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Variation of Genetic Parameters of *Pinus contorta* var. *latifolia* (Engelm.) in Central British Columbia: Some Evolutionary Implications for Multiple-Trait Selection

by

ALVIN D. YANCHUK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES A[illegible] RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Variation of Genetic Parameters of *Pinus contorta* var. *latifolia* (Engelm.) in Central British Columbia: Some Evolutionary Implications for Multiple-Trait Selection submitted by ALVIN D. YANCHUK in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Bruce P. Dancik
Supervisor
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Kenneth O. Higginbotham
....
....

....
External Examiner

Date 29 April 1986

Abstract

Patterns of genetic variation for wood, form, disease and growth traits in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) were examined at one test site using open-pollinated families from 24 provenances representing six geographic zones in British Columbia. Clinal patterns of variation were noted for traits affecting biomass production, wood specific gravity and wood moisture content. Most other traits showed large provenance variation, but geographic trends were not evident.

When families were pooled across all geographic zones, the heritability estimates for specific gravity and branch angle were over 0.40. Other traits showing moderate heritabilities were fibre length, wood moisture content and bark thickness. Genetic correlations among traits were particularly high between stalactiform blister rust and western gall rust. The correlation between specific gravity and diameter was highly negative, but that between specific gravity and height was close to zero. Genetic correlations among branching characters indicated that selection for larger branch angles should bring about a change to shorter branches with smaller branch diameter.

Selection for most traits, except specific gravity and branch angle, would yield highest gains by selection at the zone or provenance level. Multiple-trait index selection, with all traits equally weighted, indicated that: 1) a tradeoff in volume will occur at the expense of specific

gravity, 2) branch angle increases and branch diameter will decrease, and 3) stem crook tends to increase. Multiple-trait selection using combined selection indices showed that provenance information influenced the index coefficients to a large degree, particularly for growth traits.

A comparison of genetic parameters from different geographic zones indicated that differences in the amounts of additive genetic variance and covariance exist among populations. Heritabilities of specific gravity from five geographic zones were not significantly different; however, heritabilities for height growth ranged from 0.0 to over 1.0, depending on the analysis of variance model used to obtain variance components. Genetic correlations among traits, as expected, had large standard errors; however, differences in genetic correlations among populations were present between specific gravity and diameter, and height and branch diameter. Consideration of evolutionary forces that can reduce or increase amounts of additive genetic variance presents a case that "pooling" populations to obtain genetic parameters may not be wise, particularly for 1) prediction of genetic gains and 2) use in optimum index construction. From the aspect of multiple-population breeding strategies, identifying populations with unique and desirable genetic relationships already provided by nature may be an efficient way of breeding for multiple-traits.

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There are many people to thank in an undertaking such as this. Without Keith Illingworth's interest in lodgepole pine, this material would not have been established and therefore available for study. The staff at the Red Rock Seed Orchard and Nursery were extremely helpful during the nine months I was there. Also, thanks must be given to Dr. F. Yeh for arranging the study with British Columbia Ministry of Forests material, and for the enormous amount of time and help he provided. I would also like to thank Dr. B. Dancik for his support in solving the multitude of small problems that I encountered. Financial support of the Canadian Forest Service block grant to the University of Alberta, arranged by Dr. B.P. Dancik, as well as his editorial comments on the thesis, are much appreciated. Editorial and technical suggestions provided by Dr. K. Higginbotham and Dr. P. Blenis were very helpful. I must also mention that it was extremely valuable and pleasurable to have Dr. J.P. van Buijtenen as the external examiner on my committee. I would like to thank him for taking time out his busy schedule to come up to Edmonton.

This thesis is dedicated to my wife, Brenda, my son, Nicholas, and to the memories of an old friend, Branko Sedmak.

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1. Introduction

1.1 General

Lodgepole pine (*Pinus contorta* Dougl.) possesses a number of attributes that make it desirable for intensive management and improvement. Ecologically, lodgepole pine is considered to be: 1) a seral species with low shade tolerance, 2) fast growing, particularly as a young tree, and 3) capable of growth on almost any forest site (Pfister and Daubenmire 1975). Evidence of its wide adaptability to a variety of forest habitats is apparent from its success both as an exotic in Scandanavia and from provenance studies established within its native range. Martinsson (1980) estimated that since 1976, 50 million seedlings of lodgepole pine have been planted annually in Sweden. Lodgepole pine is expected to produce up to 50 percent more wood per hectare than the native Scots pine (*P. sylvestris* L.) in Sweden (Remrod 1977). In British Columbia and Idaho, sources of lodgepole pine have been successfully transferred two degrees of latitude north and 200 meters higher in elevation (Illingworth 1975, Illingworth *et al.* 1985, Rehfeldt 1985a).

Lodgepole pine has an extensive natural range from Alaska south to California and east through Alberta, Wyoming and Colorado (Fig. 1). Surveys of natural variation of lodgepole pine have shown large population differences for a number of morphological and biochemical traits (Critchfield 1957, Forrest 1981, Wheeler *et al.* 1983, Yeh *et al.* 1985).

Page 2 has been removed due to copyright restrictions. The information on this page contained the following: a range map of lodgepole pine contained in E.L. Little (1971). Atlas of United States Trees, Vol. 1. Conifers and Important Hardwoods. USDA Misc. Publ. 1146

Four subspecies of *Pinus contorta* have been proposed (Critchfield 1957), but by far the most extensive and commercially important of the four subspecies is lodgepole pine (*P. contorta var. latifolia* Engelm.). All further references to lodgepole pine will be to this variety.

The expansion of the pulp industry in interior British Columbia and Alberta has led to increased harvesting and planting of lodgepole pine (Guernsey and Dobie 1966, Illingworth 1975). Planting of lodgepole pine started in British Columbia in the mid-1960's, and by 1972, eight million seedlings were planted annually in the interior of the province (Illingworth 1975). In Alberta, over 3 million seedlings of lodgepole pine are planted annually, and this planting is expected to increase '. In both provinces, tree improvement programs were initiated in the mid 1970's, indicating a commitment in western Canada for tree improvement to play an important part in the intensive management of lodgepole pine.

1.2 Tree Improvement Strategies

The objective of most tree improvement programs is to improve the forest for better yields and better wood quality (Zobel and Talbert 1984). Therefore, the quality of wood, along with other important growth and form traits, should be considered for improvement.

'pers. com., Kerkoff, L. Alberta Forest Service, Reforestation and Reclamation Branch. Edmonton, Alberta.

Volume growth and form have been the principal traits selected for in most tree improvement programs. An improvement in growth rate and form traits, however, does not necessarily result in improvement in wood quality (Zobel and Kellison 1978). Furthermore, because plantation forests have shorter rotations, a larger proportion of juvenile wood likely will be present in these forests. Compared to mature wood, juvenile wood[1] of conifers typically is characterized by lower wood density (specific gravity), shorter tracheids, larger fibril angle, higher shrinkage and lower strength (Bendsten 1978). Therefore, in tree improvement programs it is appropriate to consider wood properties, in order to minimize the loss in wood quality in short rotation plantations.

Properties of wood such as specific gravity, fibre length, cellulose content, spiral grain and fibril angle have been investigated in determining the overall quality of wood in conifers. Of these traits, specific gravity has usually been considered the most important (Nicholls *et al.* 1963, Porterfield *et al.* 1975, van Buijtenen *et al.* 1975, Zobel 1976). Although it is often considered a single trait, a complex of characteristics (primarily summerwood percentage, wall thickness and cell diameter) contribute to the overall specific gravity of wood (Zobel 1961).

The economic aspects of wood quality in tree improvement programs have also been documented (Kellogg

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[1] Larson (1962a) referred to juvenile wood as being primarily crown-formed wood.

1982). Van Buijtenen *et al.* (1975) indicated that at short rotation ages, breeding for high wood density was always desirable for kraft pulp. However, breeding for low wood density was important especially when burst specifications had to be met. These economic considerations that affect an overall selection strategy for wood density make it difficult for a breeder to decide how much emphasis should be placed on particular wood quality traits. This will be especially difficult if tree improvement programs should also attempt to emphasize uniformity of properties, which result in freedom from spiral grain, knots, compression wood, straightness and branch characteristics (Bendsten 1978, Blair *et al.* 1974, Zobel *et al.* 1982), in addition to growth. Other traits, such as resistance to diseases and insects, are important because they will affect long-term survival and growth. Therefore, tree improvement programs need to examine how important traits interact with each other under artificial selection and how the resulting plants will respond to the various environments in which they are to be located.

1.3 Provenance Testing

When progeny of provenances are planted in different environments, adaptation is the initial criteria being screened for. Adaptation is generally inferred from survival, vigor and growth. Often, other traits of economic interest are investigated to determine if clinal or ecotypic patterns of variation have a genetic basis.

Clinal patterns of variation indicate that selection for optimal characters has occurred as a result of environmental conditions that vary continuously along geographic gradients. Within local populations, selection for characters for adaptation should be maintained by stabilizing and/or directional selection; however, migration could tend to counteract this through the introduction of new genes from neighboring populations (Stern and Roche 1974). Discontinuous provenance variation (ecotypic variation) arises from discontinuous environments that reflect adaptive strategies of populations. The nature of this variation depends primarily upon the distribution of environments, selection pressure, migration rate and founder effects (Stern and Roche 1974). These patterns are important because they may indicate geographic regions where a species exhibits traits which may be more desirable for some economic purpose. Rehfeldt (1985a) found that lodgepole pine populations from high elevations were susceptible to needle cast infections when transferred to low elevations, and provenances from relatively mild environments had the best growth potential, but suffered the most snow damage, when planted at high elevations. Generally, adaptation of lodgepole pine to biotic and abiotic environments revealed clinal patterns of differentiation that were elevationally steep but geographically gentle (i.e., latitude and longitude; Rehfeldt 1985a). In lodgepole pine provenance tests in Sweden, rate of survival and height growth generally increased with increasing latitude of seed origin (Lindgren 1983). Most of the traits indicative of adaptation showed clinal patterns of variation. Lindgren (1983) found that some provenances did not perform well anywhere in Sweden, while others performed well over a wide range of environments. Because certain provenances exhibited better growth and quality attributes in one or more environments, larger gains were possible by selecting the more stable provenances.

Studies of many tree species have shown these opposing results: 1) populations of trees that show genetic stability across a wide range of environments, or 2) populations that exhibit significant genotype x environment interactions. As an example of the first category, a population of loblolly pine (*Pinus taeda* L.) originating along the Mississippi River flood plain was shown to be consistently more resistant to fusiform rust than loblolly pine from other locations (Wells *et al*. 1982). An example of stability of growth comes from a study by Evans and Thor (1971) who reported that virginia pine (*P. virginiana* Mill.) from three stands consistently outgrew other sources at most of the six test sites.

Although provenance x environment interaction components may be significant, the interaction component usually accounts for only a small percentage of the variation (e.g., King 1965). In most cases a high degree of stability is present, and interactions, if present, appear to be random and unpredictable for particular traits. Wakeley (1961) reported that latitude of provenance with five-year height growth was negatively correlated in southern plantations and positively correlated in northern plantations in four species of southern pine.

Provenance x environment interactions may develop as trees mature. Mirov *et al*. (1961) found that two provenances of 12-year-old ponderosa pine (*P. ponderosa* Laws) from different elevations grew best at all planting sites. Callaham and Liddicoet (1961), in the same plantations at 20 years, found that progeny from high elevation sources showed best growth at two lower elevation planting sites. Examination of provenance x environment interactions appear to be the most reliable means of indicating the genetic structure of populations and response of populations in different environments.

Comstock and Moll (1961), Gardner (1961) and Matzinger (1961) concluded that as genetic diversity of crop plants increases, the relative magnitude of genotype x environment interactions decreases. Forest trees, compared to other organisms, would be considered as having to exist in course-grained environments (Levins 1968), since they must grow and reproduce in one location over a long period of time. Bradshaw (1965) discussed the importance of phenotypic flexibility (plasticity) for adaptation and evolution of populations; however, phenotypic plasticity must have a genetic basis (Waddington 1967). Therefore, trees could be expetted to be buffered by some "genetic flexibility", which is defined as the ability of a population or a species to adapt to new environments by changing its genetic composition (Stern and Roche 1974). Although selection is expected to reduce genetic variability, a number of adaptive mechanisms can maintain genetic diversity (Lerner 1954).

Namkoong (1980) stated that the special adaptation exhibited by populations variable in their adaptation could be used profitably. Those provenances which exhibit extraordinary characters on sites which have been identified as unique in their environmental characteristics could be earmarked for those specific sites. However, sources or populations that are genetically variable and stable enough to adapt to many environments may be the material that is required for tree breeding, strictly from an economic and practical standpoint. Although this generalist approach may not yield the best gains on specific sites, seed orchard strategies and management would be less difficult and the populations may be more stable in the long run. The decision of which approach to take for provenance transfer can only be made after: 1) more data are available on the types of environments or site classes in a breeding zone, and 2) more is known about the effect management practices will have on the sites and environments where these provenances are to be planted.

1.4 Breeding and Genetic Variation

The observed variation in a trait is referred to as the phenotypic variance, and can be attributed to three components: genetic variance, environmental variance and the variance caused by the interaction of genotype and environment. The improvement of metric or quantitative traits is dependent upon genetic variances associated with each trait in the population. The genetic variance can be partitioned into three components: 1) genetic variance due to additive gene effects, 2) genetic variance due to dominance gene effects (intra-allelic interactions), and 3) genetic variance due to epistatic gene effects (inter-allelic interactions)(Hanson 1961). The relative importance of heredity in determining phenotypic values is called the heritability of a character (Falconer 1981). Heritability in the broad sense considers total genetic variance in relation to phenotypic variability. Heritability in the narrow sense considers only the additive portion of the genetic variability in relation to phenotypic variability (Hanson 1961). Narrow-sense heritability determines the degree of resemblance between relatives and is of the greatest importance in breeding programs (Falconer 1981). This ratio of additive variance to total variance indicates what type of breeding program is appropriate for a particular trait. For example, Jett *et al.* (1977) suggested wood density has a large proportion of additive genetic variation, but other traits (e.g., percentage of cellulose) have very little. Therefore, little gain will be obtained for these traits with little additive genetic variance from a breeding system such as that of a seedling or multi-clonal seed orchard. Although the magnitude of this heritability dictates the gains that can be expected, the magnitude of variation among individuals in the population (phenotypic variance) and the intensity of selection also influence the expected responses in a trait. If heritability is low for the trait of interest, increasing the intensity of selection or selecting at a level which exhibits higher heritabilities (e.g., family selection) are two alternatives to increase expected gain for a trait.

Estimates of heritability of traits in forest trees require careful interpretation. The number of test sites, the number of families, the kind of propagules used (i.e., sexually-~~or~~-clonally generated), and the age of the material all influence the validity and usefulness of a heritability estimate. Stonecypher (1966) obtained a heritability of 0.2 for height growth of two-year-old loblolly pine at one site and 0.04 at another. Stonecypher (1966) attributed this to a small number of families grown in single environments, Narrow-sense heritabilities estimated at one test site are only valid if genotype x environment interactions are assumed to be zero or negligible for a particular trait (Jacquard 1983). Genotype x environment interactions arise when a genotype or genetically similar group (e.g., provenances) change rankings across test sites, or when the genotypic variance differs among environments. When only one site is used, there is no way to observe a change in rank (the particular test site may be of the type where the genotype behaves differently for the trait of interest), or a change in the genotypic variance. Also, if the experiment is not adequately replicated within or across test sites, and family numbers and size are small, the accuracy and the reliability of the heritability estimates is reduced large standard errors of the estimate).

Material typically used in narrow-sense heritability studies arises from either controlled matings or from random matings among trees (i.e., open pollination). Progeny derived from controlled matings are assumed to be full-sibs because parental identity is known. Progeny derived by random matings are assumed to be half-sibs because only the female parent is known; paternal (or pollen) parents are considered random, which typically may be the case from seed collections in wild stands. If this open-pollinated material is used in a heritability study, progeny are erroneously assumed ~~to be~~ half-sibs (Wright 1976); however, depending on the level of inbreeding (past related matings), selfing (self-fertilization) and sibling structure (which can arise from a pollen parent fertilizing a number of selected trees or progeny within a tree), family variation estimates range between one-quarter and one-half of the additive genetic variance (Cheliak *et al*. 1985, Namkoong 1966, Squillace and Bengston 1961). This bias, that may be included in open-pollinated seed, tends to overestimate heritability (Squillace 1974).

Age of the material from which heritability estimates are derived is also important. In young plants the maternal effect of seed weight variation may influence early results (Squillace *et al.* 1967). As the same plants become older, increased environmental variances or decreasing additive genetic variance can reduce the heritability estimates. For example, Kriebel *et al.* (1972) showed that the heritability estimate for height growth decreased to essentially zero as crown closure occurred in a test of coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Wearstler (1979) showed that family effects became non-significant at certain levels of crown competition in young loblolly pine.

Relationships between traits can be described in the form of phenotypic or genetic correlations. Phenotypic correlation indicates the relationship between two traits based on the observed variation among individuals. This variation is the sum of environmental and genetic influences acting on both characters. Genetic correlations, which arise from linkages and pleiotropy (Simmonds 1979), indicate the direction and relative change in one character due to a change brought about by selection of another character (i.e., indirect selection). The magnitude of this correlation is strongly influenced by heritabilities associated with each trait (Falconer 1981). Therefore, when a number of traits are being considered for improvement, these genetic interactions between traits may be of primary concern.

1.5 Genetic Structures

From the previous discussion, it is apparent that genetic variability at the population level should exist, and that the heritability of a particular trait determines what progress can be expected from selection. Many studies in forest trees have investigated among-population variability (i.e., provenance tests), and then obtained estimates of heritability across populations. While this approach of "pooling" populations to examine the genetic parameters of interest is common, it may not be wise since heritabilities are influenced by gene frequencies and therefore may differ from one population to another (Falconer 1981). Electrophoretic studies in conifers have shown that most of the variation at isozyme loci could be found within populations using average single-locus estimators such as Nei's (1973) G-statistic (e.g., Guries and Ledig 1982, Millar 1983, Yeh and Layton 1979, etc.). Multilocus analysis of allozyme variation in conifers, which accounts for interactions among loci not observable using average statistics, revealed a rich structure of genetic variation (Yeh *et al*. 1985). This genetic variation was consistent with geography and results of provenance test data (Yeh *et al*. 1985). Many other studies of the genetic architecture of variable characters indicate maintenance of stores of potential genetic variability in the form of linked polygene complexes (Simmonds 1979).

Slatkin (1981) showed that with the additive model of a quantitative character, extinction and recolonization of demes (ecotypes) can lead to significant genetic variation. Also, the average population-level genetic differences in a quantitative character can be established and maintained in local populations; this is referred to as "populational heritability". Along with the heritability affecting the rate of evolution for a trait, the genetic covariance can influence the direction of evolution (Lande 1979). According to Falconer (1981), traits that are genetically correlated will evolve together. One would expect traits that must interact in development or in the performance of a common function to show interactions in fitness and, therefore, develop some optimal correlation, whether it is zero or one (Cheverud 1982). However, Lande (1980) suggested that developmentally and functionally independent traits can evolve non-zero genetic correlations through stochastic processes. Therefore, considering the evidence available from biochemical and provenance studies, it is likely that geographic and climatic factors may have produced populations of different genetic variability (i.e., additive genetic variance and covariances) for traits of fitness as well as traits not directly related to fitness. Evolutionary (i.e., selective) forces driving or developing different genetic structures among stands or geographic areas should be due to stabilizing selection for interacting traits of fitness, drift and founder effects (i.e., non-selective) for non-fitness traits (Cheverud 1982).

One approach to examining this question is a geographic comparison of genetic parameters (Arnold 1981). Birot and Christophe (1983) noted large differences in genetic parameters estimated from different provenances of Douglas-fir and sitka spruce (*Picea sitchensis* [Bong.]Carr.). These geographic comparisons of heritabilities are interesting from a theoretical and a practical standpoint. Those traits that exhibit relatively constant proportions of additive genetic variance among geographic zones may have remained constant by mutation and recombination (Arnold 1981). If selection is weak in nature, as has been suggested by Lewontin (1974), then it is likely that genetic variance will be conserved (Lande 1976). Estimates of genetic parameters may provide a better insight into the expected stability of traits from different populations over simple phenotypic observations (Arnold 1981). From a practical aspect, this information would allow a unique opportunity to capitalize on genetic attributes of certain populations for sub-line or sub-population breeding (Namkoong 1976; 1980). Although the practicality of such an approach to breeding may be limited, populations exhibiting different stand or family structures for desirable traits (along with desirable correlations among traits) may already be present in nature and could perhaps be utilized.

1.6 Selection Schemes

Falconer (1981) defined expected response or gain as the product of selection intensity, an appropriate phenotypic variance and a heritability. Genetic gains can occur at several levels. For example, selection of the best progeny from the best families in the best populations results in gains at three levels. Calculation of expected gains for multi-stage selection such as this is computed by treating each level of improvement independently and adding the gains at each of the levels (e.g., Namkoong *et al.* 1966, Shelbourne 1969a). If more than one trait is being selected, a method of ranking each individual on the basis of all traits must be used. Hazel and Lush (1942) described three different approaches for this type of selection: 1) tandem selection, 2) independent culling levels, and 3) selection indices.

In tandem selection, a single trait in the population is improved by selection each generation. Therefore, new generations need to be quickly developed if a number of traits are important in the breeding program. This approach is acceptable for annual plants and animals where generation times are short (i.e., one to five years). Independent culling level selection is approached by defining a minimum acceptable level for each trait, and discontinuing the use of those in the breeding population which do not meet all criteria. If a number of traits are being selected simultaneously, difficulties will arise simply because it is unlikely that enough individuals will meet the acceptable minimum standard for all traits. Selection indices rank each individual by using a linear combination of breeding information for the traits of interest. Stonecypher (1970) concluded that in forest tree breeding, selection indices were the most applicable of the three approaches, because generation times are too long to warrant the application of the other two methods in multiple-trait breeding. This method theoretically yields improvement of economic value because it simultaneously selects all the characters, with the appropriate weightings given to relative economic importance, heritability and correlations among different characters (Falconer 1981).

These linear functions can be derived by a number of techniques using different information and procedures. Smith (1936) first proposed the idea of a linear index that optimizes the correlation between phenotypic values and economic worth of a genotype (i.e., its aggregate genotype). This total genetic worth, called H, is a linear function of an individual's breeding values and economic weighting factors, which express the relative importance attached to each of the n traits (Falconer 1981):

$$H = a1 \cdot g1 + a2 \cdot g2 + a3 \cdot g3 + \ldots a_n \cdot g_n,$$

where a1, a2, a3, etc. are the economic weighting factors for each of the 'n' traits and g1, g2, g3 etc. are an unknown set of genetic values for each trait (Lin 1978).

The index (I) is a linear function of the phenotypic values for 'm' traits, weighted by least-squares partial regression coefficients (b's):

$$I = b1 \cdot X1 + b2 \cdot X2 + b3 \cdot X3 + \ldots b_m \cdot X_m,$$

where b1, b2, b3, etc. are the index weighting factors and X1, X2, X3, etc. are the phenotypic values for the m traits in the index. The index weighting factors (b coefficients) are derived such that the correlation between I and H is maximized (Lin 1978).

The number of characters in H may differ from the number in I; there may be traits that are not in H but may help to improve H through their correlations if included in I (Falconer 1981). For example, if a trait such as bark thickness was correlated with volume growth, such that if bark thickness was measured on phenotypes and included in I, bark thickness would improve H (which is some aggregate breeding value). Falconer (1981) stated that if the aim is to improve economic value, then all the characters that influence economic value must be included in the definition of H.

For proper construction of selection indices, valid information on the economic importance of each trait is required, and this has been one of the primary concerns related to index construction in forestry, simply because little can be said about the economic value of traits relative to each other. Other problems, such as non-linearity of economic value for traits (Namkoong 1969) and poorly estimated genetic parameters, unfortunately can lead to poor index construction. Furthermore, as more traits are included in an index, the accuracy of the index is reduced due to the associated errors of the genetic estimates (Hayes and Hill 1980, Williams 1962). Many modifications to the standard index first discussed by Smith (1936) and Hazel (1943) exist, such as Elston (1963) for nonlinear indices and Baker (1974) for indices with no economic weightings, but they are for the most part slight alterations to a method which can assist a breeder to examine the potential worth of material. Cotterill (1985) found that of four different index approaches for improvement in radiata pine (*Pinus radiata* D. Don), the index which included genetic information proved to be more reliable than the indices estimated without genetic information.

Although these concerns in index construction are important considerations, it is likely the procedure will be used along with other selection criteria. Simmonds (1979) suggested that some traits will have a minimum acceptance level (i.e, independent culling level) in a program, and those that are acceptable can then later be treated by an index. This truncation plus intuitive-index-selection procedure described by Simmonds (1979) is primarily the method used in practical breeding programs (e.g., Wilcox *et al*. 1975).

Another use of indices is simply to examine the direction in which different traits will proceed with different economic weights or subjective rankings. Simulations of this type are helpful to the breeder for multiple-trait index selection strategies, where particular populations are bred for different objectives (e.g., Namkoong 1976). By keeping population objectives few (e.g., one for high wood density or one for volume), the corresponding indices for each sub-population would be more reliable and the breeder would have the ability to change emphasis in traits in response to changes in economic importance of traits.

In some circumstances, primarily where a negative correlation exists between two desirable traits, construction of an index that imposes a restriction on one of the traits may be required. This restriction would maintain the trait of interest at the current level in the population (i.e., no genetic change). Kempthorne and Nordskog (1959) and Cunningham *et al*. (1970) outlined procedures for constructing indices that restrict the genetic change in a desired trait. Yamada *et al*. (1975) and Lin (1978) also outlined different procedures for restriction, where the breeder can choose desired gains for traits without using economic values. Both of these approaches may be useful in a multiple-population breeding strategy such as the one outlined by Namkoong (1976).

1.7 Objectives

Much of the literature on inheritance and correlation of wood and growth characters is a result of work done on the U.S. southern pines (e.g., Dorman 1976). Two considerations are warranted in the study of inheritance and correlation patterns of growth and wood characters for any species in a particular area. First, the design of the experiment dictates what type of valid information can be obtained from the study. Second, each experiment is specific to the species, population and environment used for the study.

The objective of this study was to examine the patterns of genetic variation of economically important traits of lodgepole pine in British Columbia. There currently are only a few estimates of heritability for any trait of lodgepole pine (Rehfeldt 1985b). Some estimates are also available for shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) grown as an exotic in Europe (Cahman 1981). The lack of heritability and correlation estimates for lodgepole pine makes it difficult to develop proper selection schemes for multiple-trait improvement. This study investigated the genetic control of growth, form, wood and disease characteristics of lodgepole pine in central British Columbia. The specific questions addressed were:

1) What are the patterns of variation among geographic zones, provenances (or stands) within zones and open-pollinated families within provenances within zones?

2) What is the degree of additive genetic variance for the traits examined and do variances change among geographic zones?

3) What are the genetic and environmental correlations among the traits and do correlations vary among geographic zones?

4) What are the expected gains that will occur from individual and multiple-trait selection at the individual, family, provenance and zone levels for the traits of interest?

2. Materials and Methods

2.1 Materials

A provenance-family lodgepole pine plantation located at the British Columbia Ministry of Forests Red Rock Nursery (18 kilometers south of Prince George, British Columbia) was established in 1973 as part of a range-wide lodgepole pine provenance survey (Illingworth 1975). Fifty-three provenances of lodgepole pine ranging from the Yukon to southern British Columbia were planted on a terrace on the banks of the Fraser River (latitude 53 46'N, longitude 122 42'W, elevation 620m). Each provenance was represented by approximately 360 open-pollinated progeny (from approximately 15 parent trees per provenance). Progeny were outplanted as 2-1 seedlings in four replications of six-tree plots. Replications one, two and three were planted in 2 X 3 rectangular tree plots, while replication four was more disjunct, established primarily in six-tree, row plots. Actual field layout of the experiment was a hierarchical design of family plots randomly assigned to provenance blocks, which were randomly located in each replication. Mortality caused by rust fungi over the past ten years has reduced the number of progeny, particularly in some of the less vigorous provenances (Martinsson 1980).

Parent tree selection from each provenance was essentially random (Illingworth, pers. com.); therefore, no bias was expected in the estimates of variation due to the minimizing of variances by selection of the best trees in the stand (Goggans 1962). Only 24 of the 53 provenances were included in this study due to time and sampling constraints. From each provenance, nine families (out of the possible 15) were selected that had the most progeny in the plantation from replications 2, 3, and 4. These will be referred to as replications 1, 2 and 3, respectively, for the remainder of the text. Selection of the 24 provenances was made to include the range of lodgepole pine across the Province of British Columbia. The 24 provenances represented six physiographic regions or broad geographic zones of the province (Fig. 2; Table 1). Each provenance was basically a stand collection, but each was considered to be genetically distinct enough to be considered a provenance, as they were relatively far apart and were from a broad range of elevations (Table 1).

2.2 Measurements and Sampling

2.2.1 Disease and Form Traits

Measurements of four traits related to disease resistance and tree form were recorded on all progeny from the 24 provenances (during the summer of 1983):

a)Rust score for stalactiform blister rust (*Cronartium coleosporiodes* Arth.) and comandra blister rust (*C. comandrae* Pk.) was recorded on a scale of 1 to 10, and on a 1 to 5 scale for western gall rust (*Endocronartium harknesii*

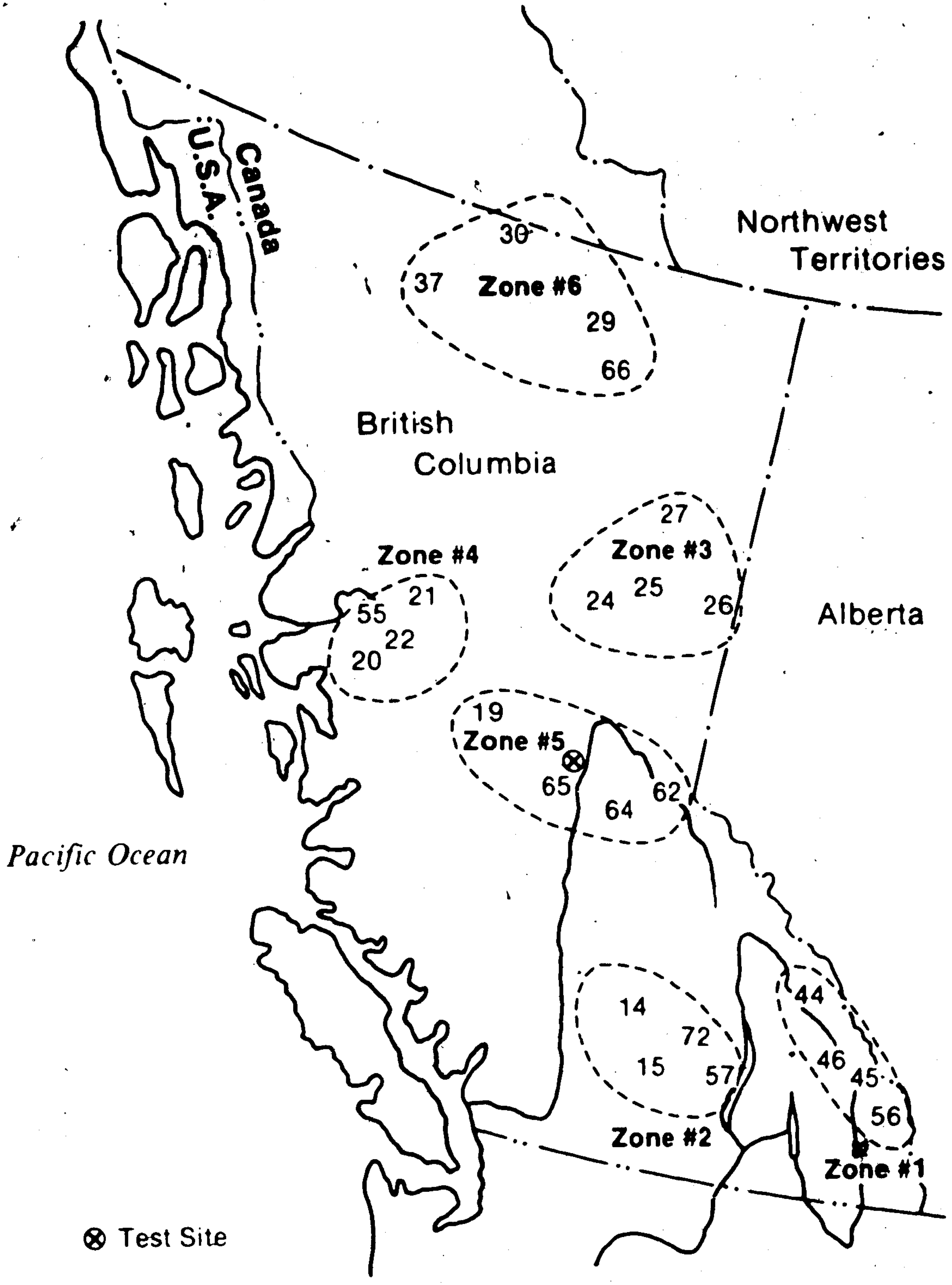

Figure 2 - Approximate locations of the 24 lodgepole pine provenances representing six geographic zones in British Columbia.

ZONE	PROVENANCE\a	NAME	ELEVATION(M)	LATITUDE	LONGITUDE
1	44	MARL CR.	945	51° 31′	117° 11′
	45	SETTLERS' RD	1036	50° 31′	115° 44′
	46	CARTWRIGHT LK.	1170	50° 49′	116° 26′
	56	ELK VALLEY	1280	49° 59′	114° 55′
2	14	WENTWORTH CR.	1060	50° 58′	120° 20′
	15	ESPERON L.	1070	50° 03′	119° 39′
	57	INONOAKLIN	580	49° 54′	118° 12′
	72	LARCH HILLS	780	50° 42′	119° 11′
3	24	FINLAY FORKS	685	55° 57′	123° 48′
	25	HUDSON HOPE	725	56° 02′	122° 05′
	26	TOWER L.	790	56° 01′	120° 37
	27	PINK MT.	1113	57° 00′	122° 24′
4	20	COLLINS L.	940	54° 08′	127° 14′
	21	DORIS L.	960	54° 59′	126° 33′
	22	TELKWA LOW	520	54° 39′	127° 03′
	55	TELKWA HIGH	1005	54° 38′	127° 26′
5	19	NITHI R.	970	54° 03′	125° 05′
	62	McKALE R.	700	53° 25′	120° 20′
	64	WENDLE PARK	1280	53° 07′	121° 30′
	65	LYNX L.	820	53° 39′	122° 59′
6	29	MUNCHO L.	[illegible]50	59° 03′	125° 46′
	30	LOWER POST	640	59° 59′	128° 33′
	37	CASSIAR	790	59° 06′	129° 44′
	66	STONE MT.	1170	58° 39′	124° 45′

TABLE 1 - Elevation, latitude and longitude for 24 lodgepole pine provenances in British Columbia.
a\ refer to Illingworth, 1975

Y. Hiratsuka). The alternate host for stalactiform blister rust is Indian paint brush (*Castilleja* spp.)(Ziller 1974). The abundance of paint brush throughout the plantation probably ensured a relatively uniform distribution of inoculum over the past several years. Actual number of stem cankers caused by stalactiform blister rust would not have been a good estimation of actual infection levels on individual trees, since one tree could have one or two large cankers whereas the next tree could have five or six small ones. Therefore, a scoring system (on a 1 to 10 scale) similar to the one used by Matziris and Zobel (1973) and Stonecypher *et al.* (1973) was used. This approach may be more appropriate in indicating a general level of resistance for individual trees, because the two trees in the previous example could possibly have a similar level of resistance. Different levels of resistance could be due to inhibition of infection or inhibition of subsequent growth of the fungus (Simmonds 1979). Therefore, a tree was considered a "1" if no cankers were visible and a "10" if there were many large cankers on the stem and branches. Initially, each tree was considered a "1" and subsequently had points added depending upon the number and size of each canker. Large cankers (i.e., those approaching 20-30 cm in length) on the stem usually dictated that "3" points were added to the tree's score. Cankers on branches were usually small and "1" point was added to the overall score with each occurrence. Trees in the category of "10" for stalactiform rust were earlier determined to have the heaviest infection in the plantation so that scoring could be graded accordingly to what was expected to be the worst situation. A distinction between stalactiform and comandra blister rust was not attempted, but stalactiform blister rust appeared to be more prevalent (Martinsson 1980). Western gall rust was scored on a scale from 1-5, since galls were primarily on branches and little judgement had to be given to ranking the severity of individual galls. A score of "1" indicated no galls were present and a score of "5" indicated approximately 10-15 galls were present in the crown. Scores between "1" and "5" for western gall rust attempted to categorize trees with intermediate number of infections.

b) Crown score was determined by a number of criteria, such as branch angle, crown shape and crown uniformity. Busby (1983), Ledig and Whitmore (1981), Matziris and Zobel (1973) and Stonecypher *et al.* (1973) also have scored crown form in a similar manner, using the same general criteria, on a 1-6 scale. A scale of 1-10 was used in this study to give more classes to categorize a tree, since a number of traits were being used to score an individual trees crown. The scoring system initially considered each tree as a "5"; this was adjusted to a "4" if branch angle was high, remained a "5" if branch angle looked to be average, or moved to a "6" if branch angle appeared to be low. The score was adjusted by "2" points if branch angle was severe. Branch diameter and the other criteria mentioned previously were similarly assessed and used to modify the score for that tree. With such a system, two trees could be judged as "3" for completely different reasons. For example, one tree could have excellent branch angle, excellent branch size, average crown form and average uniformity, whereas another tree could have poor angle, average branch size and excellent shape and uniformity. This may be considered acceptable, since the trees scored as "3" may be economically desirable to the same extent even by different criteria. Since the scoring system is subjective and prone to personal discrepancies, scoring was done by the same person within each replication.

c) Stem straightness was also measured on an scale of 1 to 10, a "1" being a perfectly straight stem and a "10" being an extremely crooked stem. Trees with substantial basal sweep had two or three points added to the score as did trees with forked tops or leaders. Minor or major crooks in the stem caused one or two points to be added to the score depending on their severity. More complex methods of assessing sweeps and crooks in stems proposed by Shelbourne and Namkoong (1966) were not used simply because of the large numbers of trees in this study. The 1-10 scale was again used to allow better discrimination among trees, rather than the 1-6 scale used by Matziris and Zobel (1973). Again, scoring within a replication was done by one person.

