SOME PROBLEMS IN TESTING PROVENANCE WITH SPECIAL REFERENCE TO THE CO-OPERATIVE DOUGLAS-FIR PROVENANCE TEST AT THE UNIVERSITY OF BRITISH COLUMBIA RESEARCH FOREST

by

FRANZ REUTER

Diplomforstwirt,
University of Freiburg, Germany, 1967

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

Master of Forestry

in the Faculty
of
Forestry

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

February, 1971

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Department of Forestry

The University of British Columbia
Vancouver 8, Canada

Date February 3rd, 1971

ABSTRACT

Importance of research on the provenance problem, which is basically one of seed transfer from collection site to outplanting area, is discussed with special emphasis on coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*).

The "Co-operative Douglas-fir provenance test," begun in 1957 and involving sixteen coastal seed sources from British Columbia, Washington and Oregon, is described in detail. Height measurements collected at the University of British Columbia Research Forest, when the trees were eleven years old, are analysed and the results are discussed. Due to site heterogeneity and young age of the Co-operative test, no significant height growth differences between provenances can be shown, although the local seed source, from the University of British Columbia Research Forest, seems to be the fastest growing and the southernmost origin, Butte Falls, the slowest of all provenances investigated. The Co-operative test is critically evaluated and specifications for further studies are recommended.

ACKNOWLEDGMENTS

Above all I wish to thank Dr. P.G. Haddock who suggested the subject for this thesis and patiently provided help and guidance.

The measurements were obtained with assistance from Mr. J. Walters who constructively criticized thesis drafts.

I am indebted to Dr. A. Kozak and Miss L. Cowdell for their assistance in analyzing the data.

Special thanks are due Dr. O. Sziklai for chairing the thesis committee.

Several graduate forestry students gave me much of their precious time. The help of Messrs. D. Ormerod, L. Lacelle and G. Paille will be gratefully remembered.

Dr. K.K. Ching of the Oregon State University obligingly answered many questions.

Mr. C. Heaman lent me his excellent report on the "Co-operative Douglas-fir provenance test" in British Columbia.

I am deeply obliged to my wife Rita for her continual support.

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I. INTRODUCTION AND OBJECTIVES

In 1954 the Oregon State Board of Forestry met to consider the possibility of studying the genetic variability of the coastal form of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) from sixteen sources in Oregon, Washington and British Columbia. The following major reasons made that study a necessity:

1. the importance of the provenance problem,
2. the lack of knowledge on the performance of Douglas-fir provenances in the Pacific Northwest.

The present thesis was written with two objectives:

1. to review literature on the provenance problem,
2. to illustrate this review by an analysis of height measurements of the "Co-operative Douglas-fir provenance test," taken at the University of British Columbia Research Forest.

II. LITERATURE REVIEW ON PROVENANCE

No attempt is made in the following to give an exhaustive review on this subject, which is far too vast to be condensed within the scope of this thesis. An excellent survey of pertinent Douglas-fir provenance literature has recently been published by Haddock *et al*. (1967).

Definition of Provenance

According to Wright (1962), provenance (or provenience) means "the geographic source of a lot of seed (or pollen)." This definition parallels very closely that given by Snyder (1959) and Lines (1967). Lines stated: "Provenance is synonymous with population. The term 'race' refers to one or more natural populations showing defined characteristics. Provenance does not carry this implication, hence the broader term provenance is more generally applicable when populations are investigated."

In the present thesis "source" or "origin" will be used synonymously with "provenance" to avoid repetition.

The Provenance Problem

Species exhibit natural variation as a result of evolutionary adaptation to different environments in space and time. According to Haddock (1967), the major factors responsible for the development of locally, genetically different populations, are believed to be "the great topographic and associated climatic and edaphic variation in the environment." This variation, the nature and extent of which are hardly explored for any tree species, can be continuous (clinal) or discontinuous (ecotypical). When transplanted to a new environment within or outside the natural range of the species, different geographic sources will react differently. This difference in reaction cannot be predicted in detail. Good performance of a particular provenance in one place is no assurance of its superiority elsewhere. It is generally believed (e.g., Silen 1966) that local sources are best adapted to their particular environment and will outperform trees of non-local origin in the long run, especially in areas with occasional climatic extremes such as exceptional frosts. Transfer of seed should only be made between regions showing as much climatic similarity as possible in order to avoid undesirable silvicultural results (Isaac 1949).

Larsen (1956), the father of modern forest genetics, does not agree with the idea of strictly adhering to climatically similar areas when transferring seed. He preaches bold optimism and illustrates his point with the superior performance in Denmark (at 56° latitude North) of Norway spruce (*Picea abies* (L.) Karst) from a Romanian source (46° latitude North), of dissimilar climate. The fact that non-local superiority has not yet been proven for Douglas-fir does not necessarily mean that local provenances are always superior, it merely indicates the lack of both knowledge and experimentation in this field. Some indications of "nonoptimality" of local sources for several species, including loblolly pine (*Pinus taeda* L.), were recently reported by Namkoong (1969). Apparently evidence is mounting that an optimal growth zone of this species exists along the southeastern border of its range. Further experiments will prove whether seed from this zone will outproduce local stock elsewhere.

Wheat (1966) listed several reasons for there being an important provenance problem with Douglas-fir in the Pacific

Northwest. They are briefly:

1. Lack of local seed in sufficient quantities due to irregular seed crops.
2. Urgency of immediate reforestation due to the capability of high site lands in the Pacific Northwest to grow a dense cover of brush as fast or faster than Douglas-fir would grow.
3. Lack of sufficient knowledge on the adaptability of other sources to the local situation, i.e. lack of field-tested seed transfer rules.
4. Lack of controls on seed movement.

Considering the number of years it takes to grow a stand to maturity and the time that might elapse before a provenance shows its inferiority, it is economically and silviculturally unsound to blindly buy a seedlot of which the origin, and therefore performance, are not known. It is better in such a case not to plant but rather to wait for good seed.

Thus, in practical forestry, the provenance problem in essence is to find populations of trees, whether the species be indigenous or not, of which the seed will grow forests that are well adapted to their environment and that produce more wood than trees from any other population of the same species during the same period of time.* The provenance problem is

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*Productivity may not simply be equal to rapid growth. In a particular provenance test, the critical factor in productivity may be the ability to withstand frost (e.g. Sitka spruce in Western Norway) or the ability to produce fertile seed (e.g. Scots pine (Pinus sylvestris L.) in Northern Finland (Lines 1967).

intimately connected with the problem of finding the best species for a particular area.

Technical problems such as statistical design, layout and control of provenance experiments have been thoroughly discussed by Edwards (1956) and Lines (1967).

According to Schmidt (1962a), provenance trials can be divided into the following categories:

1. Studies of broad geographic variation.

   Studies of broad geographic variation are not specifically designed to provide data for seed transfer rules; they usually involve a small number of provenances which may not be a sufficiently representative sample of a given species. This type of study usually indicates that local seed is best, although that might not always be correct.

2. Tests of stock from improved seed production areas.

   Studies involving stock from seed production areas can be criticized on the basis that the seed production areas may no longer be functioning by the time the results are obtained and that they usually involve too few provenances.

3. Comprehensive trials.

   Comprehensive trials require much ground work, such as climatic stratification of the range of the species in question. Such a stratification in itself is an overwhelming task in some areas. Reciprocal plantations have to be established within each zone. Seed samples may be too few to adequately capture the variation within the species.

4. Factorial tests.

   The influence of the individual climatic (and geographic) variables considered to be of major importance to ecotypic differentiation are determined by factorial tests which are of great value in areas where climate shows little, or at least, predictable variation with changes in geographic factors such as latitude.

5. Random population trials.

   Random population trials involve a large number of randomly picked provenances and a large number of outplanting sites representative of the climatic variation within the range of the species. Although some climatic data are required before establishing the test to assist in selecting the outplanting sites, the bulk of the information can be accumulated during the study. This approach was adopted by Schmidt (1967) to study the variation within the British Columbia coastal form of Douglas-fir.

Provenance trials should not be mistaken for progeny tests which follow them chronologically. Provenance studies determine the genetic worth of populations of trees; progeny tests determine the genetic worth of an individual tree (Lines 1967).

Objectives of Provenance Tests

Out of the previous paragraphs, the following major objectives can be defined:

1. To study extent and nature of the variation in parts or in the entire range of a species in order to locate populations of trees, the seed of which will produce well adapted, productive forests in a given region (Lines 1967 and Place 1969).
2. To define the genetic and environmental components of this phenotypic (i.e. morphological and/or physiological) variability between trees from different geographic sources (Lines 1967).
3. To establish seed transfer rules (Schmidt 1967).

Provenance Tests and Forest Tree Improvement

According to Nanson (1964a), tree improvement programs basically aim at three points:

1. quantity (of wood and/or other organic products),
2. quality (of visible, e.g. stem straightness and/or invisible characteristics such as specific gravity),
3. resistance (to biotic environment, to soil and to climate).

The following tools can be used to reach these objectives:

1. Provenance studies
2. Seed production areas
3. Seed orchards
4. Inter- and intra-specific hybridization
5. Induced mutations and polyploidy
6. Vegetative propagation.

According to Nanson (1964a), provenance tests should be designed statistically in such a way that growth performance, form and resistance of the various origins under investigation can be assessed. Provenance tests constitute the first logical step in genetic research. Although a relatively easy endeavour, provenance tests are able to yield practical results quickly. They often show without additional cost, which stand or region to buy seed from.

Brief History of Provenance Testing

The Frenchman de Vilmorin is traditionally considered to be the father of provenance testing. In the early 1820's he established Scots pine plantations of known geographic origin at his estate at les Barres. In 1862 he wrote a report on the growth of these trees and concluded that there was a definite difference in several important characteristics between trees from different regions. Unfortunately, these discoveries went unheeded (Larsen 1956, Revel 1960).

Cieslar (1907) and Engler (1913) demonstrated the existence of great differences between various origins of Norway spruce. The 1912 Douglas-fir heredity study constitutes the pioneer effort in provenance testing in North America. It was initiated by the United States Forest Service which also provided the seed for the Douglas-fir tests started by Schwappach and Muench around 1912 in Germany. The first tentative seed transfer rules were established in Sweden in the 1930's.

With the growing awareness of the importance of the problem and the potential gains to be derived from the selection of adequate seed sources, provenance tests became more and more popular in forest research around the world. They are too numerous to be reported here in detail.

Problems Commonly Investigated

The following is an arbitrary distillation of literature for some major autecological aspects of the provenance problem, with special reference to Douglas-fir.

Drought resistance

According to Ferrell and Woodland (1966), drought resistance may involve either drought avoidance or drought hardiness, or both. Drought avoidance is accomplished through root extension and reduction in leaf area or through early onset of dormancy. Drought hardiness is the ability to survive in a dry external environment causing severe tissue dehydration. The authors studied the effect of seed origin on drought resistance of Douglas-fir and found that interior mountain provenances showed significantly greater drought resistance than those from areas west of the Cascades. Seedlings from Corvallis were a notable exception. They proved no more drought resistant than seedlings from higher precipitation, lower temperature areas elsewhere west of the Cascades.

By two drought hardiness tests, time to death and soil moisture content at the death point, Pharis and Ferrell (1966) showed that Douglas-fir seedlings from three coastal sources were less drought resistant than those from five inland sources. They found needle moisture to be a good index for determining plant viability under well watered conditions. Seedlings could be classified into coastal and inland groups on the basis of their needle moisture content with the exception of an Arizona provenance behaving like the coastal group.

Site ecotypes

A basic tenet of genetics holds that the phenotype is affected by the genotype and the environment. Provenance studies are designed to enable the researcher to detect the genetic differences between various seed sources. This can best be done by growing the trees on a hopefully uniform site under the same environmental conditions. Since site is one of the major components of the environmental complex, it is not surprising that some foresters have tried to find out whether populations had adapted themselves genetically to growing on a particular site.

