study suggest that embryo class, dormancy time and RCD share a certain set of genes.

Juvenile-mature correlation work has been primarily concerned with the seedling traits and those of the advanced ages. Where the seed weight (weight of seed coat, endosperm and embryo) has been considered, it was found to be related with only the early ages' performance. These effects were concluded to be maternal effects which last for short periods of time, and are of very little importance in long lived organisms like forest trees (Barnes, 1973; Yao, 1971). However, this study has revealed that pre-seedling traits could also be used in predicting a correlated response at advanced ages.

5. CONCLUSION AND RECOMMENDATIONS

Results of this study suggest that dbh, root collar diameter (RCD), volume, taper, and angles of whorl branches have reasonable amounts of additive variance consequently fairly large heritabilities. In fact if the heritabilities are real (since most of them are not significant) selection based on these traits would provide considerable genetic gains. Selection of all the above-mentioned traits except RCD and angles of whorl branches should be based on best individuals in the best provenances. In case of the two exceptions; which showed significant additive variance and heritabilities; selection should be based on the best individuals within families. In the final analysis the best families are noted for more seed collection and possibly cuttings. On the whole, yearly growth, diameter of yearly growth, and branch characteristics showed very low quantities of additive variances consequently low heritabilities. However, further studies may be necessary to substantiate these findings.

Results from genetic juvenile-mature correlation analyses revealed the possibility of predicting RCD performance at age 13 from the embryo class since a strong relationship ($r_A = 0.73$) was found. The same performance can be predicted from the dormancy time of the germinants but with less precision as a result of the weaker relationship ($r_A = 0.32$).

Past investigations in forest genetics have largely been concerned with revealing the genetic architecture of species, among them the extent of variation, mode of inheritance and estimates of

heritability to measure potential gains of selection for the different traits. It is therefore clear from this study that genetic correlations between juvenile and premature or mature traits offer better alternative criteria for selection. In view of this, it is strongly recommended to continue investigations on genetic juvenile-mature correlations of certain tree characteristics in order to accumulate data that might lead to establishing reliable and quantitatively testable criteria for future selection programs in tree breeding. It would be particularly useful to carry out the analyses presented here on data obtained from the other two remaining areas, namely Haney and Lens Creek. The incorporation of larger sample sizes in future investigations should lead to more accurate estimates of genetic parameters. The recording of various traits on a yearly basis should aid in understanding possible trends of variation in these characteristics. It is further recommended that more experiments be established which include information on seed and seedling characteristics as these appear to be a possible basis for future prediction of growth performance.

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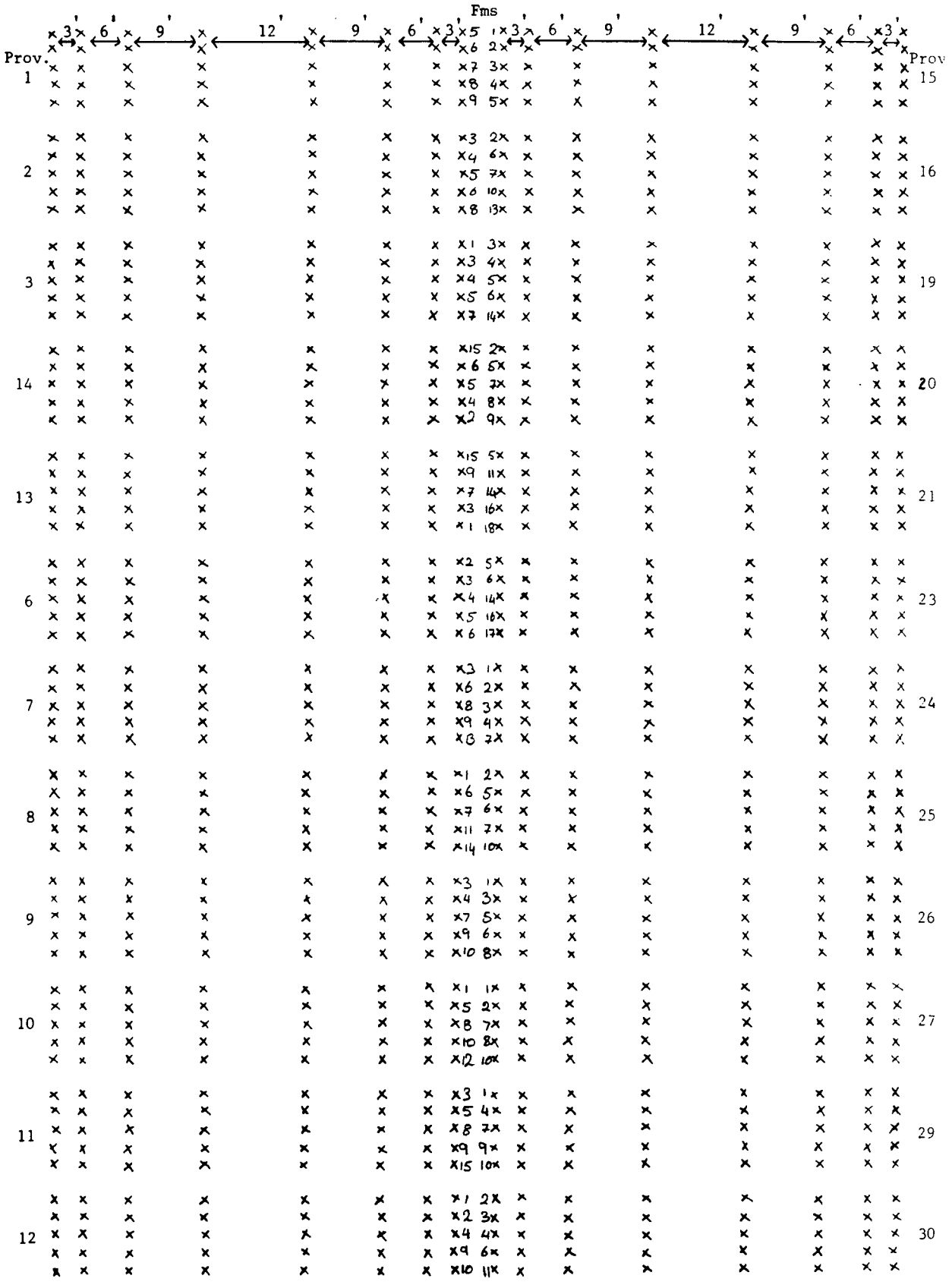
Experimental design for provenance - progeny test of Douglas-fir at the South Campus Research Nursery (University of British Columbia)



KEY

Prov - Provenances
Fms - Families
Trees are 3' within rows
× - Individual trees