2.2.2 Branch Traits

A total of three measurements (branch angle, branch diameter and branch length) was made on progeny from only 19 of the provenances, again because of sampling time constraints. Provenances from zone #6 (Yukon) and provenance #22 within zone #4 were not measured for branch angle, branch diameter and branch length. The objective behind obtaining a detailed quantitative measure of these three traits was to determine their relative genetic control, which could not be adequately distinguished in the conglomerate trait of crown form.

a) Branch angle was measured at the base of four branches on each tree, two branches each from the sixth and seventh whorls. These two whorls were chosen because they were accessible and usually were in the lower mid-crown and contained the largest live branches. The two branches measured at each whorl were the branches closest to the north and south cardinal directions. This was done to ensure that the effect that aspect might have had on branch size was reduc[illegible] and that larger or smaller branches were not favoured. Branch angle was recorded in degrees using a modified protractor that had extended arms and could be placed along the branch and the stem. Ledig and Whitmore (1981) measured branch angle using a subjective point scoring system, but they obtained low estimates of heritability, so a quantitative measure of branch angle was preferred.

b) Branch diameter (approximately 3cm from the base of the branch) of the same four branches was measured to the nearest mm.

c) Branch length was recorded to the nearest cm on these four branches to the end of the 1982-formed shoot. The branches were straightened and measured from the base of the branch so that curvature of the branch would not affect the measurement of length.

2.2.3 Wood Property Traits

From the 19 provenances with branch measurements, only 14 provenances from five zones were selected for wood property studies. One large diameter increment core (11 mm), containing wood from the pith to the bark, was removed from each tree approximately 30 cm above the ground. Each core was taken from the southern cardinal direction of each tree. Wood cores have been shown to give a reliable estimate of whole-tree wood density (Zobel and Talbert 1984). The following measurements were made on the wood samples collected from progeny of the 14 provenances:

a) Specific gravity (or wood density) from trees in three replications was measured using the oven-dry weight/green volume method (Panshin and DeZeeuw 1980). The 1983 growth ring was not complete at the time of sampling and was removed from the cores.

To assess the usefulness of a method for rapidly screening individuals or families for specific gravity, the Pilodyn instrument (e.g., Micko *et al*. 1982a) was used on progeny from 10 provenances in replications 1 and 2. A six-joule Pilodyn was used on approximately 1000 progeny in the experiment for which specific gravity values were also obtained. Two pin penetration readings were taken from each tree, each through the bark close to where the wood samples were removed.

b) Wood moisture content (Panshin and DeZeeuw 1980, pg. 201) of the cores was measured on 10 provenances from replications 1 and 2. Immediately after removal from the tree and labelling, the cores were wrapped in cellophane to avoid moisture loss. Fresh weights were obtained from cores within one hour after removal from the tree.

Although better estimates of moisture content are obtained from disk-type samples (Zobel, pers. com.), the data obtained from cores should give a good estimate of moisture-content variation and how it relates to other wood property and growth traits.

c) Tracheid (or fibre) lengths were measured from progeny of 10 provenances in all three replications (Appendix A). The ring formed in the 1982 growing season (i.e., which was usually the ninth ring from the pith) was removed from the core and width was recorded to the nearest 0.1 mm. This measure of ring width, as opposed to a larger measure of diameter growth, was recorded specifically to examine the relationship between ring width and tracheid length. Two match-stick sized samples were removed from this ring of the 11mm core (containing equal portions of spring and summerwood), macerated, and 50 tracheids per sample were measured as described by Taylor (1975) and Micko *et al.* (1982b).

d) Compression wood percentage was estimated on each sample by recording the amount of compression wood (in mm) present across the radial length of the wood sample. This measurement, although recorded quantitatively, was somewhat subjective because actual delineation of a zone of compression wood was difficult. Although the method of identifying compression wood using a light box (e.g., Shelbourne *et al.* 1969) was not used, the method was similar to that of Shelbourne *et al.* (1969) in that this measure only recorded those bands or zones which appeared to be extremely dark and characteristic of compression wood.

e) Rate of growth was measured on the core from the pith to the end of the 1982 growth ring. This measure may be a more appropriate measure than tree diameter (outside bark) for relating growth rate to wood traits. This measure would also be free of bias from the influence of bark thickness.

2.2.4 Height, Diameter, Volume and Dry-Weight

Tree height (HT) to the nearest dm and diameter (DIA) to the closest cm were recorded at the end of the 1982 growing season on 14 provenances in replications 1 and 2 of the experiment. Diameter was measured at variable heights (approximately at 25 percent of total tree height). This was required for the calculation of volume per tree by the volume function. Individual tree volumes were calculated using an Alberta Forest Service volume function of:

$$VOL(dm^3) = 0.024716 \times (DIA*2.133) \times (HT*0.987),$$

for young lodgepole pine [3]. Dry-weight was calculated (kg/tree) by multiplying the volume of each tree by the core specific gravity.

2.3 Statistical Analysis

2.3.1 Variance and Covariance Estimation

All effects in the analysis of variance and covariance model were considered to be random (Table 2). Valid error terms were present for only four sources of variation (replication x provenance with zone [RxP/Z], replication x zone [RxZ], families within provenances within zones

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[3] The volume function derived by Kovatts (1977) for young lodgepole pine gave a correlation of 0.991 (r^2) with the AFS volume function. * indicates exponent.

TABLE 2 - Expected mean squares and cross products for a completely random model of an open-pollinated lodgepole pine provenance-family trial at one site in central British Columbia. 1/

SOURCE		DF	EXPECTED MEAN SQUARES OR CROSS PRODUCTS[2]
Replications	(R)	(R-1)	$\sigma^2{}_{w/k} + \sigma^2{}_c + k_{13}\,\sigma^2{}_{rp/z} + k_{14}\,\sigma^2{}_{rz} + k_{15}\,\sigma^2{}_r$
Zones	(Z)	(Z-1)	$\sigma^2{}_{w/k} + \sigma^2{}_c + k_8\sigma^2{}_{f/p/z} + k_9\sigma^2{}_{rp/z} + k_{10}\sigma^2{}_{p/z} + k_{11}\sigma^2{}_{rz} + k_{12}\sigma^2{}_z$
Provenance /Z	(P/Z)	(P-1)Z	$\sigma^2{}_{w/k} + \sigma^2{}_c + k_5\sigma^2{}_{f/p/z} + k_6\sigma^2{}_{rp} + k_7\sigma^2{}_p$
Families /P/Z	(F/P/Z)	(F-1)ZP	$\sigma^2{}_{w/k} + \sigma^2{}_c + k_4\sigma^2{}_{f/p/z}$
R X Z		(R-1) (Z-1)	$\sigma^2{}_{w/k} + \sigma^2{}_c + k_2\sigma^2{}_{rp/z} + K_3\sigma^2{}_{rz}$
R X P/Z		(R-1) (P-1)Z	$\sigma^2{}_{w/k} + \sigma^2{}_c + k_1\sigma^2{}_{rp}$
Plot Error		(R-1)(F-1)ZP	$\sigma^2{}_{w/k} + \sigma^2{}_c$
Within Plot		RZPF (n-1)	$\sigma^2{}_w$

/1 Analysis based on plot means

where; σ^2_w = within plot error
σ^2_c = plot-to-plot error
k = harmonic mean of number of trees per plot
k_1-k_{15} = coefficients associated with variance and componenets
[2]/ COV replaces σ^2 in the expected mean cross products

[FAM/P/Z] and replications [REPS]; Table 2). Since the effects of provenances within zones (PROV/Z) and zones (ZONES) do not have true error terms in this completely random model, error terms for these two effects were derived using the Satterthwaite (1946) approximation method. Also, the relative contribution of each variance component in the model (on a percentage scale) was examined.

All traits except stalactiform blister rust score, western gall rust score and percent compression wood had normal distributions. The data obtained on a 1 to 10 scale for the two disease traits showed extremely skewed distributions simply because of the large numbers of trees that were scored as "1". Variance components obtained from data with skewed dis~~tributions~~ are unreliably estimated (Gilbert 1973).

Three statistical procedures have been proposed for data with non-normal distributions. The first would be a binomial approach where a tree was considered as a "0", (e.g., not infected by a pathogen) or a "1" (e.g., infected by a pathogen). This approach allows the estimation of heritabilities and correlations on individual tree data (Falconer 1981, Sohn and Goddard 1979). Binomial data can introduce a large amount of measurement error, which appears as environmental variance if the incidence deviates considerably from fifty percent (Falconer 1981).

The second procedure for obtaining variance components from non-normal data is the approach presented by Becker and

Marsden (1972) for white pine blister rust. This procedure is an analysis of variance on the percentage of trees infected in a plot for which the data have undergone a arcsin, square-root transformation. For this analysis the sampling variance is a constant (σ^2_{bin}=821; Fisher and Yates 1963).

The third method tests percentage of trees infected per plot using a heterogeneity c[illegible]square for a heritability estimate. This approach, desc[illegible]ed by Dempster and Lerner (1950) as "threshold chara[illegible] was used on slash pine by Goddard and Arnold (1966).

Compression wood data, when calculated as a percentage of total core sample length, were analyzed using the binomial approach, because an arcsin transformation of percent compression wood relative to the whole core (e.g., as was done by Shelbourne *et al.* 1969) was not effective in normalizing the data.

Analyses of variances and covariances were carried out by two procedures. The first analysis done on plot means included all effects in the model (Table 2). A few of the traits had an unbalanced data set for the plot means analysis (i.e., cells were missing); therefore, procedure MANOVA in SPSSx was used to obtain the sums of squares, degrees of freedom and mean squares for the plot means. Because the plot-means analyses were slightly unbalanced, coefficients relating to variance components for the expected mean squares would not be whole numbers. Therefore, the appropriate values associated with the variance components in the expected mean squares (i.e., k1, k2, k3 ... k15, in Table 2) were derived using the procedure described by King and Henderson (1954) in procedure UANOVA of SPSSX at the University of Alberta (Taerum 1984). To obtain estimates of within-plot variances (for within-plot error terms in the plot means analysis), as well as heritabilities and genetic correlations for all traits, the generalized least-squares procedure of Harvey (1977)(MTY=07) was used on individual tree data. Expected mean squares and cross products for the analysis on individuals are given in Appendix B. Standard errors of heritability estimates and genetic correlations from individual tree data were estimated from Harvey (1977) following the formulas given by Swiger *et al*. (1964) and Tallis (1959). Heritabilities that are in the range of 0 to 0.1 were considered as low, from 0.1 to 0.4 as moderate and greater than 0.4 as high.

As indicated earlier, the material used in this study was tested on one site. An upward bias may be present in the estimates of heritability if some genotype x environment interactions were present. However, the magnitude of these interactions for various traits may be inferred from the literature. Based on 10-year results for lodgepole pine in British Columbia, provenance x location interactions for height and survival appear to be relatively small (C.C. Ying, pers, com.). The assumption that all progeny are true half-sibs may not be realistic in forest trees (King *et al*.

1984, Namkoong 1966), because all parent tree selections within a stand would have to be unrelated and crosses from a large effective pollen pool at each pollination event would be required to avoid overestimates of additive genetic variance (Namkoong 1966). For true half-sib structure to exist in a test with, for example, 24 seedlings per half-sib family, 24 unrelated pollen parents would have to have contributed the male gametes. Therefore, the coefficient of four may not always be accurate in estimating additive genetic variance from family effects. However, most lodgepole pines maintain viable seeds from a number of pollination events (cones up to 10 years old with viable seed are common). Also, lodgepole pine has been shown to be a highly outcrossing species with little stand-to-stand variability in outcrossing rates (Epperson and Allard 1984). Therefore, the collection of stored, open-pollinated seed from such trees may be as close to being true half-sibs as is possible from wild-tree collections.

Formulas used for calculating heritabilities on an individual-tree basis and heritabilities for family, provenance and zone means are as follows:

$$h_i^2 = \frac{4\,\sigma_f^2}{\sigma_w^2 + \sigma_{rf}^2 + \sigma_f^2} = \frac{\sigma_A^2}{\sigma_T^2} \quad \text{(using individual tree data)}$$

$$h_i^2 = \frac{4\,\sigma_f^2}{\sigma_w^2 + \sigma_c^2 + \sigma_f^2} = \frac{\sigma_A^2}{\sigma_T^2} \quad \text{(using plot means)}$$

$$h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_w^2}{nk_4} + \frac{\sigma_c^2}{k_4} + \sigma_f^2} = \frac{\sigma_f^2}{\sigma_{HSF}^2}$$

$$h_p^2 = \frac{\sigma_p^2}{\frac{\sigma_w^2}{nk_7} + \frac{\sigma_c^2}{k_7} + \frac{\sigma_f^2}{k_6} + \frac{\sigma_{rp}^2}{k_5} + \sigma_p^2} = \frac{\sigma_p^2}{\sigma_{PROV}^2}$$

$$h_z^2 = \frac{\sigma_z^2}{\frac{\sigma_w^2}{nk_{12}} + \frac{\sigma_c^2}{k_{10}} + \frac{\sigma_f^2}{k_9} + \frac{k_9\sigma_{rp}^2}{k_{12}} + \frac{k_9\sigma_p^2}{k_{11}} + \frac{\sigma_{rz}^2}{k_8} + \sigma_z^2} = \frac{\sigma_z^2}{\sigma_{ZONE}^2}$$

where;

σ_T^2 =phenotypic variance among individuals

σ_A^2 =additive genetic variance

σ_{HSF}^2 =phenotypic variance among half-sib family means

σ_{PROV}^2 =phenotypic variance among provenance means

σ_{ZONE}^2 =phenotypic variance among zone means

σ_w^2 =within-plot variance

σ_{rf}^2 =variance due to replications x families/prov.

σ_c^2 =variance due to environmental plot-to-plot differences

σ_f^2 =variance due to families/prov./zone

σ_{rp}^2 =variance due to replications x provenance/zone

σ_p^2 =variance due to provenances/zone

σ^2_{rz} =variance due to replications x zones

σ^2_z =variance due to zones

h^2_i =heritability on an individual basis

h^2_f =heritability of family means

h^2_p =heritability of provenance means

h^2_z =heritability of zone means

n =number of trees per plot = k = harmonic mean of number of trees per plot

k4-k12 =coefficients from Table 2.

Heritabilities based on family, provenance and zone means were derived from the analysis on plot means. Standard errors for heritability estimates derived from the plot means analysis were calculated as given by Becker (1975) and are shown in Appendix C.

For the determination of heritabilities and genetic correlations within geographic zones, individual tree data were analyzed using two different analysis of variance models* in Harvey's (1977) program. The first included replications, families, replications x family and error effects as sources of variation in the model, and the second included replications, provenances, families within provenances, replications x provenance, replications x families with provenance and error effects (for both the analysis of variance and covariance). These two analysis of variance models for the within-zone analysis will elucidate on the effects provenance differences may have on heritabilities and correlations. All variance and covariance components were derived by equating the expected mean squares and expected mean cross products to the mean squares and mean cross-products, respectively (i.e., Henderson method I; Searle 1971).

2.3.2 Index Construction

The least-squares solution for regression coefficients that maximizes the correlation between H and I (i.e., the aggregate genotype and the index value for the individual) has been shown by Hazel (1943), Lin (1978), Talbert (1984), Turner and Young (1969) and Falconer (1981) to be:

$$Pb = Ca,$$

where P = phenotypic variance-covariance matrix,
b = index coefficients,
C = matrix of genetic variance and covariances, and
a = vector of economic weights.

The response of any one of the traits in the index can be predicted, because response of H is equal to the selection intensity multiplied by the standard deviation of the index. This measure provides a simple way of comparing the relative efficiencies of an index, because the response of merit is a proportion of σ_I^2 (Falconer 1981, pg. 296). The expected response (R) of the characters of the index (or aggregate genotype) as a result of selection on the index is:

$$R = (i/\sigma_I)b'C,$$

where C is the genetic variance-covariance matrix, b the vector of index coefficients, i the selection intensity and σ_I the standard deviation of the index (Lin 1978). When information from relatives is included (e.g., half-sib or full-sib family information), the aggregate genetic worth (H) remains the same, but the index (I) is expanded to include the additional phenotypic measurement just as if the measurement on a given relative was a measurement of another trait (Talbert 1984). The correlation between H and I (R^2_{HI}) is a predictor of genetic change in H when selection is on I (Nordskog 1978).

When restrictions are imposed on a trait in an index (e.g., to examine the response of other traits in the index when no genetic change is required in one trait of interest), the procedure described by Kempthorne and Nordskog (1959) was used (i.e., for indices derived for individual-tree or mass selection).

Economic weights for the traits were estimated following the procedure of Wilcox *et al*. (1975), where the inverse of the phenotypic standard deviation was used to standardize the b coefficients. This method of "economic weights" influences the index weights by the variability associated with each trait. A second set of "economic weights" was used that gave each trait an equal weighting (i.e., the a matrix with 1 for all traits). The index weights derived from this approach were affected by the heritabilities and phenotypic variances associated with each trait.

Genetic parameters used in index construction were derived from individual tree analysis. Provenance information, when included in index construction, was pooled over all provenances; therefore, the genetic variance and covariance of provenances was assumed to be the variance and covariance component from the analysis of variance and covariance (i.e., σ_p^2 and COV_p). Additive genetic variance and covariance among half-sib families was assumed to be σ_f^2 and COV_f, repectively. Outlines of the genetic and phenotypic matrices used in index construction are shown in Appendix D.

For ranking a select number of trees in the plantation, family means were expressed as deviations from provenance means. Similarly, individuals were expressed as deviations from family means. Index (b) values were then multiplied by the deviations each individual tree exhibited from its overall family mean, its family mean from the provenance mean and the provenance mean from the overall grand mean. When combined selection was only at the individual and family levels, family means were expressed as deviations from the overall mean. Deviations were also adjusted for the replication effects so that individuals were not favoured because of the replication in which they occurred.

3. Results

3.1 Provenance Variation and Heritabilities

Heritabilities estimated from individual tree data were very close to heritability estimates on a plot mean basis across all zones (Table 3), and those derived from the plot means analysis are discussed here. A listing of zone, provenance and family means for all traits is given in Appendix A. Expected mean squares, mean cross-products, variance and covariance components from the analysis on individuals are shown in Appendix B. Expected mean squares for the analysis of variance on plot means are shown in Appendix E .

3.1.1 Crown and Stem Score

Crown score on the 1 to 10 measurement scale had a grand mean of 3.3 with a coefficient of variation (CV) of 28%. These two statistics indicate a tendency to score trees somewhat lower than the mid-point of the ranking scale and that a large amount of variation was present among trees. Crown score differed significantly among REPS (Table 4). The replication means for crown score were 2.42, 4.50 and 2.96. If scorer biases were removed, it is unlikely that crown score differences would have been as great. ZONES and PROV/Z effects were not significantly different for crown score even though the heritability estimate of provenance means was 0.40(±.34)(Table 3). FAM/P/Z and ZONE heritability

Table 3 - Heritabilities, grand means, stand deviations and units for 15 traits of lodgepole pine in British Columbia. Standard errors ofestimates in parenthesis. NA indicates values not estimated from analysis on individual tree data (because of restrictions in model using Harvey's [1977] program).

TRAITS	h^2 on Ind Basis (on Ind)	h^2 on Ind Basis (Plot Means)	h^2 on Fam $\bar{x}$ Basis (Plot Means)	h^2 on Prov $\bar{x}$ Basis (Plot Means)	h^2 on Zone $\bar{x}$ Basis	GRAND MEAN	S.D.	UNITS
Stalactiform Rust	0.200 (0.045)	0.39	0.414 (0.11)*	0.866 (0.01)*	NA	0.258*	0.393	0 or 1
Western Gall Rust	0.137 (0.039)	0.213	0.331 (0.12)*	0.871 (0.01)*	NA	0.189	0.357	0 or 1
Crown Score	0.064 (0.033)	0.074 (0.06)	0.160 (0.13)	0.400 (0.34)	0.000 (1.20)	3.306	0.933	1, 10
Stem Score	0.134 (0.039)	0.128 (0.06)	0.298 (0.13)	0.587 (0.33)	0.042 (0.38)	4.416	1.420	1, 10
Branch Angle	0.415 (0.069)	0.411 (0.08)	0.607 (0.12)	0.223 (0.38)	0.000 (0.26)	69.28	6.820	DEG
Branch Diameter	0.247 (0.054)	0.250 (0.07)	0.482 (0.14)	0.826 (0.36)	0.000 (0.45)	22.30	3.480	mm
Branch Length	0.282 (0.057)	0.306 (0.08)	0.527 (0.13)	0.854 (0.35)	0.452 (0.53)	142.43	20.880	cm
Moisture Content	0.254 (0.092)	0.241 (0.14)	0.371 (0.21)	0.803 (0.54)	0.765 (0.56)	112.12	14.710	%
Specific Gravity	0.421 (0.080)	0.440 (0.10)	0.654 (0.14)	0.000 (0.47)	0.814 (0.51)	0.3846	0.0257	
Bark Thickness	0.294 (0.068)	0.306 (0.10)	0.403 (0.13)	0.481 (0.37)	0.327 (0.39)	3.178	0.474	mm
Tracheid Length	0.311 (0.083)	0.327 (0.11)	0.524 (0.17)	0.483 (0.52)	0.308 (0.56)	1.685	0.142	mm
Height	0.267 (0.078)	0.273 (0.12)	0.363 (0.17)	0.869 (0.43)	0.763 (0.56)	4.715	0.476	m
Diameter	0.225 (0.074)	0.235 (0.12)	0.347 (0.17)	0.791 (0.43)	0.743 (0.55)	7.353	0.840	cm
Volume	0.178 (0.069)	0.169 (0.11)	0.265 (0.18)	0.866 (0.43)	0.743 (0.56)	8.495	2.640	dm^3
Dry Weight	0.222 (0.075)	0.237 (0.12)	0.321 (0.17)	0.883 (0.43)	0.740 (0.57)	3.255	0.993	kg

* indicates estimated on individual tree data

TABLE 4 - Analysis of variance of Crown Score from an open-pollinated progeny test of 24 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	260.770**	1.211	47.9
Zones (Z)	5	1.108	0.000	0.0
Provenance /Z (P/Z)	18	3.295	0.049	1.9
Families /P/Z (F/P/Z)	190	0.357*	0.019	0.8
R X Z	10	1.069	0.066	2.6
R X P/Z	36	1.915**	0.180	7.1
R X F/P/Z(PLOT)	374	0.300	0.130	5.1
Error (within plot)	2786	0.871	0.871	34.5

Harmonic mean of number of trees per plot = 5.14979
Satterthwaite approximate error term for (P/Z) = 1.97 (37.8 d.f)
Satterthwaite approximate error term for (Z) = 2.45 (7.3 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

estimates were quite low (Table 3); however, FAM/P/Z effects were significant at the $P<0.05$ level (Table 4), indicating substantial variation exists within PROV/Z and within ZONES. Family means across the experiment ranged from 2.4 (provenance #45, family #14) to 4.9 (provenance #56, family #11) on the 1 to 10 point scale. RxP/Z interaction was significant ($P<0.01$) indicating some provenances changed rankings in the three replications.

Heritability of crown score was 0.07(±.03), which is low in comparison to the heritability of "branch quality" (0.18±.07) by Dean *et al*. (1983) in radiata pine. This may have been due to additional emphasis placed on other characteristics (i.e., crown uniformity and shape) in this study, making the overall measure less sensitive. Matziris and Zobel (1973) reported a heritability of 0.33 for crown score for loblolly pine, while Stonecypher *et al*. (1973) reported a heritability of 0.08 in the same species. Stonecypher indicated his relatively low estimate may have been affected by early insect damage in the plantation; however, in this study no such cause was evident. What may have influenced the heritability estimate for crown score was the large effect of RxF/P/Z and a relatively large within-plot variance (Table 4).

The grand mean score for stem straightness was 4.4, with a CV of 32%. This would indicate that trees with average straightness were close to the mid-point of the ranking scale for straightness and that a substantial amount of variability was also present among trees. Stem score had no significant REPS effects, which is in contrast to that observed for crown score (Table 5). ZONES were not significant and had a heritability estimate of only 0.04(±.38). The sources of variation PROV/Z and FAM/P/Z were significant ($P<0.01$)(Table 5), and heritabilities of provenance and family means were moderately high at 0.59(±.33) and 0.30(±.13), respectively. Provenance means for stem straightness varied from 2.77 (provenance #62) to 4.09 (provenance 45). Family means within provenance #62 varied from 2.41 (family #14) to 3.23 (family #9). Within provenance #45, family means ranged from 3.05 (family #9) to 4.82 (family #15); therefore, some overlap is present between the best and worst provenances for stem straightness. Coefficients of variation associated with these means were quite high, ranging from 25 to 50% (Appendix A3). RxZ and RxP/Z all accounted for about the same amount of variation (on a percentage basis), and of these RxP/Z was significant ($P<0.01$)(Table 5). Cause of this interaction is difficult to determine, but there may have been differential environmental stresses on the stems among replications during planting. These may have persisted to cause basal sweep as the trees grew larger.

The heritability estimate for stem score was 0.13(±.06), which is close to the heritability of 0.12(±.10) reported by Dean *et al.* (1983) for radiata pine, but substantially lower than the estimate of 0.66 reported by

TABLE 5 - Analysis of variance of Stem Score from an open-pollinated progeny test of 24 provenances of lodgepole pine at one test site in central British Columbia /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	6.372	0.0295	1.2
Zones (Z)	5	5.021	0.0031	0.1
Provenance /Z (P/Z)	18	3.296**	0.0716	3.0
Families /P/Z (F/P/Z)	190	0.701**	0.0696	2.9
R X Z	10	2.205	0.0695	2.9
R X P/Z	36	1.153**	0.0734	3.0
R X F/P/Z(PLOT)	374	0.492	0.105	4.3
Error (within plot)	2786	1.993	1.9930	82.5

Harmonic mean of number of trees per plot = 5.14979
Satterthwaite approximate error term for (P/Z) = 1.36 (16.8 d.f)
Satterthwaite approximate error term for (Z) = 4.35 (46.2 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

Matziris and Zobel (1973) for loblolly pine. Shelbourne (1969b) indicated that stem straightness is probably more heritable than growth traits. However, in this study the estimate may be lower because of the occurrence of basal sweep on many stems.

3.1.2 Bark Thickness

Bark thickness, from the 14 provenances examined, averaged 3.2 mm (CV=15%). Differences among ZONES for bark thickness were not significant (Table 6). The effects PROV/Z and FAM/P/Z were significant ($P<0.05$) and both were of the same order of magnitude (explaining approximately 6% of the variation each; Table 6). Provenance means for bark thickness ranged from 2.70mm (provenance #22) to 3.46mm (provenance #27). Family means within provenance #22 varied from 2.49mm to 3.05mm, and within provenance #27, from 3.20mm to 3.69mm. Heritability estimates for ZONE, PROV/Z and FAM/P/Z were 0.33(±.39), 0.48(±.37) and 0.40(±.13), respectively. Both the REPS and the the RxP/Z interaction were significant at the $P<0.01$ level (Table 6).

Heritability for bark thickness on an individual basis was 0.3 (±.10). Matziris and Zobel (1973), Pederick (1970) and Ledig and Whitmore (1981) also reported moderate to high heritabilities for this trait in Caribbean pine (*Pinus caribaea* Morelet) and loblolly pine (ranging from 0.28 to 0.7). Although the practical significance of bark thickness may be less important than volume growth or wood density,

TABLE 6 -.Analysis of variance of Bark Thickness from an open-pollinated progeny test of 14 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	0.8596**	0.0080	2.3
Zones (Z)	4	2.2885	0.0145	4.2
Provenance /Z .(P/Z)	9	0.9538*	0.0201	5.8
Families /P/Z (F/P/Z)	112	0.1193**	0.0200	5.8
R X Z	8	0.0476	0.0103	3.0
R X P/Z	18	0.3501**	0.0323	9.3
R X F/P/Z(PLOT)	223	0.0592	0.0170	4.9
Error (within plot)	1658	0.2248	0.2248	64.8

Harmonic mean of number of trees per plot = 5.29016
Satterthwaite approximate error term for (P/Z) = 0.41 (24.2 d.f)
Satterthwaite approximate error term for (Z) = 0.65 (3.9 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

its importance may lie in its correlations with other traits.

3.1.3 Wood Moisture Content

The average moisture content for lodgepole pine at age 10 was 112 percent (CV=13%) of dry weight of the wood. This indicates that at this age, more than half of the weight of a standing tree is water. The effect of ZONES variation was not significant (Table 7), although it accounted for 15 percent of the variation. PROV/Z and FAM/P/Z effects were significant at the P<0.05 level (heritability estimates were 0.77[±.56], 0.80[±.54] and 0.37[±.21], respectively). RxZ and RxP/Z contributed negligibly to the overall variation in wood moisture content. Although, REPS was significant effect (P<0.01; Table 7), wood moisture content in replications #1 and #2 was only 110.4% and 113.9%, respectively. The lack of significance of the effect of ZONES was apparently due to the relatively large variation in moisture content among provenances (Fig. 3). Provenance #20 had the lowest mean moisture content of 95.5%, and provenance #25 had the highest mean wood moisture content of 119.9%. Family means within provenance #20 varied from 87.3% (family #1) to 105.5% (family #11), and in provenance #25, family means varied from 116.1% (family #3) to 125.3% (family #7).

The heritability for moisture content was 0.24(±.14). Compared to Matziris and Zobel's (1973) estimate of 0.8 for loblolly pine, this is somewhat low. Although wood moisture

TABLE 7 - Analysis of variance of Moisture Content from an open-pollinated progeny test of 10 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	1	496.28**	5.199	1.6
Zones (Z)	4	2114.25	47.451	14.9
Provenance /Z (P/Z)	5	504.56*	22.517	7.1
Families /P/Z (F/P/Z)	80	78.31*	14.516	4.6
R X Z	4	9.99	0.000	0.0
R X P/Z	5	70.23	2.328	0.7
R X F/P/Z(PLOT)	80	49.28	9.650	3.0
Error (within plot)	813	216.28	216.280	68.0

Harmonic mean of number of trees per plot = 5.45742
Satterthwaite approximate error term for (P/Z) = 99.26 (9.0 d.f)
Satterthwaite approximate error term for (Z) = 444.32 (3.8 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

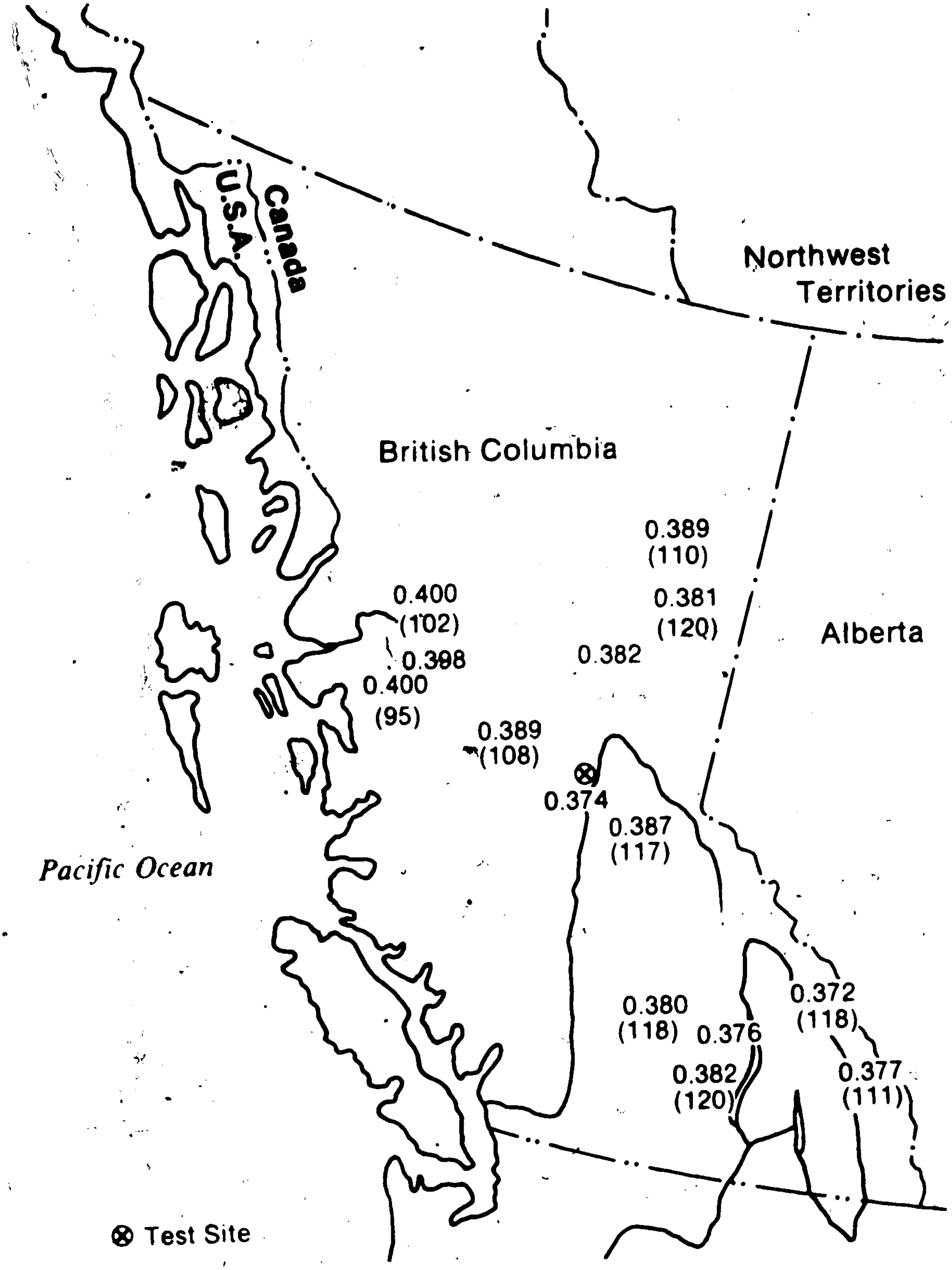

Figure 3 - Lodgepole pine provenance means for wood density and percent moisture content of wood (in parenthesis) at the Red Rock test site in central British Columbia.

content may have economic implications, its importance may again lie in its relationship to other traits.

3.1.4 Wood Specific Gravity

Although the grand mean for specific gravity was quite high (0.385), wood at this age should still be considered juvenile (i.e., rings 1-10). Specific gravity is expected to decrease in growth rings after this age, then increase again in rings 25-30 (Taylor *et al.* 1983). The CV associated with the grand mean for wood density was only 7%; therefore, the overall observed variability is low relative to the other traits. The effects of ZONES and FAM/P/Z in this study were significant and both accounted for the largest amount of variation in specific gravity (Table 8). The proportion of variation accounted for by PROV/Z was zero (Table 8); therefore, no genetic differences were present for specific gravity among stands within a geographic zone or area. The zone-mean heritability was high at 0.81(±.51). Zone means for specific gravity were lowest in zone #1 (0.375) and highest in zone #4 (0.400). Since provenances within geographic zones were not significant, variability between zones for wood specific gravity can be examined by pooling families within zones. In the low specific gravity zone (#1), family means ranged from 0.352 (family #10, provenance #44) to 0.394 (family #2, provenance #46), [illegible] the high specific gravity zone (#4), family means va[illegible] from 0.381 (family #11, provenance #22) to 0.427 (family #2, provenance

TABLE 8 - Analysis of variance of Specific Gravity from an open-pollinated progeny test of 14 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	.00108	.000011	1.3
Zones (Z)	4	.00618**	.000070	8.1
Provenance /Z [illegible]Z)	9	.00058	.000000	0.0
Families /P/Z (F/P/Z)	112	.00037**	.000082	9.5
R X.Z	8	.00032	.000013	1.5
R X P/Z	18	.00028**	.000021	2.4
R X F/P/Z(PLOT)	223	.00013	.000010	1.2
Error (within plot)	1667	.000658	.000658	76.1

Harmonic mean of number of trees per plot = 5.29016
Satterthwaite approximate error term for (P/Z) = .0005 (47.8 d.f)
Satterthwaite approximate error term for (Z) = .0006 (7.04 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

#22). Therefore, families of high specific gravity are present in geographic zones with low specific gravity.

A clinal pattern of decreasing specific gravity from the northwest to the southeast exists for lodgepole pine (Fig. 3). Henderson and Petty (1972) found similar results when coastal and inland sources of lodgepole pine from British Columbia were established in Scotland. Maeglen and Wahlgren (1972), in a study of variation of specific gravity of natural stands of lodgepole pine, reported that coastal stands (e.g., from Washington and Oregon) had higher specific gravity than did interior stands. (e.g., from Utah and Wyoming). The open-pollinated families sampled from zone #4 would be classified as the inland variety (Fig. 1), and they resembled the inland variety phenotypically (Illingworth, pers. com.). It appears, therefore, that the clinal pattern of variation expressed in this genetic test coincides with the phenotypic patterns of variation that have been reported elsewhere. However, this is not necessarily the case for specific gravity in other conifers (e.g., Zobel *et al.* 1982).