The first authors to report on this problem in Douglas-fir were Munger and Morris (1936) who found that the age of the parent tree, its growing space, its conditions as to fungus infection and its site index, had no effect upon height growth of the progeny. Gathy (1961 and 1967) tested various provenances of coastal Douglas-fir and came to similar conclusions: age and growing site of the parent trees seemed to have no bearing on height growth of their offspring. Heaman (1968) found no significant differences in height growth between two high elevation Douglas-fir provenances. One lot of seed had been collected from a stand showing relatively good phenotypic characteristics on a good site while the other lot originated from trees growing on a much poorer site, but in a similar climatic zone.

Aspect races

Although there has been no definite proof so far of site ecotypes in Douglas-fir, it is quite interesting to note that ecotypes have evolved that are adapted to the particular conditions prevailing on southerly aspects. Ferrell and Woodland (1966) found that seedlings produced from trees growing on a south slope were more drought resistant than those from trees growing on a north slope, a short distance away. Interesting results were obtained by Hermann and Lavender (1968) in a growth chamber experiment with Douglas-fir from various altitudes and aspects in southern Oregon. Progeny of trees from south facing aspects exhibited a shorter growing period and larger roots in relation to their tops than seedlings from parents on north facing slopes. This was interpreted to be a result of natural selection for early cessation of growth in habitats that are particularly dry in summer. These results are an interesting parallel to earlier findings by Squillace and Bingham (1958) suggesting the existence of aspect ecotypes in western white pine (*Pinus monticola* Dougl.).

Bud bursting

Bud bursting, as discussed in this chapter, refers to the opening of vegetative buds only and is synonymously used with "flushing."

1. The influence of genetic control on the timing of flushing. Observations by Morris *et al*. (1957) suggest strong genetic control over time of bud bursting in Douglas-fir. The most classical study on this question was made by Silen (1962), who tried to minimize environmental influences by grafting several replications of scions from trees with large, known differences in

flushing dates onto limbs of seven trees of a seventeen year old clone. As a control, a limb of the clonal tree was cut and re-grafted. Silen estimated the genetic component of the bud bursting trait at ninety-four and ninety-six percent of the total variation for the two years of observations. At the same time he presented evidence that local environmental differences may consistently delay bud bursting of genetically similar material for as much as two weeks. Similarly, publications by the United States Forest Service (1964) and Griffith (1968) show evidence of strong genetic control over flushing in Douglas-fir. The trees under observation for several years consistently flushed in the same order, within a day or two. The pattern was not altitudinal. Walters and Ching (1969) studied the pattern of bud burst in the Douglas-fir provenance tests to be reported later in this thesis, and found the University of British Columbia Research Forest provenance to be a late flusher, regardless of plantation; the Salem source proved to be the earliest flusher of terminal and lateral buds, regardless of planting area. Evidence was put forward for a strong influence of local climatic conditions on bud bursting.

2. The effects of the environment on flushing.

The publications cited in the previous chapter, stating that under uniform environmental conditions bud bursting is under very strong genetic control, also mention the effect of the environment, particularly the climatic conditions of any particular year, on the expression of this trait. Morris <u>et</u> <u>al</u>. (1957) observed that in some years flushing may occur as much as a month later than in other years. In high elevation plantations, buds may open anywhere from two weeks to two months later than at low elevations. Griffith (1968) tried to correlate date of flushing with climatic data and found that in the University of British Columbia Research Forest bud bursting was influenced by weather conditions during the forty-two day period prior to May the sixth.

3. The disadvantages of early bud bursting.

Time of flushing is important in relation to spring frosts. Since bud bursting is a highly hereditary trait, seed from early flushers cannot be planted to advantage in areas where late frosts are likely to occur. Irgens-Møller (1967) noticed a difference in time of bud bursting of fifteen to eighteen days between plants originating from areas separated by only twenty to forty miles. He stressed the importance of choosing a seed source that can be expected to be unaffected by spring frosts. Needle midges (<u>Contarinia</u> spp.) were found to threaten early flushing Douglas-fir trees (Mitchell and Nagel, 1969), while leaving late flushers more or less unharmed. Schober (1963) advised against Douglas-fir provenances from British

Columbia's Interior Wet Belt for use in areas with late frosts or widely fluctuating weather conditions during spring, such as occur in Western Europe, because they flush earlier than coastal provenances. This earlier flushing makes them more susceptible to the Douglas-fir needle blight (*Rhabdocline pseudotsugae* Syd.). Haddock *et al.* (1967) came to similar conclusions. To summarize, early flushing is hardly an asset, since spring frosts, insects and fungi may damage the trees severely.

4. Implications of time of flushing on the provenance problem. When choosing seed lots, geographic and climatic data should be supplemented with careful observations on date of bud bursting covering several years. The success of whole plantations may hinge on time of flushing in connection with spring frosts, insects or fungi. Late flushing eliminates all these dangers and has no negative effect on total height growth. Ideal provenances are those that grow fast, flush late and set their buds early, thus avoiding both spring frosts and fall frosts.

Lammas shoots

According to Walters and Soos (1961b), " ... lateral and terminal vegetative buds of young trees frequently break dormancy in late summer and produce extra-seasonal shoots named lammas shoots after the old English harvest festival of Lammas on August 1." The authors studied this phenomenon on Douglas-fir seedlings from various origins grown at several elevations on the University of British Columbia Research Forest. The conclusions were that lammas growth

1) was influenced more by environmental than genetic factors,

2) decreased with increasing age,

3) increased as site quality increased,

4) increased as current height growth increased for seedlings of a particular provenance.

Lammas growth was sometimes reflected in false annual rings. Forked leaders caused by lammas shoots were overcome quite rapidly in Douglas-fir.

Sweet (1965) found that Douglas-fir seedlings having more than one annual growth flush in their second year do not make a greater height increment than provenances with fewer such trees. Hoffman (1965) experienced other results with Norway spruce, where the incidence of lammas shoots varies geographically and decreases with increasing elevation of seed source as an adaptation to the local climate. For sites with no early frosts, Hoffman recommended provenances with a high occurrence of lammas shoots that would outgrow dangers of juvenile stages more quickly. Schmidt-Vogt (1966) also noticed that lammas growth decreases with increasing altitude of seed source in Norway spruce, and he found its occurrence on one and two-year old seedlings to be a workable early test to check on elevational authenticity of seed.

To conclude, lammas shoots constitute a disadvantage on sites where early frosts are common, since the soft shoots can be damaged easily by frost. If this happens repeatedly, trees of poor form may result. On sites free of early frost hazards, lammas shoots are an advantage in overcoming competition from lesser vegetation, and possibly from deer browsing.

Frost resistance

Schoenbach (1958) evaluated the effects of a mass selection of Douglas-fir seedlings for frost resistance. The selection had given two populations: one mainly frost sensitive, the other frost resistant. Schoenbach concluded that frost resistance has single gene inheritance and appears in a homozygous condition. He stressed the need to start provenance studies on a very large basis, that is, including as many seed sources as possible, in order to find populations containing resistance genes. According to Scheumann (1965), the following five points have to be considered when frost resistance is to be studied:

1. readiness to harden off (= early frost resistance).
2. extent of hardening off (= winter frost resistance).
3. stability of dormancy (important during winters with highly varying temperatures).
4. time of flushing and flowering (late frost resistance).
5. regeneration potential (ability to overcome frost damage).

These five points make it quite obvious that:

- frost resistance is a dynamic process that cannot be studied as a static condition, as has been done traditionally.

- there cannot be a single test with which to evaluate all aspects of frost resistance in plants.

Previous knowledge on this subject has always been based on field observations after extremely cold weather. Scheumann (1965) devised a laboratory test with which readiness, extent and stability of hardening-off can be studied under controlled temperature conditions. Seedlings, needles or young twigs can be used in this test where temperature is gradually lowered to below freezing point. After early frost resistance and extent of hardening-off have been evaluated, the temperature is repeatedly raised for some time above the freezing point and then lowered again in order to test stability of dormancy. This is a method to rapidly mass select and rank various provenances (or progenies for that matter) for several aspects of frost resistance. Scheumann tried this "simplified test" on Douglas-fir and on European larch (<u>Larix</u> <u>decidua</u> Mill). He found significant differences in frost resistance of two-year old Douglas-fir hybrids (<u>glauca</u> x <u>viridis</u>). He found correlations between the climate in which the larch trees grew and the behaviour of the twigs in the frost resistance test. Scheumann concluded that this possibility of finding genetic differences in frost resistance among plus-trees and their progenies gives new hope for successfully testing frost resistance in forest trees. Schoenbach and Bellmann (1967) reported on the same <u>glauca</u> x <u>viridis</u> hybrids. The hybrids were all significantly more frost resistant than the "green" parents. Since they were also growing faster than the "blue" variety, the hybrids were recommended by Schoenbach and Bellmann for the cold climates of western Europe's mountains.

In a study involving thirty-one seed sources of coastal Douglas-fir from Washington and Oregon, Gathy (1961) found three Washington provenances from medium and low elevations (Yacolt, 200 feet, Castle Rock, 1300 feet, and Forks, 400 feet above sea level) to be most frost resistant and therefore best suited for the maritime climate of Belgium. Nanson (1964b) studied the effect of the severe winter of 1962-1963 on coastal Douglas-fir provenances in Belgium, but could not confirm the superiority of Washington sources over Oregon origins in terms of frost resistance. According to Nanson, all provenances of coastal Douglas-fir tested require adequate protection from severe frost, especially when they are young. Lacaze (1964) examined Douglas-fir seedlings in France after the 1962-1963 "deep freeze" and found considerable variation in frost resistance which generally increased with increasing latitude and altitude of the seed source. A line joining the points 49° latitude North, 1800 feet elevation, roughly divides the resistant from the non-resistant provenances. In a note by Stern (1966), reviewing results of a recent experiment, Douglas-fir seedlings from Arizona, New Mexico and Mexico were found to be more frost resistant than provenances from coastal British Columbia, Washington and Oregon, traditionally tested in Europe and recommended by Schober (1963). Silen (1966), evaluating the 1912 Douglas-fir heredity study (see below) after the 1955 November frost, formulated the hypothesis that local provenances have adapted themselves over the centuries to long-term weather extremes and are therefore less damaged by severe frosts than are non-local sources.

Cline or ecotype?

In 1936 Langlet published an article on the physiological variability and its relation to climate for Scots pine in Sweden. The dry matter content of needles proved to be highly correlated with the number of days during the growing season with an average temperature of six degrees Celsius (43° Fahrenheit), or more. Langlet showed a north-south variation in Scots pine in Sweden and claimed this variation to be continuous. Wright and Baldwin (1957) based their criticism of Langlet's article on observations from a Scots pine provenance test in New Hampshire. They agreed that there is a north-south variation in Scots pine, but their statistical analysis indicated that most of the geographic variation is discontinuous, not clinal. This would mean that the Swedish seed transfer rules based on the clinal hypothesis and limiting cone collections to areas within 250 kilometers (approximately 150 miles) north or south and 300 meters (approximately 1000 feet) difference in elevation from the planting site, should be revised to collecting seed within the boundaries of the ecotype best suited for the planting area. This may permit the safe transfer of seed for several hundred miles or limit it to a few miles. Langlet (1959) used Wright and Baldwin's data to show where they had gone wrong and he stated that variability continues in the same degree as the determining environmental factors vary continuously.

Neither the clinal nor the ecotypical hypothesis has been disproven. It is possible that in isolated occurrences Scots pine has developed ecotypes that cannot be explained by differences in the environment, whereas in large, contiguous areas of its vast range the variation is clinal, reflecting gradual changes in the environment. In other words, ecotypes are not necessarily in contrast with clinal variation. Haddock _et al_. (1967) mentioned the variability of ponderosa pine (_Pinus ponderosa_ Laws.) studied by various authors, some of whom support the clinal, some the ecotypical hypothesis. Haddock _et al_. concluded that no matter which alternative one subscribes to,

> " ... one cannot dispense with a thorough knowledge of the geography of a region and an understanding of the influence of topography on local climate, especially in regions as continuously mountainous as southern British Columbia."

Climate

Since weather measurements can only indicate part of the complex called climate, and since the establishment and maintenance of weather stations in remote areas are costly, Schmidt (1962b) tried to interpret climate from phenological observations. For this purpose, time of initial pollen release in Douglas-fir was chosen, because it is the first external indication of physiological activity in spring and it is easy to assess, compared for instance with determining the start of cambial activity. The results were not encouraging, and they raised further problems because male bud development does not seem to be related to a simple expression of temperature.

Irgens-Møller (1965) questioned the value of climatic data in assigning off-source seed to planting site. Both planting location and seed source may be far away from the nearest weather station. In addition, some provenances may tolerate a wide variety of conditions, others might be narrowly adapted to specific conditions. Haddock and Sziklai (1966) divided the range of Douglas-fir in British Columbia and western Alberta into nine seed collection zones based primarily on the influence of climate on geographic variability of populations and the distribution of associated species. Both authors were aware of the merits and limitations of such a zonation, and admitted that populations within the individual zones are far from being homogeneous, since remarkable climatic differences due to elevation, topography and precipitation exist within these zones. It is not sufficient for a forester to indicate the general zone from which he wants seed. He should provide detailed climatic data for the plantation site, including at least mean annual temperature, absolute minimum temperature, mean annual precipitation during growing season, and length of frost free period or dates of earliest and latest frosts. This way the seed collector may have a better chance of providing suitable seed (Haddock and Sziklai, 1966).

Newnham (1968) published an article on the classification of climate and its relationship to tree species, including Douglas-fir, using data from seventy weather stations from many parts of British Columbia. With principal component analysis on the matrix of correlation coefficients with nineteen variables recorded by the weather stations, he computed three new variables accounting for ninety-two percent of the total variation between weather stations. The first variable was a general index of winter and fall climate and of the length of the growing season, the second represented the contrast between spring and summer temperatures and precipitation, the third variable, of lesser importance, represented merely a measure of latitude. When the weather stations were grouped, the parallels to Chapman's (1952) climatic regions were surprising. Newnham's approach, with further refinements, may prove very useful for zoning the natural range of trees and assist in finding good matches for tree species introduction elsewhere. Newnham believes that " ... the components can be used as measures of climatic similarity between different provenances within a species."

Seed movement

Isaac (1949) based his rules for Douglas-fir seed collections on Langlet's (1945) publication dealing with seed movement limitations in Sweden. These rules, still valid, were as follows:

1. Collect seed within 100 miles north or south of planting site if at similar elevations.

2. A 500 foot rise or drop in elevation from planting site is allowable if seed source is not more than ten miles to the north or south.

3. For each additional ten miles north of planting site, the allowable elevation for seed collection is reduced by fifty feet, up to 100 miles north.

4. For each additional ten miles south, the elevation may be increased by fifty feet, up to 100 miles south.

5. In a rough, broken country, climate should guide more than distance or elevation. Average annual temperature of the seed source should be within two degrees Fahrenheit plus or minus and frost-free period should be similar to that of the planting site.

6. The seed source stand should be thrifty and making average or better than average growth for the locality.

7. Individual seed trees should be of good form and should not be excessively limby.

Isaac (1949) stated explicitly that these rules are not to be considered optimum conditions but rather limitations for seed collections. He recommended to collect seed during heavy crop years and store it for poor years. Isaac noted the lack of seed certification laws. Despite the concern about the provenance problem, no refined seed transfer rules have been devised yet for Douglas-fir, and local seed is still recommended as safest and probably best (Bingham 1966). Wheat (1966) felt that the increase in artificial reforestation with Douglas-fir in Washington and Oregon and the lack of seed from adequate sources made it easy to ignore rules of safe practice. He also deplored the lack of controls on the movement of seed.

Haddock (1966) noted that neither distance of seed movement in miles nor the change in elevation itself are really the question of importance, but rather the effects of these changes on the local total environment. Haddock stressed the importance of a thorough knowledge of the geography of a region and the influence of topography on local climate in respect to seed movement problems. Schmidt's (1967) provenance test will hopefully yield enough information for new seed transfer rules for coastal Douglas-fir in British Columbia less than fifteen years from now.

Physical properties of wood have been shown to be an important aspect of the provenance problem, but one which needs further investigation (Haigh, 1961; Silen, 1964; Bramhall, 1966; McKimmy, 1966).

Early Tests

The long rotations represent one of the major handicaps of forestry. Whereas most agricultural crops ripen after one growing season, it usually takes a forest stand longer than an average human life to grow to maturity. In an effort to overcome this shortcoming in provenance and progeny testing, some foresters have been trying to develop early tests. Pioneer work in this field was done by Schmidt (Germany) and Langlet (Sweden) around 1930 (Nanson 1965).

Early tests investigate provenance variation in order to give the earliest indication of the later performance of the trees (Lines 1967). If statistically significant correlations can repeatedly be found between early and later performance (five, ten or even fifteen years are not good enough for management) in several tests of the same species or variety, covering a large range of environmental conditions, it should be possible to set up equations predicting later performance on the basis of measurements taken at an early age. In this way the relative inferiority or superiority of a particular provenance (or parent tree in the case of progeny testing) could be recognized early and foresters would know which stand to choose for seed collection for large scale planting programs.

Early testing begins with the seed, although climatic and geographic data on seed source constitute very important background information. Growth chambers facilitate the study of the differential reaction of provenances under a controlled environment. Irgens-Møller's (1957) investigations on the effects of various temperatures and photoperiods on Douglas-fir seedlings from different sources are a good example of this. Although laboratory tests are very helpful in provenance trials, caution must be used in projecting the results to later growth in the field. Nursery performance (e.g. Ching and Bever, 1960) may yield some useful information, but again the true value of those observations will be confirmed only many years later. Orr-Ewing (1967) stressed this need for caution when basing premature conclusions on early results. He stated: "Progeny tests can yield enough information at twelve to fifteen years after planting for at least the poorer provenances to be recognized." The same thing can probably be said of provenance trials. McKimmy (1966), studying specific gravity of Douglas-fir from several seed sources, concluded that trees should be over twenty-five years old for stand predictions. According to another publication on the 1912 Douglas-fir heredity study (United States Forest Service 1964), the results were disappointing when seedling heights were compared to mature heights. In a provenance study with European larch, Leibundgut (1962) found that height growth during the first years was poorly correlated with later height growth.

Some experiments, however, showed high correlations: Wright and Baldwin (1957) found a statistically significant correlation ($r = 0.933$ and 0.861 respectively) between three or four year's height and seventeen year's height in a Scots pine provenance test in New Hampshire. Nanson (1965), reporting on an international Norway spruce experiment in Belgium dating back to 1938, found the twenty-five year growth to be strongly correlated with the following "early" characteristics:

- length of growing season at seed source
- 1000 seed weight
- fresh weight of seedlings
- dry weight of seedlings
- bud bursting date
- heights at various ages.

Nanson felt that the length of the testing cycle could be considerably reduced if the planting check could be eliminated. Haddock <u>et</u> <u>al</u>. (1967) found a correlation coefficient of over 0.938 at the 0.01 probability level between height at age two and height at five, six, seven, eight and eleven years in a Douglas-fir study at the University of

British Columbia Research Forest. For the same species, Lacaze (1968) could show a highly significant correlation between height growth at two, five, eight and thirteen years after planting (r between two and thirteen years was 0.96).

Early tests can also be used as a check on the authenticity of seed lots collected by commercial seed dealers. Sweet (1965) found that both two-year height growth and time lag between lateral and terminal bud burst of Douglas-fir provenances tested in New Zealand were sufficiently strongly correlated to climate at seed source to do a check on the data of origin supplied with commercial seed lots. Schmidt-Vogt (1967) showed the same thing for Norway spruce and Scots pine.

III. MAJOR PROVENANCE TESTS WITH DOUGLAS-FIR

Tests Made Outside Its Natural Range

Douglas-fir was discovered by Archibald Menzies in 1797 at Nootka Sound on Vancouver Island (Krajina 1956). David Douglas sent cones and other material, collected on the banks of the Columbia River, to Europe as early as 1827. The first provenance experiments with Douglas-fir were started much later. In 1909 and 1910, the United States Forest Service sent Douglas-fir seed, collected under the aegis of Zon at different points of its range from the Pacific Coast to the Rocky Mountains, to Professor Schwappach at Eberswalde, Germany, and to Count von Berg in Livonia, Russia. The Count noted that trees from Chelan " ... in the same range of the Cascades as the seed from

Snoqualmie, but on the eastern slope, have grown very nearly as high as the seedlings from Snoqualmie, but stand upright and have scarcely suffered at all from the frost." (Zon 1913). In 1912, Professor Muench started another provenance test in Kaiserslautern, Germany, with seed from ten provenances, sent by Professor Schwappach who was experimenting with nineteen provenances himself, two from low elevations in Western Washington, three from high elevations in California, west of the Sierra Nevada summit, the remainder from more continental climates. In 1933, three other provenance tests were started in Germany: series one at the foot of Mount Feldberg in the Black Forest, series two in Freienwalde and Braunlage, series three in Gahrenberg. These experiments have been reported by Schober (1954), Schober and Meyer (1954, 1955), Jahn (1955), Rohmeder (1956) and others. In Germany it soon appeared that there were great differences between provenances as to growth rate, frost and disease resistance, as well as morphology. The seed for the 1933 experiments was from ill-defined provenances, therefore morphology was sometimes resorted to for clues on origin (Decker 1967). Although this did not prove very easy due to the great morphological variability of Douglas-fir, the provenances were ascribed to three varieties:

<u>viridis</u> = green or coastal form, called varietas <u>menziesii</u> in North America

<u>glauca</u> = blue or Colorado or Rocky Mountain Douglas-fir by Little (1953)

<u>caesia</u> = grey form from the intermountain or more northern interior provenances from Schenck's (1939) climatic region 110 B.

At present most North American authorities on Douglas-fir do not universally agree beyond the *menziesii-glauca* separation (Fowells 1965), although many German foresters still frequently write about the *caesia* variety.

Another minor controversy raging among English speaking foresters and botanists regards the hyphenation problem in spelling Douglas (-) fir. Although there are valid arguments for and against the hyphen, this problem could easily be solved by calling *Pseudotsuga menziesii* (Mirb.) Franco simply "Douglas" as some Europeans do.

The great variability of Douglas-fir was stressed by Larsen (1956), who wrote as follows:

> " ... one has to travel very widely throughout the natural range of Douglas-fir in order to get an impression of differences in geographical type, but standing in one place one can, without moving a foot, see many individuals differing widely in their structure; it is often more difficult to pick out those that resemble another ... It does not matter if one chooses in California a site in the Coast Range or in the Sierra Nevada, passes through Oregon and Washington, or in British Columbia selects a place on Vancouver Island or in the Rocky Mountains; everywhere one is bound to be impressed by the great individual variation of this tree species ... "

Orr-Ewing (1968) concluded from his inbreeding studies that Douglas-fir is a most heterozygous species, leaving ample opportunities for further selection.

In a comprehensive paper presented in Stockholm, Schober (1963) summed up European provenance studies with Douglas-fir. He concluded that in Central Western Europe, provenances from areas west of the Cascades in Washington, especially from elevations below 700 meters (2000 feet) were fast growing and fairly resistant to Rhabdocline pseudotsugae Syd. but at the same time rather sensitive to winter frost. However, late frosts did not affect them because of their late bud burst. In the cooler climates of Northeastern Europe, the Central European Mountains and the transition zones to continental Eastern Europe, certain provenances from the interior of British Columbia grew as fast or faster than trees from coastal Washington. However, they showed greater susceptibility to both Rhabdocline and late frosts, due to their early flushing, although they were resistant to winter frosts. In coastal regions or in maritime European climates, the provenances from British Columbia's Interior showed only average to poor performance. Schober expanded on the great variability of these sources and tried to explain it with information from Galoux's (1952) publication on the phytogeography and paleobotany of Douglas-fir. Unfortunately, many European foresters lack Galoux's knowledge on the subject and do not recognize the existence of British Columbia's Interior Wet Belt and the extreme climatic variation in British Columbia. This is particularly significant for provenances of Douglas-fir around Shuswap Lake, for instance. Haddock and Sziklai's (1966) seed zone map can help seed collectors to avoid gross errors in the future. Hopefully these seed zones will be interpreted ecologically and not considered to be uniform entities. Schober (1963) recommended the Interior Wet Belt origins for appropriate parts of Europe. Those from British Columbia's dry Interior, corresponding to Haddock and

Sziklai's (1966) seed zones five and eight or to Rowe's (1959) Montane Forest Region, were found to be slow growing and susceptible to Rhabdocline in Europe. Seed from coastal Oregon and California showed good results in the warmer climates of Italy, but they proved unsatisfactory in Central and Northern Europe where they grew slowly and suffered from winter frosts. Provenances from east of the Cascades, particularly those from the Rocky Mountains, always showed great susceptibility to Rhabdocline and exhibited poor growth (Schober 1963).