Photoperiodism may be affecting growth and wood formation. O'Reilly (pers. com.) noted that in the same plantation, southern sources continued shoot elongation for two to three weeks longer than sources from near or north of the test site. This may be a large factor causing low specific gravity in the southern sources. The extension of the growing season (by photoperiod extension) causes auxin synthesis to continue resulting in a continuation of the production of large diameter cells (Larson 1960; 1964, Zahner 1963). Larson (1962b) demonstrated this indirect effect of photoperiod on cell diameter and wall thickening in red pine (*Pinus resinosa* Ait.). Rees and Brown (1954), Thor and Brown (1962) and Saucier and Taras (1966) observed a similar wood density response in provenance tests examining growth and specific gravity in other species.

As mentioned previously, not all of the observed variation among provenances for wood density may be attributed to latitudinal transfers. Henderson and Petty (1972) reported that coastal lodgepole pine had a significantly higher proportion of latewood and higher earlywood and latewood densities than inland material. Average tree heights and diameters were similar for the two sub-species; therefore, the observed lower density from the inland variety was probably due to genetic factors and not a growth rate/specific gravity relationship.

The heritability appropriate for mass selection for specific gravity (h_i^2) was estimated to be 0.44(±.10). This estimate is similar to that reported for wood density in other conifers (e.g., Dean *et al.* [1983] for radiata pine, Ernst *et al.* [1983] for jack pine, and Matziris and Zobel [1973], Shelbourne *et al.* [1969], Stonecypher *et al.* [1973], Talbert *et al.* [1982] for loblolly pine). The heritability estimate of family means for wood density was the highest (0.65±.15) among all traits measured in this study.

As mentioned previously, the occurrence of genotype x environment interactions can substantially influence heritability in a study with only one test site. For specific gravity, however, a large number of studies with more than one test site indicate that specific gravity is a relatively stable trait (e.g., Matziris 1979, Sprague *et al.* 1983, Talbert *et al.* 1982), although exceptions to this rule have been reported (McKimmy and Campbell 1982, Zobel *et al.* 1982).

The general pattern that seems to emerge from the literature on this topic is that the genotype x environment interaction may be negligible for specific gravity if locally adapted populations are tested in "compatible" environments. Interactions may develop, however, when trees are moved to environments with substantial edaphic, photoperiodic and climatic differences.

3.1.5 Branch Angle, Diameter and Length

Grand means for branch angle, branch diameter and branch length were 69.3 degrees (CV=10%), 22.3 mm (CV=16%) and 142.4 cm (CV=15%), respectively. The overall ranges for branch angle could only vary from 45 to 90%; the mean of the plantation is relatively intermediate and the level of variation quite moderate. No significant differences were noted among ZONES and PROV/Z for branch angle (Table 9), and heritabilities of zone and provenance means for branch angle were quite low (0.0 and 0.14±.24, respectively). Geographic

TABLE 9 - Analysis of variance of Branch Angle from an open-pollinated progeny test of 19 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	270.358	1.151	2.0
Zones (Z)	4	23.467	0.000	0.0
Provenance /Z (P/Z)	14	47.086	0.390	0.7
Families /P/Z (F/P/Z)	151	27.493**	5.561	9.5
R X Z	8	62.614*	1.691	2.9
R X P/Z	28	19.881**	1.008	1.7
R X F/P/Z(PLOT)	300	10.811	1.915	3.3
Error (within plot)	2259	46.541	46.541	79.9

Harmonic mean of number of trees per plot = 5.23137
Satterthwaite approximate error term for (P/Z) = 36.56 (68.5 d.f)
Satterthwaite approximate error term for (Z) = 89.82 (12.2 d.f)

* - significant at the $P<.05$ level
** - significant at the $P<.01$ level

/1 Analysis based on plot means

origin, therefore, has little effect on branch angle. FAM/P/Z effects, however, were significant (P<0.01) and accounted for a large percentage of the variation in branch angle (9.5%). Family means across all zones ranged from 59.7 degrees (family #6, provenance #44) to 75.7 degrees (family #10, provenance #57). The heritability of the family means estimate (0.61±.12) and the heritability on an individual basis (0.41±.08) were quite high. This heritability estimate is much higher than the estimates of 0.07 and 0.04 obtained by Erhenberg (1966) for Scots pine (*Pinus sylvestris L.*) and Ledig and Whitmore (1981) for Caribbean pine. Their procedure of scoring branch angle rather than actually measuring it may have caused poor separation among families.

The effects of ZONES on branch diameter and branch length were non-significant; however, the effects of REPS, PROV/Z and FAM/P/Z were significant (P<0.01)(Table 10 and 11). Provenance means for branch diameter varied from 20.1mm (provenance #20) to 24.8mm (provenance #72) and for branch length from 119.0cm to 170.5cm, again from provenance #72 and #20, respectively. Family means within provenance #72 ranged from 158.9cm (family #6) to 185.0cm (family #14). Family means for provenance #20 ranged from 100.4cm (family #1) to 127.5cm (family #5). As mentioned previously, the effect of ZONES was not significant for branch length but the heritability estimate was high at 0.45(±.53; Table 3). The large standard error of this estimate indicates large within-zone variability for branch length.

TABLE 10 - Analysis of variance of Branch Diameter from an open-pollinated progeny test of 19 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	97.752**	0.534	3.3
Zones (Z)	4	50.715	0.000	0.0
Provenance /Z (P/Z)	14	58.559**	1.791	10.9
Families /P/Z (F/P/Z)	151	5.200**	0.835	5.1
R X Z	8	4.723	0.195	1.2
R X P/Z	28	7.683**	0.554	3.4
R X F/P/Z(PLOT)	300	2.695	0.378	2.3
Error (within plot)	2259	12.123	12.123	73.9

Harmonic mean of number of trees per plot = 5.23137
Satterthwaite approximate error term for (P/Z) = 10.19 (44.9 d.f)
Satterthwaite approximate error term for (Z) = 55.60 (55.6 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

TABLE 11 - Analysis of variance of Branch Length from an open-pollinated progeny test of 19 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	1396.10*	0.000	0.0
Zones (Z)	4	7506.53	35.780	5.3
Provenance /Z (P/Z)	14	3377.35**	106.869	15.8
Families /P/Z (F/P/Z)	151	214.15**	37.588	5.5
R X Z	8	291.22	12.987	1.9
R X P/Z	28	379.11**	30.858	4.6
R X F/P/Z(PLOT)	300	101.39	18.071	2.7
Error (within plot)	2259	435.87	435.876	64.3

Harmonic mean of number of trees per plot = 5.23137
Satterthwaite approximate error term for (P/Z) = 491.87 (44.2 d.f)
Satterthwaite approximate error term for (Z) = 3289.46 (13.0 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

Heritabilities of provenance and family means were 0.83(±.35) and 0.48(±.13) for branch diameter and 0.85(±.35) and 0.53(±.13) for branch length, indicating selection for desirable provenances and desirable families within provenances for these two branch traits would be possible. Individual tree heritabilities were moderate for branch diameter (0.25±.07) and branch length (0.31±.08).

3.1.6 Tracheid Length

The grand mean for tracheid length measured on a composite sample of earlywood and latewood from the ninth growth ring was 1.7mm with a CV of 8%. In mature wood of lodgepole pine tracheid lengths are expected to be over 3 mm (Taylor *et al*. 1983); therefore, fibre length at this age is still indicative of juvenile wood. The source of variation REPS was significant at the $P<0.05$ level and accounted for more than 10 percent of the variance (means for replications 1, 2 and 3 were 1.75, 1.62 and 1.67 mm, respectively; Table 12). Therefore, some micro-environmental differences among replications may influence tracheid development. The effects of ZONES and PROV/Z were not significant. Heritability of zone means for tracheid length was moderate (0.31±.56), but a large amount of variation was present within zones (Appendix A), making this effect non-significant. The effect of FAM/P/Z was significant ($P<0.01$) and the heritability of family means was also high (0.52±.17), suggesting that a large amount of variation exists among families for tracheid

TABLE 12 - Analysis of variance of Tracheid Length from an open-pollinated progeny test of 14 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	0.37953*	.00353	11.6
Zones (Z)	3	0.10533	.00049	1.6
Provenance /Z (P/Z)	6	0.03406	.00061	2.0
Families /P/Z (F/P/Z)	80	0.01098**	.00192	6.3
R X Z	6	0.04046**	.00155	5.1
R X P/Z	12	0.01191**	.00074	2.4
R X F/P/Z(PLOT)	159	0.00523	.00136	4.5
Error (within plot)	1158	0.02023	.02023	66.5

Harmonic mean of number of trees per plot = 3.22682
Satterthwaite approximate error term for (P/Z) = 0.018 (23.1 d.f)
Satterthwaite approximate error term for (Z) = 0.063 (8.2 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

length. Interactions for RxZ and RxP/Z were significant (P<0.01); therefore, environmental differences within replications were probably large enough to cause a change in the ranking of variances for these two effects. Family means across the experiment ranged from 1.51mm for family #9 (provenance #27) to 1.89mm for family #2 (provenance #57) for the 1982 growth ring. As mentioned previously, family differences were significant and the heritability estimate on an individual basis for tracheid length was moderate (0.31±.09). For radiata pine, broad-sense heritabilities have varied from 0.2 to 0.8 (Dadswell *et al*. 1961, Nicholls 1967) and for loblolly pine, Stonecypher *et al*. (1973) and Matziris and Zobel (1973) reported narrow-sense heritabilities of 0.44 and 0.97, respectively. Although the heritability estimate for tracheid length from this study is somewhat lower than those reported for southern pines, it had the third highest heritability for all traits measured in this study and should probably be considered a highly heritable trait in lodgepole pine.

3.1.7 Height and Diameter

Trees in the Red Rock plantation averaged 4.7m (CV=10%) tall and had an average diameter of 7.4 cm (CV=11%) at age 10. Because height and diameter may be considered closely related traits, it was not unexpected that both would exhibit similar patterns of variation at the zone, provenance and family levels. ZONES and FAM/P/Z were significant at the $P<0.05$ level and REPS and PROV/Z were significant at the $P<0.01$ level for height at age 10 (Table 13). Results of significance tests for diameter growth in the model were the same as for height, except that ZONES was significant only at the 0.05 level (Table 14). Zone means for height varied from 4.4m to 5.2m and for diameter from 6.9cm to 8.0cm (zones #2 and #4, respectively). The heritability of zone means for both traits were also very close (Table 3). Provenance means for height growth ranged from 4.2m for provenance #27, to 5.6m for provenance #72. Provenance means for diameter ranged from 6.6cm to 8.6cm, again for provenances #27 and #72, respectively. Heritability of provenance means was 0.87 (±.43) for height and 0.79(±.43) for diameter, indicating that selection for increased growth can easily be achieved by selection at the provenance level.

Family means for height growth within provenance #27 ranged from 4.1m to 4.3m, and in provenance #72, ranged from 5.5m to 6.1m. Heritabilities of family means were moderate at 0.36(±.17) for height and 0.35(±.17) for diameter, as were heritabilities on an individual basis (0.27±0.08 and 0.23±.07, respectively).

Height and diameter growth typically have lower heritabilities than those reported here, which may be explained by the fact that the test site at Red Rock was extremely homogeneous, thereby reducing environmental variation. This would reduce the within-plot variance (σ_w^2)

TABLE 13 - Analysis of variance of height from an open-pollinated pro[illegible] test of 14 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	1	5.5425**	.04111	8.1
Zones (Z)	4	7.6374*	.11[illegible]5	22.0
Provenance /Z (P/Z)	9	1.3324**	.06437	12.7
Families /P/Z (F/P/Z)	112	0.1004*	.01822	3.6
R X Z	4	0.2564	.01476	2.9
R X P/Z	9	0.1372*	.00813	1.6
R X F/P/Z(PLOT)	112	0.0640	.0223	4.5
Error (within plot)	1134	0.2262	.2262	44.6

Harmonic mean of number of trees per plot = 5.4792
Satterthwaite approximate error term for (P/Z) = 0.174 (13.6 d.f)
Satterthwaite approximate error term for (Z) = 1.452 (9.8 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

TABLE 14 - Analysis of variance of Diameter from an open-pollinated progeny test of 14 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	1	7.0156*	.0520	4.4
Zones (Z)	4	12.4687*	.1817	15.3
Provenance /Z (P/Z)	9	2.2101**	.0971	8.2
Families /P/Z (F/P/Z)	112	0.2720*	[illegible]	4.0
R X Z	4	0.5231	[illegible]	2.5
R X P/Z	9	0.3677*	[illegible]	1.8
R X F/P/Z(PLOT)	112	0.1776	.0487	4.1
Error (within plot)	1134	0.7064	.7064	59.7

Harmonic mean of number of trees per plot = 5.4792
Satterthwaite approximate error term for (P/Z) = 0.462 (13.4 d.f)
Satterthwaite approximate error term for (Z) = 2.366 (8.9 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

which is usually a major component in the denominator of the heritability calculation. Heritability of height growth at age six in this same plantation (using a larger data set) was estimated to be 0.16 (Yeh, pers. com.). Rehfeldt (1985b) estimated a heritability of 0.22 for six-year height growth of lodgepole pine in Idaho. When plantations of lodgepole pine are established in these "farm field" sites, superior height growth should be expressed well from the better families.

3.1.8 Volume and Dry-Weight Production

The average volume for trees in the experiment was 8.5 dm^3, and for dry weight, 3.3 kg/tree, both of which had CV's of 31%, indicating overall variability is greater for these two traits than for height and diameter. Volume and dry weight, which are functions of both diameter and height, exhibited the same trends of variation as diameter and height. REPS, ZONES and FAM/P/Z were significant ($P<0.05$ level) and PROV/Z was significant at the $P<0.01$ level for both volume and dry-weight production (Table 15 and 16). Zone and provenance means indicated a north to south increase in volume and dry-weight production (Fig. 4). Provenance #27 produced the lowest volumes (5.8 dm^3) and provenance #72 the highest (13.8 dm^3). These two provenances also produced the smallest (2.3 kg/tree) and largest (5.1 kg/tree) estimated dry weights, respectively. Therefore, volume production appears to be the major factor influencing

TABLE 15 - Analysis of variance of Volume from an open-pollinated progeny test of 14 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replication (R)	1	133.728*	0.973	6.3
Zones (Z)	4	203.119*	2.902	18.9
Provenance /Z (P/Z)	9	35.111**	1.690	11.0
Families /P/Z (F/P/Z)	112	2.872*	0.380	2.5
R X Z	4	10.622	0[illegible]74	3.7
R X P/Z	9	3.938	0.203	1.3
R X F/P/Z(PLOT)	112	2.111	0.656	4.3
Error (within plot)	1134	7.970	7.970	51.9

Harmonic mean of number of trees per plot = 5.4792
Satterthwaite approximate error term for (P/Z) = 4.70 (12.02 d.f)
Satterthwaite approximate error term for (Z) = 41.79 (10.5 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level.

/1 Analysis based on plot means

TABLE 16 - Analysis of variance of Dry Weigh[illegible] an [illegible]pen-pollinated progeny test of 14 provenances of lodgepole pine at [illegible] site in central British Columbia. /1

SOURCE	DF	MEAN SQ[illegible]	[illegible]ARIANCE [illegible]NENT	% VARIANCE
Replications (R)	1	18.07[illegible]	.1323	6.8
Zones (Z)	4	24.208*	.3426	17.7
Provenance /Z (P/Z)	9	4.464**	.2192	11.3
Families /P/Z (F/P/Z)	112	0.430*	.0691	3.6
R X Z	4	1.422*	.0677	3.5
R X P/Z	9	0.381	.0099	0.5
R X F/P/Z(PLOT)	112	0.292	.1122	5.8
Error (within plot)	1134	0.985	.9851	50.8

Harmonic mean of number of trees per plot = 5.4792
Satterthwaite approximate error term for (P/Z) = 0.519 (14.5 d.f)
Satterthwaite approximate error term for (Z) = 5.505 (11.1 d.f)

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

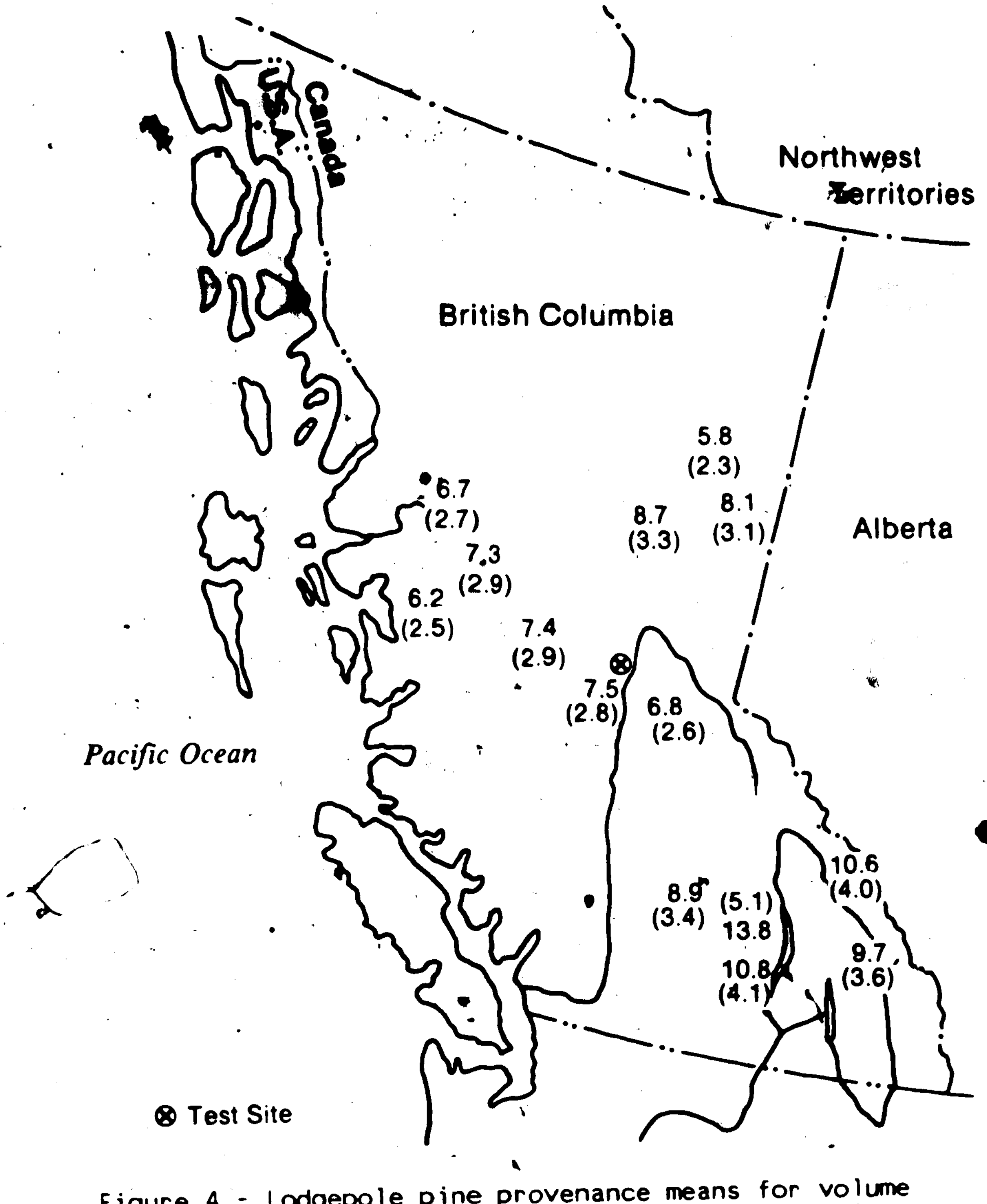

Figure 4 - Lodgepole pine provenance means for volume production (dm^3) and dry-weight production (kg/tree; in parenthesis) at the Red Rock test site in central British Columbia.

dry-weight production. Variation among family means for these two traits in provenance #27 varied from 4.7 dm' to 6.9 dm' for volume and from 1.8 kg/tree to 2.6 kg/tree for dry-weight. In provenance #72 family means varied from 12.0 dm' to 15.7 dm' for volume, and from 4.4 kg/tree to 5.7 kg/tree for dry-weight. Heritabilities of zone, provenance and family means were similar to those for height and diameter (Table 3). Heritabilities for volume and dry-weight production were slightly lower compared to those for height and diameter (Table 3). In the Stonecypher [illegible] (1973) study, heritability estimates for dry-weigh[illegible]uction (0.19) and volume (0.18) also were intermediate to those for height and diameter and were similar to the estimates reported here for lodgepole pine.

3.1.9 Rust Resistance

Of the total number of trees examined for rust infection from the 24 provenances, 25.6% were infected with stalactiform blister rust and 18.9% with western gall rust. From the [illegible]lysis of stalactiform blister rust on the percentage of trees infected per plot, REPS, PROV/Z, FAM/P/Z and RxP/Z were significant ($P<0.01$)(Table 17). The largest two sources of variation found in the analysis were for REPS (19.4%) and PROV/Z (15.4%)(Table 17). Replication means for trees infected (i.e., scored on a scale of 1 to 10) were 1.6, 1.4 and 2.1 for replications 1, 2 and 3, respectively. The REP effect could again have been influenced by scorer

TABLE 17 - Analysis of variance of Stalactiform Blister Rust from an open-pollinated test of 24 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	35783.0**	315.13	19.4
Zones (Z)	5	20113.8	107.70	6.6
Provenance /Z (P/Z)	18	8484.5**	249.40	15.4
Families /P/Z (F/P/Z)	190	1334.9**	161.54	9.9
R X Z	10	740.9	0.0	0.0
R X P/Z	36	1749.3**	99.90	6.1
R X F/P/Z(PLOT)	374	850.2	690.82	42.5
Error (within plot)		821		

Satterthwaite approximate error term for (P/Z) = 2234 (51.8 d.f.)
Satterthwaite approximate error term for (Z) = 7476.1 (13.5 d.f.)

σ^2 bin = 821

$$\frac{1}{m}\sigma_b^2 = 159.424$$

$$\sigma_e^2 - \frac{1}{m}\sigma_d^2 = 690.816$$

$$\frac{1}{m} = 5.15$$

$$h^2 = \frac{4\ (161.54)}{821 + 690.82 + 161.54} = 0.39$$

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plot means

bias as well as by variation in Indian paint brush densities acting differentially among replications as inoculum sources. Differences among replications in micro-meteorological factors influencing infection may also have been a factor. Provenance means based on the 1-10 ru[illegible] infection scale ranged from 1.04 (provenance #62) to 2.4 (provenance #15). Family means within provenance #62 ranged from 1.0 (family #5) to 1.2 (family #4). Family means in the least resistant of the 24 provenances (provenance #15) varied from 1.3 (family #5) to 2.9 (family #6). Heritability for stalactiform blister rust score from the transformed plot mean (percent infection) data was 0.39, from the binomial analysis 0.20(±.05), and from the threshold chi-square analysis, 0.53 (Table 17, 18, 19). Sohn and Goddard (1979) reported that gain calculations using genetic estimates from the binomial analysis were closest to the realized gain calculations for fusiform blister rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f.sp. *fusiforme*). Individual tree heritabilities for fusiform rust resistance in loblolly pine ranged from 0.02 to 0.39, depending on the resistance index used, location, and year of planting (Barker 1973, Blair 1970). As stated by Sohn and Goddard (1979) differences in heritability estimates may be due to differences in infection level at the site, because with low infections, the chance for a "non-resistant" tree to escape is high.

TABLE 18 - Analysis of variance of Stalactiform Blister Rust and Western Gall Rust based on binomial data for infection.

SOURCE		DF	MS STALACTIFORM RUST	MS WESTERN GALL RUST	EXPECTED MEAN SQUARES
Replications	(R)	2	8.7650 **	2.3322 **	$\sigma^2_r + 5.52\ \sigma^2_{rf} + 48.25\ \sigma^2_{rp} + 1139.38\ \sigma^2_r$
Provenance	(P)	23	2.6050 **	1.9887 **	$\sigma^2_r + 5.50\ \sigma^2_{rf} + 16.10\ \sigma^2_f + 47.97\ \sigma^2_{rp} + 142.53\ \sigma^2_p$
Family/P	(F/P)	190	0.3265 **	0.2247 **	$\sigma^2_r + 5.46\ \sigma^2_{rf} + 15.94\ \sigma^2_f$
R & P		46	0.3522 **	0.3937 **	$\sigma^2_r + 5.45\ \sigma^2_{rf} + 47.26\ \sigma^2_{rp}$
R X F/P		374	0.1904 **	0.1497 **	$\sigma^2_r + 5.32\ \sigma^2_{rf}$
Error		2786	0.1542	0.1272	σ^2_r

$$h^2_{\text{STALACTIFORM RUST}} = \frac{4\ (.008475)}{0.1542 + .006809 + .008470} = 0.20$$

$$h^2_{\text{WESTERN GALL RUST}} = \frac{4\ (.004662)}{0.1272 + 0.004234 + .004662} = 0.14$$

** Significant at P<.01 Level

MS^1 Satterthwaite approximate MS for testing (P) = 0.488 (~~72~~ d.f.)

MS^2 Satterthwaite approximate MS for testing (P) = 0.2197 (59 d.f.)

TABLE 19 - Heritability estimates of Stalactiform Blister Rust and Western Gall Rust analyzed as threshold traits (Dempster and Lerner method).

STALACTIFORM BLISTER RUST	WESTERN GALL RUST
$n = 3422$	$n = 3422$
$\Sigma x = 884$	$\Sigma x = 647$
$\Sigma xp = 349.844$	$\Sigma xp = 213.358$
$\overline{p} = 0.25833$	$\overline{p} = 0.1891$
$\overline{q} = 0.7417$	$\overline{q} = 0.8109$
$\overline{pq} = 0.1916$	$\overline{pq} = 0.1533$
$\chi^2 = \frac{349.844 - 0.25833\ (844)}{0.1916} = 634.03$	$\chi^2 = \frac{213.358 - .1891\ (647)}{0.1533} = 593.72$
$h^2 = \frac{634.03 - 213}{0.25\ (3192.82)^{**}} = 0.53\ (\pm.02)^{***}$	$h^2 = \frac{593.72 - 213}{0.25\ (3192.36)^{**}} = 0.48\ (\pm .02)^{***}$

* = # of families

** = $No = 3422 - \frac{55226}{3422} - 213 = 3192.816$

*** = S.e. of heritability estimate (See Appendix C).

For western gall rust, REPS was significant ($P<0.01$) and ZONES, PROV/Z and FAM/P/Z were significant at the 0.05 level (Table 20). ZONES accounted for approximately 19.5% of the variation, which is quite different than the case for stalactiform blister rust (Table 20). No clinal patterns were evident. The population from zone #1 had the lowest mean infection (1.1) while the population from zone #3 had the highest mean infection (1.7). The effect of PROV/Z and FAM/P/Z both accounted for a small amount of the variation (6 and 7 %, respectively). Provenance #57 had the lowest level of infection at 1.04, and provenance #20 had an infection level of 1.88 (on the 1 to 5 scale). Family means within provenance #57 ranged from 1.0 (no infection) to 1.2. Family means in the least resistant provenance (#20) ranged from 1.3 to 2.4. The heritability estimate for western gall rust score from the transformed plot means data was 0.21, from the binomial analysis, 0.14 and from threshold chi-square analysis, 0.48 (Table 20, 18, 19, respectively).

It would be difficult to speculate whether or not these results indicate there is less additive genetic variance for western gall rust resistance than for stalactiform blister rust, or whether infection levels in the plantation primarily determined the outcome. Western gall rust was present on only 19% of the trees (compared to 26% for stalactiform blister rust); this may indicate that less inoculum was present for western gall rust than stalactiform blister rust.

TABLE 20 - Analysis of variance of Western Gall Rust from an open-pollinated test of 24 provenances of lodgepole pine at one test site in central British Columbia. /1

SOURCE	DF	MEAN SQUARE	VARIANCE COMPONENT	% VARIANCE
Replications (R)	2	8677.5**	39.40	3.5
Zones (Z)	5	27793.2*	221.96	19.5
Provenance /Z (P/Z)	18	3821.9*	67.88	6.0
Families /P/Z (F/P/Z)	190	1023.4*	81.20	7.1
R X Z	10	160.5	0.00	0.0
R X P/Z	36	745.4	107.29	9.4
R X F/P/Z(PLOT)	374	779.8	620.38	54.5
Error (within plot)		821		

Satterthwaite approximate error term for (P/Z) = 989 (12.8 d.f.)
Satterthwaite approximate error term for (Z) = 3237 (6.2 d.f.)

$$\frac{1}{m}\sigma_b^2 = 159.424$$

$$\sigma_e^2 - \frac{1}{m} = \sigma_\sigma^2 = 620.376$$

$$\frac{1}{m} = 5.15$$

$$h^2 = \frac{4\,(81.2)}{821 + 620.376 + 81.2} = 0.21$$

* - significant at the P<.05 level
** - significant at the P<.01 level

/1 Analysis based on plo[illegible]eans

The mechanisms of rust resistance cannot be elucidated from information gathered in this study, except that a sufficient amount of additive genetic variance for resistance breeding appears to be present in these lodgepole pine populations (i.e., family differences were significant). Also, provenance and zone effects were significant, indicating populations have different levels of resistance; these may be caused by gross maladaptation (i.e., severe stress) of some populations to the test site or some inherent level of resistance built in by coadaptation with the pathogen.

3.1.10 Structure of Genetic Variance

Assuming the clinal pattern of variation exhibited here for wood density (as well as the clinal or ecotypic patterns of variation for any of the other traits) has a genetic basis, it could be proposed that selective and/or non-selective factors have led to the observed pattern of variation in lodgepole pine. To further extrapolate the differences among families from different zones, the three components of variance that go into the calculation of these heritabilities (i.e., error variance, replication x family variance and family variance) were estimated independently for zones #1 through #5 using two analysis of variance models (Tables 21a and 21b). These indicated that the ratio of additive genetic variance estimates to the error variance were relatively constant for specific gravity across all

TABLE 21a - Variance components for family effects (σ^2_f), replication x family effects (σ^2_{rf}), error variance (σ^2_e) and total variance (σ^2_T) for seven traits of lodgepole pine from five different geographic zones in British Columbia. Based on an analysis of variance model of Replications, Families, Reps. x Fam. and error on individual tree data.

ZONE	σ^2	BARK THICKNESS	SPECIFIC GRAVITY	DIAMETER	HEIGHT	VOLUME	BRANCH DIAMETER	BRANCH ANGLE
1	σ^2_f	0	.000048	.1262	0	.789	.72	12.92
	σ^2_{rf}	.0555	.000076	.0529	.0470	1.841	.17	0
	σ^2_e	.2359	.000462	.7310	.1850	8.897	10.45	47.55
	σ^2_T	.2914	.000587	.9101	.2320	11.528	11.34	60.47
2	σ^2_f	0	.000074	.2043	.1282	4.177	2.83	7.58
	σ^2_{rf}	.0654	.000089	.1282	.0266	1.861	1.19	.33
	σ^2_e	.2459	.000613	.8250	.2480	11.582	15.63	48.02
	σ^2_T	.3113	.000776	1.1575	.4028	17.620	19.65	55.93
3	σ^2_f	.0645	.000049	.1862	.0857	1.800	1.81	5.48
	σ^2_{rf}	.0611	.000048	.0290	.0108	.353	.24	1.39
	σ^2_e	.1986	.000576	.5725	.1601	4.684	13.04	40.02
	σ^2_T	.3242	.000672	.7877	.2566	6.837	15.09	47.35
4	σ^2_f	.0567	.000064	.0806	.0542	.992	1.95	1.56
	σ^2_{rf}	.0389	0	.0001	.0142	.068	.52	2.64
	σ^2_e	.1738	.000677	.5989	.2072	4.314	10.74	44.85
	σ^2_T	.2694	.000740	.6805	.2756	5.374	13.21	49.05
5	σ^2_f	.0834	.000046	.0265	.0350	.217	.48	5.67
	σ^2_{rf}	.0480	.000053	.0467	.0710	.747	.83	3.30
	σ^2_e	.1885	.000604	.5833	.2066	4.603	11.61	43.51
	σ^2_T	.3199	.000703	.6565	.2726	5.573	12.92	52.48

TABLE 21b - Variance components for family effects (σ^2_f), replication x family effects (σ^2_{rf}), error variance (σ^2_e) and total variance (σ^2_T) for seven traits of lodgepole pine from five different geographic zones in British Columbia. Based on an analysis of variance model of Replications, Provenances, Families within Prov., Reps. x Prov., Reps. x Fam/Prov. and error on individual tree data.

ZONE	σ^2	BARK THICKNESS	SPECIFIC GRAVITY	DIAMETER	HEIGHT	VOLUME	BRANCH DIAMETER	BRANCH ANGLE
1	σ^2_f	0	.000051	.1190	0	.81	.49	12.94
	σ^2_{rf}	.3447	.000086	.0397	.0450	1.58	0	0
	σ^2_e	.2359	.000462	.7309	.1847	8.90	10.45	47.55
	σ^2_T	.2706	.000599	.8896	.2297	11.284	10.94	60.49
2	σ^2_f	0	.000078	.0093	.00001	0	2.89	6.34
	σ^2_{rf}	.0684	.000080	.1196	.0309	1.97	.92	0
	σ^2_e	.2459	.000613	.8248	.2484	11.58	15.63	48.02
	σ^2_T	.3143	.000771	.9537	.27931	13.55	19.44	54.36
3	σ^2_f	.0201	.000047	.0548	.0250	.47	.13	5.61
	σ^2_{rf}	.0235	.000046	.0076	.0102	.17	0	1.44
	σ^2_e	.1986	.000576	.5725	.1601	4.68	13.04	40.02
	σ^2_T	.2422	.000669	.6349	.1953	5.32	13.17	47.07
4	σ^2_f	.0086	.000062	.0706	.0396	.83	.79	1.28
	σ^2_{rf}	.0272	0	.0046	.0132	.06	.43	2.78
	σ^2_e	.1738	.000677	.5990	.2072	4.31	10.74	44.85
	σ^2_T	.2096	.000739	.6742	.2600	5.20	11.96	48.91
5	σ^2_f	.0358	.000027	.0417	.0262	.32	.36	6.04
	σ^2_{rf}	.0055	.000012	.0271	.0164	.47	1.00	2.38
	σ^2_e	.1884	.000604	.5833	.2066	4.61	11.61	43.51
	σ^2_T	.2287	.000643	.6521	.2492	5.40	12.97	51.93

five zones regardless if provenance effects were removed from the analysis (Table 21a and 21b). This is no doubt due to the lack of significant differences among provenances within zones. Significant family effects, when present, are due to differences among trees and not among stands (Table 22a and 22b). For branch angle, the differences among estimates of additive genetic variation were quite large (from σ_A^2 =4x1.6 and 1.3 for zone #4 to σ_A^2 =4x12.9 for zone #1; Table 21a and 21b) and were the major components affecting heritability differences among zones (Table 22a and 22b). The inclusion of provenance effects in the analysis of variance model, as expected, did not affect estimates of variance for branch angle (Table 21a and 21b). No clear pattern was evident with respect to different populations expressing more or less additive genetic variance for all traits, except the population from zone #5 had five of the lowest heritabilities (Table 22a and 22b).

Although a few of the heritabilities were poorly estimated (i.e., heritabilities greater than one in Table 22a), and the standard errors among heritability estimates were large, heritabilities were generally reliable (i.e., standard errors were usually lower than the heritability estimate; Table 22a and 22b). Although heritabilities within zones were usually greater than 0.2, which would indicate that a large amount of additive genetic variance is present for most traits, significance tests for family effects (F-tests) was quite variable across zones for the same trait

TABLE 22a - Heritability (S.e. in parenthesis), significance of family effects (NS - non-significant; * significant at P< .05; ** significant at P< .01) and heritability of family means (in square brackets) for seven traits from five different geographic zones of lodgepole pine in British Columbia. Based on an analysis of variance of Replications, Families, Reps. x Fam. and error on individual tree data.

ZONE	BARK THICKNESS	SPECIFIC GRAVITY	DIAMETER	HEIGHT	VOLUME	BRANCH DIAMETER	BRANCH ANGLE
1	NS NA	NS 0.33 (.23) [0.38]	* 0.56 (.28) [0.58]	NS NA	NS 0.27 (.22) [0.31]	NS 0[illegible].21) [illegible]	** 0.86 (.34) [0.75]
2	NS NA	NS 0.38 (.20) [0.43]	* 0.71 (.25) [0.60]	** 1.30 (.32) [0.78]	** 0.95 (.28) [0.68]	* 0.58 (.23) [0.59]	** 0.54 (.22) [0.63]
3	* 0.80 (.26) [0.57]	NS 0.29 (.18) [0.39]	** 0.96 (.28) [0.74]	** 1.30 (.32) [0.81]	** 1.10 (.30) [0.75]	* 0.48 (.21) [0.59]	* 0.46 (.21) [0.55]
4	** 0.84 (.28) [0.61]	* 0.34 (.19) [0.50]	* 0.47 (.22) [0.59]	** 0.79 (.27) [0.67]	** 0.74 (.26) [0.69]	* [illegible]9 (.24) [illegible]0.60]	NS 0.13 (.15) [0.22]
5	** 1.0 (.30) [0.67]	NS 0.26 (.17) [0.36]	NS 0.16 (.15) [0.26]	* 0.52 (.22) [0.50]	N[illegible] 0.16 (.15) [0.21]	NS [illegible]15 (.15) [illegible]0.25]	* 0.43 (.21) [0.50]

TABLE 22b - Heritability (S.e. in parenthesis), significance of family effects (NS - non-significant; * significant at P< .05; ** significant at P< .01) and heritability of family means (in square brackets) for seven traits from five different geographic zones of lodgepole pine in British Columbia. Based on an analysis of variance model of Replications, Provenances, Families within Prov., Reps. x Prov., Reps x Fam./Prov. and error on individual tree data.