According to Schober (1959), the caesia and glauca provenances are susceptible to Rhabdocline because they are not used to the high air humidity of the European climates which does not bother the coastal form. In the tables attached to the 1963 publication, Schober clearly showed that in most European countries, suitable Douglas-fir provenances outproduce all indigenous species. Many European foresters (e.g. Schober 1954, Rohmeder 1956) felt that it was time to sample in more detail the populations from the general areas where the provenances that have proven suitable for Europe, originated. This is exactly what some Danish foresters (Barner 1966) had in mind when they sent a team of cone pickers to western North America for several consecutive years, starting in 1966. The seed is distributed by I.U.F.R.O. to interested research groups. Many more experiments with Douglas-fir are going on in Europe. Stern (1966) for instance reported on three to four years' performance of so far "unexplored" origins from high elevation stands in Arizona, New Mexico and Mexico, grown at Schmalenbeck. He pointed out their advantages of faster growth, longer growing period, greater frost and drought resistance.

The majority of European countries, including Luxembourg (Decker 1967) and Russia "where the coastal form of Douglas-fir is one of the most rapidly growing, valuable and promising forestry species in the western Ukraine" (Brodovich 1967), are interested in growing suitable provenances of this species, which some authorities hail as Europe's most important exotic.

Douglas-fir is also grown in other parts of the world, for instance in New Zealand (Sweet 1965) where it is doing extremely well (Spurr 1963). In eastern North America, that is, in areas outside its natural range, Douglas-fir has mainly been grown for Christmas tree purposes. Byrnes _et al_. (1958) tested several provenances in Pennsylvania and found that the _glauca_ variety was best in terms of survival, growth and hardiness. _Viridis_, though slightly faster in growth, suffered most from cold and drought. Likewise, Baldwin and Rock (1961) rated _glauca_ superior to _viridis_ after nine growing seasons in New Hampshire.

Major Provenance Tests With Douglas-fir Within Its Range

The most famous Douglas-fir provenance test in North America is the classical 1912 heredity study of the United States Forest Service. It consists of progenies from 120 recorded mother trees, representing thirteen coastal provenances ranging elevationally from 100 to 3,850 feet and planted at five elevations between 1,100 and 1,400 feet in western Oregon and Washington. It is both a provenance study and a progeny test from which a wealth of useful information has been derived. Munger and Morris (1936) found for instance that the age of the parent tree, the quality of its growing site, its growing space and its condition as to fungus infection had no effect upon the height growth of its progeny. Wright (1962), using data from that publication, criticized the statistical design of the study for lack of replication and randomization and concluded prematurely that " ... in all five test areas one or more non-local provenances grew faster than the local provenance." The 1955 November frost, killing many non-dormant trees, local and non-local, was going to change this picture drastically, leading Silen (1966) to stress the importance of survival and growth combined, instead of growth performance alone, when discussing provenance performance. Silen hypothesized that inherent growth rate of a race has developed toward the maximum that can be sustained in each locality against impacts of long-term weather extremes. This hypothesis does not exclude the possibility of non-local races outproducing local ones at short rotations on protected sites. Among other important findings, the following points are worth remembering (United States Forest Service 1962).

1. Seed origin was more critical in high-elevation (above 2,000 feet) than in low-elevation plantations.

2. Superior performance of a given provenance at one planting site was no assurance of superior performance elsewhere.

3. Slenderness or stockiness of progeny was consistently related to its female parent in all plantations. Mortality resulting from the severe freeze of November 1955 was also related to the individual parent.

According to the United States Forest Service (1964), no result was more striking than the evidence of a gene-environment interaction. Low elevation sources performed poorly at high elevations and vice-versa. It was also found that environment generally has a larger effect on growth than source of seed. The pattern of bud burst did not appear to be altitudinal. Wide valley origins burst their buds first, followed by those on open slopes. Those from narrow valleys flushed last, probably representing a selection against late frosts. Sweet (1965) came to similar conclusions in New Zealand.

Other authors have used data from the 1912 study. For instance Isaac (1949) established seven seed transfer rules or limitations relative to the collection of Douglas-fir seed. These rules, listed on page 22, are based primarily on average annual temperature and frost free period and roughly parallel Langlet's (1945) system used in Sweden for Scots pine. Jahn (1955) compared North American with German experience on Douglas-fir provenance.

In 1954, foresters in Oregon, realising the lack of knowledge on the Douglas-fir provenance problem, planned a regionwide study which comprised sixteen provenances from Oregon, Washington and British Columbia. This so-called "Co-operative Oregon Douglas-fir provenance study" will be discussed in detail later in this thesis. Orr-Ewing (1966) reported on intraspecific crosses with Douglas-fir from various origins in the United States and Canada. Some North American research institutes are growing seed from the I.U.F.R.O. collection mentioned earlier. Schmidt (1967) reported on the critical stages of an intensive provenance study the major aim of which is to set up seed transfer rules for the coastal range of Douglas-fir in British Columbia. The area was stratified observing two criteria:

1) recognition of known or suspected climatic differences,

2) possibility that geographically separated areas might have produced different ecotypes despite only minor climatic differences.

From a total of ninety provenances to be tested, sixty-nine are from the coast (fifty-seven from British Columbia, twelve from Washington and Oregon), thirteen from continental climates of British Columbia's Interior, and eight from Coast-Interior transition zones. Cones for that study were collected in 1966, partly in connection with I.U.F.R.O. to avoid duplication of time and effort. Field testing will be conducted at over forty outplanting areas, distributed over a comprehensive range of climates within the coastal range of Douglas-fir. Meteorological data will be obtained at the field test sites.

In 1967 Haddock et al. published a paper comparing coastal with interior Douglas-fir origins. The authors, who stressed the importance of a thorough knowledge of the geography of an area and an understanding of the influence of topography on local climate, confirmed European experience that coastal provenances outgrow interior sources in mild climates, while being at the same time less frost resistant and less susceptible to Rhabdocline infections. Once more, local or near-local origins were found to produce the best growth. Many more publications have appeared on Douglas-fir provenance in North America.

Morphological problems have been investigated for instance by Allen (1960a, 1961) who described an easy method of separating coastal from British Columbia interior sources. Tusko (1963) concluded after an extensive study on the variability in certain Douglas-fir populations in British Columbia, that there are only two subspecies - one coastal, and one interior. Sziklai (1969) studied variation in cone and seed morphology of 1,335 trees from the I.U.F.R.O. collection between $42^{o}07$ and $53^{o}37$ latitude north and found " ... a clearly expressed clinal variation in cone and seed length with an increasing trend from north to south. The other characteristics such as wing length, wing width and seed width, did not show a similar clinal variation pattern."

Growth chamber experiments under controlled light, were carried out by Irgens-Møller (1957) who found ecotypic response to temperature and photoperiod. High elevation plants appeared to have a definite photoperiodic response with regard to date of bud bursting. The magnitude of this response was increased by low night temperatures. Irgens-Møller concluded that the natural selection to which Douglas-fir at high elevations has been exposed may have resulted in plants for which the optimal length of the day for bud bursting occurs at a time when the danger of night frost is usually low. Vaartaja (1959) concluded that photoperiodic ecotypes have evolved as an individual mechanism of trees to seasonally changing climatic factors. Allen (1960b) separated coastal from interior seed lots on the basis of their germination behaviour at various temperatures, following a short period of stratification. Revel (1960) compared coastal with interior provenances grown in a greenhouse, and found that germination was faster and height growth ceased much sooner for interior provenances which also require more chilling to break dormancy for vegetative growth. Similarly, Nicholson (1963) found higher germination for interior provenances. He separated interior from coastal provenances by using short day treatments. However no definite regional grouping of the coastal provenances was distinguishable. Sorensen (1967) was able to separate two year-old seedlings representing several provenances from a west-east transect in Oregon into three distinct groups, on the basis of their height growth and the date of bud formation in the first year.

Haddock and Schmidt (1957) wrote that it is best to assume that there are a large number of unexplored ecotypes since the ecological behaviour of Douglas-fir obviously varies greatly with site, " ... even within the Pacific Coast portion of its range." Bingham (1966) felt that many cases of aberrant performance in "local" sources involve movement of seed between unrecognized, but nevertheless distinctly different environments. He recommended adherence to the maxim: local seed is safest and probably best, and he cautioned against stretching the concept of "local," especially where steep climatic gradients or soil changes are known or suspected between seed source and planting area. Haddock and Sziklai (1966) established seed collection zones for Douglas-fir in Canada, based primarily on climatic data and the distribution of associated species. The authors recommended that seed users who cannot indicate a specific locality or stand from which they want seed, should provide pertinent climatic data for the proposed plantation site in order to avoid undesirable results. Haddock (1967) stressed the need for more precise provenance designations because of the great topographic and associated climatic and edaphic variation believed to have shaped the evolution and development of locally, genetically different populations over long periods of time. The author also warned against relying too much on morphological features used by taxonomists " ... we should rely more on less easily measured characteristics such as general physiology, phenology, cold, heat and drought resistance, susceptibility to insects and disease, growth form and wood quality."

IV. THE CO-OPERATIVE DOUGLAS-FIR PROVENANCE TEST*

General

The great importance of Douglas-fir in the regional economy and the lack of knowledge on the variation within this

*In this thesis "co-operative test" or "co-operative study" are used as abbreviations for "the co-operative Douglas-fir provenance test."

species lead in 1954 to a publication by the Pacific Northwest Forest and Range Experiment Station, entitled "A Program of Tree Improvement for the Pacific Northwest," stating that the tolerance of Northwest species to changes in geography, elevation and climate, had not been fully explored and a comprehensive program of provenance testing should be initiated as soon as possible. That same year, staff of the Research Division of the Oregon State Board of Forestry (now in the Forest Research Laboratory, Oregon State University) began to organize a regionwide provenance study of coastal Douglas-fir, after conferring with many interested parties (Anon. 1955a).

Hypotheses to be Tested

After reviewing literature on the Douglas-fir provenance problem, Ching and Bever (1960) felt that in the experiments reviewed, the sampling of the variables of altitude, latitude and longitude was neither precise nor systematic enough to elucidate the question whether variation is clinal or discontinuous. To improve on this, an effort was made to get as many co-operators as possible in order to test the following hypotheses (Anon. 1955a).

1. Distinct races of Douglas-fir are associated with temperature as measured by frost free days during the growing season.

2. Distinct races of Douglas-fir are associated with altitude.

3. Distinct races of Douglas-fir are associated with latitude.

4. Distinct races of Douglas-fir are associated with temperature, altitude and latitude, as measured

by comparable frost free days and comparable photoperiods during the growing season.

5. Distinct races of Douglas-fir have resulted from the development of genetic strains in localized areas, and not from any of the variables or combinations of variables stated in the preceding four hypotheses.

6. Distinct races of Douglas-fir do not exist within the area covered by this study.

Design

The design was to follow the working plan for the southern pine provenance study by Wakeley (1953) who had found at least one of the following six weaknesses in other provenance studies:*

1. Occasional aimless and illogical selection of seed sources. This mistake was to be avoided through relatively systematic sampling within the range of coastal Douglas-fir in Oregon, Washington and British Columbia.

2. Mixing of single tree and bulk cone collections. A rigid cone collection prospectus, asking for a sample of at least fifty trees per seed source was aimed at overcoming this shortcoming.

3. Inadequate test plantings. This error was to be corrected by establishing plantations of all sources near each collection site to compare the local provenance with the other provenances.

4. Inadequate statistical design. Four replications with random provenance allocation was to satisfy the prerequisites for statistical analysis (see Fig. 1).

5. Insufficient number of trees planted for adequate survival and measurement up to rotation age. An eight by eight foot spacing in square plots with

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*Since Wakeley's publication was not seen, the information on "design" is mainly taken from Heaman's (1963) thesis.

eleven times eleven seedlings was to be adopted; the two outer rows were to act as a buffer strip, minimizing edge effects (see Fig. 2).

6. Lack of maintenance after establishment of the test, and subsequent irregular measurements. Good co-operation and the ratification of a ten-year agreement by all co-operators was to remedy this.

In addition to the above points, confounding nursery effects were to be eliminated by growing all stock in one nursery, namely Corvallis.

Fig. 1 Diagram of plot designations.

Block A=1				Block B=2				Block C=3				Block D=4			
13	8	14	7	4	10	1	13	14	6	1	10	2	11	14	8
6	1	4	12	9	15	5	2	8	2	16	4	16	6	4	12
15	5	11	16	7	8	11	14	5	13	9	12	5	3	7	10
9	3	10	2	12	3	6	16	11	3	15	7	1	9	13	15
Plantation I								Plantation II							

Each outplanting area has two "plantations," usually from one-quarter mile to one-half mile apart, and consisting each of two adjacent blocks.

Co-operators and Seed Sources

Tables 1 and 2 show the names of the co-operators as well as the distribution of the seed sources. Figure 3 illustrates the geographic distribution of the provenances included in the co-operative test. The provenances were first assigned letters (A to P), then given numbers following the order in

Fig. 2 Blow-up of plot X in plantation Y.

```
X   X   X    X    X    X    X    X    X    X   X

X   X   X    X    X    X    X    X    X    X   X
        1    2    3    4    5    6    7
X   X   X    X    X    X    X    X    X    X   X
        14   13   12   11   10   9    8
X   X   X    X    X    X    X    X    X    X   X
        15   16   17   18   19   20   21
X   X   X    X    X    X    X    X    X    X   X
        28   27   26   25   24   23   22
X   X   X    X    X    X    X    X    X    X   X
        29   30   31   32   33   34   35
X   X   X    X    X    X    X    X    X    X   X
        42   41   40   39   38   37   36
X   X   X    X    X    X    X    X    X    X   X
        43   44   45   46   47   48   49
X   X   X    X    X    X    X    X    X    X   X

X   X   X    X    X    X    X    X    X    X   X

X   X   X    X    X    X    X    X    X    X   X
```

Features of each small plot:

- 121 trees
- 8 x 8' spacing
- all trees of the same provenance
- only 49 trees in the inner groups will be measured. They are marked with numbered cedar stakes.

Table 1 Co-operators and Location of the Test Sites

	Seed Source	Provenance Number	Co-operator	Latitude	Elevation (Feet) range of collection	Year of Collection	Location of Test Site
British Columbia	A	4	Canadian Forest Products Ltd.	$50^{\circ}30'$	400-600	1956	Nimpkish River Valley
	B	2	Crown Zellerbach (Canada) Ltd.	$49^{\circ}45'$	1300-1700	1956	Courtenay
	C	1	MacMillan Bloedel Limited	$49^{\circ}10'$	2600-2900	56/57	Sugar Loaf Mountain, Chemainus River
	D	3	B. C. Forest Service	$48^{\circ}50'$	570-750	1955	Robertson Valley near Lake Cowichan
	E	15	University of British Columbia	$49^{\circ}10'$	500-700	1957	University of British Columbia Research Forest
Washington	F	16	Weyerhaeuser Company	$47^{\circ}30'$	39-4100	1957	Snoqualmie Area
	G	6	Simpson Olympic Tree Farm	$47^{\circ}15'$	100-500	1956	Shelton Area
	H	5	Dept. Nat. Resources, State of Wash.	$46^{\circ}45'$	1850-2000	1956	Elbe Area
Oregon	I	7	State Board of Forestry, Oregon	$45^{\circ}30'$	1600-2200	54/55	Tillamook Area
	J	9	Crown Zellerbach Corporation	$45^{\circ}10'$	1600-2000	1956	Clackamas Tree Farm
	K	10	Crown Zellerbach Corporation	$45^{\circ}10'$	3200-3800	1956	Molalla Area
	L	8	Jack Stump and Kenneth McCrae	$44^{\circ}50'$	200	1956	Willamette Valley, Salem Area
	M	11	Oregon State College	$44^{\circ}30'$	1800-2000	55/56	McDonald Forest, Corvallis Area
	N	12	U.S. Forest Service	$43^{\circ}45'$	1800-2000	1954	Oakridge Area
	O	13	U.S. Forest Service	$43^{\circ}45'$	2500-3000	1956	High Prairie, Oakridge Area
	P	14	Medford Corporation	$42^{\circ}20'$	2700-3300	1955	Butte Falls

Table 2 Distribution of the Seed Sources

a) British Columbia

Location	Elevation (feet)		
	0-1000	1000-2000	2000 +
N. Vancouver Island	Nimpkish(A)		
C. Vancouver Island		Courtenay(B)	
S. Vancouver Island	Robertson Valley(D)		Sugarloaf Mtn.(C)
Mainland	University of British Columbia Research Forest(E)		

b) U.S.A.

Location	Coast Zone			Valley Zone	Cascade Zone		
	0-1000	1000-2000	2000 +		1000-2000	2000-3000	3000 +
Washington	Shelton(G)	Elbe(H)					Snoqualmie(F)
Oregon		Tillamook(I)		Willamette(L)	Molalla(J)	Oakridge(O)	Molalla(K)
		Corvallis(M)	Butte Falls(P)		Oakridge(N)		

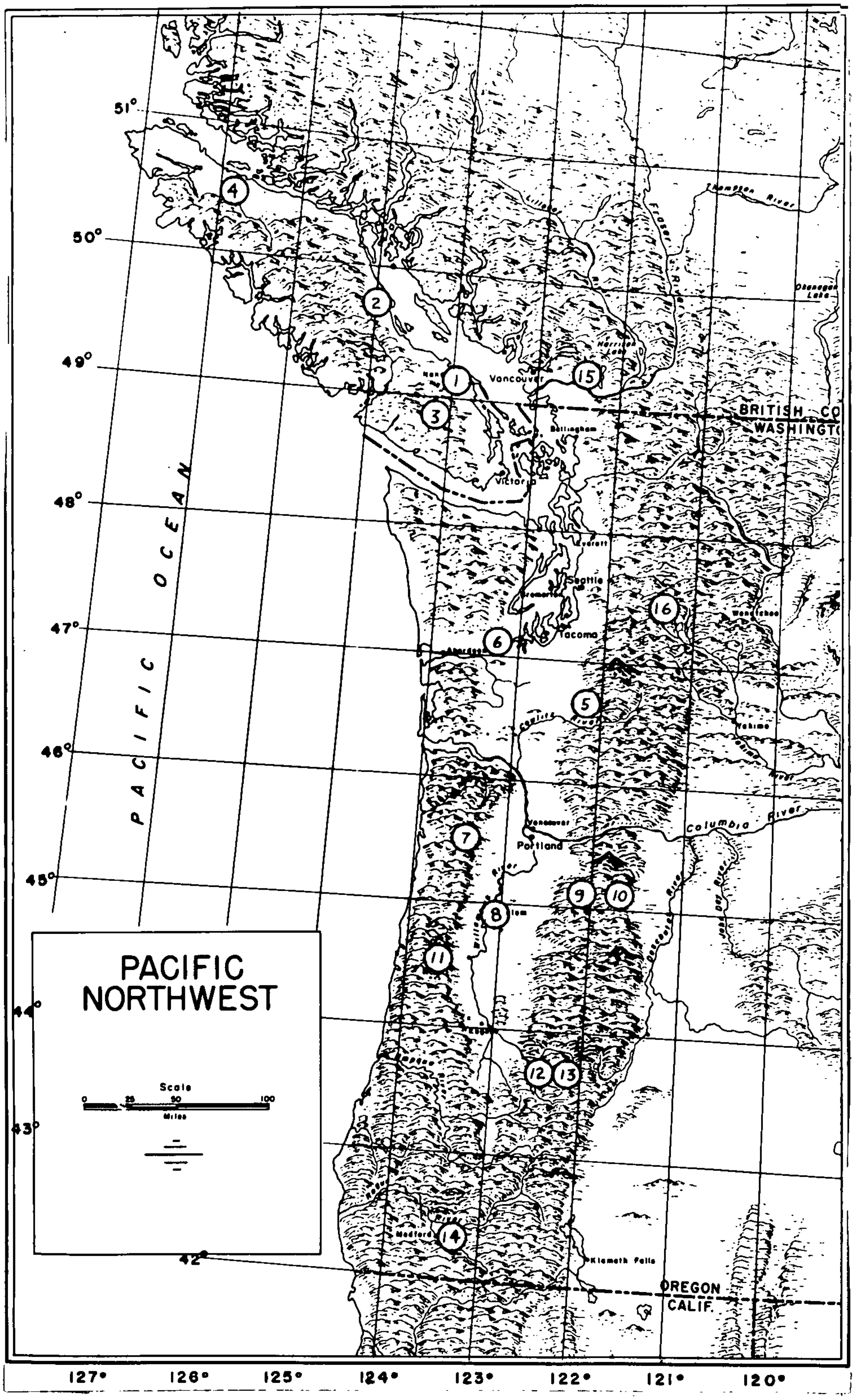

Figure 3 Geographic distribution of seed sources in the Pacific Northwest Douglas-fir provenance test.

which the seed lots reached the nursery (Table 1). For example, provenances E and F were the last ones to be sent to Corvallis and were thus assigned the numbers 15 and 16.

The following persons acted as regional co-ordinators:

Oregon	:	J.F. Gartz
Washington	:	J.W. Duffield
British Columbia	:	A.L. Orr-Ewing

The first overall co-ordinator was D.N. Bever of the Oregon State Board of Forestry; Professor K.K. Ching of the Oregon State University replaced him later on.

Phases

The study was separated into four distinct phases:

Selection of outplanting areas and seed collection

The selection of the test sites was left to the individual co-operator with approval by the regional co-ordinator. The test sites were to meet the following requirements:

i) be in the Douglas-fir type

ii) north to northwest aspect

iii) large enough to handle two six-acre plantations

iv) be on land expected to remain in permanent ownership

v) not to be relogged or have a heavy brush or herbaceous cover.

In areas where excessive deer browsing was expected, an eight foot fence was recommended.

It was not always possible to strictly meet all the requirements. Most good growing sites suffer from a brush invasion. Also, mountainous soils are extremely variable and therefore there may be undesirable site heterogeneity within as small an area as six acres. The cone collection areas were defined as having a radius of twenty-five miles in a designated area, at an elevation not differing from that of the outplanting area by more than two hundred feet (or exceptionally up to four hundred feet). A maximum of fifty trees should be picked at random to sample as much variation as possible, and to provide 3.2 pounds of seed from each area (Anon. 1955b). Seed crop permitting, the collections were started in the fall of 1954. The last two lots of seed (from the University of British Columbia Research Forest, i.e. seed source 15, and Snoqualmie, i.e. seed source 16) arrived at the nursery in Corvallis in fall 1957. The number of trees sampled ranged from fourteen to eighty-nine. Seed was extracted by various organisations. After an eighty-five percent cutting test was obtained, the clean seed was stored in a cold storage at zero degree Fahrenheit at the Oregon State Forest Nursery in Corvallis (Ching and Bever, 1960).

Nursery phase

In order to avoid confounding nursery effects, all seed was raised in Corvallis. Naked stratification was used by soaking the individual seed lots in plastic bags with water for forty-eight hours. After the water was drained off, the bags were placed in a cool room at 34 - 37 degrees Fahrenheit and 95 percent relative humidity, for three weeks (Ching and

Bever, 1960). The seeding rate was adjusted according to the viability of the seed lot. Sowing of fourteen seed lots was started on May 15 and completed on May 17, 1957. The first indication of field germination was noticed on May 28. The seedlings were lifted in late February 1959 (i.e. as 2-0 stock) and culled according to criteria advocated by Edwards (1956). All seedlings with less than a four inch top, were discarded. Due to a poor cone crop, seed lots E (from the University of British Columbia Research Forest) and F (Snoqualmie) were shipped to the nursery one year after the other provenances, and sown in the spring of 1958; consequently trees from these two origins were to remain one year younger than the others throughout the duration of the co-operative study.