ZONE	BARK THICKNESS	SPECIFIC GRAVITY	DIAMETER	HEIGHT	VOLUME	BRANCH DIAMETER	BRANCH ANGLE
1	NS NA	NS 0.31 (.23) [0.38]	* 0.47 (.28) [0.58]	NS NA	NS 0.27 (.22) [0.42]	NS 0.17 (.19) [0.34]	** 0.71 (.34) [0.75]
2	NS NA	NS 0.37 (.20) [0.45]	NS 0.04 (.12) [0.07]	NS 0.0 (.11) [0.00]	NS NA	* 0.52 (.23) [0.61]	* 0.42 (.21) [0.60]
3	NS 0.31 (.19) [0.41]	NS 0.27 (.18) [0.39]	* 0.32 (.19) [0.50]	** .45 (.22) [0.56]	NS .32 (.19) [0.48]	NS 0.04 (.12) [0.10]	* 0.43 (.21) [0.58]
4	NS 0.16 (.16) [0.22]	* 0.31 (.19) [0.50]	* 0.38 (.21) [0.55]	* 0.53 (.24) [0.60]	** 0.55 (.26) [0.66]	NS 0.25 (.18) [0.39]	NS 0.10 (.14) [0.19]
5	** .54 (.24) [0.24]	NS 0.16 (.15) [0.31]	NS 0.24 (.17) [0.39]	* 0.38 (.20) [0.50]	NS 0.22 (.17) [0.33]	NS 0.11 (.14) [0.20]	* 0.42 (.21) [0.54]

and also depended on the analysis of variance model used (Table 22a and 22b). Significant family differences in specific gravity were present only in the population from zone #4 ($P<.05$) and did not change when provenance effects was added to the analysis of variance model (Table 22b). Heritability on an individual basis (h^2_i) for bark thickness were quite close across all zones from which estimates could be obtained; however, significant family differences were not present when provenance effects were included in the analysis. Therefore, a heritability without significant family effects is probably not a meaningful statistic. Height growth for the population from zone #2 had a heritability (h^2_i) of over one, whereas, height growth for the population from zone #5 had a heritability estimate of 0.52(±.22)(Table 22a). When provenance effects are included in the analysis, heritability estimates dropped considerably (Table 22b). For diameter, the estimate from zone #3 was close to one (0.97±.28) and that obtained from zone #5 had an estimate of only 0.16(±.15), and these similarly became smaller when provenance effects was in the model. Large differences were also present between the heritabilities for branch angle in zone #1 (0.86±.34) and zone #4 (0.13±.15). Likewise, family differences were significant for branch angle in the zone #1 population ($P<.01$) and non-significant in the zone #4 population. As indicated earlier, this trait was not influenced by provenance effects. These large scale changes in heritability estimates caused by changing the analysis of variance model to included provenance effects, indicates that significant family effects may in fact be due to provenance (or stands) differences and little variation exists within a provenance. What is particularly interesting, is that these differences in variances change among zones and among traits in different zones.

Family heritability (h_f^2) may be a more reliable estimate to compare family variation across zones, simply because in comparison to h_i^2 it is free of bias from stand-to-stand differences in relatedness and full-sib structure in the progeny (as previously discussed). The heritabilities of family means ranged from 0.00 to 0.78 and corresponded closely to the F-tests for family differences (Table 22a and 22b). Heritability estimates in the range of 0.00 to 0.41 corresponded with non-significant family differences, those from 0.5 to 0.60 corresponded with significant family differences at $P<.05$ and from 0.61 and greater, corresponded with significant family differences at the $P<.01$ level (Table 22a and 22b).

Even though there are large errors associated with these estimates, the genetic parameters may provide some insight into the expected stability of traits over all populations. Making the assumption that a trait such as height growth may be more important than wood density to overall reproductive fitness, selective forces might exert differential pressures depending upon the environments associated with different geographic zones. Therefore, in situations where the selective pressure for height growth was weak, additive genetic variance might be conserved and heritability estimates from such populations would be high. In environments where selection for height growth is strong, additive genetic variance would be low if it was not maintained at high levels by mutation and recombination. When selective pressure was more uniform across the geographic distribution, additive genetic variance may be expected to be constant across all populations. The above considerations suggest that when populations are pooled to obtain estimates of genetic parameters (for heritability estimates used in expected gain calculations), the reliability of the values is obviously questionable as genetic parameters have been shown to vary across the geographic range.

Within a zone, significant stand-to-stand differences may contribute most of the additive genetic variance, whereas in other zones, additive genetic variance may be "spread" across stands (i.e., stand differences non-significant). For example, there were significant PROV/Z effects for height, diameter, volume and branch diameter; therefore, these traits are influenced by the genetic structures among stands within zones. For specific gravity and branch angle, PROV/Z effects were not significant, indicating that variation within zones is primarily influenced by genetic differences among individuals, irrespective of the stand (or provenance) structure.

However, significant differences of family effects for specific gravity were only present in the zone #4 population (Table 22). Of particularly interest, the heritabilities for specific gravity were relatively constant over all five populations, whereas the heritabilities for branch angle were quite variable. From the generalization that characters more closely related to reproductive fitness have less additive genetic variance, it could be suggested that stabilizing selection may be more uniform for specific gravity across the species range, whereas branch angle may be more tightly related to fitness in some zones (as both additive genetic variance and phenotypic variance were reduced in zone #4; Table 21). Not knowing, however, how natural selection acts on the character makes this type of speculation difficult, since selection may be occurring on one of its correlated characters (Falconer 1981). Also, additive genetic variance may have been reduced simply by genetic drift and/or selection, as the more northern populations (i.e., population from zone #4) tended to occur in smaller isolated stands and may have had to undergo greater adaptation to narrower ecological niches (Yeh *et al.* 1985).

3.2 Correlations Among Traits and Relationships of Traits with Information of Provenance Origin

Relationships among traits measured in this study can be examined at a number levels. Relationships between provenance means for the various traits and geographic origin information can be used to examine the influence that latitude, longitude and elevation have had on developing differences among provenances.

Correlations between traits have two distinct causes, genetic and environmental (Falconer 1981). Genetic correlations arise primarily from pleiotropic effects of genes and, to a lesser extent, linkage among genes, particularly if selection is weak (Falconer 1981). Most genes are thought to be pleiotropic, affecting many different aspects of the phenotype (Wright 1980). Environmental correlations between traits occur in situations where two characters are influenced by the same changes in environmental conditions (Falconer 1981). Phenotypic correlations, therefore, are a combination of genetic and environmental causes. If the heritabilities of the two traits are high, then the phenotypic correlation is determined chiefly by the genetic correlation; if both traits have low heritabilities, then it is the environmental correlation that is more important (Falconer 1981).

Because of the large number of correlations that can be generated in this study, only those which were considered economically important have been discussed in this section (Table 23). A matrix of all possible correlations, based on the maximum number of trees for each combination among traits, is provided (Appendix F).

TABLE 23 - Genetic, phenotypic and environmental correlations for growth and wood property traits for lodgepole pine at the Red Rock test site in central British Columbia.

TRAITS	GENETIC CORRELATION (S.e.)	PHENOTYPIC CORRELATION	ENVIRONMENTAL CORRELATION
SG w. HT	0.034 (.20)	-.032	-.071
SG w. DIA	-0.401 (.20)	-.155	-.018
SG w. VOL	-0.364 (.22)	-.121	-.007
SG w. DW	-0.124 (.21)	.090	.190
SG w. MC	-0.336 (.28)	-.513	-.595
SG w. CW	0.601 (.24)	.176	.016
HT w. DIA	0.415 (.18)	.574	.627
HT w. DW	0.797 (.09)	.720	.698
HT w. VOL	0.680 (.13)	.730	.751
DIA w. DW	0.915 (.04)	.913	.916
BL w. HT	0.301 (.18)	.418	.467
BL w. DIA	0.120 (.21)	.430	.555
BL w. BD	0.742 (.06)	.835	.870
BL w. SS	0.310 (.20)	.067	.018
BA w. BD	-0.561 (.14)	-.360	-.272
BA w. BL	-0.420 (.14)	-.251	-.164
BA w. HT	-0.041 (.18)	.082	.163
BA w. DIA	-0.051 (.18)	.028	.078
BA w. VOL	-0.099 (.20)	.051	.132
BD w. HT	-0.210 (.20)	.225	.411
BD w. DIA	0.129 (.20)	.389	.494
CS w. BA	-0.970 (.20)	-.298	-.114
CS w. BD	0.656 (.15)	.271	.194
CS w. BL	0.390 (.17)	.195	.155
SS w. BA	0.343 (.18)	.061	-.013
SS w. BD	0.226 (.20)	.063	.033
SS w. DIA	0.414 (.25)	.078	-.009
SS w. HT	0.437 (.26)	-.084	-.231
SS w. VOL	0.343 (.28)	.040	-.028
SS w. DW	0.400 (.28)	.037	-.043
SS w. CS	0.120 (.27)	.239	.256
BT w. HT	-0.175 (.24)	.112	.202
BT w. DIA	0.628 (.20)	.253	.149
RS w. GS	0.588 (.17)	.055	-.051

where;
SG - specific gravity
HT - 10 year height growth
VOL - volume growth
MC - wood moisture content
DW - stem dry weight
BL - branch length
BD - branch diameter
DIA - diameter
BA - branch angle
SS - stem score for straightness
CS - crown score for form
CW - compression wood
BT - bark thickness
RS - stalactiform rust score
GS - western gall rust score

3.2.1 Wood Specific Gravity

The relationships of latitude and elevation to specific gravity were not significant, but that between specific gravity and longitude was significant ($P<.01$; Table 24). However, photoperiodic responses could indirectly be the primary cause of this relationship, as western provenances were from latitudes higher than the test site. Therefore, some confounding of latitudinal effects may be present in regressions of traits with longitude.

The relationship of most interest in tree breeding is usually the one between specific gravity and volume. The economic implication of specific gravity being reduced by selection for volume production is a major concern (e.g., Kellogg 1982). Rank correlations between specific gravity and volume growth at the provenance level were significant ($P<.01$), indicating that the fastest growing provenances also had the lowest wood densities (Table 25).

The genetic correlation of specific gravity with height was essentially zero (0.03±.20), but for diameter the relationship was moderately negative (-0.40±.20). Because the volume calculation is heavily weighted by diameter, the genetic correlation of volume with specific gravity was also negative (-0.36±.22). Phenotypic and environmental correlations among these traits, however, were low (Table 23). Therefore, selection for increased volume growth should have a negative genetic effect on specific gravity. Dean *et al*. (1983) and Loo *et al*. (1985) reported similarly high

TABLE 24 - Significant linear regressions between elevation, latitude and longitude and provenance means from 15 traits of lodgepole pine in central British Columbia.

DEPENDENT	INDEPENDENT	EQUATION	F	R^2
Specific Gravity	Longitude	SG=0.121 + 0.00216 Long.	29.7**	0.84
Height	Longitude	HT=1466.98 - 8.158 Long.	12.0**	0.71
Height	Latitude	HT=1202.62 - 13.71 Lat.	13.74**	0.73
Tracheid Length	Latitude	TL=2.509 - 0.0154 Lat.	10.65*	0.76
Branch Diamter	Elevation	BD=25.53 - 0.00358 Elev.	7.8*	0.56
Branch Length	Longitude	BL=348.47 - 1.706 Long.	6.2*	0.27
Moisture Content	Longitude	MC=303.91 - 1.575 Long.	9.4*	0.54
Diameter	Longitude	DIA=204.43 - 1.073 Long.	13.1*	0.52
Stalactiform Rust	Elevation	RS=0.579 + 0.00122 Elev.	11.2**	0.34

* - Significant at P<.05
** - Significant at P<.01

Table 25 -Ranking of 14 lodgepole pine provenances at one site in central B.C. for mean wood density from increment cores against provenance means for volume growth (in cubic decimeters). Standard deviations for each provenance mean are in parenthesis. * indicates ranking position relative to wood density.

PROVENANCE MEAN FOR WOOD DENSITY (FROM 11mm CORES)				PROVENANCE MEAN FOR VOLUME GROWTH (dm^3)		
Wood Density	Provenance No.	Ranking		Volume (dm^3)	Provenance No.	Ranking*
.400(.030)	55	1		13.8(4.5)	72	12
.400(.025)	20	2		10.9(3.7)	57	8
.398(.029)	22	3		10.7(3.8)	44	14
.389(.027)	19	4		9.7(3.2)	46	11
.389(.024)	27	5		9.0(3.6)	14	10
.387(.023)	64	6		8.7(2.5)	24	7
.382(.032)	24	7		8.[illegible](2.7)	25	9
.382(.031)	57	8		7.5(2.6)	65	13
.381(.030)	25	9		7.4(2.6)	22	3
.381(.024)	14	10		7.4(2.5)	19	4
.377(.023)	46	11		6.8(2.2)	64	6
.376(.033)	72	12		6.7(2.6)	55	1
.374(.025)	65	13		6.2(2.0)	20	2
.372(.026)	44	14		5.9(1.8)	27	5

SPEARMAN RANK CORRELATION =-0.785 significant at the P<.01

negative genetic correlations between wood density and volume for radiata and loblolly pine. Whereas Dean *et al.* (1983) reported a negative genetic correlation between height and specific gravity, the relationship for lodgepole pine in this study was essentially zero (.03±.20). These results suggest that selection based on height growth alone should not adversely affect specific gravity from mass selection.

Cheverud (1982) suggested that if genetic correlations were higher than the corresponding phenotypic correlations, the morphology of traits under study is more tightly integrated in the genotype. Therefore, it may be that these genetic correlations indicate that height growth and specific gravity are functionally and developmentally independent. Diameter growth and specific gravity have a dependency such that selection for diameter will cause a negative response in specific gravity.

Wood moisture content and specific gravity at the provenance level had a rank correlation of -0.81, indicating that sources with low specific gravity have high moisture content (Table 26). The genetic correlation of wood moisture content with specific gravity was moderately negative (-0.34±.28) and, considering the standard error associated with this correlation, is comparable to the value of -0.51 reported by Matziris and Zobel (1973) for loblolly pine. The environmental correlation between the two traits was highly negative (-0.60), indicating the environmental factors

Table 26 -Ranking of 10 lodgepole pine provenances at one site in central B.C. for mean wood density from increment cores against provenance means for moisture content (in percent). Standard deviations for each provenance mean are in parenthesis. * indicates ranking position relative to wood density.

PROVENANCE MEAN FOR WOOD DENSITY (FROM 11mm CORES)				PROVENANCE MEAN FOR % MOISTURE CONTENT		
Wood Density	Provenance No.	Ranking		% Moisture	Provenance No.	Ranking*
.400(.030)	55	1		119.9(11)	25	6
.400(.025)	20	2		119.7(15)	72	9
.389(.027)	19	3		118.4(18)	44	10
.389(.024)	27	4		118.3([illegible]8)	14	7
.387(.023)	64	5		116.7([illegible]1)	64	5
.381(.030)	25	6		110.7(17)	46	11
.381(.024)	14	7		110.0(17)	27	5
.377(.023)	46	8		107.8(15)	19	4
.376(.033)	72	9		102.8(16)	55	1
.372(.026)	44	10		95.5(16)	20	2

SPEARMAN RANK CORRELATION =-0.861 significant at the P<.01

causing a decrease in specific gravity also cause an increase in wood moisture content. Moisture content was not significantly influenced by latitude or elevation, but the relationship between longitude and moisture content was significant ($P<0.05$) (Table 24).

The only large genetic correlation with specific gravity was that with compression wood (treated as binomial data) (0.64±.22; Table 23). Therefore, selection for families with high specific gravity, without noting the families with high compression wood content, could lead to a substantial decrease in wood quality by inadvertently increasing compression wood content.

Correlations of dry weight with height, diameter and specific gravity were examined to determine the relative magnitude each may have when dry-weight production is the goal. The genetic correlation for stem dry weight with specific gravity was negative and low (-0.12±.21), but its correlation with height and diameter was very high and positive (0.80±.09 and 0.92±.04, respectively). Environmental correlations between dry weight and height and diameter were, as expected, quite large, and between dry weight and specific gravity only 0.19 (Table 23). This may indicate that specific gravity is not a large factor influencing dry weight of a stem and that height and diameter are the critical factors. This is in general agreement with what has been reported for loblolly pine (Bridgwater *et al.* 1983).

3.2.2 Height and Diameter Growth

As mentioned earlier, the fastest growing sources at the Red Rock site were those from lower latitudes. There was also a significant negative relationship between longitude and height and diameter ($P<0.01$ and $P<0.05$, respectively)(Table 24). This was again probably influenced by a sampling bias of more western provenances being from higher latitudes relative to other provenances sampled in this study. As expected, the effect of latitude was significant ($P<.01$; Table 24).

Height and diameter were highly genetically correlated with volume and biomass (Table 23). However, the genetic correlation between height and diameter was only 0.42±.18, suggesting that height and diameter growth are not strongly related genetic traits. Dean *et al*. (1983) and Bridgwater *et al*. (1983) reported genetic correlations greater than 0.79 between these two traits in radiata and loblolly pine, respectively. The phenotypic correlation between height and diameter was only slightly higher than the genetic correlation in this study (Table 23). The largest genetic correlation was between volume and dry weight (0.97±.01), indicating that selecting for volume should bring about an increase in dry weight.

Bark thickness had a small negative genetic correlation with height growth (-0.18±.24). With diameter growth, however, it had a genetic correlation of 0.63(±.20). Ledig and Whitmore (1981) found a high genetic relationship between bark thickness and diameter growth for Caribbean pine in Puerto Rico, and suggested that bark thickness could be incorporated into a selection index to improve selection for volume. However, the moderate heritability found in this study for bark thickness (0.29±.0[illegible]), compared to the value obtained by Ledig and Whitmore ([illegible]1; $h_i^2=0.53$) may make it a less valuable trait in improving selection for diameter growth in lodgepole pine.

Provenances from higher latitudes (i.e., slow growing provenances) tended to have shorter tracheids ($P<0.05$) (Table 24). Correlations of fibre length with height growth were both positive (phenotypic 0.14 and genetic 0.55±.27), but the genetic correlation of fibre length with diameter was negative (-0.39±.31). Matziris and Zobel (1973) reported a similar relationship between height and tracheid length in loblolly pine, but did not find a negative correlation between diameter and tracheid length. Because volume is proportional to diameter squared, the genetic correlation between tracheid length and volume was also negative (-0.13±.35). Again, the environmental correlations were all quite low (Table 23).

3.2.3 Branching Characteristics

Of all the linear regressions of provenance means against origin information, only branch diameter was significantly influenced by elevation ($P<.05$; Table 24). This indicates that provenances originating from higher elevations tend to have smaller bran[illegible]meters.

The genetic correlation of branch diameter with branch length was positive and high (0.74±.06), but genetic correlations for these two traits with branch angle were negative (-0.56±.14 and -0.42±.14, respectively; Table 23). Genetic correlations between branch angle and height and between branch angle and diameter were essentially zero, although that between branch diameter and stem diameter was slightly positive (0.13±.20). The genetic correlation between height and branch diameter was small and negative (-0.21±.20).

What may be surmised from this complex of genetic interactions of branch characteristics with growth variables is that selection for the more desirable higher branch angles (i.e., those approaching 90 degrees) should bring about smaller branch diameters and shorter branches. This is a very desirable genetic relationship for tree breeders concerned with reducing branch biomass and the relative size of knots in the stems of trees (Blair *et al.* 1974).

3.2.4 Crown and Stem Score

Crown score was not related to geographic origin of provenance. Crown score had a stongly negative genetic correlation with branch angle (-0.97±.20) and a strongly positive genetic correlation with branch diameter and branch length (0.66±.15 and 0.39±.17, respectively; Table 23). Unfortunately, correlation estimates with the growth traits had large standard errors (Appendix F) and are probably of little value. It should be mentioned, however, that these correlation estimates were all negative, indicating that selection for better growth may increase the quality of the crown form.

Genetic correlations of stem straightness with the four growth traits (i.e., height, diameter, volume and dry-weight) ranged from 0.34 to 0.44 (all estimates had standard errors close to ±.28; Table 23), suggesting that faster growing families tend to produce more crooked stems. Explanations for this phenomenon include nutrient depletion at the microsite level (Kolari 1982), wind damage and lean in individuals that were larger at the time of establishment, or a true genetic correlation between the traits; however, none of these can be substantiated by this study. Ledig and Whitmore (1981) also found a positive relationship between stem crook and volume production.

The genetic correlation between crown score and stem score in this study was small but positive (0.12±.27). Stonecypher *et al*. (1973) also reported a positive genetic relationship between crown and stem score and Matziris and Zobel (1973) reported a genetic correlation between the two score traits that exceeded 1.0. Dean *et al*. (1983), however, found a strong negative genetic correlation between these two traits in radiata pine. It should be surmised, therefore, that selection for increased volume production will generally reduce the occurrence of desirable crown traits.

3.2.5 Disease Traits

At the provenance level, stalactiform blister rust score had a significant ($P<0.01$) positive relationship with elevation (Table 24); therefore, those provenances from higher elevations were more susceptible to these infections.

Genetic correlations for stalactiform blister rust and western gall rust with the other traits were quite small, with the exception of the correlation between the two rust scores (0.59±.17). Therefore, families that were susceptible to stalactiform blister rust also seemed to be susceptible to western gall rust. Stalactiform blister rust was not noticeably related to crown or stem score, but western gall rust had a slightly positive genetic correlation with crown score and a slightly negative genetic correlation with stem score (Table 23).

3.2.6 Structure of Genetic Covariance

Genetic correlations among traits within zones can be examined to see whether or not genetic structures of correlations were the same among geographic zones. The number of families included in the within-zone analysis, as expected, was substantially smaller; therefore, a few of the genetic correlations had large standard errors, or could not be estimated due to negative variance components (Table 27a and 27b). What is noticeable are the large differences in

TABLE 27a - Genetic correlations (S.e. in parenthesis) and environmental correlations (in square brackets) among six traits for lodgepole pine from five geographic zones in British Columbia. NA - indicates not available due to a negative variance component. Based on an analysis of variance model of Replications, Families, Reps. x Fam. and error on individual tree data.

ZONE	SG w. HT.	SG w. VOL	SG w. DIA	BA w. BD	BA w. HT.	HT w. BD	HT w. VOL	HT w. DIA
1	NA	-1.7 (.59) [.48]	-1.1 (.37) [.49]	-.48 (.45) [-.28]	NA	NA	NA	NA
2	-.12 (.29) [-.10]	-.33 (.30) [.36]	-.46 (.31) [.14]	.65 (.30) [-.08]	.12 (.27) [-.13]	.02 (.27) [-.53]	.97 (.03) [2.3]	.92 (.07) [.74]
3	-.42 (.30) [-.33]	-.36 (.32) [-.33]	-.27 (.33) [-.04]	.09 (.36) [-.49]	.00 (.28) [-.04]	.52 (.21) [.03]	.95 (.03) [-2.6]	.85 (.08) [2.6]
4	-.18 (.33) [-.02]	-.23 (.34) [-.19]	-.23 (.38) [-.22]	-.95 (.68) [-.25]	-.23 (.45) [.36]	.59 (.21) [-.41]	.96 (.05) [-.04]	.91 (.12) [-.23]
5	-.06 (.38) [-.19]	.04 (.55) [.16]	-.14 (.54) [-.08]	-.12 (.51) [-.45]	-.03 (.33) [.09]	.80 (.36) [.09]	.97 (.15) [.79]	.54 (.32) [.68]

TABLE 27b - Genetic correlations (S.e. in parenthesis) and environmental correlations (in square brackets) among six traits for lodgepole pine from five geographic zones in British Columbia. NA - indicates not available due to a negative variance component. Based on an analysis of variance model of Replications, Provenances, Families within Prov., Reps. x Prov., Reps x Fam/Prov. and error on individual tree data.

ZONE	SG w. HT.	SG w. VOL	SG w. DIA	BA w. BD	BA w. HT.	HT w. BD	HT w. VOL	HT w. DIA
1	NA	-1.7 (.59) [.29]	-1.2 (.38) [.24]	-.40 (.54) [-.33]	NA	NA	NA	NA
2	NA	NA	.61 (1.2) [-.08]	-.75 (.31) [-.16]	NA	NA	NA	NA
3	-.13 (.38) [.01]	-.07 (.42) [-.07]	.11 (.43) [-.14]	-.01 (.85) [-.34]	-.28 (.33) [.15]	-2.4 (3.0) [.68]	.78 (.15) [.68]	.41 (.30) [.54]
4	-.10 (.36) [-.07]	-.13 (.36) [-.21]	-.12 (.40) [-.24]	-1.1 (1.0) [-.36]	-.01 (.54) [.13]	.29 (.36) [.23]	.96 (.07) [.49]	.91 (.15) [.18]
5	.08 (.49) [-.11]	-.28 (.58) [-.04]	-.72 (.57) [.05]	-.37 (.65) [-.40]	-.01 (.36) [-.01]	.89 (.48) [.16]	.93 (.11) [.74]	.72 (.23) [.55]

genetic correlations for specific gravity with volume and diameter growth between zones #1 and #5 (Table 27a and 27b). The genetic correlation from the overall analysis was -0.36 for volume with specific gravity, whereas this value ranged from 0.04 to -1.7 in zones #5 and #1, respectively (Table 27a). Therefore, selection for volume production in the population from zone #5 is not expected to bring about a decrease in specific gravity, whereas the converse would apply for the population from zone #1. However, when provenance effects where included in the analysis, correlations changed from 0.04 to -0.28 in zone #5, and from -0.36 to -0.07 in zone #3. Although standard errors of these correlations indicate that these would not be significant differences, it does exhibit the sensitivity of the analysis to changes in the model by including provenance effects. Height and volume growth had high genetic correlations that were relatively constant across zones. Height and diameter growth, however, exhibited significant differences in genetic correlations between zone #2 and #5 (Table 27a). The relatively low genetic correlation for height and diameter in zone #5, suggests these traits may be more independent in this particular population.

Although correlations between branch angle and branch diameter varied substantially, particularly for zone #3 (0.09±.36) and #4 (-0.95±.68), there were no significant differences among zones in the correlations between these two traits (Table 27a and 27b). Since the overall trend was for a negative correlation between branch angle and branch diameter, the correlation across all populations was also negative (-0.56; Table 23).

Comparisons of genetic parameters are probably most appropriate for zones #1 and #2, since they are geographically proximate (Fig. 2) and have been displaced a similar distance from the test site in central B.C. One would expect then that the increased growth rates exhibited by provenances from these two zones (primarily due to the response to increased daylengths by southern sources) should be free of a bias due to latitudinal transfer, and that these differences in genetic correlations are real. Unfortunately, correlations with height growth in zone #1 were not estimated because of the negative variance component obtained for height growth. However, specific gravity and volume showed large differences in this relationship between zones #1 and #2 (Table 27a). What is noteworthy is that the best overall provenance in the plantation was from zone #2 (provenance #72), which exhibited a negative genetic correlation of -0.33(±.30) between specific gravity and volume. Therefore, selection for volume production in the population from zone #2 would not bring about the drastic reduction in specific gravity that would occur from selection for volume in the population from zone #1. The inclusion of provenance effects in the model did not affect correlations in zone #1, suggesting that the negative covariance at the family level was not affected by stand-to-stand differences within a zone (Table 27b).

It may be safe to say that specific gravity and volume growth are not entirely independent traits, simply because growth in trees depends on the production of wood. Falconer (1981) suggested that when two characters (which are pleiotropic) are intensively selected, the genetic correlation eventually becomes negative. For this to have occurred for the height-specific gravity relationship, selection would have had to reduce genetic variance, and therefore the covariance, to fixation. In zone #1, both height and specific gravity showed no significant family differences, and if a genetic correlation could have been estimated, it undoubtedly would have been negative (based on the large negative correlations which were calculated for specific gravity with volume and diameter). Although the reliability of these correlations may be limited (because of large standard errors and large changes when the model is changed), these differences in genetic correlations may indicate differences in genetic structures among zones simply by the magnitude of some of the differences in the estimates. These differences could be valuable for multiple-population breeding strategies.

3.3 Gain from Individual and Multiple-trait Selection

3.3.1 Individual-Trait Selection

Genetic information is available from this study at four levels (i.e., individual, family, provenance and zone). The heritability at each of the four levels acts as a predictor of what may be expected in the next generation if selection is practiced on that level. If the heritability is one, the mean of the new population would equal that of the selected parents (Simmonds 1979). Expected gain or response can be calculated for a single trait by multiplying the heritability by a selection differential (Falconer 1981). The selection differential is derived by multiplying the phenotypic standard deviation [illegible] a trait by an appropriate selection intensity (i) to estimate a genetic gain. The heritability estimate for calculation of gain from mass selection is, of course, the narrow-sense heritability and the heritability for estimating gain from family, provenance and zone selection is the heritability estimate of family, provenance and zone means, respectively (based on the plot means analysis[4]). Expected gain from within-family selection is also possible to calculate and was derived following the procedure outlined by Shelbourne (1969a).

If proportions of selection ranging from 1/10 to 7/10 (i.e., i=1.75, 1.4, 1.16, 0.966, 0.798, 0.644 and 0.497,

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[4] Fig. 5b-h are based on the plot means analysis. Fig. 5a, for the two disease traits, were based on individual tree data.

respectively) are practiced independently on the five levels available for selection, it is apparent that the best gains, for a majority of the traits, are achieved simply by selection at the zone or provenance level (Fig. 5a-h).

If volume production is the primary objective, selection of material from the best zone would yield gains of approximately 30 percent (at i=1.75; Fig. 5g). Selection of the best 10% of the provenances for volume would theoretically yield gains of only 25 percent; however, since provenance means make up the zone mean it is only the function of the phenotypic standard deviation among zone means that makes expected gains larger for selection of zones [*]. Nevertheless, it is obvious that selection for overall volume production should be made from the best provenances in zone #1. For other traits, such as specific gravity, branch angle and tracheid length, genetic gains may be best achieved through mass selection. Expected gain for specific gravity by mass selection was 5.2 percent and from selection at the family or zone level only 3.3 percent (Fig. 5c). Although the family heritability is substantially larger than the heritability based on individuals (Table 3), the large phenotypic variation present among progeny within families increases the expected gain. Predicted gains from family selection over mass selection were usually lower and was probably due to lower phenotypic standard deviations of

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[*] In practice the selection intensity of 0.1 could not be used for zones since only five zones were used in this study; therefore, the gains presented for zones are for comparative purposes only.

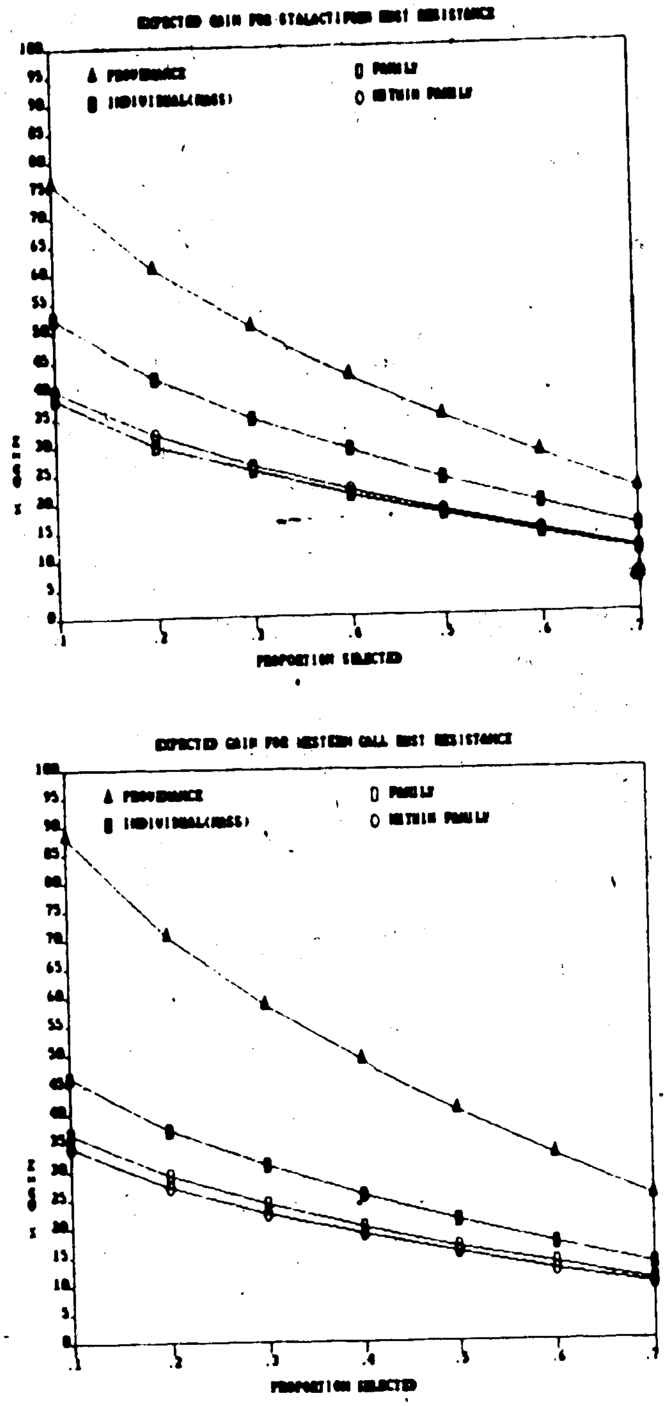
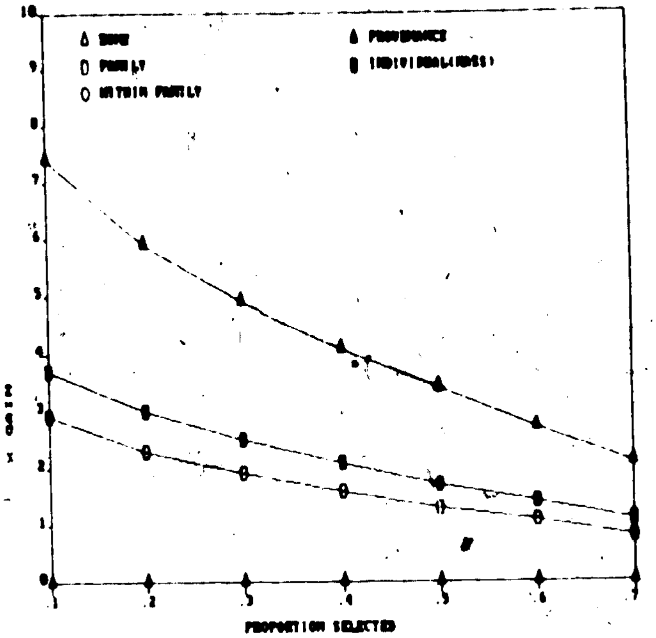


Figure 5a - Expected genetic gains from selection at the within-family, individual, family and provenance levels for stalactiform blister rust resistance and western gall rust resistance at seven proportions of selection for lodgepole pine. Gains for selection at the zone level not calculated because of restrictions in variance component estimation using Harvey's program.

EXPECTED GAIN FOR CROWN SCORE



EXPECTED GAIN FOR STEM SCORE

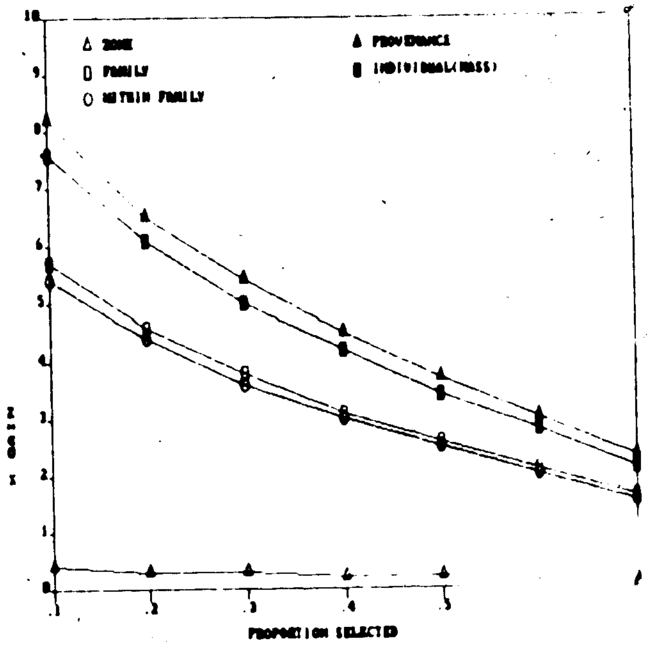


Figure 5b - Expected genetic gains from sele[illegible] at the within-family, individual, family, prove[illegible] levels for crown score and stem score for [illegible] at seven proportions of selection for [illegible] line.