Planting of the nursery stock

The original plan specified one planting crew in each region (Oregon, Washington, British Columbia). This did not prove feasible, and planting was carried out by individual co-operators in fall 1959 or spring 1960. The test sites had previously been adequately prepared.

Field examinations

Co-operators were provided with thermometers, rain gauges and standardized field tally sheets. Current and total height growth was to be assessed in metric units and records kept on flushes, frost and other damage.

Results

Ching (1958) reported on first year performance of fourteen provenances (the University of British Columbia Research Forest seedlot and the Snoqualmie source were sown one year later than the others) in the nursery at Corvallis. Height growth, bud burst and bud set, as well as frost damage were assessed and genetic variations found. Seedlings from the Nimpkish Valley, Vancouver Island, and from Butte Falls, Oregon, i.e. from both latitudinal extremes of the study, showed a definite trend of inferior growth. Some significant differences in the susceptibility to frost damage were found, but caution was expressed to avoid premature conclusions.

Ching and Bever (1960) reported on two years' nursery performance. They found no correlation between the height of the seedlings and the altitude of their place of origin, although they did find significant differences in needle length between various provenances and some correlation between needle length and total height growth. Except for the Nimpkish Valley provenance, the Vancouver Island sources compared favorably with the local Willamette Valley provenance, as far as height growth was concerned. Under the shorter photoperiod in Oregon, the Vancouver Island sources, excepting the Nimpkish one, formed their buds earlier and terminated their growth earlier than others. The fact that the southernmost provenance (Butte Falls) did not show increased height growth under the slightly longer photoperiod at Corvallis, was interpreted to be a result of natural selection for early cessation of growth in an environment characterized by severe summer droughts. High elevation origins showed a tendency toward late bud bursting, as an adaptation to late spring frosts. No correlation was found between time of bud burst and annual height growth.

Ching (1960) reported on survival of fourteen provenances on eleven test sites after the first growing season in the field. Height was measured in four plantations.* Except for the Nimpkish Valley provenance, the Vancouver Island sources compared very favorably with all others, the Sugar-Loaf Mountain origin (C) being among the three best in all four plantations.

Walters and Soos (1961b) based their studies regarding lammas growth on the University of British Columbia Research Forest on Douglas-fir seedlings, including the co-operative test. Their findings, e.g. that lammas growth is greatly influenced by environment have been reviewed above. The same authors (1961a) investigated the efficiency of various chemicals to prevent hares from damaging the young Douglas-fir trees. The repellents used did not prove adequate; protection of the natural predators of the hares was suggested as a better means of keeping the varying hare population in check.

Heaman (1963) reported on the project in British Columbia for the years 1954-1961. Mortality and height growth after the 1960 and the 1961 growing seasons were assessed for the five outplanting areas in the province and weather data

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*Unless otherwise defined, "plantation" is synonymous with "test site" or "outplanting area."

were discussed. Heaman's criticism covered the following points:

1. Scope of the study.

   The scope of the co-operative study was too wide, covering eight degrees of latitude. According to Schmidt's (1962a) classification, the co-operative test falls into the category of "studies of broad geographic variation." This type of study cannot be expected to yield more than broad generalizations. Information gained from such a project can be used to design a more intensive one in the future, but as the results cannot be reliably interpreted for at least twenty years, this is a lengthy approach. Practical applications, such as seed transfer rules, cannot be expected.

2. Cone collection.

   The cone collection was not carried out in a uniform way by all co-operators. Apart from this, the twenty-five mile collection radius was too large, despite the limitation of collecting within four hundred, preferably within two hundred feet of the elevation of the testing site. Heaman supported his criticism with records from five weather stations lying within those limitations in a twenty-five mile radius of the Robertson Valley. The average frost free period, the major climatic criterion of the co-operative study, between two extreme stations, varied from fifty-one to two hundred and forty-four days!

3. Weather records.

   Heaman deplored the lack of continuity and standardization. Some co-operators measured temperatures at two feet, others at four, others still at five feet above the ground. At the Nimpkish test site in 1960, a frost free period of eleven weeks was recorded at two feet above the ground and twenty-two weeks at five feet above the ground.

4. Site selection.

   Heaman felt that more care could have been exercised in site selection. For instance, it might have been recognized from the start that the Robertson Valley plantation was located in a frost pocket. A frost free period of only six weeks was measured at two feet above the ground in 1960.

Heaman found no correlation between height growth and elevation or latitude of seed source. There was no correlation between either seed weight and height growth or between germination percentage and seed weight during the first year.

At Nimpkish and Courtenay, the low elevation source G (Shelton) and the high elevation source C (Sugar-Loaf Mountain) showed best performance, although they did not prove significantly superior on all British Columbia test sites.* The

*Heaman did not test the provenance x block interaction, although he pointed to the site heterogeneity at the University of British Columbia Research Forest.

unusual early growth of Shelton (G), if endorsed by more reliable data in the future, was interpreted as a possible confirmation of the hypothesis that " ... distinct races of Douglas-fir have resulted from the development of genetic strains in localized areas ... " Heaman concluded that significant deductions could not be made because of the short duration of the experiment, the incompleteness and lack of standardization of weather data, and because of the excessive damage at some test sites by frost* and browsing.

The following were Heaman's recommendations:

1. Provenance studies should be of a smaller scope than the co-operative test, and sample the range of a species much more intensively within much narrower latitudinal limits.

2. Standardization and controls in all phases of a co-operative study by one co-ordinator in constant personal contact with all involved, are essential.

3. Cone collection areas have to be clearly defined and based on a thorough local knowledge.

4. Growth studies should be based on phenological observations instead of tedious weather measurements.

5. A comprehensive study of all outplanting areas is necessary regarding climate, soil and micro-topography.

6. The plantations have to be protected efficiently from animal damage, if early assessments are to have any meaning, unless it can be established that the damage is evenly distributed over all sources.

Ching (1965) assessed survival and growth after the

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*The Robertson Valley plantation was seriously damaged by frost.

first three years in the field for fourteen provenances at eight outplanting areas. Early survival was highest near Nimpkish. At most plantations, trees from the local source grew as well as those from the three best sources. Trees from seed collected at the northern and southern extremes (Nimpkish and Butte Falls, respectively) grew least in the three years (as they had in the nursery). Never damaged trees were no more than slightly different in height growth from those that had been damaged.

Christmas tree growers systematically evaluated trees in three locations in 1964 (Douglass 1967). The Salem provenance (L) was found to be the best Oregon source and Shelton (G) the best representative from Washington. The Robertson Valley (D) origin ranked highest in all three locations investigated. It combined a number of desirable qualities, such as high vigor, dark green colour, upright growth habit, natural tendency for bushiness, and an attractive needle arrangement.

Walters and Ching (1969) studied the pattern of bud burst of the sixteen provenances* at the University of British Columbia Research Forest and in the Willamette Valley. The results have been reviewed on page 12. In a report on field performance at age nine, Ching (1967) assessed survival and height growth in ten locations.** Trees from Oakridge (N) and from the

* Sources E (University of British Columbia Research Forest) and F (Snoqualmie) were included for the first time.

**Since their establishment in 1959, the following plantations southernmost source P (Butte Falls) were consistently poor in height growth. Ching concluded that high elevation stock can safely be planted at lower altitudes, whereas it would be unwise to do the opposite. Plotting height growth against elevation and latitude did not reveal a significant correlation. Finally, another investigation (Mitchell and Nagel, 1969) revealed that attack by Douglas-fir needle midges (mainly *Contarinia pseudotsugae* Condrashoff) was correlated to date of bud burst, the damage being highest on early flushing trees.

V. METHODS

The Study Area

General description of the University of British Columbia Research Forest

The University of British Columbia Research Forest, at $49^{o}18'$ latitude north and $122^{o}35'$ longitude west, is situated four miles north of Maple Ridge, formerly Haney, in the Fraser Valley of British Columbia, on the south fringe of the Coast Mountains, at a distance of 36 miles from the University

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have been lost:
1. D - Robertson Valley, both plantations abandoned due to frost damage.
2. G - Shelton. One plantation lost to grass fire.
3. I - Tillamook. Both plantations heavily damaged by rabbits.
4. J - Molalla. Both plantations suffered from rabbit damage.
5. N - Oakridge area. Both plantations lost to deer damage.
6. P - Butte Falls. Both plantations lost to drought. (Ching 1969, personal communication.)

of British Columbia Campus in Vancouver (U.B.C. Forest Committee 1959). It comprises approximately twelve thousand seven hundred acres of forested land, and is bounded on the north and east by Garibaldi Provincial Park and by Pitt Lake on the northwest. Elevations range from sea level to 2600 feet. The area lies within the southern Pacific coast section (C.2) of the coastal forest according to Rowe (1959) and in the coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone according to Krajina (1959). The main association comprises the two coastal dominants western red cedar (*Thuja plicata* Donn.) and western hemlock, with coastal Douglas-fir and scattered western white pine, Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) (Walters and Soos, 1961b).

Climate

The climate, described in detail by Griffith (1968) who used data from the four weather stations on the Research Forest, is considerably influenced by the relatively warm and moist air of the Pacific Ocean and by the Coast Mountains. The summers are warm and dry, the winters relatively mild and wet. Temperature seldom reaches 90 degrees Fahrenheit, the absolute minimum on record being five degrees Fahrenheit below zero. The annual precipitation averages about 89 inches in the southern part of the Forest, where the provenance test site is located, but increases in the higher elevation areas to the north. The high amount of precipitation has a pronounced effect on the soils which are strongly leached podsols and are very acidic.

The weather station outside the Administration Building at an elevation of 475 feet above sea level is the one closest to the study area, the climate of which can be assumed to be practically the same. For the years 1959 to 1967 inclusive, i.e. the years relevant to this thesis, the following data were published by Griffith (1968):

Precipitation:

Annual average	89.09" (Min. 75.88" - Max. 95.83")
October to March	63.57" or 71.35% of the annual total
April to September	25.52" or 28.65% " " " "
July (driest month)	2.70" or 2.97% " " " "
December (wettest month)	12.64" or 14.19% " " " "
Winter snowfall	24.4"
Number of days with measurable precipitation	192

Temperature:

Annual mean	49.1°F (Min. 47.6 degrees - Max.
July (hottest month)	63.2°F 51.0 degrees Fahrenheit)
January (coldest month)	35.9°F
Absolute minimum	2°F
Absolute maximum	98°F
Frost free period, average	200 days (Min. 165 - Max. 243)

Average date of last spring frost: April 14
Average date of first fall frost : November 1

May frosts are fairly frequent but September frosts are rare. For the five-year period 1953-1957, average length of the growing season, as indicated by cambial activity resulting in diameter increment, was 146 days (ranging from a minimum of 107 days to a maximum of 163 days) according to Griffith

(1960). Since the co-operative provenance test sites, at an elevation of approximately 500 feet above sea level, are at a slightly lower elevation than the weather station used by Griffith in his 1960 study, the growing season there can be assumed to be of slightly longer duration.

Location of the co-operative provenance test on the Research Forest

Plantation I (i.e. blocks 1 and 2) is situated between Mainroad F and Spur A-10; plantation II (i.e. blocks 3 and 4) is adjacent to Branch Road A on the eastern side of the North Alouette River. Both plantations are within less than one-half mile of each other and less than a mile from the Administration Building in the southeast corner of the Research Forest (see Fig. 5).

History of the test site

Prior to logging in 1955-1956, the area supported the following volumes (in thousand board feet, B.C. rule):

	Live Douglas -fir	Dead Douglas -fir	Live Cedar	Dead Cedar	W.Hem- lock	Total	Vol/ acre	Cedar poles
Pltn I*	15	9	95	4	132	255	18.4	--
Pltn II**	260	-	435	69	208	972	43.2	69

The area of plantation I was logged by high-lead which caused relatively little soil disturbance, the area of

*Area was part of a 14 acre stand.