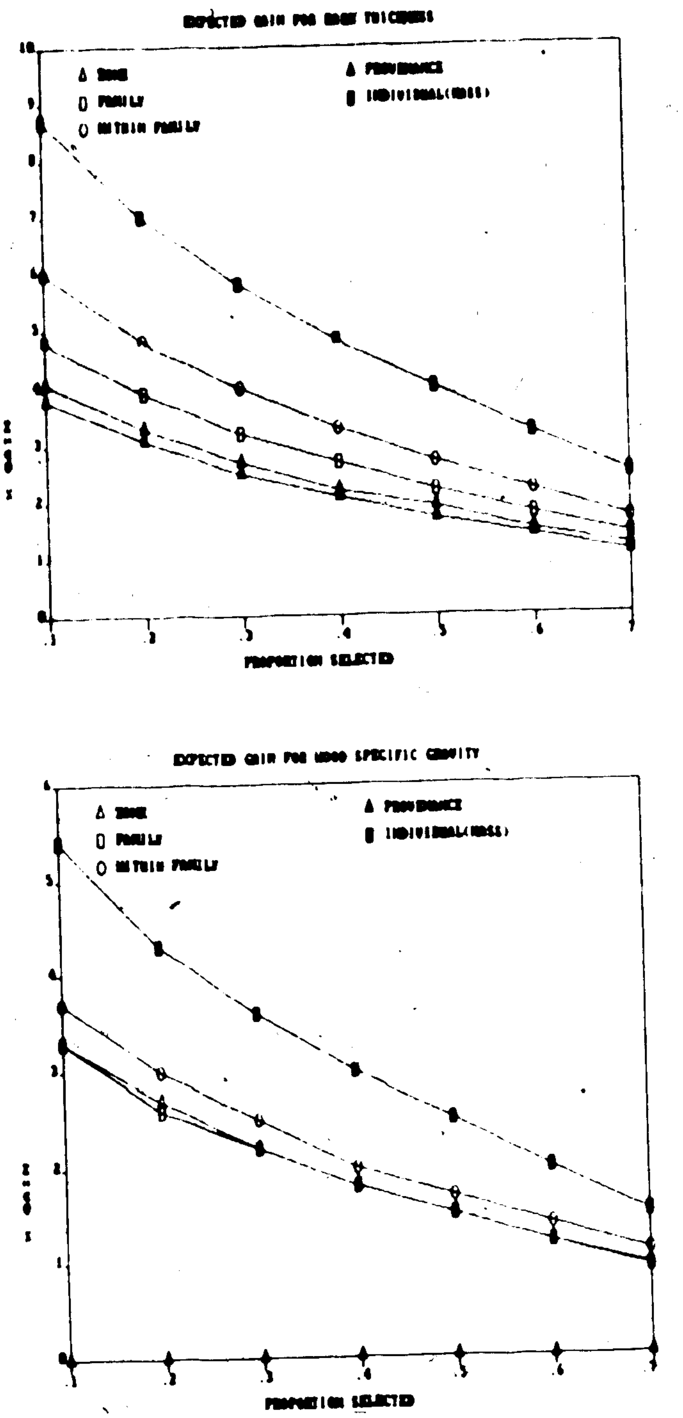
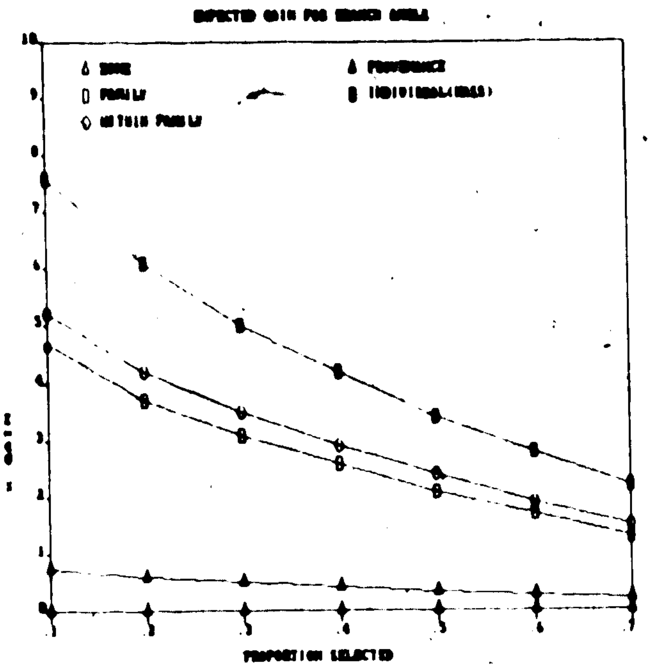


Figure 5c - Expected genetic gains from selection at the within-family, individual, family, provenance and zone levels for bark thickness and wood specific gravity at seven proportions of selection for lodgepole pine.



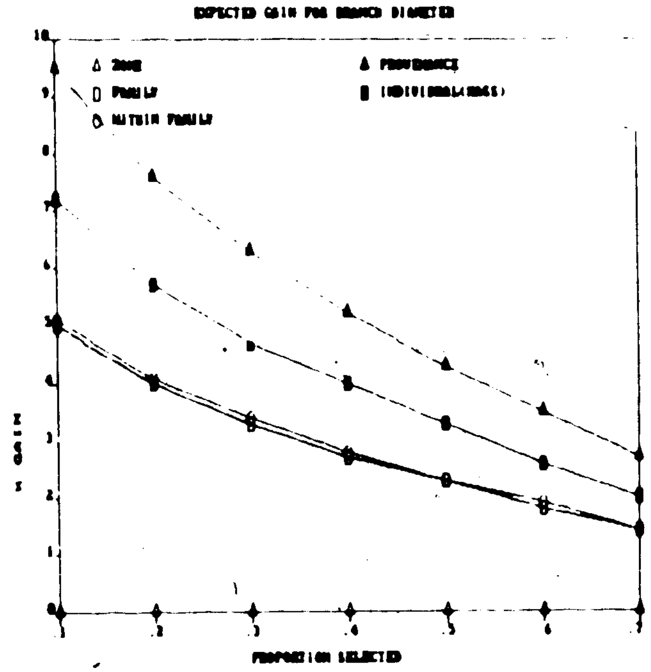


Figure 5d - Expected genetic gains from selection at the within-family, individual, family, provenance and zone levels for branch angle and branch diameter at seven proportions of selection for lodgepole pine

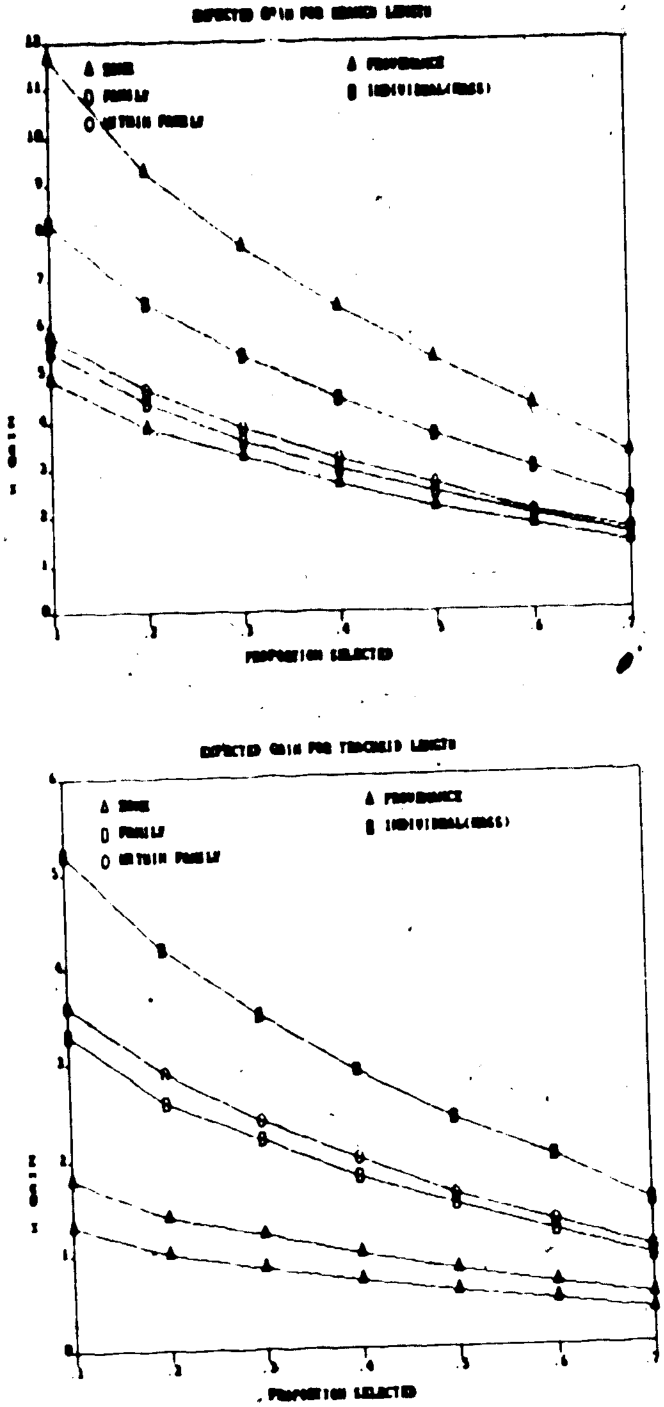


Figure 5e - Expected genetic gains from selection at the within-family, individual, family, provenance and zone levels for branch length and tracheid length at seven proportions of selection for lodgepole pine

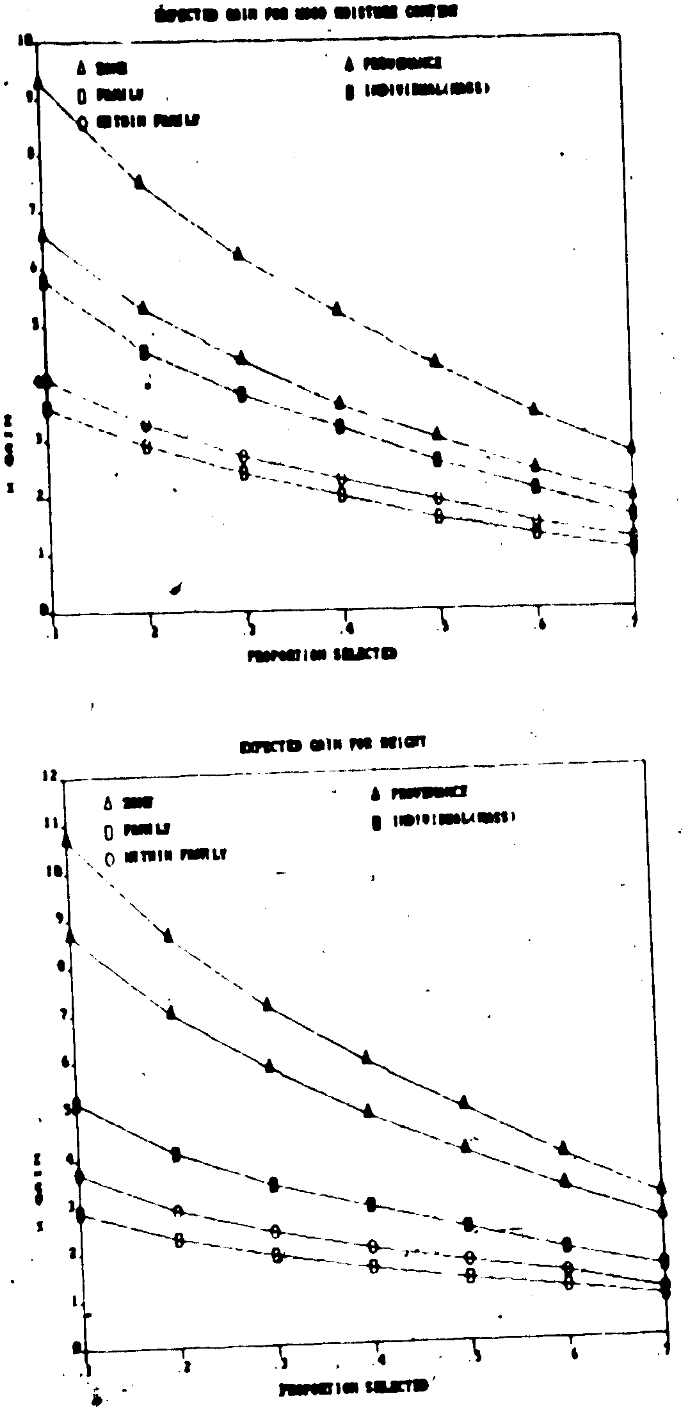


Figure 5f - Expected genetic gains from selection at the within-family, individual, family, provenance and zone levels for wood moisture content and height growth at seven proportions of selection for lodgepole pine

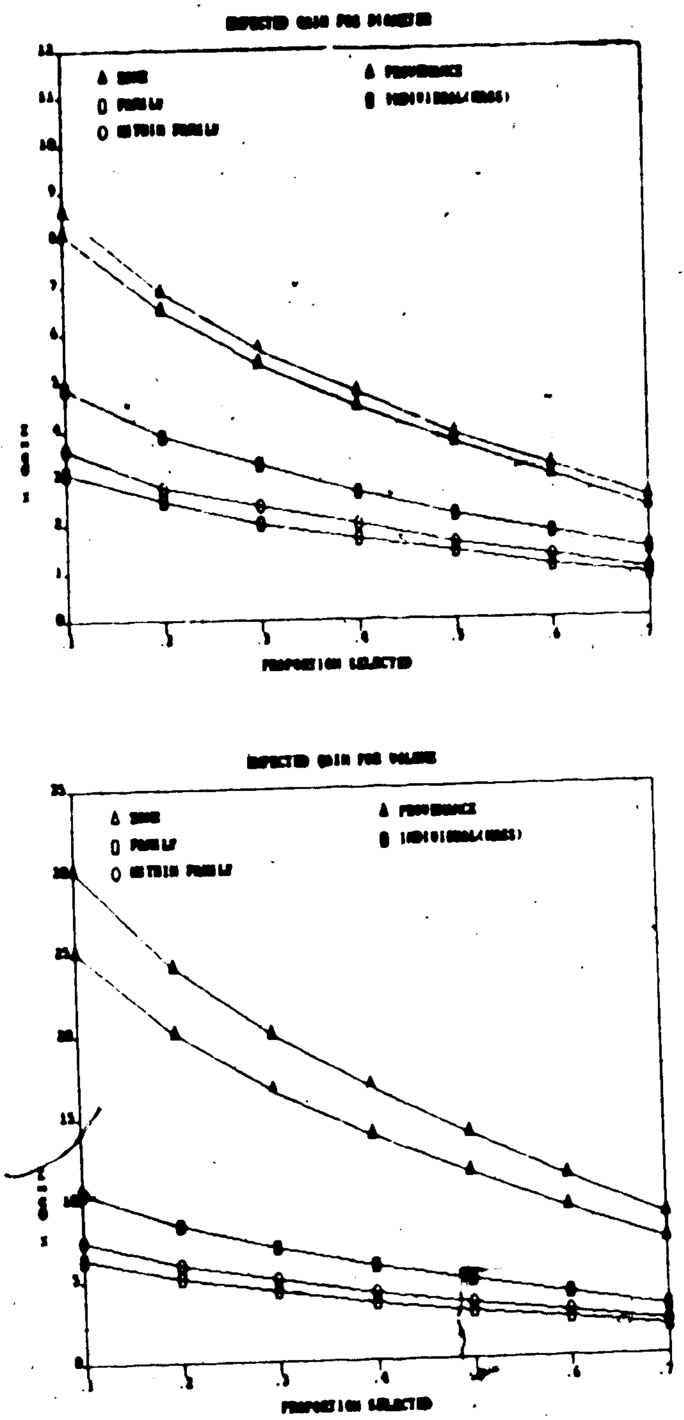


Figure 5g - Expected genetic gains from selection at the within-family, individual, family, provenance and zone levels for stem diameter and volume production at seven proportions of selection for lodgepole pine

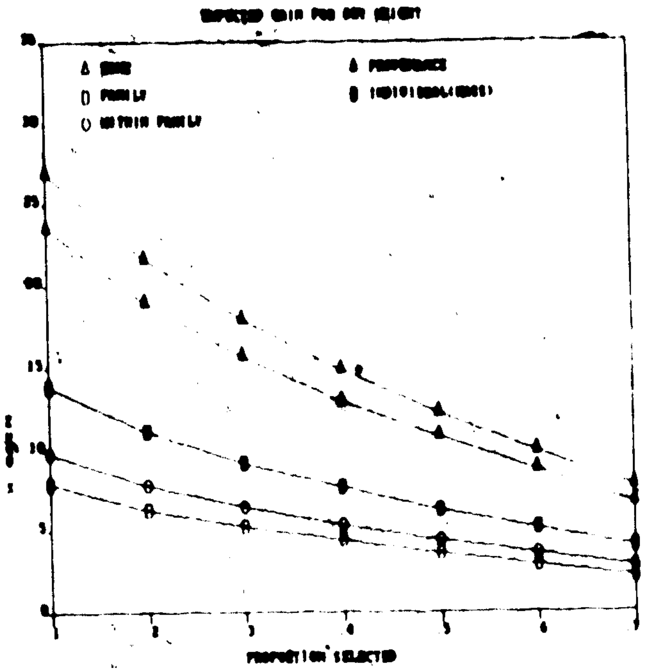


Figure 5h - Expected genetic gains from selection at the within-family, individual, family, provenance and zone levels for dry-weight production at seven proportions of selection for lodgepole pine.

family means. Within-family selection usually corresponded closely to the gains derived from family selection. A possible reason why gains from individual selection for the two rust traits are so high is that the standard deviations were very high relative to the means. This again was due to the binomial analysis approach, and it is difficult to understand what economic value a 75% or 85% gain in rust resistance has (i.e., at a selection intensity of 1.75). What should be noted for the two rust traits is that best gains are achieved by selection first at the provenance level, then by the selection of individuals (Fig 5a).

3.3.2 Correlated Responses from Index Selection

Dean *et al.* (1983) calculated indices combining volume, stem straightness, branch quality and wood density for radiata pine and found that it was not possible to achieve significant improvement simultaneously in wood density and growth. For comparison purposes similar indices were derived for lodgepole pine combining volume, branch angle, branch diameter, stem straightness and specific gravity using economic weightings similar to that of Dean *et al.* (1983). Although it has been shown that the genetic parameters required to construct accurate indices could vary from population to population, estimates from the pooled analysis were used. These give an "average" effect for lodgepole pine for expected responses from multiple-trait selection [*].

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[*] Genetic estimates used here were derived from mean squares and cross products in Appendix B; correlations are given in

Also, genetic parameters estimated from the pooled analysis had smaller standard errors; therefore, indices would theoretically be more precise. The expected genetic response in these traits from mass selection in the test plantation (at a selection intensity of 2.67, or proportion selected of 1/100), as expected, indicated that trade-offs occur between wood density and volume growth (Table 28). [illegible]tering the economic weightings on volume and wood density changed the expected gain of the traits at the expense of the other. This, of course, was primarily due to the genetic correlation of -0.36 (from the pooled analysis over all zones; Table 23) between the two traits and the relatively low phenotypic standard deviations as compared to the grand means associated with specific gravity (CV=7%) relative to volume (CV=31%). As reported for radiata pine by Dean *et al.* (1983), selection for both volume and wood density would not lead to substantial gains in both traits in lodgepole pine. The best example of this can be seen in index equations 8 and 12 (Table 28). When the genetic change in wood density was restricted using a restriction index approach, volume growth would increase 0.04 dm^3 (0.5%) over the plantation average. If volume growth is restricted, the response in specific gravity is expected to [illegible] 0.0005 (1.3%) higher than the plantation average. With equal weighting on all five traits in the index (equation 1; Table 28), the expected response in volume is 0.5%; in branch angle, 10.1%; in

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•(cont'd) Appendix F.

Table 28 - Correlated responses from selection indices for volume(dm^3), branch angle(degrees), branch diameter(mm), stem score(1-10 scale) and specific gravity from mass selection for lodgepole pine at one test site in central British Columbia. R indicates the trait restricted for a particular equation (i=2.67)

E Q/	Economic Weights					b Coefficients					Expected Genetic Gain					R^2
	VOL	BA	BD	SS	SG	VOL	BA	BD	SS	SG	VOL	BA	BD	SS	SG	
1/	1	1	1	1	1	0.034	0.350	0.15	0.573	-4.58	0.0448	6.984	-0.952	0.5121	-0.00001	.36
2/	1	20	20	20	1	-3.071	7.522	4.33	9.615	67.76	-0.2806	7.209	-0.955	0.4587	0.00368	.39
3/	1	20	20	20	5	-3.073	7.523	4.33	9.611	69.42	-0.2814	7.210	-0.955	0.4585	0.00371	.40
4/	1	20	20	20	1000	-3.656	7.786	4.57	8.760	483.63	-0.4583	7.259	-1.077	0.3949	0.00965	.41
5/	1	20	20	20	2000	-4.242	8.049	4.80	7.905	899.93	-0.5977	7.043	-1.146	0.3248	0.01455	.43
6/	5	20	5	20	1	-1.068	8.144	0.71	8.705	131.12	-0.2018	7.605	-1.485	0.3961	0.00489	.42
7/	5	5	1	5	5	0.493	1.944	-0.13	2.491	3.36	0.0223	7.440	-1.517	0.4203	0.00249	.40
8/	1R	1	1	1	1	0.010	0.353	0.16	0.556	-3.48	0.0	7.031	-0.958	0.5010	0.00051	.36
9/	1	1R	1	1	1	0.082	0.034	0.18	0.351	-13.29	0.7312	0.0	1.498	0.5276	-0.01517	.07
10/	1	1	1R	1	1	-0.430	0.303	0.37	0.651	-10.91	0.071	5.46	0.0	0.576	-0.00374	.31
11/	1	1	1	1R	1	-0.050	0.194	-0.03	-0.42	12.77	-0.582	6.53	-1.93	0.0	0.01192	.13
12/	1	1	1	1	1R	0.034	0.350	0.15	0.568	-4.58	0.044	6.98	-0.95	0.506	0.0	.36
13/	1	-	-	-	1	0.170	-	-	-	-7.65	1.4800	-	-	-	-0.018	.21

branch diameter, -4.3%; in stem score points, 11.6%; and for specific gravity, essentially no change (-.003%). Because of the equal weighting each trait received in equation 1 (Table 28), the heritabilities and phenotypic standard deviations for each trait influence the b coefficients (index weights) and the expected responses. The expected response in branch angle is large because of the high heritability and large phenotypic standard deviation. Interestingly, branch diameter was always reduced except when branch angle was restricted. Branch angle always increased (which is a desirable change); however, stem score also tended to increase by approximately 0.5 points, except when stem score and specific gravity were restricted (Table 28).

If branch angle, b[illegible]h diameter and stem score are removed from the index, the trade-off between specific gravity and volume becomes larger, because the interrelationships among traits are reduced to two. The magnitude of the reduction in specific gravity is substantially higher (-4.7% from -0.003%) and the expected gain in volume goes up considerably (17.4% from 0.5%). The actual gain that would be obtained by single-trait selection at an intensity of 2.67 for volume in the plantation (using the heritability estimate and phenotypic standard deviation derived from Table 15) would be 1.26 dm^3 (14.9%). This indicates that even though wood density has a substantially higher heritability than volume, the small phenotypic standard deviation associated with it causes little (or in this case negative) emphasis to be placed on wood density. Therefore, this index, with equal weighting to both specific gravity and volume, yields gains greater for volume than those expected by simply selecting on volume alone. This theoretical improvement for volume, using an index approach over single-trait mass selection, arises from the additional information specific gravity provides to the index. Specific gravity, therefore, is useful as it had a higher heritability than volume.

3.3.3 Combined Index Selection

The previously discussed indices are all based on mass selection in the plantation using index coefficients based on heritabilities and correlations based on individuals. The inclusion of more genetic information in the index (i.e., family and provenance) could increase the efficiency of the index because more or less weight is placed on the index coefficient depending on heritabilities and correlations among traits at the individual, family and provenance levels.

Two traits, volume and wood density, were considered for construction of combined indices (which include provenance, family and within-family information). These two traits were considered ideal for treatment by index selection as they exhibited 1) low phenotypic correlation, and 2) could be considered to have the highest economic interest currently in tree improvement. Efficiency of an index is measured by a percentage gain for each trait as compared to the overall plantation mean. Also, the correlation between H and I (R^2_{HI}), the predictor of genetic change in H when selection is practiced on I (Nordskog 1978), can be used to compare the index equations. Economic weights will be of two types; the first a weighting proportional to the inverse of the phenotypic standard deviations of the trait, similar to that explained by Wilcox *et al*. (1975), and the second, an equal weighting of traits to examine the changes that occur to the expected gain assuming absolute equality in the value of both traits in the index.

As pointed out in the previous section, simultaneous improvement for volume and specific gravity would not occur using both traits in an index based on mass selection (equations 1 and 2; Table 29). Using a combined index, where half-sib family information is included, no significant changes occur in the expected responses of volume and specific gravity (equations 3 and 4; Table 29). However, if provenance information is included to make the index a combined index at three levels, responses are expected to be approximately 40% larger for volume than combined selection with individuals and half-sib family information (equations 5 and 6; Table 29). This is due primarily to the large b values associated with the provenance mean relative to the family mean and individual b values (Table 29).

Table 29 - Index (b) values, expected responses, correlations (R^2_{HI}) and overall response (ΔHI) for combined index selection at the provenance, family and individual level for specific gravity (SG) with volume (VOL) and height (HT). Values in parenthesis are % gain over the plantation mean. x-indicates both genetic and phenotypic information included in index.

E	VOL.			HT.			SG			b VALUES									EXPECTED RESPONSE					ECONOMIC WEIGHTS	
										VOL.			HT.			SG									
q.	P	F	I	P	F	I	P	F	I	Prov.	Fam.	Ind.	Prov.	Fam.	Ind.	Prov.	Fam.	Ind.	Vol.	HT.	SG	$R^2_{(HI)}$	ΔHI	VOL/HT	SG
1			x						x	-	-	.044	-	-	-	-	-	12.7	-.220 (-2.6)	-	.027 (7.0)	.29	0.95	.385	37.736
2			x						x	-	-	.170	-	-	-	-	-	- 7.65	1.48 (17.4)	-	-.018 (-4.7)	.21	1.46	1	1
3		x	x					x	x	-	.078	.047	-	-	-	-	19.66	12.59	-.200 (-2.4)	-	.032 (8.3)	.31	1.12	.385	37.736
4		x	x					x	x	-	.239	.170	-	-	-	-	-10.19	- 7.62	1.72 (20.2)	-	-.020 (-5.2)	.22	1.70	1	1
5	x	x	x				x	x	x	.254	.078	.047	-	-	-	12.58	19.66	12.59	4.12 (48.5)	-	.004 (1)	.52	1.77	.385	37.736
6	x	x	x				x	x	x	.898	.239	.170	-	-	-	-18.00	-10.19	- 7.62	5.77 (67.9)	-	-.025 (-6.5)	.75	5.74	1	1
7						x			x	-	-	-	-	-	.329	-	-	16.47	-	.137 (2.9)	.028 (7.3)	.32	1.33	2.1008	37.736
8						x			x	-	-	-	-	-	.144	-	-	.700	-	.269 (5.7)	.006 (1.6)	.15	0.28	1	1
9					x	x		x	x	-	-	-	-	.170	.329	-	24.61	16.47	-	.137 (2.9)	.033 (8.6)	.34	1.54	2.1008	37.736
10					x	x		x	x	-	-	-	-	.079	.144	-	.904	.700	-	.287 (6.1)	.007 (1.8)	.14	0.29	1	1
11				x	x	x	x	x	x	-	-	-	.189	.170	.347	-48.8	24.61	16.47	-	.755 (15.9)	.012 (3.1)	.44	2.05	2.1008	37.736
12				x	x	x	x	x	x	-	-	-	.124	.079	.153	-35.7	.904	.706	-	1.03 (21.8)	-.016 (-4.2)	.56	1.01	1	1

If the 1390 individuals within the plantation are considered to be the population undergoing selection, using equations 5 and 6 (Table 29), it is apparent that at a proportion of selection of 1/100 all individuals selected would come from the best provenance (Table 30 and 31). Comparing this to the individuals that would be selected if using equation 4 (i.e., provenance information excluded), the select population would also have a large number of individuals from provenance #72. However, when more weight is placed on specific gravity (i.e., equation 3; Table 32), the number of individuals from provenance #72 is greatly reduced (Table 33). As mentioned earlier, the corresponding gains in volume are substantially reduced without provenance information being included. The correlation between H and I also is increased with the addition of provenance information (Table 29). This indicates an increase in the variance of H (economic merit) is more predictable from the index with provenance information included. Individual selection for volume production gives an expected gain of 14.9%, while combined-index selection of volume and specific gravity is expected to give a 48.5% increase in volume and a 1% increase in specific gravity using equation 5 (Table 29). The large weighting given to specific gravity relative to volume in equation 5 overrides the strong weighting given to provenance means for volume. Although a compromise between volume and specific gravity is being made at the expense of volume, as compared to the gains that could be obtained

					Phenotypic Value					
R	Z	PR	F	T	SG	DIA	HT	VOL	DW	INDEX SCORE
1	2	72	10	1	.3177	10.9280	6.4500	26.2500	8.2572	7.7246
1	2	72	2	2	.3737	10.1280	7.1100	24.5390	9.1321	6.9156
2	2	72	3	1	.3768	10.7770	6.1550	23.0298	8.6969	6.5676
1	2	72	6	5	.3367	9.7280	6.7500	21.3540	7.1299	6.5524
2	2	72	12	4	.3588	10.4770	5.9550	21.0178	7.5718	6.4390
2	2	72	6	2	.3398	10.1770	5.8550	19.4568	6.6547	6.2062
1	2	72	12	5	.3677	9.8280	6.1500	19.8950	7.2808	6.1803
1	2	72	2	4	.3477	9.0280	7.0500	18.9660	6.5466	6.1663
2	2	72	9	1	.3518	9.9770	6.1550	19.5978	6.9288	6.1657
2	2	72	12	3	.3378	9.6770	6.1550	18.3898	6.2556	6.1522
1	2	72	10	6	.3697	9.4280	6.3500	18.7670	6.9069	6.0562
2	2	72	10	3	.3478	9.6770	5.8550	17.5198	6.1282	6.0111
1	2	72	10	3	.3437	9.4280	5.7500	16.9890	5.7917	5.9521
1	2	72	14	3	.3217	9.8280	5.3500	17.3080	5.5038	5.9410
1	2	72	2	6	.3647	9.4280	6.1500	18.1750	6.5945	5.9023
1	2	72	8	2	.3397	9.3280	6.1500	17.7570	5.9804	5.8431
1	2	72	8	3	.3997	9.7280	6.3500	20.0900	8.0187	5.7825
1	2	72	12	1	.3587	9.5280	5.6500	17.0820	6.0908	5.7706
2	2	72	4	4	.3278	9.5770	5.5550	16.2948	5.3900	5.7564
2	2	72	3	4	.3638	9.8770	5.6550	17.6738	6.4525	5.7561

Table 30 - Ranking of the best 23 individuals based on index score from equation 6; Table 29, at the Red Rock plantation. The top 14 individuals after random mating would yield the expected responses in Table 29. R-replication, Z-zone, PR-provenance, F-family, T-tree, SG-specific gravity, HT-height(dm), DIA-diameter(cm), VOL-volume(dm^3) and DW-dry-weight(kg/tree)

					Phenotypic Value					
R	Z	PR	F	T	SG	DIA	HT	VOL	DW	INDEX SCORE
1	2	72	3	5	.4727	9.7280	6.3500	20.0900	9.5392	3.0370
1	2	72	9	2	.4587	9.8280	8.3500	20.5410	9.4537	2.8527
2	2	72	2	4	.4658	8.7770	5.8550	14.3148	6.6088	2.6474
2	2	72	3	1	.3768	10.7770	6.1550	23.0298	8.6969	1.9669
1	2	72	2	2	.3737	10.1280	7.1100	24.5390	9.1321	1.9643
2	1	44	13	4	.4758	7.8770	5.4550	10.7268	5.0328	1.9181
2	2	72	3	5	.3918	9.4770	6.2550	17.8848	7.0089	1.9162
1	2	72	8	3	.3997	9.7280	6.3500	20.0900	8.0187	1.8626
1	2	72	3	6	.3917	9.0280	6.0500	16.2630	6.3595	1.8395
1	2	72	12	2	.4217	7.6280	5.6500	10.4550	4.4302	1.8345
2	2	72	9	3	.4108	8.0770	5.2550	10.8948	4.4544	1.8008
2	2	72	2	1	.3968	8.4770	6.3550	14.4128	5.7127	1.7836
1	2	72	12	3	.4227	7.2280	5.4100	8.8580	3.7691	1.7728
1	2	72	4	3	.3897	9.6280	5.9500	18.4060	7.1570	1.7543
1	2	57	15	1	.4287	9.0280	6.3500	17.0740	7.3349	1.6882
2	2	72	9	4	.4028	7.5770	5.7550	10.4278	4.1847	1.6784
2	2	72	4	5	.3968	8.9770	5.7550	14.7488	5.8464	1.6734
1	2	72	6	3	.4037	8.8280	5.3500	13.6750	5.5231	1.6609
1	2	72	10	5	.3897	9.3280	5.7500	16.5980	6.4555	1.6289
1	2	72	9	5	.3887	8.7280	5.2500	13.0830	5.0778	1.6246

Table 31 - Ranking of the best 23 individuals based on index score from equation 5; Table 29, at the Red Rock plantation. The top 14 individuals after random mating would yield the expected responses in Table 29. R-replication, Z-zone, PR-provenance, F-family, T-tree, SG-specific gravity, HT-height(dm), DIA-diameter(cm), VOL-volume(dm^3) and DW-dry-weight(kg/tree)

					Phenotypic Value					
R	Z	PR	F	T	SG	DIA	HT	VOL	DW	INDEX SCORE
1	2	72	10	1	.3177	10.9280	6.4500	26.2500	8.2572	4.0710
1	2	72	2	2	.3737	10.1280	7.1100	24.5390	9.1321	3.2621
2	2	14	12	6	.3708	11.2770	5.6550	23.3088	8.6671	2.9203
2	2	72	3	1	.3768	10.7770	6.1550	23.0298	8.6969	2.9140
1	2	72	6	5	.3367	9.7280	6.7500	21.3540	7.1299	2.8988
2	2	72	12	4	.3588	10.4770	5.9550	21.0178	7.5718	2.7854
1	1	44	10	6	.3657	10.5280	5.6500	21.2310	7.7258	2.7250
1	2	57	4	1	.3397	10.1280	6.1500	21.2380	7.1569	2.7078
1	1	44	10	5	.3597	10.5280	5.5500	20.8570	7.4601	2.7071
2	2	72	6	2	.3398	10.1770	5.8550	19.4568	6.6547	2.5527
1	2	72	12	5	.3677	9.8280	6.1500	19.8950	7.2808	2.5267
1	2	72	2	4	.3477	9.0280	7.0500	18.9660	6.5466	2.5128
2	2	72	9	1	.3518	9.9770	6.1550	19.5978	6.9288	2.5122
2	2	72	12	3	.3378	9.6770	6.1550	18.3898	6.2556	2.4987
1	1	44	5	3	.3507	10.3280	5.4500	19.6460	6.8431	2.4349
1	2	72	10	6	.3697	8.4280	6.3500	18.7670	6.9069	2.4027
1	2	57	12	3	.3677	9.8280	6.1500	19.8950	7.2808	2.3954
2	2	72	10	3	.3478	9.6770	5.8550	17.5198	6.1282	2.3575
1	1	44	10	4	.3487	9.5280	6.0500	18.2940	6.3332	2.3553
2	1	46	5	4	.3668	10.3770	5.7550	19.9258	7.3320	2.3266
1	2	72	10	3	.3437	9.4280	5.7500	16.9890	5.7917	2.2985
1	2	14	12	3	.3647	10.4280	5.2500	19.3290	7.0134	2.2902
1	2	72	14	3	.3217	9.8280	5.3500	17.3080	5.5038	2.2874

Table 32 - Ranking of the best 23 individuals based on index score from equation 4; Table 29, at the Red Rock plantation. The top 14 individuals after random mating would yield the expected responses in Table 29. R-replication, Z-zone, PR-provenance, F-family, T-tree, SG-specific gravity, HT-height(dm), DIA-diameter(cm), VOL-volume(dm^3) and DW-dry-weight(kg/tree)

R	Z	PR	F	T	SG	DIA	HT	VOL	DW	INDEX SCORE
					Phenotypic Value					
1	2	72	3	5	4727	9.7280	6.3500	20.0900	9.5392	1.8770
2	4	55	9	4	5318	6.7770	3.7650	5.6728	2.8970	1.8769
2	4	55	3	1	5138	8.0770	4.6650	9.7368	4.9016	1.7833
1	2	72	9	2	4587	9.8280	6.3500	20.5410	9.4537	1.6927
2	2	72	2	4	4658	8.7770	5.8550	14.3148	6.6088	1.4875
2	5	19	8	2	5068	6.7770	4.4550	6.5978	3.2442	1.4372
1	3	24	3	5	4967	7.0280	4.6500	7.0910	3.6046	1.4162
2	3	24	15	2	4918	7.2770	5.1550	8.6748	4.1806	1.3932
2	1	44	13	4	4758	7.8770	5.4550	10.7268	5.0328	1.3628
2	5	65	9	2	4908	6.7770	4.2550	6.3298	3.0190	1.2125
2	5	19	14	2	4808	7.1770	3.9650	6.6338	3.1098	1.2025
1	4	20	7	4	4847	6.0280	3.8500	4.0160	2.0254	1.1999
1	2	57	15	1	4287	9.0280	6.3500	17.0740	7.3349	1.1785
1	4	55	14	6	4667	7.0280	4.8500	7.4130	3.5194	1.1445
1	3	24	3	2	4497	8.0280	6.3500	13.1980	5.9725	1.1090
1	2	14	9	1	4267	9.7280	6.1500	19.4580	8.3124	1.0818
2	5	19	9	4	4538	9.2770	4.3650	12.0998	5.4383	1.0799
2	5	19	7	5	4628	8.3770	4.8550	10.8838	4.9761	1.0625
2	4	20	7	3	4608	6.8770	4.8650	7.3548	3.3255	1.0546
2	2	57	8	6	4618	6.7770	4.8550	7.1328	3.2293	1.0341
2	4	22	2	6	4688	5.7770	3.5550	4.0228	1.8122	1.0298
1	5	19	4	6	4567	7.4280	4.8500	8.4090	3.8911	1.0122
1	4	20	15	2	4667	6.0280	4.3600	4.6130	2.2174	1.0084

Table 33 - Ranking of the best 23 individuals based on index score from equation 3; Table 29, at the Red Rock plantation. The top 14 individuals after random mating would yield the expected responses in Table 29. R-replication, Z-zone, PR-provenance, F-family, T-tree, SG-specific gravity, HT-height(dm), DIA-diameter(cm), VOL-volume(dm^3) and DW-dry-weight(kg/tree)

using equation 6, the reduction in volume gain may be acceptable from the point of view of maintaining or slightly increasing specific gravity.

Because of the non-negative genetic correlation between height and specific gravity (.034), expected gains from individual and combined individual-family index selection for height and specific gravity were positive in all cases (equations 7 to 10; Table 29). However, when provenance information is also included, expected gain in specific gravity was reduced when height and specific gravity were weighted equally (equation 12; Table 29). When specific gravity was weighted by the inverse of its standard deviation, however, expected gain became positive (equation 11; Table 29). This situation undoubtedly arises from the large inverse relationship at the provenance level between height growth (which is strongly related to volume growth) and specific gravity. Examining the b values for equation 11, it is clear that family means and individuals are weighted heavily for specific gravity, since this is where the genetic correlation between height and specific gravity is influential (Table 29). The provenance effect, when included in the height/specific gravity index, puts a large amount of emphasis on the provenance mean; therefore, a large reduction in specific gravity is expected (equation 12; Table 29).

It is difficult to say which of the indices are best for a particular objective (i.e., those based on individuals or family means and individuals or provenance means, family means and individuals), simply because correlations between H and I covered such a broad range. Typically, correlations were higher when all three levels of information were included. Equations 1 through 12 appear to be relatively reliable, particularly equations 5, 6, 11 and 12. Depending upon the objectives of the breeder, it may be best to use equation 6 if he is solely interested in obtaining gains in volume in the Red Rock population, or equation 5, if he is inte[illegible]ted in making gains in volume while slightly in[illegible]ng specific gravity. What will happen, however, is th[illegible]st all of the individuals selected by the index will be from the same provenance, because of the heavy weightings given to provenance means from both equations 5 and 6 (Table 29). Some arbitrary restrictions likely will have to be placed on individuals selected from the same provenance or family to reduce inbreeding; therefore, expected gains calculated from index selection are likely to be reduced.

These indices basically indicate the strong effect that provenance information can have on indices and subsequent selection based on them. Because population genetic parameters are likely to be quite different, selection procedures might best be approached by independent culling of populations based on their means for the traits of interest. Index selection could then be practiced within these sub-populations. The high R^2 obtained between H and I is probably an artifact of the "pooled" genetic relationship values used among provenances (i.e., σ^2_p = the variance or covariance [COV_p] from the analysis of variance).

The inclusion of half-sib family information is usually expected to increase the predictability of H selecting on I in index selection (e.g., Bridgwater *et al*. 1982, Talbert 1984); however, half-sib family information for the indices constructed here did not increase the R^2_{HI} correlations to a large extent. Family selection is expected to be more efficient over individual selection when traits have low heritabilities (Falconer 1981), which was not the case here (Fig. 5a-h). Again, this may be due to the relatively low phenotypic standard deviation among family means found in this study.

4. Discussion and Conclusions

4.1 Measurements of Traits

Although a substantial amount of time is required to thoroughly test stability of sources for growth and performance (e.g., Wakeley and Bercaw 1965), it is likely most programs will be making a large number of initial selections at early ages. Lambeth *et al.* (1983) found that selection of loblolly pine families at age five for volume was acceptable for predicting 20-year volume. It may be reasonable to expect some changes in family rankings as trees mature, but such changes in family ranking are likely to come from those families in the middle of the rank distribution. Perhaps then, other quality traits may also be relatively stable at ages earlier than half the expected rotation age. From the 18 characters examined in this study, inferences can be made about characters that can be assessed at age 10 for multiple-trait improvement.

The first relationships that became apparent were among branch angle, branch diameter and branch length. No significant effects were noted for any of the three traits at the ZONE level; however, PROV/Z effects were significant for both branch diameter and branch length. All three branch traits had significant FAM/P/Z effects; therefore, branch size (branch diameter and branch length) can be manipulated by selection at the provenance and individual level, and branch angle could be changed by selection at the individual level. Genetic correlations indicated that selection for smaller branch diameters should result in shorter branches. This is desirable since knot sizes would be reduced and trees would reduce allocation of biomass to branch wood. However, the genetic relationships among branch angle, diameter and length are such that if larger branch angles are selected, improvement should occur in all three traits.

Physical measurement of branch angle gave excellent family discrimination (based on four branches per tree) and may be worth considering; however, physical measurement in large tests would be costly. Assessment of four major branches, from two whorls on each tree using a 1-5 or 1-10 point scoring system may provide good discrimination among lodgepole pine families for branch angle. This contrasts sharply with the lack of family discrimination for branch angle in Caribbean pine, using a subjective scale (Ledig and Whitmore 1981). The lack of differences among families of Caribbean pine, however, could be due to 1) the presence of small genetic differences, 2) the insensitivity of the subjective scale, or 3) the fact that only 16 families were assessed in their study.

Crown and stem form measures are subject to large personal bias; therefore, it is imperative that rigorous scoring standards are established and maintained across replications. The scoring system used in this study did follow guidelines for scoring individual trees for the traits making up crown score (see page 29), but significant replication differences still became evident. Stem score, using the 1-10 point system, was not biased, as replication differences were not significant.

No significant effects were present for crown score at the ZONE or PROV/Z level. Stem score, however, had significant differences at the PROV/Z level (P<0.01), which indicated stem straightness has a significant stand component. Both of these traits had significant FAM/P/Z effects; therefore, selection for crown form should require screening only at the individual level, whereas stem straightness requires screening at both the provenance and individual level. Family selection, typically had higher heritabilities, but tended to have corresponding low phenotypic standard deviations among family means making expected gain relatively low. Genetic correlations between crown form and branch angle were almost minus one (-0.97). In this study, heavy weighting was given to branch angle in the synthetic trait of crown form, so a strong relationship should be expected. A reliable trait to measure on lodgepole pine at age 10 may be a branch quality trait similar to that used by Dean *et al*. (1983). Because of the correlation patterns exhibited among the branch traits, selection based on branch quality (i.e., branch angle and branch diameter assessed on a few major branches) should bring about a desirable change in most of the other characters affecting crown form. Rehfeldt's (1985b) concern about branch length increasing through selection for growth is valid, but selection for branch angle along with growth may minimize the overall increase in the width of the crown.

Selection for high wood density will also decrease wood moisture content at both the family and zone levels, which could be considered a desirable change. This should be beneficial from the view that transportation of logs to the mill will be more cost effective since less water will be hauled relative to the amount of wood. Collection and measurement of wood samples from test trees is expensive, and depending on the goals of the program, probably not worthwhile. This does not mean that a measurement of wood specific gravity is unimportant, but other devices which can give a reasonably indirect measure of specific gravity could be more cost effective.

The study of the correlations of specific gravity with pin penetration using the Pilodyn (e.g., Micko *et al*. 1982, Sprague *et al*. 1983) indicated that the instrument could give significant rankings for an indirect measure of specific gravity at the provenance level (Spearman rank correlation [r=-0.65]; P<0.05). The genetic correlation between pin penetration of the Pilodyn and wood density was -0.95(±.22), indicating that the device would be quite effective for obtaining a reliable correlated response in specific gravity by selecting on pin penetration. Sprague *et al*. (1983) using the Pilodyn reported similar results in loblolly pine.

Bark thickness had a high positive genetic correlation with diameter growth and a low negative genetic correlation with height growth. Although bark thickness is easily measured on 10-year-old lodgepole pine, and may have its own economic and biological implications, it is probably a trait that can be ignored in a large scale progeny test. The correlations indicate that selection for height should reduce bark thickness.

As mentioned in the results, compression wood content has a high genetic correlation with specific gravity; therefore, once selected families have been assessed for wood density, some wood sampling is required to ensure that compression wood content is not the trait being selected.

There was a moderate negative genetic correlation between the width of the ninth growth ring and tracheid length (-0.39±.27). It should be expected that tracheid length will decrease slightly as selection occurs for diameter. However, selection for height growth should increase tracheid length (r_g=0.55±.27). This seems to be a contradictory relationship, but may follow the correlation patterns shown for bark thickness with height and diameter. Once fibres have average lengths of at least of 2.5mm, burst and tear strengths appear to be adequate (Kellogg, pers. com.). This length is normally attained by ages 20-30 in lodgepole pine (Taylor *et al.* 1983). Selection for height is likely to reduce the time required before fibres at least 2.5mm in length are formed, according to the genetic correlations found here.

If dry-weight production is the goal of a program, the correlations indicate that volume should be an excellent means of indirect selection for dry weight. Bridgwater *et al.* (1983) estimated stem dry weight by destructive sampling, and concluded that volume was also the major factor contributing to ~~stem~~ dry weight.

The two disease traits examined in this study are not true metric traits and do not lend themselves to standard analysis. The scoring system gives good discrimination among trees; however, variance estimates would be unreliable from this data set. If rust infection levels are relatively low, a large number of trees are scored "1", skewing the data set. Heritability estimates derived by three alternative procedures for dealing with levels of resistance indicated moderate levels of resistance for stalactiform blister rust and western gall rust, but it is difficult to attach any economic meaning to incremental gains in genetic resistance without commercial checks being included in the test. Practically, a presence/absence (threshold character) scoring approach, with significance testing determining if family differences are present, might be effective for selection. What is required in rust-resistance testing is a method to ensure each individual has been exposed to the causal agent to the same degree; therefore, artificial inoculation techniques followed by field testing would be the only way that the entire population is shifted in relation to a threshold value. This trait is probably best treated as a trait for independent culling at the provenance and individual level.

4.2 Geographic Patterns

Substantial variation was found in most of the traits examined in this study of lodgepole pine in British Columbia. Variation patterns in wood density and growth traits have been reported in a number of other studies (e.g., Rees and Brown 1954, Saucier and Taras 1966); however, little information has been reported on variation of some of the other quality traits at the zone and provenance levels. Several aspects of the genetic structure of lodgepole pine can by elucidated from the results of this study. In a range-wide provenance study of black spruce (*Picea mariana* Mill.), Morgenstern (1969) used two criteria to classify the variation pattern for thirteen characters. If the populations (zones in this present study) component of variance was larger than the subpopulation (provenance within zone) and the family (families within provenance within zone) component, the variation was considered clinal. If the subpopulation component of variance was larger than the population and family component, the variation was considered ecotypic in nature. On the basis of the criteria suggested by Morgenstern, it could be concluded that clinal patterns are present for wood moisture content (Fig. 3), specific gravity (Fig. 3) height, diameter, volume, dry-weight and incidence of western gall rust infection (i.e., variance attributable to ZONES was higher than that for PROV/Z and FAM/P/Z; Fig. 4; Tables 13, 14 and 20, respectively) in this study. However, the effect of ZONES was not statistically significant for moisture content; therefore, this trait should not be considered as having a significant clinal pattern of variation. The clinal patterns of variation noted for these traits are, therefore, probably influenced by continuous ecological factors such as regional patterns of precipitation, temperature, daylength, etc.

Geographic variation in wood specific gravity of slash pine (*Pinus elliotii* Engelm.) was significantly related to the occurrence of early and late rainfall (Goddard and Strickland 1962). Ledig *et al*. (1975) reported that in pitch pine (*Pinus rigida* Mill.) specific gravity and tracheid length variation was related to climatic variables. They hypothesized that these two traits varied as ecoclines across the sampled range of pitch pine. Of the traits that exhibited clinal variation, only specific gravity had non-significant PROV/Z effects, which is similar to the report of Ledig *et al*. (1975). Therefore, gradual environmental factors probably have influenced specific gravity more than five other traits that exhibited clinal variation. Perhaps a modification of Morgenstern's (1969) criteria is in order, by adding that ecoclinal patterns of variation to the two previously described categories. This would be the case for height, diameter, volume, dry-weight and western gall rust resistance (i.e., significant PROV/Z differences were found for these traits).

Ecotypic patterns of variation were noted for all others, except branch angle and tracheid length (i.e., PROV/Z variances were higher than the variances associated with ZONES and FAM/P/Z effects). However, no significant differences were observed among provenances for crown score, so this trait should not be considered as having a significant ecotypic pattern of variation. Stem score showed significant provenance differences, which may indicate some stands may be inherently prone to producing higher than average stem crooks. This suggests that more discrete factors such as local climate, soil, aspect and elevation are more important in determining differences among provenances for these traits. Branch angle and tracheid length have no geographic patterns associated with them, and appear to be primarily determined by the genetic constitution of the individual.

4.3 Genetic Variation

When all populations were pooled for estimation of additive genetic variance and covariance, which would give an "average effect" for lodgepole pine, heritabilities and genetic correlations generally concur with findings in other pine species. The wood traits (specific gravity, moisture content, compression wood and tracheid length) all had heritabilities lower or equal to those reported by Matziris and Zobel (1973) and Shelbourne *et al*. (1969) in loblolly pine. The heritability reported here for height growth corresponded closely to that reported by Rehfeldt (1985b) for lodgepole pine at age six.

The only trait that exhibited an unexpectedly high heritability was branch angle (0.42). Very few papers have dealt with this trait alone. Cahman (1981) found a heritability of 0.72 in clonal material of lodgepole pine, and Velling and Tigerstedt (1984) reported a heritability of 0.22 using full-sib material of Scots pine. Merrill and Mohn (1985) reported a heritability of 0.44 from a half-sib material of white spruce (*Picea glauca* [Moench] Voss), which corresponds closely to the value reported here.

More important than a discussion of general trends across the populations examined in this study is the determination of whether the estimates of heritabilities and correlations were consistent across the five zones. The extensive and large distribution of lodgepole pine has led to population differentiation at the single-locus (Yeh and Layton 1979) and multi-locus level (Yeh *et al*. 1985). Evolutionary factors, such as 1) random genetic drift, 2) divergent selection of macrogeographical adaptation, 3) balancing selection for microgeographical adaptation, and 4) historically recent events such as migration, have had a significant role in the generation and maintenance of the genetic structure of natural populations of lodgepole pine (Yeh *et al*. 1985). Three different refugia appear to have been the major sources for reinvasion of lodgepole pine in British Columbia following the last glaciation (Wheeler and Critchfield 1985, Wheeler and Guries 1982). A general expectation, therefore, is that the expression of variability in the amount of additive genetic variances (i.e., heritabilities) and covariances (i.e., correlations) may be due to underlying genetic processes such as selection and migration for characters with or without some adaptive value. Most of the traits related to growth in zone #1 and #5 had non-significant family effects with a corresponding low heritability (Table 22a and 22b). Populations from zones #2, #3 and #4 had significant family effects and correspondingly high heritabilities for the growth traits (Table 22a); however, this changed for zone [illegible] when the analysis of variance model was altered to include provenance effects. Although the implication that some evolutionary forces may have caused the relative decreases in both additive and phenotypic variances in zone #1 (relative to zone #2 for volume) is speculative, differences in genetic structures do become apparent from these statistical analyses. Whether these structures are a manifestation of sampling errors within a zone or true genetic structures within a zone (i.e., significant or non-significant provenance differences), it does imply that populations need to be considered separately. Non-significant family effects in a zone suggest either 1) not enough provenances were included to fairly represent a zone, or 2) provenance and family differences are not inherent in the population. Interestingly, zone #5 material (which tended to exhibit the lowest heritabilities and non-significant family differences) was the population closest to the test site. Height differences, however, were significant (P<.05), indicating that the locally adapted population had either provenance differences and/or family differences within provenances.

Although wood specific gravity had the highest heritability in the combined analysis (0.42), values ranged from 0.26-0.38 in the zone-by-zone comparison, with significant family differences only present for zone #4. Although heritability estimates were moderate, significant family differences probably were lacking because of the relatively low coefficient of variation for specific gravity (7%) and the small number of families within each zone. If more families within a zone had been sampled, the differences may have been significant. This is interesting because heritability intuitively seems high, but the actual F-test for the family variance component indicated it was not significantly different from zero.

Genetic correlations generally showed that a negative relationship existed between specific gravity and the three growth traits (height, diameter and volume). Similar trends have been reported for radiata pine (Dean *et al.* 1983) and loblolly pine (Loo *et al.* 1984). As discussed earlier, genetic correlations among branch traits are interesting, since selection for higher branch angles should reduce overall branch size. In the combined analyses, correlations of branch angle and branch diameter with height, stem diameter and stem volume all were close to zero. The correlations of branch length with the three growth traits were all positive, but quite low.

Genetic correlations calculated for the five populations indicated that specific gravity and the growth traits expressed moderate negative genetic correlations in zones #2, #3 and #4; however, zones #1 and #5 had contrasting correlations between growth and specific gravity. Zone #1 had a correlation less than -1.0; and in zone #5, the correlations were 0.04 and -0.28 for the specific gravity/volume relationship (depending on ~~the~~ which analysis of variance model used; Table 27a or 27b). This could have a large impact on selection for volume, since the correlations can affect specific gravity in two ways, depending on the genetic structure of two seemingly different populations. Other correlations, particularly either between height and branch diameter or between height and stem diameter for zone #5 are significantly different relative to the other four zones. Selection for height in zone #2 should not bring about a large change in branch diameter, whereas selection for height in zone #5 material should bring about an almost perfect increase in branch diameter (Table 22). Across all zones, selection for height should not affect branch angle (which was also indicated from the combined analysis). However, the previously described scenario for decreasing branch diameter by selection of branch angle would not be present for all five zones. Genetic correlations ranged from 0.09 to -0.95 (without provenance effects in the model) and from -0.01 to -1.1 (with provenance effects in the model)(Tables 27a and 27b). What it particularly interesting in relation to changes in the analysis of variance model is the large change in the correlation in zone #2. Without provenance effects the correlation between branch angle and branch diameter was 0.65, and with provenance effects accounted for, the correlation became large and negative (-0.75). This again indicates the large influence provenance effects may have on genetic parameter estimation.

Practically, some pooling of individual trees will have to occur to delimit a breeding population, and this will more than likely be based on rather arbitrary data. One should expect that breeding zones will include provenances (or stands) with different gene frequencies and that errors associated with genetic parameters will be substantial, simply because we are dealing with wild populations. The level to which a breeder should explore differences in genetic structure is difficult to say, since among- and within-provenance variability may or may not be substantial for all the traits of interest. Grouping wild stand selections according to similar environmental criteria for a base population may be an approach that would minimize the pooling populations of diverse genetic structures. In this case, we would ho[illegible]t that similar evolutionary forces (i.e., selection, drift and migration) have acted according to some environmental structures.

It is possible, therefore, that heritability and correlation estimates are unlikely to be close to the true expression of additive genetic variance and covariance in the population. The problem appears to be that selections will be made in a breeding program after initial testing, and these selections will undergo recombination by some mating design to generate a new population for recurrent selection. This new population will likely exhibit linkage disequilibrium, because individuals in the mating design are likely to have come from populations of differing gene frequencies. Hanson (1959) concluded that four generations of random intermating were needed to bring a population back to equilibrium. It is likely, therefore, that forest tree populations will always be in some disequilibrium, since selection will occur each time a new generation is produced and random mating is unlikely to occur. Therefore, estimates of genetic components of variance will likely always be affected by linkage disequilibrium, but the change in the mean of the offspring by selection of parents will be permanent since it is due to a change in gene frequencies. If there are epistatic interactions between loci then part of the change in the mean may be due to linkage disequilibrium (Bulmer 1980).

4.4 Accuracy of Estimates

If a standard error of an estimate is lower than the estimate itself, it could be indicative of a reasonably estimated parameter. All heritabilities calculated on an individual basis had standard errors substantially lower than the estimates themselves (Table 3). Standard errors for heritability estimates were much larger for family, provenance and zone values, but most were still below the estimates themselves.

Standard errors reported here from the combined analysis were in the order of 20-47% of the errors reported for heritability estimates in radiata pine by Dean *et al.* (1983). Genetic correlations typically are more poorly estimated than heritabilities (Falconer 1981), but standard errors of the estimates reported here for lodgepole pine were usually lower than the values reported by Dean *et al.* (1983), which may have been due to the larger data set in this study.

In the estimation of genetic parameters within zones, standard errors of heritabilities and genetic correlations varied from 25-100% of the estimates. This could be expected as the number of families was substantially smaller in the within-zone analysis.

The bias that may have been included in the estimates of additive genetic variance and covariance may be due to some full-sib structure in the test material. As previously discussed, the nature of the serotinous cones in lodgepole pine may reduce this bias; however, relatedness among trees in the stand may be substantial, simply because fire has been a major factor in stand formation of lodgepole pine. Nearby individual trees may have substantial half-sib structure, since the mother tree may have released a large amount of seed in a localized area immediately after a burn. However, this may have been minimized by selecting trees at least 50m apart (Illingworth, pers. com.).

As more open-pollinated progeny from single tree collections are used in a half-sib family test, the chances are greater that they all did not have different pollen parents, which would be necessary for the true half-sib structure to exist. In this study, a maximum of 18 open-pollinated individuals were used to assess a family for a particular trait. Therefore, it is likely that this bias is quite minimal, simply because of the relatively low number of open-pollinated progeny used to attain a family mean. Epperson and Allard (1984) reported high outcrossing rates, with little spatial variation, in lodgepole pine. Therefore, one would not expect a large bias in the estimate of heritabilities among zones because of the high outcrossing rates.

4.5 Selection Methods

It is apparent that tandem selection in the real sense is not appropriate in tree breeding, simply because only one trait can be selected for each generation.

Independent culling levels, however, may be appropriate for resistance to stalactiform blister rust and western gall rust. No clear patterns of genetic correlations were noted with the two rust-resistance traits, with the exception of diameter growth with western gall rust (0.60±.39). This may indicate that fast growing trees may be more susceptible to gall infections. indicating they may be the most effective traits to select before selection occurs for growth and quality. It was found that selection at the provenance level would be the most effective, followed by individual selection, for the two rust resistance traits (Fig. 5a). What has to be assumed in these gain estimates is that individuals had equal exposure to the causal agents and that apparently resistant trees were not in fact escapes. Next, those provenances that have performed best in terms of growth should be considered. The best provenances for volume production were not local sources which indicates that selection for growth should occur for material that can fully utilize the biomass potential of the site. This suggests that moving lodgepole pine one to two degrees north to capitalize on photoperiod response would be appropriate, assuming that they have been sufficiently tested in the new environment.

Once these populations have been identified as relatively disease resistant and capable of maximizing the biomass-potential of the local environment, the use of selection indices may be an appropriate procedure. Hallauer and Miranda (1981) concluded from other studies that the superiority of index selection was at a maximum when traits were considered to be equal in importance. Efficiency is more dependent on genetic correlations than phenotypic correlations, and small changes in economic weights do not appreciably influence efficiency (Smith 1983). In terms of efficiencies of indices over simple selection, it was shown that an index including specific gravity and volume (with equal weighting) would yield higher expected gains than selection for volume alone. This may be an approach that could be used by a breeder interested in increasing volume, but the indices would require proper genetic estimates for the construction of the index. It has been demonstrated that these genetic estimates depend on the population and may lead to poor index construction if populations differ drastically in gene frequencies affecting the traits in the index. It seems an appropriate strategy in tree breeding to locate populations exhibiting desirable correlations, and to practice index selection within these populations. For example, if volume is the goal of the program, index selection could be practiced on the population that would give the best volume response using an index. If an overall goal of increasing volume while maintaining specific gravity at the current level was the approach, a restricted index for zone #2 would be appropriate, or one could practice index selection from populations with a zero correlation between volume and specific gravity.

There are numerous options in regard to the many approaches that can be taken once good information is available on population structures and economic objectives. It seems appropriate then, to construct indices with equal weightings on the traits, and concentrate on changing expected responses by dealing with populations that have the desired correlation patterns, instead of simply changing the economic values associated with each trait. Index selection is expected to be a better approach when correlations are low and heritabilities are similar (Smith 1983). Therefore, traits such as growth, specific gravity, branch angle and perhaps stem straightness could be selected by index selection. This approach could be considered an extension of the multiple-index selection strategy (Namkoong 1976), by breaking down populations according to their genetic structures rather than by aggregate breeding values derived from genetic estimates in different populations. Of course practical considerations along with clear economic objectives and goals are still required for both multiple-population approaches; however, capitalizing on the genetic structures which are present in wild populations, may lead to more accurate multiple-population breeding.

This whole strategy would be the intuitive-plus-index selection described by Simmonds (1979). As described earlier, high specific gravity may be [illegible] compression wood content and the selection would [illegible]id. Some arbitrary decisions by the breeder [illegible]ave to be made to exclude certain individuals with high aggregate breeding values because of a poor score for a trait not included in the index or because of relatedness; therefore, the expected gains may not be realized in the next generation. Practically then, index selection should be considered a theoretical tool that can identify trends from selection, as well as indicate potential candidates for selection based on multiple-trait selection.

4.6 Recommendations

This study indicates a number of important features that should be considered in the breeding of lodgepole pine. When dealing with material from natural populations, it is important to consider the zone, provenance (or stand) and individual tree effects. For lodgepole pine, open-pollinated seed provides a valuable sample of genes from a provenance. A number of trees sampled from a stand will increase the reliability of a stand mean as well as indicate the better stands. The stand-to-stand variation can then be examined to determine if individual tree selection or provenance selection (with best trees within a provenance) is appropriate for a particular trait.

Breeding within zones should be the starting point for improvement since it would give valuable information on stand differences and genetic parameters for local populations. Once these are understood, movement of the material to test the ability of genotypes to realize the biomass potential of the environments and to monitor genetic parameters may be appropriate. Ideally, these should be initiated at the same time; however, this is usually an undertaking of large proportions.

The heritabilities reported here cannot be directly used in gain calculations for wild-tree selections; they may be applicable in so-called "farm-field" plantations. Rankings of heritabilities in natural stands probably are similar to those in test plantations, but the environmental effects in natural stands are likely to be substantially higher. Therefore, heritabilities in the wild are expected to be substantially lower than those reported in designed plantation experiments. Assuming the relative ranking of the heritabilities among traits stays the same, it may be appropriate to select for branch angle and specific gravity on the phenotypic observation of individual trees. Selection for rust resistance can occur at all levels, particularly at the provenance level. Ideally, natural stands that have been noted as heavily infected would provide the best material for selection, since both pathogen and tree probably have been exposed to each other for some time. Growth traits are most efficiently selected at the provenance or stand level. However, a new program should include both local and non-local sources, simply to guard against long-term instability of non-local sources. If, however, non-local populations express better long-term growth potential, as they appear to do in the Red Rock plantation, then multiple-trait selection should be practiced in this material. Potential genetic gains are simply too high to be ignored by this relatively simple approach.

With this approach, the proper genetic parameters will be available and sublines constructed with the desired goals (e.g., for high specific gravity and growth or strictly for growth). This, of course, can occur from both local and non-local material, depending upon which populations exhibit the desired growth potentials and genetic relationships. Once these breeding populations are established, multiple-trait selection, whether it be by indices or culling levels, will basically involve partitioning growth into the desirable components of trees, as it is unlikely that selection within a population for growth potential will yield substantial gains.

4.7 Future Research

The Red Rock provenance-family plantation offers an interesting opportunity to examine genetic parameters and their expression within zones. The sub-sampling of provenances within zones in this study was based on sampling constraints to some extent; therefore, a large number of families from a large number of provenances could not be sampled to obtain extremely reliable estimates of additive genetic covariances. The estimates obtained for additive genetic variance gave a reliable indication of different heritabilities for different traits in different geographic areas. More intensive restructuring of zones and provenances within zones using all available material in the plantation should yield reliable information about how the various populations exhibit genetic parameters in the Prince George region of British Columbia. Particular emphasis should perhaps be placed on materials from zones #1 and #2. Whether the observed results are representative of the area is uncertain.

An additional undertaking that may prove valuable in the long run would be to make inter-provenance or inter-zone crosses. Because gene frequencies are expected to be different among populations, the composite population would probably be in linkage disequilibrium (Harvey and Townsend 1985). However, if the composite population were allowed to inter-mate randomly, linkage should be reduced each generation by the recombination factor, and new unique gene complexes may become available for selection. Genetic correlations may also be broken and new recombinants may exist for positive genetic correlations between specific gravity and volume. Controlled matings within provenances would yield information on dominance genetic variance, which would be helpful in examining the genetic structures within populations further. The design II mating scheme (Comstock and Robinson 1948) would be effective for estimating dominance genetic variance; to ensure that a number of parents were in the test, crosses could be set up as small four- to- eight tree factorials (i.e., disconnected factorial design). With this material planted on reciprocal test sites, an observation could be made on the means, phenotypic variance, and additive and dominance genetic variance for each of the populations. The presence of differences in dominance to additive genetic variance and phenotypic variance may provide more precise data on which to make comments on possible evolutionary forces causing population differences in quantitative inheritance.

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Appendices

Appendix A

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
1			1.92 (84)	1.14 (41)	3.38 (44)	4.47 (39)	3.29 (16)	0.375 (6)	69.45 (11)	22.15 (17)	147.3 (17)		114.5 (16)	5.04 (10)	7.83 (13)	10.18 (35)	3.80 (35)
2			1.811 (93)	1.23 (53)	3.32 (46)	4.70 (32)	3.35 (17)	0.380 (8)	69.38 (11)	22.76 (20)	152.0 (18)	1.73 (10)	118.9 (14)	5.29 (13)	8.00 (14)	11.24 (39)	4.22 (39)
3			1.43 (78)	1.11 (33)	3.24 (43)	4.42 (33)	3.28 (17)	0.384 (8)	68.40 (10)	22.88 (17)	140.7 (18)	1.63 (10)	115.0 (13)	4.95 (11)	7.14 (13)	7.57 (35)	2.90 (35)
4			1.79 (83)	1.66 (63)	3.44 (39)	[illegible].07 (38)	2.97 (18)	0.399 (7)	69.64 (11)	21.09 (18)	129.0 (18)	1.69 (9)	99.10 (17)	4.37 (13)	6.89 (13)	6.74 (36)	2.72 (34)
5			1.25 (63)	1.36 (54)	3.25 (44)	4.32 (37)	3.11 (10)	0.384 (7)	69.60 (11)	22.20 (17)	139.0 (16)	1.67 (10)	112.3 (12)	4.47 (12)	7.06 (12)	7.25 (34)	2.79 (32)
6			1.85 (91)	1.18 (40)	3.20 (41)	4.49 (53)											

Table A1 - Zone means for 15 traits of lodgepole pine from central British Columbia: where, RS=stalactiform blister rust(1,10), GS=western gall rust(1,5), CS=crown score(1,10), SS=stem score (1,10), BT=bark thickness(mm), SPGR=specific gravity, BA=branch angle(deg.), BD=branch diameter(mm), BL=branch length(cm), TL=tracheid length(mm), MOIS=moisture content(%), HT=height(m), DIA=diameter(cm), VOL=volume(dm^3), DW=dry weight(kg/tree). Coefficient of variation in parenthesis.

[illegible]	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	HDIS	HT	DIA	VOL	DW
	64		1.74 (79)	1.20 (49)	3.39 (39)	3.75 (43)	3.30 (15)	0.372 (7)	68.03 (13)	23.10 (14)	153.8 (15)		118.4 (15)	5.08 (10)	7.88 (13)	10.65 (36)	3.90 (35)
	45		1.71 (79)	1.08 (28)	4.09 (42)	5.13 (29)			70.48 (12)	23.45 (17)	158.1 (15)						
	46		2.03 (75)	1.13 (44)	3.13 (42)	4.68 (29)	3.21 (17)	0.377 (6)	70.08 (9)	21.48 (15)	144.2 (14)		110.7 (15)	5.02 (10)	7.60 (12)	9.72 (33)	3.63 (33)
	56		2.21 (94)	1.16 (38)	2.88 (43)	4.29 (33)			68.21 (10)	20.36 (18)	132.5 (17)						
	14		2.43 (95)	1.36 (99)	3.23 (40)	4.53 (34)	3.22 (17)	0.380 (6)	68.43 (11)	23.19 (18)	147.9 (17)	1.72 (9)	118.3 (14)	[illegible] (15)	7.55 (14)	9.01 (40)	3.42 (40)
	15		2.39 (84)	1.40 (60)	3.70 (44)	4.43 (36)			68.29 (12)	20.27 (19)	134.5 (17)						
	57		1.31 (61)	1.04 (22)	2.79 (41)	4.73 (30)	3.35 (19)	0.382 (8)	71.18 (10)	22.49 (19)	152.7 (16)	1.77 (10)		5.30 (11)	7.98 (13)	10.91 (34)	4.09 (34)
	72		1.22 (55)	1.14 (46)	3.39 (43)	5.05 (28)	3.42 (15)	0.376 (9)	68.54 (12)	24.80 (18)	170.5 (15)	1.69 (11)	119.7 (13)	5.64 (11)	8.57 (13)	13.80 (32)	5.13 (32)
	24		1.30 (61)	1.16 (35)	3.18 (43)	4.66 (32)	2.99 (17)	0.382 (8)	67.89 (9)	24.05 (14)	147.1 (14)			4.79 (10)	7.48 (11)	8.67 (29)	3.30 (29)
	25		1.08 (80)	1.07 (20)	3.55 (41)	4.16 (37)	3.33 (17)	0.381 (8)	68.84 (11)	23.81 (16)	151.5 (16)	1.67 (9)	119.9 (9)	4.64 (10)	7.35 (12)	8.13 (34)	3.12 (33)
	26		1.23 (60)	1.09 (49)	3.15 (43)	4.51 (28)			70.00 (10)	22.12 (17)	132.1 (17)						
	27		2.10 (81)	1.14 (37)	3.05 (44)	4.37 (34)	3.46 (13)	0.389 [illegible]	67.24 (11)	21.24 (17)	128.8 (18)	1.60 (10)	110.0 (16)	4.20 (9)	6.59 (11)	5.86 [illegible]	2.27 [illegible]
	20		2.08 (81)	1.88 (64)	3.33 (37)	3.62 (39)	3.12 (16)	[illegible]	69.62 (12)	20.14 (18)	119.0 (18)	1.66 (9)	95.5 (17)	4.21 (12)	6.77 (12)	[illegible]	[illegible]
	21		2.15 (85)	1.44 (48)	3.31 (40)	4.84 (42)											
	22		1.50 (78)	1.69 (68)	3.49 (41)	4.58 [illegible]	2.70 (18)	0.398 (7)	68.19 (10)	22.54 (16)	140.5 (14)			4.55 (13)	7.05 (13)	7.35 (35)	2.93 (33)
	55		1.59 (77)	1.60 (61)	3.59 (37)	3.92 (36)	2.99 (16)	0.400 (7)	71.16 (10)	20.41 (16)	125.5 (18)	1.73 (9)	102.8 (16)	4.37 (14)	6.83 (13)	6.66 (39)	2.71 (37)
	19		1.25 (53)	1.35 (51)	3.74 (39)	4.52 (38)	3.26 (15)	0.389 (7)	68.16 (11)	21.70 (17)	135.4 (16)	1.67 (10)	107.8 (14)	4.50 (12)	7.11 (13)	7.42 (33)	2.91 (32)
	62		1.04 (28)	1.31 (51)	2.77 (41)	4.05 (37)			70.02 (10)	23.95 (15)	147.9 (13)						

Table A2 - Provenance means for 15 traits of lodgepole pine from central British Columbia.