**Area was part of a 22 acre stand.

plantation II was yarded by tractor, requiring an intensive network of skidroads resulting in heavy soil disturbance. The slash, burning poorly in a first attempt, particularly in plantation I, was piled and re-burnt in 1958 (Heaman 1963). Since the material was collected by hand and no heavy equipment was used for site preparation, there was minimal mechanical soil disturbance. Much debris remained. Vine maple (Acer circinatum Pursh.) was successfully sprayed in spring 1959 with 2,4-D, 2,4,5-T. Draining was carried out in portions of plantation II by blasting a ditch.

The seedlings were planted in the spring of 1959. The nursery planting stock (2-0 Douglas-fir) was generally of poor quality and despite close supervision of the planting operation, examination of Armillaria mellea (Fr) Kumm. infected root systems several years later suggested that the presence of the disease could possibly be related to a poor planting technique (Walters 1964). The area was covered by fireweed (Epilobium augustifolium L.) six feet tall, but the real problem the first year was browsing by hares. In addition to a trap line, chemical repellents were used in May 1959, but they did not prove adequate if used alone (Walters and Soos, 1961a). By 1961 it appeared that almost all of the seedlings had grown away from the browsing zone for hares, therefore no additional treatments were planned (Walters 1961).

Mortality was fairly high: 365 trees were found dead in fall 1959, 380 died in 1960, and 140 in 1961. These figures apply only to the "inner blocks" with forty-nine numbered stakes (see under "design"). All mortality was replaced in the spring of 1960 and 1961 by seedlings that were themselves frequently of poor quality. In 1963 the area was weeded by machete and brush hooks, and then concentrations of vine maple and salmonberry (*Rubus spectabilis* Pursh.) sprayed with 2,4-D, and 2,4,5-T in diesel oil (Walters 1964). *Vaccinium* spec. was never treated but possibly impeded tree growth wherever it occurred in thick concentrations (see below). The four blocks were again treated chemically in August 1965. Infections by *Armillaria* continued during that year (Walters 1966). In 1966 the sixteen provenances produced flowers and cones for the first time (Walters 1967). Height growth had been assessed at the end of 1960, 1961, 1964 and 1965.

Height Measurements

For this thesis, the height of all surviving numbered trees was measured after the 1967 growing season when most trees were eleven years old. Since trees of the local source (University of British Columbia Research Forest) and from Snoqualmie (F) were one year younger than the rest, it seemed reasonable to measure them one year later, although no two growing seasons are quite the same. The primary objective in analyzing the height measurements taken at the University of British Columbia Research Forest, was to determine whether significant growth differences between provenances were showing at an early age, and if so, to try and correlate them with geographic variables. A secondary objective was to evaluate the site homogeneity at the Research Forest.

Statistical Analysis

Height measurements for simple analysis of variance were analyzed on computers at the University of British Columbia.

VI. RESULTS AND DISCUSSION

Height at Age Eleven

The analysis of variance of height measurements showed the block x provenance interaction to be significant. This means that:

a) The individual provenances behave differently in the four blocks.

b) The plantation site is not homogeneous.

c) The four blocks have to be evaluated separately.

d) No statistical conclusion as to the overall performance, such as superior growth, of any particular provenance, can be drawn, i.e. the provenances cannot be ranked on a statistically sound basis.

e) Unless the prerequisites for co-variance analysis can be met, which would allow comparisons of overall performance of all provenances, the results at the University of British Columbia Research Forest do not justify at this stage a confirmation or rejection of any hypothesis that the co-operative study set out to test, nor do the results justify a positive answer to the question whether significant growth differences between provenances are showing at an early stage. Similarly, seed transfer rules cannot be established with these results.

An attempt was therefore made to find a quantifiable parameter related to site, that would allow an accurate explanation of the different behaviour of the individual provenances in the four blocks, after bringing everything down to the same basis. Griffith (1960) studied the growth of Douglas-fir in relation to climate and soil at the Research Forest and found that available soil moisture in the B-horizon during the growing season was the most important single variable affecting tree growth. Theoretically it is easy to get a valid idea of the soil moisture regime of an area by breaking it down into its major indicators: slope (percent), soil depth, position on slope, aspect. It would indeed be helpful to know what percentage of each plot* suffers from adverse conditions, such as excessive moisture or abnormal soil disturbance, for instance. By weighing the performance of each plot accordingly, that is, by trying to eliminate varying environmental influences, a better picture of the growth potential of that particular provenance could be arrived at. The following map was drawn by Mr. D. Ormerod, in an attempt to illustrate the soil moisture regime in the four blocks (see Fig. 4).

Despite the help of the map, it proved difficult in the field to get an accurate estimate of soil moisture, due to the extreme variability in microtopography even within the various plots. It was felt that such an evaluation would too easily be subjective and therefore incorrect and inadequate.

Mr. L. Lacelle, a graduate student in soil science

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*Plot means any provenance in any block.

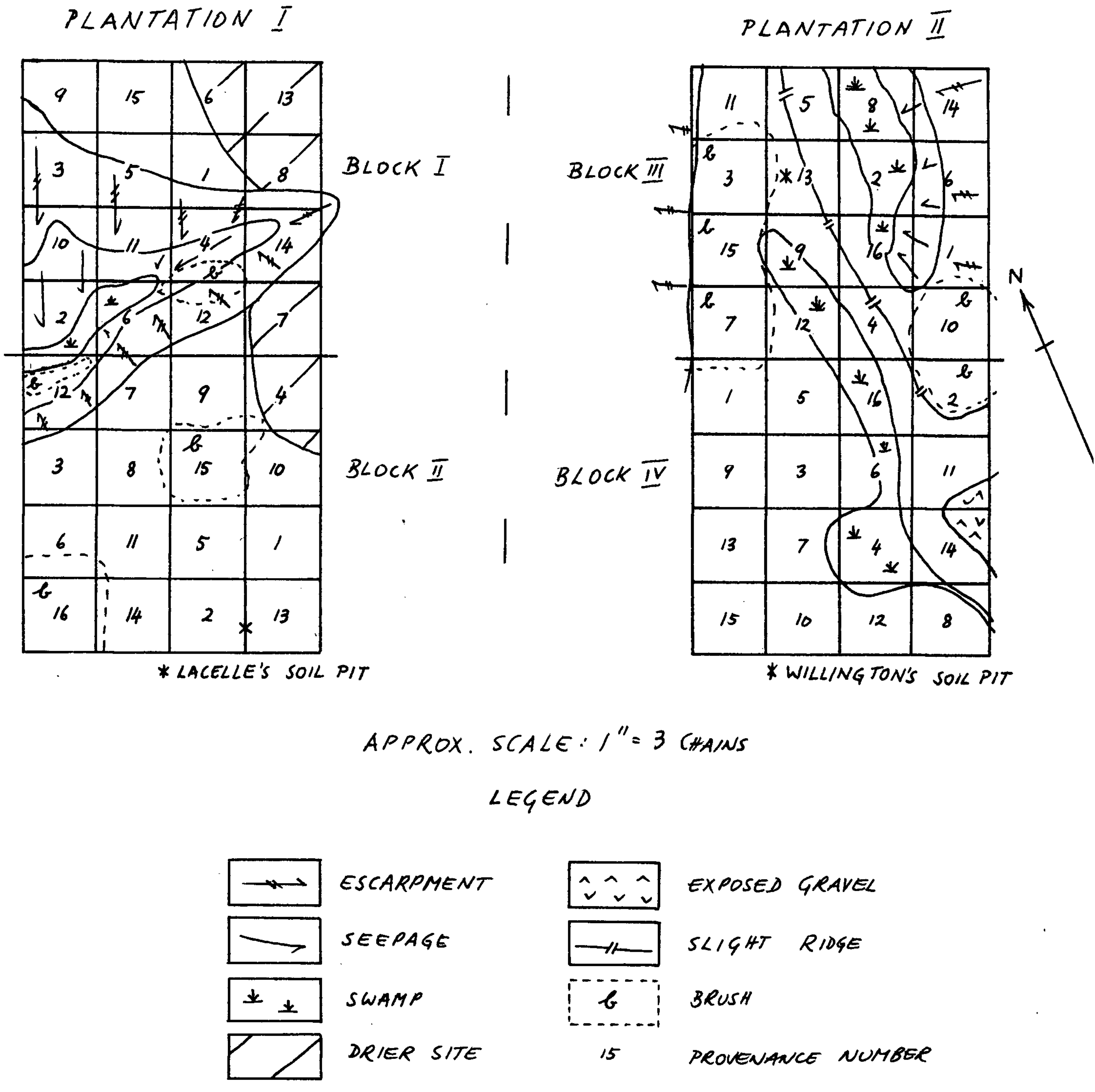

Figure 4 Ormerod's map.

at the University of British Columbia, kindly dug several soil pits in both plantations and came to the conclusion that the soil was roughly the same in all four blocks, except for small areas that showed the effects of mechanical disturbance due to logging, and also excepting areas with a different water regime due to their microtopography. Mr. Lacelle described the soil in block B, plantation I, as a mini-orthic-humoferric podzol, moderately well drained to well drained. According to Willington (1968), the soil in block C, plantation II, is a moderately well drained orthic podzol, developed in outwash parent material overlying Whatcom glaciomarine. Walters (1970) thinks that the cemented layer underlying the soil at varying depths, has to take part of the blame for the variability in site in some plots by affecting the direction of the seepage flow.

A co-variance analysis therefore could not be carried out due to the lack of a detailed analysis of the physical, chemical and hydrological soil properties of the different plots which would each require a great number of samples due to the extreme variability in microtopography. It is hoped that such a study will be made and more conclusive information will be gained from the provenance study at the Research Forest. According to a personal communication by Ching (1970), a graduate student of Oregon State University, collected many soil samples from eleven outplanting areas. His results will probably throw some light on the effect of microedaphic differences on tree growth. Heaman (1963) pointed out the site variability at the University of British Columbia Research Forest, as exemplified by a gulley in plantation I, caterpillar roads, a gravel pit, and swampy areas in plantation II. However it should be noted that, given the limited area and the knowledge at the time of the soils, the site chosen was by far the best one available. In another Douglas-fir provenance study at the Research Forest, Haddock et al. (1967) found a significant provenance x block interaction, too, reflecting possibly " ... the heterogeneous nature of the site, typical for coastal mountain country in British Columbia."

Results by Individual Blocks

Separate analyses of variance for height performance were carried out. The results are listed in Table 3.

The wide range, strikingly exemplified by three provenances (Nimpkish, Tillamook and higher elevation Molalla), showing a difference of thirteen ranks, out of a possible maximum of fifteen, between their shortest and their tallest performance, can be interpreted to mean either that:

1. The genetic variability of Douglas-fir is such that four replications of 49 trees each for every provenance are not enough to cover it.

To support this one could point to the fact that, when walking through the study area at the Research Forest, one is struck not only by the variability in growth between some provenances (e.g. seed source 4, Nimpkish, and 16, Snoqualmie in block III) but also by the fact that in every plot, no matter how poor its average performance, there is at least one tree doing much better than the rest. The best example of this can be found in block IV, plot 4, Nimpkish, where one particular

Ranking of Provenances

Provenance #	Origin	Block I	Block II	Block III	Block IV	Average	Range
1=C	Sugar Loaf Mountain, Vancouver Island	6	3	1	8	4.5	7
2=B	Courtenay area, Vanc. Island	8	2	7	12	7.2	10
3=D	Robertson Valley, " "	3	8	13	9	8.2	10
4=A	Nimpkish Valley, " "	10	11	2	15	9.5	13
5=H	Elbe area, Washington	12	7	8	5	8.0	7
6=G	Shelton area, "	4	1	3	4	3.0	3
7=I	Tillamook area, Oregon	5	6	16	3	7.5	13
8=L	Salem area, "	11	13	12	6	10.5	7
9=J	Molalla, lower elevation "	13	5	11	10	9.8	8
10=K	Molalla, higher elevation "	2	15	15	2	8.5	13
11=M	Corvallis area, "	9	9	9	13	10.0	4
12=N	Oakridge, lower elevation "	14	16	4	14	12.0	12
13=O	Oakridge, higher elevation "	16	4	14	7	8.2	12
14=P	Butte Falls, "	15	12	10	16	13.2	6
15=E	U.B.C. Research Forest, British Columbia	1	10	5	1	4.2	9*
16=F	Snoqualmie area, Washington	7	14	6	11	9.5	8

Table 3 Height performance at age eleven. Ranking is from tallest (1) to shortest (16).

tree is growing vigorously in a swampy place, with most of its neighbours looking chlorotic and stunted in apparently the same micro-environment. This is an interesting parallel to a finding in the 1912 Douglas-fir heredity study by the U.S. Forest Service (1964): "An anomaly to the interaction exists in the following sense: Almost without exception the progenies of every parent include at least one superior individual at each

*The local provenance.

location. This indicates surprising genetic diversity within a restricted source of germ-plasm such as a single seed lot."