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	WT	DIA	VOL	DU
	64		1.54 (81)	1.60 (59)	3.28 (42)	4.05 (40)	3.22 (16)	0.387 (6)	68.74 (11)	21.44 (17)	153.9 [illegible]	[illegible] (11)	116.7 (6)	4.38 (12)	7.88 (12)	6.83 (32)	2.63 (30)
	65		1.15 (46)	1.19 (46)	3.23 (50)	4.66 (32)	2.82 (19)	0.374 (7)	71.96 (10)	21.97 (17)	138.6 (16)	1.68 (10)		4.62 (13)	7.86 (12)	7.51 (35)	2.84 (33)
	29		1.54 (64)	1.15 (33)	3.49 (36)	4.43 (33)											
	30		1.80 (82)	1.10 (30)	3.19 (41)	4.55 (34)											
	37		2.20 (96)	1.29 (45)	3.01 (44)	4.36 (36)											
	66		2.13 (92)	1.22 (46)	3.08 (45)	4.64 (29)											

Table A2 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
1	44	03	3.00 (71)	1.31 (46)	3.94 (36)	4.44 (38)	3.32 (14)	0.371 (5)	69.47 (11)	24.80 (14)	162.4 (18)	1.67 (6)	121.6 (14)	5.00 (8)	7.61 (12)	9.42 (35)	3.50 (35)
1	44	04	2.87 (67)	1.13 (46)	3.47 (34)	3.07 (45)	3.21 (17)	0.384 (5)	67.50 (14)	22.58 (16)	146.0 (11)	1.72 (8)	105.5 (21)	5.18 (16)	7.49 (17)	9.83 (52)	3.98 (51)
1	44	05	1.39 (50)	1.11 (29)	3.67 (31)	3.67 (47)	3.17 (18)	0.359 (6)	72.18 (13)	21.26 (13)	141.4 (12)	1.69 (7)	127.8 (9)	5.16 (7)	8.45 (10)	12.07 (28)	4.33 (27)
1	44	06	1.87 (67)	1.47 (51)	4.13 (38)	3.67 (41)	3.43 (11)	0.382 (4)	59.70 (7)	24.02 (9)	158.1 (8)	1.68 (8)	119.4 (9)	4.95 (8)	7.57 (12)	9.20 (27)	3.49 (27)
1	44	07	1.35 (64)	1.00 (0)	2.82 (34)	3.53 (45)	3.19 (11)	0.368 (5)	71.44 (11)	21.44 (16)	143.1 (17)	1.75 (9)	119.3 (6)	5.02 (8)	7.71 (11)	9.67 (29)	3.68 (29)
1	44	10	1.35 (52)	1.35 (74)	3.41 (40)	4.12 (35)	3.25 (9)	0.352 (8)	66.05 (15)	24.16 (13)	167.0 (13)	1.71 (9)	119.9 (9)	5.26 (10)	8.76 (15)	13.62 (39)	4.78 (42)
1	44	13	1.28 (45)	1.28 (59)	3.28 (49)	2.67 (53)	3.25 (16)	0.389 (8)	61.47 (9)	22.82 (11)	145.1 (15)	1.84 (9)	108.3 (26)	4.82 (15)	7.88 (14)	10.08 (43)	3.89 (41)
1	44	14	1.06 (24)	1.13 (44)	3.13 (39)	4.50 (32)	3.43 (17)	0.366 (5)	69.92 (9)	23.63 (14)	161.1 (16)	1.64 (8)	121.6 (11)	5.01 (8)	8.30 (8)	11.20 (22)	4.12 (22)
1	44	15	1.69 (94)	1.06 (24)	2.75 (28)	4.19 (39)	3.48 (16)	0.379 (10)	74.23 (8)	24.22 (13)	162.7 (13)	1.75 (11)	121.8 (21)	5.16 (8)	7.74 (12)	10.07 (30)	3.79 (30)
1	45	01	1.31 (67)	1.19 (34)	4.43 (36)	5.06 (30)			70.13 (10)	24.0 (16)	156.6 (12)						
1	45	02	1.71 (65)	1.06 (23)	3.88 (47)	5.06 (28)			72.56 (10)	22.69 (20)	156.3 (19)						
1	45	06	1.35 (90)	1.00 (0)	3.94 (41)	5.35 (37)			70.16 (9)	24.26 (16)	163.6 (14)						
1	45	07	1.12 (43)	1.06 (23)	4.12 (36)	5.12 (18)			71.24 (10)	24.90 (11)	164.1 (11)						
1	45	08	1.41 (90)	1.00 (0)	3.94 (44)	5.00 (31)			66.19 (20)	23.57 (13)	164.5 (12)						
1	45	09	1.44 (49)	1.28 (45)	3.06 (31)	4.72 (35)			75.47 (8)	20.68 (17)	144.2 (17)						
1	45	12	1.94 (76)	1.06 (22)	3.89 (49)	5.89 (25)			74.92 (12)	22.14 (24)	151.1 (21)						
1	45	14	3.19 (59)	1.06 (24)	4.88 (38)	5.38 (24)			65.86 (12)	24.67 (17)	164.5 (14)						

Table A3 - Family means for 15 traits of lodgepole pine from central British Columbia

(continued)

ZONE	PROV	FAM	RS	BS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
1	45	15	2.00 (87)	1.06 (23)	4.82 (40)	5.12 (28)			66.26 (9)	24.46 (13)	159.7 (13)						
1	46	01	2.17 (80)	1.06 (22)	3.22 (45)	4.67 (28)	3.18 (17)	0.386 (5)	70.22 (8)	22.10 (16)	139.2 (14)		109.1 (16)	4.90 (9)	7.38 (9)	8.57 (25)	3.27 (28)
1	46	02	2.47 (67)	1.47 (72)	3.27 (50)	4.33 (32)	3.13 (17)	0.394 (4)	69.40 (10)	20.41 (17)	137.8 (18)		110.2 (8)	4.63 (6)	7.10 (11)	7.45 (26)	2.93 (22)
1	46	03	1.38 (64)	1.00 (0)	2.75 (43)	4.44 (28)	3.15 (13)	0.377 (5)	73.06 (5)	21.22 (13)	147.4 (14)		117.7 (11)	5.35 (5)	8.36 (12)	12.21 (27)	4.57 (27)
1	46	05	2.88 (70)	1.18 (33)	3.35 (39)	5.00 (28)	3.63 (17)	0.379 (6)	67.87 (10)	23.41 (10)	157.0 (11)		107.2 (14)	5.22 (8)	8.40 (9)	12.04 (26)	4.50 (27)
1	46	07	1.55 (74)	1.18 (45)	3.24 (50)	5.00 (21)	3.26 (15)	0.382 (6)	71.85 (9)	20.73 (17)	142.7 (14)		91.6 (19)	5.31 (13)	7.80 (10)	10.51 (28)	4.00 (27)
1	46	10	2.07 (70)	1.07 (24)	2.93 (33)	4.47 (38)	3.39 (12)	0.375 (6)	70.52 (10)	20.33 (17)	140.3 (14)		121.8 (12)	5.09 (9)	7.67 (8)	10.00 (21)	3.54 (19)
1	46	11	3.06 (68)	1.06 (22)	3.17 (35)	5.11 (20)	3.12 (15)	0.364 (3)	72.58 (10)	21.89 (12)	139.8 (10)		117.8 (16)	4.88 (9)	7.97 (14)	10.28 (39)	3.75 (42)
1	46	13	1.67 (44)	1.00 (0)	3.39 (39)	4.61 (29)	3.82 (17)	0.375 (8)	67.54 (11)	21.90 (17)	149.0 (14)		106.5 (10)	4.93 (11)	7.43 (14)	8.97 (39)	3.27 (38)
1	46	14	1.59 (63)	1.23 (61)	2.82 (50)	4.36 (36)	3.20 (18)	0.365 (6)	67.85 (9)	20.94 (16)	144.2 (11)		118.6 (12)	4.92 (7)	7.14 (12)	8.07 (30)	2.95 (33)
1	56	02	1.13 (44)	1.06 (24)	2.94 (49)	4.50 (26)			69.09 (8)	23.28 (16)	149.3 (11)						
1	56	05	1.40 (65)	1.47 (57)	3.33 (49)	4.35 (36)			68.90 (12)	18.50 (24)	110.6 (22)						
1	56	06	3.06 (50)	1.19 (34)	2.69 (40)	4.50 (31)			71.73 (7)	20.47 (18)	133.5 (20)						
1	56	07	2.47 (77)	1.18 (45)	3.41 (46)	4.29 (40)			64.98 (9)	21.66 (13)	142.6 (11)						
1	56	09	1.88 (121)	1.06 (24)	2.88 (42)	4.13 (34)			70.00 (7)	21.31 (15)	139.5 (12)						
1	56	10	1.73 (99)	1.00 (0)	2.67 (42)	4.80 (28)			75.27 (9)	18.77 (17)	127.7 (20)						
1	56	11	1.73 (135)	1.07 (25)	2.47 (21)	4.20 (31)			71.17 (8)	18.23 (10)	128.6 (12)						

Table A3 - continued

ZONE	PROV.	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
1	56	13	2.83 (88)	1.22 (35)	2.89 (41)	4.11 (32)			65.61 (10)	20.43 (19)	127.8 (20)						
1	56	14	3.41 (83)	1.18 (33)	2.65 (35)	3.82 (45)			67.44 (11)	20.18 (16)	130.8 (12)						
2	14	01	1.13 (30)	1.25 (36)	3.44 (51)	4.00 (33)	3.10 (20)	0.363 (5)	65.47 (15)	23.38 (13)	141.7 (14)		127.8 (10)	4.59 (11)	7.44 (12)	8.29 (31)	2.99 (30)
2	14	04	2.50 (70)	1.50 (73)	2.94 (47)	4.19 (34)	3.31 (13)	0.375 (5)	68.59 (11)	24.31 (17)	155.8 (13)		123.4 (10)	4.58 (13)	7.12 (8)	7.47 (30)	2.76 (28)
2	14	05	2.22 (92)	1.44 (84)	3.50 (42)	5.83 (25)	3.43 (15)	0.370 (6)	67.86 (9)	24.84 (12)	157.8 (19)		115.5 (11)	4.60 (13)	7.67 (11)	8.87 (32)	3.24 (32)
2	14	06	2.06 (81)	1.53 (41)	4.12 (54)	4.71 (39)	3.21 (18)	0.388 (5)	66.80 (11)	23.85 (22)	152.7 (17)		111.3 (19)	4.80 (13)	7.36 (14)	8.43 (34)	3.25 (36)
2	14	08	2.00 (71)	1.35 (74)	2.59 (56)	3.71 (37)	3.09 (14)	0.394 (5)	69.15 (11)	21.16 (20)	146.8 (17)		116.2 (7)	4.95 (8)	7.08 (11)	7.97 (30)	3.14 (29)
2	14	09	4.71 (85)	1.06 (23)	3.99 (41)	5.35 (24)	3.06 (22)	0.382 (8)	69.23 (9)	22.47 (19)	140.2 (12)		127.4 (16)	4.93 (15)	7.89 (13)	10.31 (47)	3.96 (52)
2	14	10	1.88 (95)	1.13 (44)	2.69 (42)	4.13 (37)	3.04 (18)	0.376 (4)	70.69 (11)	21.16 (16)	143.9 (15)		116.1 (8)	4.97 (12)	7.49 (16)	9.37 (43)	3.54 (43)
2	14	12	3.00 (68)	1.43 (45)	3.13 (50)	4.87 (24)	3.45 (16)	0.366 (6)	72.88 (8)	24.00 (24)	147.2 (22)		113.8 (26)	4.82 (16)	8.40 (19)	11.79 (50)	4.64 (42)
2	14	13	2.36 (106)	1.57 (82)	3.00 (39)	3.78 (24)	3.33 (11)	0.406 (4)	65.09 (10)	23.61 (13)	143.6 (17)		111.7 (13)	4.95 (18)	7.40 (14)	9.02 (36)	3.62 (38)
2	15	02	1.79 (103)	1.71 (77)	3.65 (48)	4.07 (38)			69.66 (12)	19.70 (20)	130.1 (14)						
2	15	03	1.69 (51)	1.08 (26)	3.76 (45)	4.69 (31)			69.29 (10)	19.58 (17)	133.2 (16)						
2	15	05	1.27 (63)	1.20 (34)	4.27 (48)	4.73 (40)			63.20 (12)	23.65 (19)	158.4 (14)						
2	15	06	2.93 (84)	1.25 (46)	3.44 (44)	4.26 (30)			68.70 (14)	18.98 (19)	124.9 (16)						
2	15	10	2.67 (82)	1.40 (59)	3.67 (43)	4.40 (36)			67.18 (9)	20.37 (18)	134.5 (15)						
2	15	11	2.56 (72)	1.72 (59)	3.39 (52)	3.89 (39)			71.56 (13)	20.19 (18)	138.6 (20)						

Table A3 - continued

ZONE	PROV	FAM	RS	BS	CS	SS	BT	SPGR	BA	BD	BI	TL	NDIS	HT	DIA	VOL	DW
2	15	13	3.39 (87)	1.15 (33)	3.69 (40)	4.62 (34)			72.32 (9)	19.56 (17)	128.6 (14)						
2	15	14	2.88 (71)	1.59 (67)	3.65 (35)	4.24 (45)			68.76 (12)	19.66 (15)	128.1 (14)						
2	15	15	2.15 (65)	1.38 (63)	3.92 (46)	5.31 (22)			73.62 (10)	20.83 (19)	135.7 (18)						
2	57	02	1.06 (23)	1.00 (0)	3.00 (33)	4.94 (44)	3.25 (14)	0.377 (5)	72.31 (10)	21.04 (13)	146.8 (9)	1.89 (8)		5.33 (7)	7.64 (11)	10.08 (28)	3.72 (28)
2	57	04	1.56 (59)	1.11 (29)	2.96 (31)	4.33 (33)	3.28 (19)	0.378 (7)	71.35 (8)	22.17 (19)	151.7 (18)	1.75 (10)		5.18 (10)	8.15 (16)	11.49 (41)	4.28 (38)
2	57	05	1.44 (59)	1.06 (22)	2.56 (28)	4.44 (25)	3.44 (17)	0.361 (7)	70.64 (9)	23.31 (20)	150.7 (15)	1.80 (11)		5.21 (11)	7.80 (8)	10.29 (26)	3.57 (25)
2	57	08	1.00 (0)	1.00 (0)	2.75 (54)	5.00 (25)	3.50 (18)	0.401 (7)	67.34 (11)	24.50 (15)	158.1 (16)	1.77 (8)		5.11 (11)	7.58 (11)	9.56 (30)	3.75 (29)
2	57	10	1.22 (45)	1.0[illegible] (0)	[illegible]	4.89 (23)	3.62 (25)	0.386 (8)	75.72 (10)	19.93 (21)	144.5 (16)	1.71 (12)		5.59 (9)	8.13 (8)	12.01 (25)	4.58 (27)
2	57	12	1.41 (90)	1.00 (0)	3.06 (34)	4.71 (35)	3.47 (15)	0.365 (6)	65.90 (9)	28.97 (15)	174.1 (18)	1.70 (9)		5.38 (11)	8.35 (20)	12.88 (45)	4.70 (47)
2	57	13	1.39 (56)	1.17 (48)	2.9[illegible] (36)	4.50 (33)	3.13 (14)	0.393 (9)	72.54 (7)	20.95 (15)	142.0 (13)	1.72 (12)		5.18 (9)	7.98 (9)	9.59 (26)	3.68 (24)
2	57	14	1.65 (71)	1.00 (0)	2.65 (33)	4.71 (22)	3.11 (17)	0.381 (6)	75.37 (7)	20.71 (19)	145.1 (16)	1.86 (10)		5.06 (14)	7.29 (12)	8.81 (37)	3.32 (34)
2	57	15	1.00 (0)	1.00 (0)	3.31 (64)	5.19 (29)	3.78 (21)	0.403 (11)	68.78 (11)	23.23 (16)	163.3 (15)	1.75 (9)		5.61 (12)	8.55 (8)	13.38 (22)	5.23 (25)
2	72	02	1.00 (0)	1.00 (0)	4.00 (46)	5.13 (29)	3.49 (11)	0.384 (9)	68.28 (12)	28.09 (21)	175.5 (16)	1.65 (10)	127.9 (11)	6.09 (11)	8.70 (10)	15.24 (32)	5.73 (30)
2	72	03	1.33 (45)	1.33 (45)	3.61 (44)	5.39 (23)	3.36 (14)	0.391 (10)	73.25 (9)	24.36 (23)	164.3 (19)	1.72 (9)	107.0 (16)	5.53 (15)	8.33 (21)	13.46 (45)	5.64 (41)
2	72	04	1.31 (54)	1.19 (46)	3.50 (52)	4.69 (36)	3.77 (16)	0.378 (7)	69.50 (9)	25.03 (15)	171.8 (14)	1.71 (13)	119.9 (17)	5.50 (8)	8.57 (12)	13.34 (29)	4.94 [illegible]
2	72	06	1.17 (44)	1.22 (35)	3.61 (43)	4.67 (35)	3.42 (16)	0.365 (5)	65.82 (14)	22.27 (19)	158.9 (17)	1.71 (8)	125.8 (13)	5.58 (11)	8.45 (13)	13.16 (33)	4.76 (31)
2	72	08	1.11 (42)	1.11 (29)	3.17 (27)	4.33 (26)	3.18 (10)	0.372 (8)	71.10 (11)	24.86 (16)	174.8 (15)	1.70 (14)	119.5 (10)	5.45 (14)	8.16 (11)	12.02 (36)	4.38 (39)

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
2	72	09	1.17 (44)	1.06 (22)	3.56 (45)	5.89 (22)	3.31 (14)	0.391 (10)	70.26 (10)	23.89 (18)	164.8 (15)	1.67 (12)	119.5 (8)	5.78 (11)	8.69 (9)	14.31 (27)	5.49 (30)
2	72	10	1.81 (81)	1.00 (0)	3.38 (48)	4.94 (17)	3.63 (14)	0.355 (5)	72.20 (8)	24.77 (14)	175.0 (14)	1.70 (9)	119.4 (11)	5.70 (9)	9.09 (11)	15.69 (32)	5.53 (30)
2	72	12	1.12 (30)	1.06 (23)	3.47 (41)	4.53 (31)	3.19 (15)	0.380 (10)	62.96 (8)	24.90 (13)	167.4 (12)	1.70 (10)	120.1 (10)	5.83 (8)	8.81 (11)	14.93 (28)	5.46 (25)
2	72	14	1.00 (0)	1.31 (95)	4.13 (40)	5.88 (20)	3.53 (14)	0.371 (11)	63.08 (12)	27.47 (12)	184.9 (9)	1.69 (12)	120.4 (16)	5.38 (6)	8.39 (11)	12.35 (26)	4.39 (23)
3	24	02	1.13 (44)	1.19 (34)	2.69 (32)	4.88 (34)	3.21 (16)	0.392 (5)	68.13 (9)	24.91 (12)	151.2 (11)			7.86 (8)	6.72 (6)	9.38 (20)	3.75 (21)
3	24	03	1.06 (24)	1.13 (44)	3.07 (35)	4.81 (30)	3.08 (17)	0.386 (11)	71.06 (8)	23.20 (15)	146.9 (12)			5.07 (11)	7.48 (11)	9.19 (30)	3.62 (37)
3	24	05	1.67 (33)	1.11 (29)	3.28 (38)	5.28 (31)	2.78 (15)	0.365 (10)	63.10 (10)	25.58 (13)	158.9 (11)			4.68 (7)	7.20 (14)	7.87 (34)	2.[illegible] (35)
3	24	06	1.12 (44)	1.18 (33)	3.47 (47)	4.35 (38)	3.22 (14)	0.378 (6)	70.33 (10)	24.48 (20)	145.0 (20)			4.53 (11)	7.26 (8)	7.68 (26)	2.93 (25)
3	24	10	2.06 (81)	1.11 (29)	3.56 (46)	4.94 (24)	3.04 (20)	0.398 (9)	68.97 (8)	25.70 (14)	142.8 (14)			4.49 (12)	7.18 (11)	7.36 (25)	2.86 (27)
3	24	11	1.24 (46)	1.29 (45)	3.47 (48)	4.24 (40)	2.83 (12)	0.381 (8)	66.92 (10)	23.75 (15)	141.9 (14)			4.50 (8)	7.41 (12)	8.02 (31)	3.04 (28)
3	24	13	1.00 (0)	1.18 (33)	2.88 (47)	4.53 (30)	3.04 (15)	0.387 (5)	66.63 (9)	23.53 (13)	138.2 (14)			4.99 (8)	7.36 (7)	8.57 (17)	3.24 (17)
3	24	14	1.28 (45)	1.00 (0)	2.78 (36)	4.72 (25)	2.72 (17)	0.376 (7)	67.76 (7)	23.46 (12)	146.2 (11)			5.06 (8)	7.58 (12)	9.45 (31)	3.50 (30)
3	24	15	1.59 (55)	1.12 (43)	3.35 (43)	4.18 (36)	3.08 (17)	0.380 (10)	68.51 (6)	23.65 (13)	152.8 (12)			5.11 (4)	8.03 (10)	10.67 (29)	4.00 (24)
3	25	01	1.22 (53)	1.11 (42)	3.44 (38)	3.28 (37)	3.41 (14)	0.371 (5)	66.50 (9)	24.78 (19)	146.3 (20)	1.61 (6)	122.0 (6)	4.63 (14)	7.37 (12)	8.24 (36)	3.09 (35)
3	25	02	1.00 (0)	1.00 (0)	3.28 (34)	4.22 (31)	3.80 (20)	0.374 (7)	75.42 (7)	24.74 (13)	164.8 (12)	1.65 (11)	118.7 (8)	4.58 (4)	7.47 (8)	8.14 (19)	3.04 (19)
3	25	03	1.12 (43)	1.24 (35)	3.82 (47)	4.12 (45)	3.29 (15)	0.379 (5)	65.68 (15)	23.09 (16)	160.9 (19)	1.77 (7)	116.0 (12)	4.83 (11)	7.01 (7)	7.5[illegible] (25)	2.90 (24)
3	25	04	1.06 (23)	1.06 (23)	3.53 (36)	4.88 (35)	3.31 (19)	0.380 (10)	69.75 (7)	22.73 (19)	154.8 (17)	1.66 (11)	119.8 (10)	4.31 (9)	7.31 (12)	7.47 (35)	2.94 (35)

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	NODS	HT	DIA	VOL	DW
3	25	05	1.00 (0)	1.06 (22)	3.50 (37)	4.67 (22)	3.14 (15)	0.368 (5)	66.68 (11)	25.07 (14)	153.6 (13)	1.67 (8)	117.6 (9)	4.88 (7)	8.11 (12)	10.51 (29)	3.96 (50)
3	25	07	1.00 (0)	1.06 (22)	3.61 (32)	4.06 (30)	3.13 (14)	0.372 (5)	69.72 (9)	23.58 (13)	149.1 (11)	1.75 (8)	125.3 (9)	4.31 (11)	6.95 (10)	6.68 (29)	2.90 (27)
3	25	09	1.06 (22)	1.11 (42)	3.22 (31)	4.11 (32)	3.13 (14)	0.409 (13)	70.10 (6)	22.72 (19)	149.3 (17)	1.63 (9)	119.2 (10)	4.85 (11)	6.94 (17)	7.78 (50)	3.10 (48)
3	25	13	1.25 (80)	1.00 (0)	3.69 (34)	4.44 (37)	3.67 (20)	0.394 (5)	68.50 (7)	23.90 (10)	149.1 (14)	1.56 (11)	118.1 (8)	4.56 (8)	7.42 (11)	8.14 (31)	3.22 (29)
3	25	14	1.06 (22)	1.00 (0)	3.89 (63)	3.72 (57)	3.10 (16)	0.385 (7)	67.03 (15)	23.54 (19)	155.0 (18)	1.68 (6)	121.4 (11)	4.85 (10)	7.36 (14)	8.56 (34)	3.30 (28)
3	26	03	1.14 (47)	1.21 (35)	3.14 (39)	4.64 (25)			70.46 (12)	23.50 (10)	148.9 (11)						
3	26	04	1.77 (84)	1.08 (26)	3.15 (43)	4.77 (24)			71.17 (8)	21.13 (13)	127.5 (12)						
3	26	05	1.36 (99)	1.00 (0)	3.45 (49)	4.27 (21)			67.66 (10)	22.55 (15)	136.3 (10)						
3	26	06	1.00 (0)	1.13 (46)	3.07 (44)	4.53 (30)			68.75 (9)	22.10 (20)	135.7 (20)						
3	26	07	1.23 (49)	1.15 (33)	3.08 (45)	4.00 (32)			65.79 (11)	22.79 (17)	127.2 (15)						
3	26	08	1.21 (66)	1.00 (0)	3.00 (39)	4.07 (28)			69.48 (10)	22.43 (18)	128.9 (19)						
3	26	09	1.00 (0)	1.12 (30)	3.12 (47)	5.29 (24)			76.32 (8)	20.97 (24)	122.1 (25)						
3	26	10	1.21 (48)	1.00 (0)	3.29 (48)	4.29 (32)			68.39 (10)	21.80 (17)	132.1 (14)						
3	27	01	2.13 (66)	1.07 (24)	2.80 (36)	3.93 (37)	3.34 (16)	0.390 (5)	66.58 (12)	21.93 (19)	131.0 (20)	1.44 (9)	114.9 (19)	4.24 (12)	7.05 (12)	6.85 (36)	2.65 (38)
3	27	02	2.19 (75)	1.00 (0)	3.31 (36)	4.31 (28)	3.42 (13)	0.381 (5)	70.53 (14)	20.36 (14)	128.1 (12)	1.69 (7)	114.8 (10)	4.08 (8)	6.07 (10)	4.73 (25)	1.77 (24)
3	27	03	2.83 (82)	1.28 (52)	2.56 (36)	4.44 (42)	3.49 (11)	0.402 (7)	70.75 (7)	20.44 (18)	126.6 (15)	1.62 (11)	93.67 (24)	4.30 (9)	6.79 (9)	6.30 (25)	2.52 (25)
3	27	05	1.71 (70)	1.29 (36)	3.29 (50)	5.14 (32)	3.40 (12)	0.391 (7)	63.64 (10)	20.88 (17)	128.8 (18)	1.63 (9)	117.3 (5)	4.15 (9)	6.36 (12)	5.39 (33)	2.09 (32)

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
3	27	07	2.40 (96)	1.00 (0)	3.13 (45)	3.81 (41)	3.90 (15)	0.399 (6)	67.78 (12)	20.44 (21)	117.9 (25)	1.58 (8)	110.4 (11)	4.23 (8)	6.31 (8)	5.29 (22)	2.12 (22)
3	27	09	2.00 (81)	1.12 (30)	3.12 (47)	4.29 (24)	3.64 (13)	0.388 (6)	65.29 (12)	24.37 (13)	142.0 (16)	1.51 (9)	110.9 (13)	4.10 (10)	6.62 (15)	5.87 (42)	2.32 (46)
3	27	10	1.94 (95)	1.31 (54)	3.19 (49)	4.38 (20)	3.69 (11)	0.368 (4)	67.22 (12)	20.86 (17)	127.2 (14)	1.64 (10)	112.5 (17)	4.13 (11)	6.41 (10)	5.39 (29)	1.98 (29)
3	27	11	2.00 (77)	1.06 (22)	[illegible].67 (44)	5.33 (26)	3.20 (13)	0.387 (5)	69.10 (7)	21.31 (15)	130.4 (15)	1.60 (9)	108.6 (18)	4.24 (10)	6.75 (8)	6.15 (25)	2.34 (26)
3	27	12	1.60 (66)	1.13 (31)	3.53 (46)	3.60 (36)	3.46 (9)	0.396 (5)	62.98 (12)	20.47 (19)	126.3 (22)	1.69 (8)	109.6 (11)	4.32 (10)	6.95 (12)	6.73 (29)	2.65 (27)
4	20	01	1.75 (79)	1.25 (37)	2.63 (40)	2.75 (38)	3.67 (17)	0.402 (4)	69.34 (11)	19.50 (15)	100.4 (17)	1.60 (13)	87.29 (18)	4.08 (13)	6.58 (7)	5.60 (27)	2.24 (27)
4	20	05	1.86 (96)	1.79 (80)	3.14 (35)	3.50 (38)	2.84 (14)	0.419 (6)	70.54 (11)	19.00 (23)	127.5 (20)	1.70 (9)	95.90 (14)	4.33 (7)	6.56 (12)	5.93 (28)	2.44 (28)
4	20	06	2.15 (56)	2.15 (62)	3.92 (34)	3.85 (37)	3.05 (21)	0.382 (3)	68.88 (12)	19.75 (13)	116.8 (15)	1.68 (5)	99.84 (18)	4.09 (5)	6.48 (10)	5.33 (21)	2.03 (20)
4	20	07	1.93 (66)	1.43 (36)	2.50 (28)	3.71 (16)	3.14 (15)	0.414 (8)	75.80 (6)	19.07 (17)	118.2 (19)	1.66 (10)	97.49 (21)	4.23 (14)	6.73 (14)	6.19 (37)	2.58 (36)
4	20	08	1.60 (57)	1.53 (60)	3.00 (42)	3.47 (45)	3.15 (18)	0.405 (5)	70.63 (14)	19.90 (28)	114.7 (22)	1.71 (8)	96.16 (11)	4.27 (17)	6.93 (11)	6.70 (33)	2.83 (24)
4	20	09	1.93 (114)	2.43 (64)	3.50 (31)	2.93 (21)	3.02 (11)	0.396 (5)	68.36 (13)	21.27 (9)	122.5 (10)	1.66 (5)	88.75 (12)	4.25 (12)	7.04 (12)	6.79 (31)	2.88 (31)
4	20	10	2.64 (93)	2.14 (79)	3.36 (40)	3.29 (58)	3.24 (17)	0.401 (7)	67.67 (11)	21.70 (18)	123.5 (24)	1.64 (9)	91.98 (21)	4.40 (7)	6.62 (10)	6.13 (28)	2.46 (30)
4	20	11	1.93 (74)	2.00 (50)	4.00 (28)	4.20 (39)	3.14 (16)	0.381 (5)	65.50 (12)	21.67 (18)	121.3 (16)	1.62 (8)	105.5 (14)	3.86 (14)	6.67 (13)	5.51 (28)	2.24 (14)
4	20	15	2.85 (67)	2.00 (41)	3.62 (37)	4.54 (32)	3.08 (13)	0.405 (7)	69.92 (14)	18.82 (19)	118.2 (13)	1.62 (10)	97.54 (13)	4.35 (12)	7.27 (14)	7.50 (37)	3.03 (34)
4	21	01	2.87 (84)	1.80 (39)	3.20 (45)	4.47 (52)	0.02 (41)										
4	21	03	2.40 (53)	1.10 (29)	3.50 (49)	5.00 (40)	0.013 (43)										
4	21	04	3.00 (84)	1.44 (44)	3.13 (33)	4.19 (42)	0.023 (43)										

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	BW
4	21	05	1.43 (53)	1.50 (57)	3.64 (43)	4.29 (38)	0.023 (25)										
4	21	06	1.94 (102)	1.19 (34)	3.31 (33)	3.25 (50)	0.015 (38)										
4	21	07	2.73 (60)	1.82 (41)	4.09 (46)	3.36 (28)	0.017 (35)										
4	21	10	1.09 (28)	1.27 (37)	2.91 (39)	3.18 (34)	0.200 (0)										
4	21	11	1.69 (62)	1.73 (46)	2.93 (27)	4.53 (26)	0.017 (35)										
4	22	02	1.60 (88)	1.67 (59)	3.27 (36)	5.87 (40)	2.83 (15)	0.427 (5)	71.32 (8)	21.00 (14)	130.1 (14)			4.13 (11)	6.29 (8)	5.16 (28)	2.15 (24)
4	22	03	1.00 (0)	1.50 (52)	3.61 (49)	4.61 (21)	2.62 (16)	0.394 (6)	69.38 (10)	22.25 (15)	140.2 (9)			4.38 (14)	6.78 (13)	6.73 (32)	2.67 (34)
4	22	04	1.33 (51)	1.72 (62)	3.28 (45)	4.56 (32)	3.05 (13)	0.398 (6)	67.24 (8)	24.69 (11)	153.6 (11)			4.85 (9)	7.65 (8)	9.12 (22)	3.05 (21)
4	22	05	1.69 (80)	1.94 (58)	3.94 (34)	3.94 (35)	2.73 (13)	0.388 (8)	65.02 (12)	22.72 (16)	147.7 (15)			4.62 (10)	7.14 (15)	7.75 (42)	2.91 (40)
4	22	09	1.36 (62)	1.07 (25)	3.57 (51)	5.36 (25)	2.54 (21)	0.393 (5)	71.78 (12)	22.04 (17)	132.3 (16)			4.64 (11)	7.15 (15)	7.72 (40)	2.99 (38)
4	22	11	1.35 (45)	2.06 (65)	3.53 (40)	4.29 (26)	2.49 (24)	0.381 (7)	65.31 (10)	23.53 (16)	143.6 (13)			4.18 (13)	7.05 (11)	6.66 (30)	2.80 (28)
4	22	12	2.60 (86)	2.07 (50)	3.20 (41)	5.07 (37)	2.85 (23)	0.411 (6)	70.47 (10)	20.00 (20)	130.6 (16)			4.76 (11)	7.54 (11)	8.85 (35)	3.37 (33)
4	22	13	1.59 (74)	1.65 (117)	3.88 (39)	5.47 (29)	2.63 (10)	0.396 (11)	67.66 (11)	23.28 (13)	141.2 (11)			4.49 (10)	7.11 (11)	7.19 (22)	2.77 (17)
4	22	14	1.17 (44)	1.50 (57)	3.11 (36)	4.22 (40)	2.70 (19)	0.398 (6)	66.71 (11)	22.64 (18)	140.8 (16)			4.48 (20)	6.89 (14)	6.49 (38)	2.86 (30)
4	55	03	1.38 (79)	1.19 (46)	3.56 (34)	3.63 (33)	3.03 (20)	0.395 (9)	70.17 (12)	18.53 (21)	103.8 (23)	1.66 (8)	101.7 (14)	3.77 (21)	6.77 (17)	5.89 (43)	2.62 (38)
4	55	04	1.24 (61)	1.47 (73)	3.82 (43)	4.53 (31)	2.92 (12)	0.402 (5)	71.60 (14)	19.67 (19)	125.4 (17)	1.73 (8)	103.9 (12)	4.16 (12)	6.98 (10)	5.64 (20)	2.29 (28)
4	55	06	1.27 (47)	1.80 (52)	3.87 (44)	4.47 (32)	3.16 (11)	0.386 (6)	70.30 (8)	20.63 (12)	129.3 (15)	1.74 (8)	102.1 (8)	4.33 (12)	6.69 (6)	6.10 (20)	2.32 (21)

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
4	55	07	2.13 (73)	1.94 (48)	3.06 (33)	4.00 (35)	2.82 (16)	0.401 (5)	74.52 (7)	20.70 (10)	130.3 (12)	1.66 (9)	104.1 (9)	4.53 (8)	6.74 (11)	6.56 (29)	2.65 (27)
4	55	09	1.82 (69)	2.27 (66)	4.36 (21)	3.82 (35)	3.18 (14)	0.405 (15)	73.80 (12)	20.64 (16)	115.7 (19)	1.75 (12)	103.0 (50)	4.38 (14)	7.35 (10)	7.65 (31)	3.06 (31)
4	55	10	1.94 (74)	1.29 (45)	3.41 (40)	4.12 (26)	2.88 (17)	0.401 (6)	69.63 (9)	20.65 (21)	128.4 (28)	1.69 (8)	109.2 (10)	4.15 (12)	6.48 (13)	5.63 (35)	2.36 (27)
4	55	13	1.71 (94)	1.88 (42)	3.88 (44)	3.76 (47)	2.95 (15)	0.409 (7)	68.62 (12)	20.04 (12)	119.9 (15)	1.71 (8)	105.4 (10)	4.30 (11)	6.47 (13)	5.78 (34)	2.40 (33)
4	55	14	1.59 (63)	1.82 (73)	3.29 (23)	3.71 (41)	3.22 (17)	0.403 (7)	70.71 (8)	21.94 (16)	146.0 (15)	1.85 (8)	95.68 (15)	5.10 (12)	7.74 (13)	10.12 (40)	4.00 (38)
4	55	15	1.29 (94)	1.00 (0)	3.35 (35)	3.29 (44)	2.81 (17)	0.397 (6)	72.57 (7)	20.85 (12)	127.0 (12)	1.77 (7)	102.3 (6)	4.63 (10)	6.95 (13)	7.22 (32)	2.90 (32)
5	19	03	1.22 (45)	1.67 (54)	3.56 (42)	4.44 (33)	3.74 (15)	0.380 (6)	69.63 (11)	21.35 (12)	131.8 (13)	1.66 (8)	117.2 (16)	4.55 (13)	7.18 (8)	7.58 (28)	2.88 (28)
5	19	04	1.13 (31)	1.47 (51)	3.93 (37)	4.40 (28)	3.34 (16)	0.401 (6)	70.80 (10)	22.70 (13)	137.4 (15)	1.69 (6)	108.4 (11)	4.43 (14)	7.00 (18)	7.24 (44)	2.91 (44)
5	19	06	1.27 (52)	1.39 (50)	4.44 (40)	5.11 (31)	3.10 (19)	0.400 (6)	62.78 (11)	24.64 (14)	152.9 (13)	1.72 (8)	108.4 (19)	4.75 (6)	7.81 (11)	8.85 (25)	3.42 (22)
5	19	07	1.17 (45)	1.24 (61)	4.00 (34)	4.53 (37)	3.18 (13)	0.385 (7)	67.73 (10)	21.71 (12)	140.0 (11)	1.71 (10)	112.0 (15)	4.95 (9)	7.25 (9)	8.36 (26)	3.17 (30)
5	19	08	1.33 (54)	1.33 (46)	2.93 (27)	4.80 (31)	3.34 (12)	0.384 (10)	69.48 (9)	21.10 (22)	133.2 (23)	1.58 (11)	102.2 (8)	4.36 (9)	6.73 (16)	6.46 (30)	2.65 (32)
5	19	09	1.12 (43)	1.18 (33)	4.00 (39)	5.35 (39)	3.27 (11)	0.393 (7)	69.21 (13)	21.34 (18)	138.1 (14)	1.68 (16)	115.2 (12)	4.60 (9)	7.30 (15)	7.99 (38)	3.05 (39)
5	19	12	1.17 (64)	1.50 (57)	3.44 (38)	3.87 (47)	3.08 (16)	0.382 (4)	69.46 (9)	20.51 (14)	129.3 (16)	1.60 (8)	98.95 (6)	4.12 (12)	7.08 (10)	6.50 (38)	2.50 (32)
5	19	14	1.39 (50)	1.17 (44)	3.61 (34)	4.17 (47)	3.31 (9)	0.392 (8)	68.10 (12)	21.32 (18)	127.2 (18)	1.67 (9)	105.5 (7)	4.47 (17)	7.17 (15)	7.62 (38)	3.21 (31)
5	19	15	1.47 (77)	1.20 (35)	3.60 (49)	4.27 (38)	3.00 (14)	0.394 (6)	66.98 (11)	20.47 (19)	127.8 (15)	1.66 (7)	102.5 (11)	4.27 (8)	6.69 (9)	6.86 (23)	2.39 (25)
5	62	01	1.00 (0)	1.06 (24)	2.75 (41)	4.13 (33)			71.66 (12)	22.06 (14)	134.7 (12)						
5	62	04	1.24 (54)	1.65 (64)	3.00 (35)	3.88 (41)			68.37 (10)	24.78 (16)	155.5 (13)						

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	DW
5	62	05	1.00 (0)	1.07 (24)	2.73 (40)	4.20 (29)			69.60 (9)	24.73 (12)	144.5 (9)						
5	62	06	1.00 (0)	1.44 (39)	2.67 (36)	4.39 (32)			72.64 (8)	23.26 (12)	151.4 (8)						
5	62	07	1.00 (0)	1.11 (29)	2.61 (46)	4.00 (39)			74.32 (9)	23.99 (18)	148.2 (14)						
5	62	08	1.00 (0)	1.22 (35)	2.56 (33)	3.89 (28)			69.03 (10)	25.03 (16)	142.8 (13)						
5	62	09	1.00 (0)	1.67 (50)	3.22 (38)	4.22 (43)			65.11 (11)	24.89 (12)	150.2 (12)						
5	62	14	1.12 (43)	1.39 (52)	2.41 (36)	4.06 (36)			72.22 (10)	22.97 (12)	144.8 (13)						
5	62	15	1.06 (22)	1.17 (44)	3.00 (52)	3.72 (51)			67.38 (11)	25.73 (17)	149.4 (16)						
5	64	02	1.69 (94)	2.06 (98)	3.23 (43)	4.47 (36)	3.00 (13)	0.378 (6)	66.01 (13)	23.00 (16)	143.5 (13)	1.69 (11)	114.7 (7)	4.49 (7)	6.73 (9)	6.42 (22)	2.42 (21)
5	64	05	1.29 (55)	1.31 (60)	3.30 (37)	4.29 (33)	3.22 (15)	0.396 (4)	73.66 (11)	20.09 (18)	130.6 (16)	1.59 (9)	119.5 (8)	4.26 (9)	6.92 (11)	6.56 (30)	2.59 (29)
5	64	07	2.00 (73)	1.76 (76)	3.47 (40)	3.82 (38)	3.46 (11)	0.382 (7)	66.06 (9)	23.91 (15)	147.4 (15)	1.74 (12)	122.7 (11)	4.49 (14)	7.29 (11)	7.60 (30)	2.84 (29)
5	64	08	1.78 (85)	1.28 (45)	3.28 (43)	4.17 (47)	3.25 (18)	0.379 (5)	66.08 (10)	20.50 (16)	128.2 (17)	1.62 (10)	117.1 (7)	4.36 (12)	7.70 (11)	8.46 (31)	3.16 (32)
5	64	11	1.00 (0)	1.56 (52)	3.38 (51)	3.88 (35)	3.08 (19)	0.391 (5)	68.39 (11)	21.59 (15)	128.6 (18)	1.77 (8)	107.4 (11)	3.89 (11)	6.45 (11)	5.15 (34)	2.88 (32)
5	64	12	1.75 (92)	1.44 (44)	3.13 (35)	3.81 (48)	3.43 (19)	0.388 (5)	71.19 (9)	20.28 (13)	124.3 (14)	1.65 (9)	117.6 (9)	4.18 (11)	6.82 (10)	6.21 (27)	2.41 (28)
5	64	13	1.94 (82)	1.59 (45)	3.82 (43)	3.59 (49)	3.01 (16)	0.405 (5)	67.59 (11)	21.56 (15)	137.1 (18)	1.57 (13)	111.3 (16)	4.07 (16)	6.56 (17)	5.81 (43)	2.53 (35)
5	64	14	1.06 (22)	1.61 (57)	3.28 (47)	4.89 (29)	3.48 (19)	0.374 (6)	73.60 (7)	20.61 (18)	126.9 (16)	1.64 (7)	123.0 (8)	4.43 (9)	7.38 (8)	7.74 (24)	2.86 (21)
5	64	15	1.41 (71)	1.76 (68)	2.94 (59)	3.53 (46)	2.99 (17)	0.389 (5)	66.38 (9)	21.41 (15)	138.8 (16)	1.66 (12)	117.0 (8)	4.95 [illegible]	7.19 (9)	7.51 (25)	2.89 (28)
5	65	01	1.22 (35)	1.06 (22)	2.67 (43)	4.78 (28)	3.21 (17)	0.374 (4)	76.85 (7)	21.93 (18)	135.4 (17)	1.60 (11)		4.89 (10)	7.60 (10)	9.17 (31)	3.40 (28)

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MOIS	HT	DIA	VOL	BW
5	65	03	1.00 (0)	1.21 (35)	3.36 (50)	4.71 (32)	2.58 (12)	0.366 (7)	71.57 (11)	23.38 (13)	132.2 (11)	1.66 (4)		4.33 (14)	6.85 (12)	6.40 (31)	2.40 (32)
5	65	05	1.28 (52)	1.17 (33)	3.44 (53)	4.17 (38)	2.56 (17)	0.371 (6)	67.38 (9)	21.13 (18)	136.4 (13)	1.71 (8)		4.40 (12)	6.89 (15)	7.85 (40)	2.60 (45)
5	65	07	1.13 (46)	1.07 (24)	3.47 (41)	4.47 (43)	2.75 (21)	0.376 (6)	70.33 (9)	24.15 (20)	151.0 (16)	1.74 (9)		4.02 (11)	7.21 (8)	8.85 (28)	2.97 (28)
5	65	09	1.00 (0)	1.71 (65)	3.41 (56)	4.12 (37)	2.86 (18)	0.384 (10)	73.43 (10)	23.63 (18)	141.0 (14)	1.62 (9)		4.56 (10)	7.02 (9)	7.17 (25)	2.74 (24)
5	65	11	1.06 (23)	1.06 (23)	3.00 (62)	4.82 (31)	2.71 (21)	0.361 (5)	70.26 (11)	21.45 (14)	141.0 (16)	1.72 (12)		4.55 (10)	7.06 (10)	7.27 (29)	2.62 (28)
5	65	12	1.08 (26)	1.29 (40)	3.14 (39)	4.29 (21)	3.15 (18)	0.376 (6)	71.02 (9)	22.09 (18)	136.3 (22)	1.65 (8)		4.60 (18)	7.30 (12)	8.88 (38)	3.22 (27)
5	65	13	1.00 (0)	1.00 (0)	3.69 (54)	5.63 (30)	2.73 (17)	0.371 (5)	70.67 (9)	21.14 (14)	137.2 (16)	1.73 (12)		4.32 (14)	6.52 (11)	5.88 (31)	2.29 (24)
5	65	14	1.50 (77)	1.13 (44)	3.00 (49)	5.00 (15)	2.73 (18)	0.390 (6)	72.23 (11)	20.03 (17)	137.0 (15)	1.72 (9)		4.90 (14)	7.88 (34)	8.28 (44)	3.35 (40)
6	37	02	2.85 ([illegible])	1.21 (40)	2.71 (49)	3.93 (35)											
6	37	03	2.64 (82)	1.36 (47)	2.70 (25)	4.43 (32)											
6	37	04	1.41 (87)	1.24 (35)	3.18 (32)	4.12 (39)											
6	37	05	2.36 (103)	1.07 (25)	3.50 (47)	5.64 (28)											
6	37	06	1.42 (47)	1.25 (50)	2.83 (54)	4.17 (39)											
6	37	07	2.29 (83)	1.33 (37)	2.83 (33)	3.67 (47)											
6	37	11	2.31 (111)	1.38 (47)	2.92 (80)	4.46 (31)											
6	37	13	1.40 (60)	1.50 (47)	3.30 (32)	5.10 (23)											
6	37	14	2.94 (90)	1.31 (60)	3.00 (54)	3.94 (36)											

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	ST	SPOR	BA	BC	BL	TL	MDIS	HT	DIA	VOL	BM
6	66	01	2.13 (90)	1.27 (47)	3.00 (28)	5.07 (26)											
6	66	02	3.07 (49)	1.50 (63)	3.29 (33)	4.79 (28)											
6	66	06	2.06 (113)	1.13 (30)	3.75 (46)	4.44 (27)											
6	66	09	1.60 (62)	1.00 (0)	3.47 (46)	4.73 (27)											
6	66	11	1.29 (48)	1.21 (48)	2.86 (49)	3.86 (38)											
6	66	12	2.39 (90)	1.28 (45)	3.06 (57)	4.33 (27)											
6	66	13	1.54 (57)	1.38 (55)	2.02 (47)	5.38 (22)											
6	66	14	2.18 (124)	1.00 (0)	2.82 (44)	4.71 (33)											
6	66	15	2.75 (97)	1.25 (46)	2.56 (32)	4.56 (32)											
6	29	01	1.38 (63)	1.05 (21)	3.90 (34)	4.62 (27)											
6	29	05	1.08 (24)	1.00 (0)	3.56 (37)	4.38 (30)											
6	29	06	1.14 (32)	1.29 (36)	3.29 (53)	5.00 (24)											
6	29	07	1.41 (62)	1.12 (30)	3.29 (32)	4.71 (27)											
6	29	08	1.11 (29)	1.11 (29)	3.20 (29)	4.85 (30)											
6	29	10	2.08 (83)	1.17 (33)	3.42 (44)	4.83 (38)											
6	29	12	1.56 (59)	1.22 (35)	3.33 (25)	3.67 (40)											
6	29	14	1.31 (67)	1.31 (36)	3.50 (36)	3.38 (42)											

Table A3 - continued

ZONE	PROV	FAM	RS	GS	CS	SS	BT	SPGR	BA	BD	BL	TL	MDIS	MT	DLA	WBL	DW
6	29	15	1.10 (62)	1.12 (43)	3.71 (37)	4.65 (32)											
6	30	02	1.31 (48)	1.08 (26)	3.15 (53)	5.23 (26)											
6	30	03	3.06 (87)	1.06 (24)	3.38 ([illegible])	4.81 (34)											
6	30	04	1.73 (67)	1.07 (24)	4.00 (33)	4.47 (36)											
6	30	05	1.15 (46)	1.13 (46)	2.87 (49)	4.40 (30)											
6	30	06	2.00 (94)	1.07 (25)	3.07 (27)	3.88 (32)											
6	30	08	1.29 (56)	1.21 (35)	2.86 (41)	4.07 (37)											
6	30	10	1.56 (62)	1.06 (24)	3.00 (34)	4.94 (32)											
6	30	11	1.89 (72)	1.11 (29)	3.20 (30)	4.17 (29)											
6	30	12	2.00 (61)	1.12 (30)	3.06 (39)	4.82 (38)											

Table A3 - continued.

Appendix B

SOURCE	DF	Expected Mean Squares or Cross Products a/
PROV (P)	DF_6	$COV_e + k_9COV_{rf} + k_{10}COV_f + k_{11}COV_{rp} + k_{12}COV_p$
FAM/P (F/P)	DF_5	$COV_e + k_7COV_{rf} + k_8COV_f$
REP (R)	DF_4	$COV_e + k_4COV_{rf} + k_5COV_{rp} + k_6COV_r$
RxP	DF_3	$COV_e + k_2COV_{rf} + k_3COV_{rp}$
RxF/P	DF_2	$COV_e + k_1COV_{rf}$
Error	DF_1	COV_e

a/ COV is replaced by σ^2 for the expected mean squares

k_1 - k_{12} coefficients associated with the expected means squares and cross products terms in the completely random model

DF_1-DF_6 degrees of freedom associated with the source of variation

Table B1 - Expected means squares and cross products for the analysis on on individual tree data for a completely random model.

SOURCE	Mean Squares or Cross Products					
	RS	RS w. GS	GS	CS	SS	CS w. SS
PROV (P)	2.605	0.546	1.989	15.22	18.86	3.321
FAM/P (F/P)	0.326	0.062	0.225	1.84	3.68	0.560
REP (R)	8.765	4.228	2.332	1388.89	39.66	-234.681
RxP	0.352	0.032	0.394	9.44	7.65	0.995
RxF/P	0.190	0.004	0.149	1.56	2.51	0.490
Error	0.154	0.005	0.127	0.87	2.00	0.324

k values = k_1=5.32 k_2=5.45 k_3=47.26 k_4=5.52 k_5=48.25 k_6=1139.38 k_7=5.46
k_8=15.94 k_9=5.50 k_{10}=16.10 k_{11}=47.97 k_{12}=142.53

DF's = DF_1=2786 DF_2=374 DF_3=46 DF_4=2 DF_5=190 DF_6=23

TABLE B2 - Mean squares and cross products for stalactiform blister rust (RS), stalactiform blister rust with western gall rust, western gall rust (GS), crown score (CS), stem score (SS) and crown score with stem score.

SOURCE	Mean Squares or Cross Products					
	BA	BD	BA w. BD	BL	BA w. BL	BD w. BL
PROV (P)	225.27	289.19	-29.45	21968.6	53.92	2195.41
FAM/P (F/P)	150.59	27.99	-29.38	1114.4	-136.77	138.13
REP (R)	392.68	517.24	-85.92	5489.2	-2693.21	-213.15
RxP	146.16	38.42	-26.46	2029.8	-64.53	180.66
RxF/P	58.59	14.47	- 9.64	548.1	-40.83	73.28
Error	46.52	12.12	- 8.25	436.1	-33.81	61.60

k values = k_1=5.39 k_2=5.50 k_3=48.29 k_4=5.57 k_5=49.14 k_6=921.57 k_7=5.53

k_8=16.24 k_9=5.56 k_{10}=16.36 k_{11}=48.95 k_{12}=145.58

DF's = DF_1=2259 DF_2=300 DF_3=36 DF_4=2 DF_5=151 DF_6=18

TABLE B3 - Mean squares and cross products for branch angle (BA), branch diameter (BD), branch angle with branch diameter, branch length (BL), branch angle with branch length and branch diameter with branch length.

SOURCE	Mean Squares or Cross Products		
	CS w. BA	CS w. BD	CS w. BL
PROV (P)	-5.651	4.729	100.642
FAM/P (F/P)	-8.512	2.904	11.927
REP (R)	-189.578	789.325	-209.611
RxP	-8.042	10.879	96.433
RxF/P	-2.033	1.213	5.412
Error	-1.741	0.812	3.583

k values = $k_1=5.39$ $k_2=5.50$ $k_3=48.29$ $k_4=5.57$ $k_5=49.14$ $k_6=921.57$ $k_7=5.53$

$k_8=16.24$ $k_9=5.56$ $k_{10}=16.36$ $k_{11}=48.95$ $k_{12}=145.58$

DF's = $DF_1=2259$ $DF_2=300$ $DF_3=36$ $DF_4=2$ $DF_5=151$ $DF_6=18$

TABLE B4 - Mean cross products for crown score with branch angle, crown score with branch diameter and crown score with branch length.

SOURCE	Mean Squares or Cross Products			
	SG	SG w. BA	SG w. BD	SG w. SS
PROV (P)	0.01000	-0.1478	-1.0761	-0.182
FAM/P (F/P)	0.00200	0.0393	-0.0432	-0.006
REP (R)	0.00573	-3.1598	0.2786	-0.054
RxP	0.00163	-0.0119	-0.0769	-0.020
RxF/P	0.00073	-0.0065	-0.0140	-0.005
Error	0.00066	-0.0029	-7.9179	0.0005

k values = k_1=5.36 k_2=5.48 k_3=48.40 k_4=5.56 k_5=49.17 k_6=680.98 k_7=5.52

k_8=16.21 k_9=5.55 k_{10}=16.33 k_{11}=49.07 k_{12}=145.96

DF's = DF_1=1667 DF_2=223 DF_3=26 DF_4=2 DF_5=112 DF_6=13

TABLE B5 - Mean squares and cross products for specific gravity (SG), specific gravity with branch angle, specific gravity with branch diameter and specific gravity with stem score,

SOURCE	Mean Squares or Cross Products			
	HT	DIA	VOL	HT w. DIA
PROV (P)	18.109	29.907	483.62	22.758
FAM/P (F/P)	0.560	1.514	16.04	0.527
REP (R)	30.692	39.216	756.18	34.693
RxP	0.897	2.384	33.78	1.137
RxF/P	0.357	1.002	11.87	0.392
Error	0.226	0.706	6.98	0.224

k values = k_1=5.52 k_2=5.66 k_3=50.19 k_4=5.68 k_5=50.37 k_6=703.80 k_7=5.63
k_8=11.16 k_9=5.68 k_{10}=11.26 k_{11}=50.37 k_{12}=100.57

DF's = DF_1=1156 DF_2=112 DF_3=13 DF_4=1 DF_5=112 DF_6=13

TABLE B6 - Mean squares and cross products for height (HT), diameter (DIA), volume (VOL) and height with diameter.

SOURCE	Mean Squares or Cross Products			
	SG w. VOL	SG w. HT	SG w. DIA	DW
PROV (P)	-1.687	-0.3270	-0.4265	58.021
FAM/P (F/P)	-0.227	0.0003	-0.0095	2.291
REP (R)	-1.104	-0.2260	-0.2540	104.329
RxP	-0.081	-0.0150	-0.0230	3.963
RxF/P	-0.003	-0.0001	-0.0018	1.571
Error	-0.0066	-0.0006	-0.0025	0.985

k values = $k_1=5.43$ $k_2=5.60$ $k_3=49.52$ $k_4=5.62$ $k_5=49.77$ $k_6=694.83$ $k_7=5.57$
$k_8=11.02$ $k_9=5.62$ $k_{10}=11.12$ $k_{11}=49.75$ $k_{12}=99.28$

DF's = $DF_1=1138$ $DF_2=112$ $DF_3=13$ $DF_4=1$ $DF_5=112$ $DF_6=13$

TABLE B7 - Mean cross products and squares for specific gravity with volume, specific gravity with height, specific gravity with diameter and dry weight (DW).

SOURCE	Mean Squares or Cross Products	
	HT w. VOL	DIA w. VOL
PROV (P)	92.41	119.39
FAM/P (F/P)	2.22	4.69
REP (R)	152.35	172.20
RxP	4.76	8.56
RxF/P	1.60	3.27
Error	0.91	2.09

k values = k_1=5.52 k_2=5.66 k_3=50.19 k_4=5.68 k_5=50.37 k_6=703.80 k_7=5.63

k_8=11.16 k_9=5.68 k_{10}=11.26 k_{11}=50.37 k_{12}=100.57

DF's = DF_1=1156 DF_2=112 DF_3=13 DF_4=1 DF_5=112 DF_6=13

TABLE B8 - Mean cross products for height with volume and diameter with volume.

SOURCE	Mean Squares or Cross Products		
	BA w. VOL	BA w. HT	BA w. DIA
PROV (P)	-19.685	0.567	-7.781
FAM/P (F/P)	- 1.356	-0.019	-0.410
REP (R)	774.596	158.628	178.127
RxP	10.793	1.515	3.045
RxF/P	0.480	0.139	-0.078
Error	1.372	0.343	0.274

k values = k_1=5.43 k_2=5.60 k_3=49.52 k_4=5.62 k_5=49.77 k_6=694.83 k_7=5.57

k_8=11.02 k_9=5.62 k_{10}=11.12 k_{11}=49.75 k_{12}=99.28

DF's = DF_1=1138 DF_2=112 DF_3=13 DF_4=1 DF_5=112 DF_6=13

TABLE B9 - Mean cross products for branch angle with volume, branch angle with height and branch angle with diameter.

SOURCE	Mean Squares or Cross Products			
	BL W. HT	BL w. DIA	BD w. HT	BD w. DIA
PROV (P)	556.577	715.180	40.695	53.983
FAM/P (F/P)	8.246	13.847	0.233	1.992
REP (R)	-51.241	-57.539	-144.672	-162.456
RxP	27.582	48.418	1.099	2.928
RxF/P	5.596	11.996	0.547	1.648
Error	3.905	7.007	0.419	1.131

k values = k_1=5.43 k_2=5.60 k_3=49.52 k_4=5.62 k_5=49.77 k_6=694.83 k_7=5.57

k_8=11.02 k_9=5.62 k_{10}=11.12 k_{11}=49.75 k_{12}=99.28

DF's = DF_1=1138 DF_2=112 DF_3=13 DF_4=1 DF_5=112 DF_6=13

TABLE B10 - Mean cross products for branch length with height, branch length with diameter, branch diameter with height and branch diameter with diameter.

SOURCE	Mean Squares or Cross Products		
	SS w. VOL	BT w. HT	BT w. DIA
PROV (P)	29.65	2.624	4.171
FAM/P (F/P)	1.29	0.038	0.308
REP (R)	37.81	-3.574	-4.013
RxP	1.36	-0.062	0.266
RxF/P	0.56	0.065	0.142
Error	-0.0004	0.022	0.084

k values = k_1=5.43 k_2=5.60 k_3=49.52 k_4=5.62 k_5=49.77 k_6=694.83 k_7=5.57

k_8=11.02 k_9=5.62 k_{10}=11.12 k_{11}=49.75 k_{12}=99.28

DF's = DF_1=1138 DF_2=112 DF_3=13 DF_4=1 DF_5=112 DF_6=13

TABLE B11.- Mean cross products for stem score with volume, bark thickness with height and bark thickness with diameter.

SOURCE	Mean Squares or Cross Products		
	CW	CW w. SG	TL
PROV (P)	1.096	0.019	0.305
FAM/P (F/P)	0.327	0.008	0.056
REP (R)	2.765	0.059	1.926
RxP	0.687	0.010	0.107
RxF/P	0.245	0.002	0.027
Error	0.176	0.002	0.020

k values = $k_1=5.22$ $k_2=5.37$ $k_3=47.17$ $k_4=5.47$ $k_5=48.21$ $k_6=475.21$ $k_7=5.43$

$k_8=15.84$ $k_9=5.47$ $k_{10}=15.98$ $k_{11}=48.13$ $k_{12}=142.62$

DF's = $DF_1=1158$ $DF_2=159$ $DF_3=18$ $DF_4=2$ $DF_5=80$ $DF_6=9$

TABLE B12 - Mean squares and cross products for compression wood (binomial data) (CW), compression wood with specific gravity and tracheid length.

SOURCE	Mean Squares or Cross Products	
	MC	MC w. SG
PROV (P)	6508.61	-7.277
FAM/P (F/P)	417.35	-0.278
REP (R)	3079.57	0.315
RxP	215.90	-0.358
RxF/P	210.29	-0.167
Error	216.28	-0.202

k values = k_1=5.45 k_2=5.60 k_3=49.55 k_4=5.62 k_5=49.76 k_6=496.49 k_7=5.57
k_8=11.02 k_9=5.61 k_{10}=11.13 k_{11}=49.73 k_{12}=99.29

DF's = DF_1=813 DF_2=80 DF_3=9 DF_4=1 DF_5=81 DF_6=9

TABLE B13 - Mean squares and cross products for moisture content (MC) and moisture content with specific gravity.

SOURCE	Mean Squares or Cross Products BT
PROV (P)	7.342
FAM/P (F/P)	0.625
REP (R)	4.236
RxP	1.364
RxF/P	0.313
Error	0.225

k values = k_1=5.33 k_2=5.47 k_3=48.20 k_4=5.54 k_5=48.95 k_6=678.03 k_7=5.50

k_8=16.14 k_9=5.53 k_{10}=16.27 k_{11}=48.84 k_{12}=145.31

DF's = DF_1=1658 DF_2=223 DF_3=26 DF_4=2 DF_5=112 DF_6=13

TABLE B14 - Mean squares for bark thickness.

Appendix C

TABLE C1 - Standard error formulas for heritability and repeatability estimates for family, provenance and zone effects based-on plot means analysis.

$$S.e.\ (\sigma^2{}_f) = \sqrt{\frac{2}{K^2{}_4}\left(\frac{MS^2{}_f}{DF_f+2} + \frac{MS^2{}_{plot}}{DF_{plot}+2} + \frac{MS^2{}_w}{DF_w+2}\right)}$$

$$S.e.\ (h^2{}_i) = \frac{S.e.\ (\sigma^2{}_f)4}{\sigma^2{}_T}$$

$$S.e.\ (h^2{}_f) = \frac{S.e.\ (\sigma^2{}_f)}{\sigma^2_{\overline{HSF}}}$$

$$S.e.\ (\sigma^2{}_p) = \sqrt{\frac{2}{K^2{}_7}\left(\frac{MS^2{}_{P/Z}}{DF_{P/Z}+2} + \frac{MS^2{}_{RxP/Z}}{DF_{RxP/Z}+2} + \frac{MS^2{}_f}{DF_f+2} + \frac{MS^2{}_{plot}}{DF_{plot}+2} + \frac{MS^2{}_w}{DF_w+2}\right)}$$

$$S.e.\ (h^2{}_p) = \frac{S.e.\ (\sigma^2{}_p)}{\sigma^2_{\overline{PROV}}}$$

$$S.e.\ (\sigma^2{}_z) = \sqrt{\frac{2}{K^2{}_{12}}\left(\frac{MS^2{}_z}{DF_z+2} + \frac{MS^2{}_{RxZ}}{DF_{RxZ}+2} + \frac{MS^2{}_{P/Z}}{DF_{P/Z}+2} + \frac{MS^2{}_{RxP/Z}}{DF_{RxP/Z}+2} + \frac{MS^2{}_f}{DF_f+2} + \frac{MS^2{}_{plot}}{DF_{plot}+2} + \frac{MS^2{}_w}{DF_w+2}\right)}$$

$$S.e.\ (h^2{}_z) = \frac{S.e.\ (\sigma^2{}_z)}{\sigma^2_{\overline{ZONE}}}$$

- $\sigma^2_{\overline{ZONE}}$, $\sigma^2_{\overline{PROV}}$, $\sigma^2_{\overline{HSF}}$, $\sigma^2{}_T$ - as in page 41

Table C2 - Standard error calculations for heritability estimates for stalactiform blister rust and western gall rust using the Dempster and Lerner (1950) approach (from page 220).

Stalactiform Blister Rust

$$\sigma_t = \frac{[1 + (n-1)t^{*}]\,(1-t)\,\sqrt{2}}{\sqrt{n(n-1)\;(N-2)}}$$

$$\sigma_t = \frac{[1 + (14.15)0.132]\,(1-0.132)\sqrt{2}}{\sqrt{15.45(14.45)(3422-2)}}$$

$$\sigma_t = 0.0041$$

$$\text{S.e. } (h^2) = \frac{\sigma_t}{r} = \frac{.0041}{.25} = 0.016$$

Western Gall Rust

$$\sigma_t = \frac{[1 + (n-1)t^{**}]\,(1-t)\,\sqrt{2}}{\sqrt{n(n-1)\;(N-2)}}$$

$$\sigma_t = \frac{[1 + (14.45)0.119]\,(1-0.119)\,\sqrt{2}}{\sqrt{15.45(14.15)\;(3422-2)}}$$

$$\sigma_t = 0.0039$$

$$\text{S.e. } (h^2) = \frac{\sigma_t}{r} = \frac{.0039}{.25} = 0.015$$

$t^{*} = rh^2 = 0.25(0.529)$, where $r = 0.25$

$t^{**} = rh^2 = 0.25(0.477)$

Appendix D

Table D1 - Outline of phenotypic variance-covariance matrix (P) for volume (VOL) and specific gravity (SG).

	PROV mean for VOL	HSF mean for VOL	IND-Tree VOL	PROV mean for SG	HSF mean for SG	IND-Tree SG
PROV mean for VOL	$\sigma^2_{\overline{PROV}(VOL)}$	0	0	$COV_{\overline{PROV}(SG,VOL)}$	0	0
HSF mean for VOL	0	$\sigma^2_{\overline{HSF}(VOL)}$	0	0	$COV_{\overline{HSF}(SG,VOL)}$	0
IND-Tree VOL	0	0	$\sigma^2_{T(VOL)}$	0	0	$COV_{T(SG,VOL)}$
PROV mean for SG	$COV_{\overline{PROV}(VOL,SG)}$	0	0	$\sigma^2_{\overline{PROV}(SG)}$	0	0
HSF mean for SG	0	$COV_{\overline{HSF}(VOL,SG)}$	0	0	$\sigma^2_{\overline{HSF}(SG)}$	0
IND-Tree SG	0	0	$COV_{T(VOL,SG)}$	0	0	$\sigma^2_{T(SG)}$

where; $\sigma^2_{\overline{PROV}}$ = phenotypic variance among provenance means

$\sigma^2_{\overline{HSF}}$ = phenotypic variance among half-sib family means

σ^2_{T} = phenotypic variance among individuals

$COV_{\overline{PROV}}$ = phenotypic covariance among provenance means

$COV_{\overline{HSF}}$ = phenotypic covariance among half-sib family means

COV_{T} = phenotypic covariance among individuals

Table D2 - Outline[illegible] genetic variance-covariance matrix (C) for vo[illegible] (VOL) and specific gravity (SG) for derivation of a combined index including provenance, half-sib family and individual information.

Breeding Value / Phenotypic Value	VOL	SG
PROV mean for VOL	$\hat{\sigma}^2_{\text{PROV(VOL)}}$	$c\hat{o}v_{\text{PROV(VOL,SG)}}$
HSF mean for VOL	$\hat{\sigma}^2_{\text{HSF(VOL)}}$	$c\hat{o}v_{\text{HSF(VOL,SG)}}$
IND-Tree VOL	$\hat{\sigma}^2_{\text{A(VOL)}}$	$c\hat{o}v_{\text{A(VOL,SG)}}$
PROV mean for SG	$c\hat{o}v_{\text{PROV(SG,VOL)}}$	$\hat{\sigma}^2_{\text{PROV(SG)}}$
HSF mean for SG	$c\hat{o}v_{\text{HSF(SG,VOL)}}$	$\hat{\sigma}^2_{\text{HSF(SG)}}$
IND-Tree for SG	$c\hat{o}v_{\text{A(SG,VOL)}}$	$\hat{\sigma}^2_{\text{A(SG)}}$

where; $\hat{\sigma}^2_{\text{PROV}}$ = "genetic" covariance of an individual with its provenance mean = σ^2_P

$\hat{\sigma}^2_{\text{HSF}}$ = additive covariance of an individual with its half-sib family mean = σ^2_f

$\hat{\sigma}^2_A$ = additive covariance of an indivi[illegible]l with itself = $4\sigma^2_f$

$\hat{COV}_{\text{PROV}}$ = "genetic" covariance of an individual with its provenance mean = COV_P

$\hat{COV}_{\text{HSF}}$ = additive covariance of an individual with its half-sib family mean = COV_f

$\hat{COV}_A$ = additive covariance of an individual with itself = $4COV_f$

$$H = a_1(\text{VOL}) + a_2(\text{SG})$$

$$I = b_1(\text{VOL}_{\text{PROV}}) + b_2(\text{VOL}_{\text{HSF}}) + b_3(\text{VOL}_{\text{IND}}) + b_4(\text{SG}_{\text{PROV}}) + b_5(\text{SG}_{\text{HSF}}) + b_6(\text{SG}_{\text{IND}})$$

$\hat{\sigma}$

Appendix E

	TABLE No.					
	4,5,17,20	6,8	7	9,10,11	12	13,14,15,16
k_1	8.81	8.97	9.0	8.91	8.97	9.0
k_2	8.86	8.97	9.0	8.92	8.96	9.0
k_3	35.32	25.01	18.0	33.77	22.10	18.0
k_4	2.97	2.99	2.0	2.99	2.99	2.0
k_5	2.98	2.99	2.0	2.99	2.99	2.0
k_6	8.84	8.98	9.0	8.91	8.97	9.0
k_7	26.48	26.93	18.0	27.73	26.92	18.0
k_8	2.98	3.0	2.0	2.99	2.99	2.0
k_9	8.87	8.98	9.0	8.92	8.96	9.0
k_{10}	26.56	26.94	18.0	26.76	26.87	18.0
k_{11}	35.35	25.01	18.0	33.77	22.11	25.07
k_{12}	108.99	75.02	36.0	101.31	66.31	50.14
k_{13}	8.87	8.98	9.0	8.92	8.97	9.0
k_{14}	35.77	25.64	18.0	34.26	23.36	25.71
k_{15}	211.98	125.67	90.0	169.33	89.66	126.0

Table E1 - K coefficients associated with variance components in Table 2 for the analysis on plot means.

Appendix F

Table F1 - Genetic (above diagonal; S.e in parenthesis) and phenotypic correlations among 18 traits of lodgepole pine at one test site in central British Columbia. Each correlation was derived from the largest data set available for each combination of traits (i.e., correlations among traits were derived from mean squares and cross products shown in Appendix B). Variances associated with each correlation are derived from the same data set as the covariance; therefore, variances derived from tables in Appendix B may not give the same values used to determine correlations shown here.

rg rp	RS	CS	SS	GS	BA	BD	BL	MC	SG	BT	CW	RM	W9	TL	HT	DIA	VOL	DW
Rust Score (RS)	-	-.018 (.24)	.097 (.18)	.588 (.17)	.029 (.15)	-.086 (.16)	-.082 (.16)	.454 (.36)	.119 (.20)	.093 (.20)	.98 (1.3)	.203 (2.4)	1.116 (1.4)	-.954 (.86)	-.106 (.23)	.382 (.23)	.190 (.28)	.198 (.28)
Crown Score (CS)	.023	-	.119 (.27)	.526 (.27)	-.968 (.20)	.656 (.15)	.390 (.17)	*	-.282 (.23)	-.139 (.29)	-.310 (.39)	.352 (.36)	.047 (.37)	.085 (.28)	-1.00 (.90)	-.553 (.58)	-.794 (.74)	-.801 (.75)
Stem Score (SS)	.025	.239	-	-.299 (.21)	.343 (.18)	.226 (.21)	.308 (.20)	.493 (.25)	-.207 (.18)	.166 (.19)	-.495 (.30)	-.003 (.29)	.397 (.27)	-.134 (.22)	.437 (.26)	.414 (.25)	.343 (.28)	.400 (.28)
Gall Score (GS)	.076	.062	-.027	-	-.246 (.16)	.224 (.17)	.172 (.17)	*	.051 (.18)	.403 (.19)	-.325 (.31)	.237 (.30)	-.021 (.29)	-.227 (.22)	-.311 (.38)	.600 (.39)	.331 (.39)	.444 (.40)
Branch Angle (BA)	-.031	-.33	.074	-.099	-	-.561 (.14)	-.421 (.14)	.123 (.22)	.136 (.14)	.187 (.16)	.220 (.27)	-.256 (.26)	.216 (.24)	-.051 (.19)	-.041 (.18)	-.051 (.18)	-.099 (.20)	-.026 (.20)
Branch Diameter (BD)	-.017	.286	.069	.044	-.374	-	.742 (.06)	-.144 (.36)	-.221 (.16)	.288 (.16)	.508 (.28)	-.037 (.28)	.114 (.27)	-.343 (.20)	-.209 (.19)	.129 (.20)	.084 (.22)	.007 (.23)
Branch Length (BL)	-.051	.203	.076	.031	-.264	.829	-	.046 (.30)	-.090 (.16)	.173 (.17)	-.339 (.30)	-.183 (.27)	-.200 (.27)	.065 (.21)	.301 (.18)	.119 (.21)	.280 (.21)	.184 (.22)
Moisture Content (MC)	-.127	.021	.003	-.030	.037	.055	.078	-	-.336 (.28)	-.216 (.43)	-.428 (.47)	*	.568 (.73)	-.053 (.59)	-.124 (.30)	.078 (.25)	-.082 (.30)	-.165 (.32)
Specific Gravity (SG)	.023	-.052	-.015	.013	.011	-.128	-.130	-.301	-	-.132 (.16)	.637 (.22)	.255 (.24)	.148 (.24)	.129 (.18)	.034 (.20)	-.401 (.20)	-.364 (.22)	-.124 (.21)
Bark Thickness (BT)	.049	.051	.045	.044	.017	.238	.181	-.019	.041	-	.208 (.27)	.357 (.23)	.437 (.23)	-.271 (.20)	-.175 (.24)	.628 (.20)	.338 (.24)	.248 (.25)
Comp. Wood (CW)	.042	.029	-.016	.025	-.038	-.027	-.009	-.227	.201	.058	-	.481 (.31)	1.35 (.35)	-.194 (.28)	.273 (.28)	.382 (.29)	.692 (.32)	.754 (.28)
Radial Measure (RM)	.047	.132	.083	.018	-.140	.443	.437	-.084	.015	.316	.276	-	.821 (.19)	-.726 (.27)	-.099 (.35)	.662 (.21)	.511 (.29)	.604 (.24)
Width 9th (W9)	.044	.031	.066	-.017	.026	.204	.181	.022	.005	.229	.135	.309	-	-.387 (.27)	-.094 (.31)	.293 (.30)	.286 (.34)	.360 (.30)
Tracheid Length (TL)	-.053	.040	.003	.007	-.011	-.001	.085	.071	-.137	-.161	-.040	-.138	-.251	-	.552 (.27)	-.385 (.31)	-.177 (.35)	-.114 (.32)
Height (HT)	.009	-.171	-.098	-.017	.071	.195	.410	-.028	-.052	.096	.029	.419	.170	.138	-	.815 (.18)	.881 (.13)	.797 (.09)
Diameter (DIA)	.053	.048	.094	.080	.022	.371	.410	-.040	-.155	.272	.084	.630	.310	-.044	.569	-	.968 (.02)	.915 (.04)
Volume (VOL)	.046	-.014	.053	.041	.040	.336	.436	.007	-.121	.234	.080	.597	.296	-.010	.728	.943	-	.968 (.01)
Dry-Wt. (DW)	.046	-.021	.052	.049	.042	.310	.404	-.098	.090	.248	.128	.593	.298	-.042	.724	.913	.973	-

* not estimated due negative variance components