The wide range in ranking could also mean that:

2. This site is extremely heterogeneous. This alternative is supported by the significance of the interaction term and illustrated for instance by the above-cited source 4 (Nimpkish). It is second tallest in block III where its outstanding performance can be detected from a 1 : 6300 scale aerial photograph. In block IV it is the third poorest in terms of height growth, probably because it has to grow in a rather swampy place.

Aerial photographs of the study area show evidence in favour of the "site heterogeneity" - rather than the "genetic variability" alternative. Patches of poor growth (marked with "P" on Figure 5) show up very well. They ignore plot boundaries and quite likely reflect edaphic differences.

Tables 4 to 7 show height performance within the individual blocks for 1967. 1964 and 1961 are included for comparison. The brackets show the results of Duncan's New Multiple Range Test.

Early Tests

Trying to find correlations between the 1960, 1964 and 1967 measurements (at age 4, 8 and 11 years) is almost an exercise in futility for the following reasons:

1. Duncan's New Multiple Range Test shows that

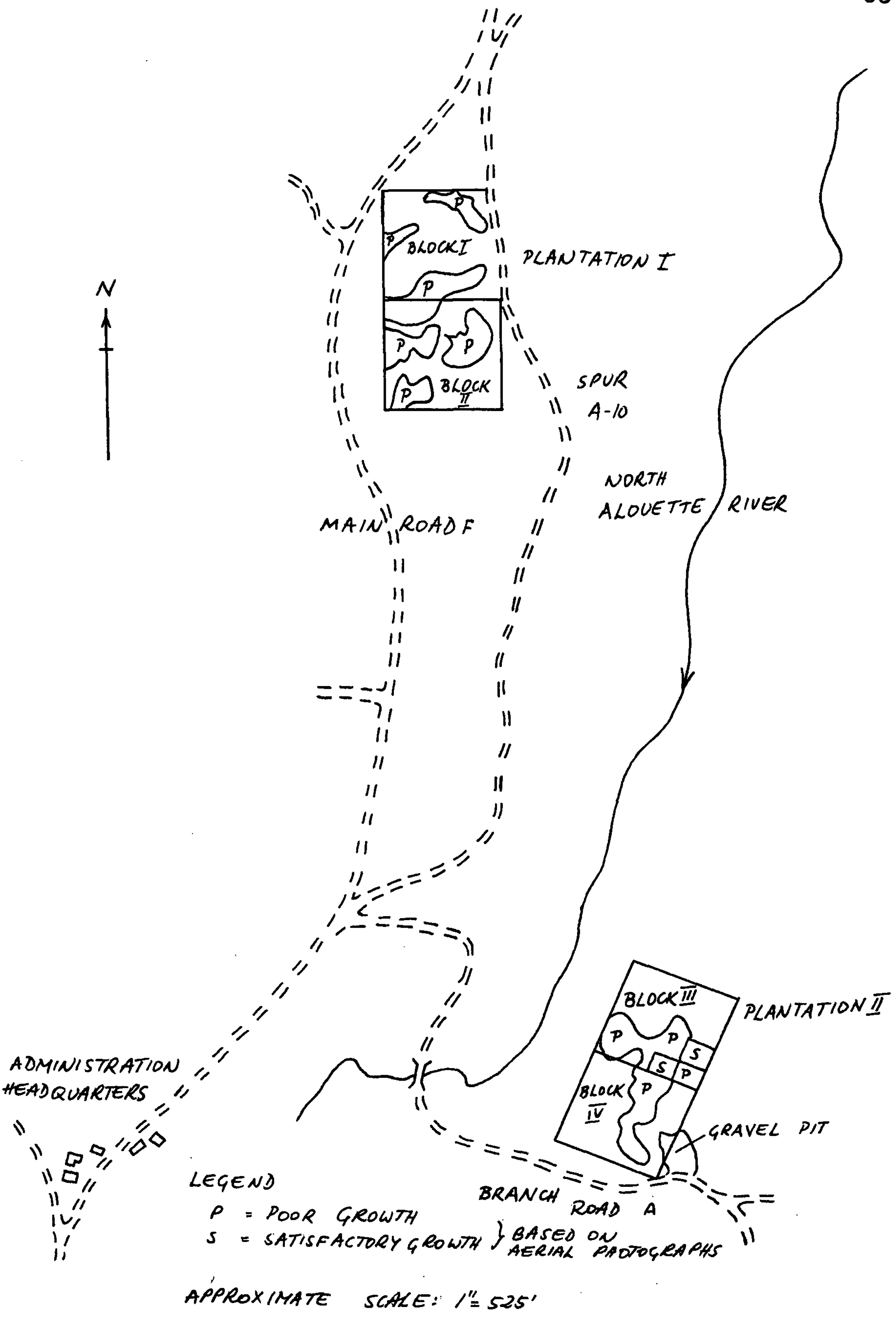

Figure 5 Location map of the co-operative provenance test at the University of British Columbia Research Forest.

	1960			1964			1967			
	Prov.	Ht(cm)	% of Mean	Prov.	Ht(m)	% of Mean	Prov.	Ht(m)	% of Mean	Rank
Rank 1	10	49.27	139	15	2.5980	125	15	5.7333	124	1
2	2	39.71	112	10	2.5927	119	10	5.2458	114	2
3	1	38.92	110	3	2.3959	110	3	5.1694	112	3
4	15	38.02	108	6	2.3857	109	6	5.1163	111	4
5	3	37.65	106	1	2.3653	109	7	4.7766	103	5
6	6	37.57	106	7	2.2687	104	1	4.7633	103	6
7	11	36.47	103	2	2.2330	103	16	4.6405	100	7
8	14	35.67	101	11	2.1787	100	2	4.6045	100	8
9	16	34.59	98	16	2.1511	99	11	4.5410	98	9
10	7	34.31	97	4	2.1142	97	4	4.5349	98	10
11	5	33.43	95	8	2.0777	96	8	4.4957	97	11
12	9	33.31	94	5	2.0719	95	5	4.4043	95	12
13	4	32.84	93	9	1.9826	91	9	4.2523	92	13
14	12	32.14	91	14	1.8511	85	12	3.8682	84	14
15	8	31.49	89	12	1.7789	82	14	3.7109	80	15
16	13	20.65	58	13	1.5447	71	13	3.6081	78	16

Table 4 Height performance. Block I

Any two provenances covered by the same bracket are not significantly different.

	1960			1964			1967			
	Prov.	Ht(cm)	% of Mean	Prov.	Ht(m)	% of Mean	Prov.	Ht(m)	% of Mean	Rank
Rank 1	6	47.76	132	6	2.7354	127	6	5.2543	116	1
2	5	43.94	121	2	2.4056	112	2	5.0133	110	2
3	1	43.81	121	9	2.3833	111	1	4.9556	109	3
4	2	41.71	115	1	2.3830	111	13	4.8581	107	4
5	9	40.39	112	7	2.3605	110	9	4.8045	106	5
6	7	39.96	110	5	2.3372	109	7	4.7905	105	6
7	13	39.89	110	13	2.3262	108	5	4.6804	103	7
8	11	37.33	103	14	2.1228	97	3	4.5974	101	8
9	14	35.47	98	11	2.0292	94	11	4.4109	97	9
10	3	34.85	96	3	2.0273	94	15	4.4043	97	10
11	10	31.35	87	10	1.9939	93	4	4.3667	96	11
12	4	30.33	84	8	1.9622	91	14	4.3200	95	12
13	12	29.12	80	4	1.9221	89	8	4.3111	95	13
14	8	28.53	79	15	1.9156	89	16	4.0958	90	14
15	15	27.39	76	16	1.8323	85	10	4.0673	89	15
16	16	26.58	73	12	1.6664	77	12	3.8930	86	16

Table 5 Height performance. Block II

Any two provenances covered by the same bracket are not significantly different.

	1960			1964			1967			
	Prov.	Ht(cm)	% of Mean	Prov.	Ht(m)	% of Mean	Prov.	Ht(m)	% of Mean	Rank
Rank 1	6	40.61	133	1	2.4781	134	1	5.1375	132	1
2	4	38.35	125	4	2.3553	128	4	5.0000	128	2
3	1	36.71	120	6	2.3178	126	6	4.3238	111	3
4	2	34.47	115	11	1.9087	103	12	4.0804	105	4
5	5	34.10	111	14	1.8967	103	15	4.0390	103	5
6	11	31.81	104	2	1.8890	102	16	3.9786	102	6
7	7	30.86	101	12	1.8670	101	2	3.8317	98	7
8	3	30.10	98	5	1.8062	98	5	3.8062	98	8
9	14	29.96	98	8	1.7512	95	11	3.7111	95	9
10	12	29.96	98	15	1.7354	94	14	3.6795	94	10
11	9	29.29	96	16	1.7198	93	9	3.6565	94	11
12	8	26.17	85	9	1.6796	91	8	3.6325	93	12
13	13	25.90	85	3	1.6459	89	3	3.5980	92	13
14	16	24.42	80	7	1.5844	86	13	3.2907	84	14
15	15	23.77	78	13	1.4844	80	10	3.2675	84	15
16	10	21.78	71	10	1.3400	73	7	3.2646	84	16

Table 6 Height performance. Block III

Any two provenances covered by the same bracket are not significantly different.

	1960 Prov.	1960 Ht(cm)	1960 % of Mean	1964 Prov.	1964 Ht(m)	1964 % of Mean	1967 Prov.	1967 Ht(m)	1967 % of Mean	Rank
Rank 1	10	43.88	137	15	2.7622	137	15	5.9204	140	1
2	7	41.00	128	10	2.6435	131	10	5.1404	122	2
3	15	40.67	127	7	2.4098	120	7	4.9128	117	3
4	5	38.22	120	5	2.2940	114	6	4.5889	109	4
5	1	33.30	104	8	2.1596	107	5	4.5755	109	5
6	3	32.86	103	6	2.1000	104	8	4.4553	106	6
7	6	32.50	102	1	2.0600	102	13	4.3683	104	7
8	2	31.94	100	13	2.0284	101	1	4.0911	97	8
9	9	31.39	98	3	1.8378	91	3	4.0347	96	9
10	13	30.06	94	9	1.7937	89	9	3.8612	92	10
11	16	27.32	85	11	1.7735	88	16	3.8372	91	11
12	4	26.66	83	2	1.7232	86	2	3.7275	88	12
13	12	26.47	83	16	1.7170	85	11	3.6163	86	13
14	8	25.79	81	12	1.6625	83	12	3.6159	86	14
15	11	24.67	77	4	1.5133	75	4	3.2441	77	15
16	14	22.69	71	14	1.4685	73	14	2.9545	70	16

Table 7 Height performance. Block IV

Any two provenances covered by the same bracket are not significantly different.

the provenances do not respond similarly in the four blocks.

2. Three observations of such variability are not enough for significant regression equations. Assuming these observations to be on a straight line is making a very rough approximation.

It was therefore not surprising that multiple regression analysis did not lead to any spectacular findings. Although the trend in height growth within the same block seems to be comparable, the slopes are similar, the heights themselves are not, except within very small groups of two or three provenances, since the intercepts are significantly different. Even if the site were homogeneous the trees might still be too young for meaningful early tests.

<u>Brush Competition</u>

Vine maple, salmonberry and other species were repeatedly treated chemically and mechanically in an effort to prevent them from competing with Douglas-fir. There is no doubt that <u>Vaccinium</u> spp. occurring in several concentrations (marked "b" for brush on Ormerod's map, page 63) and growing up to four feet tall, account for some of the variability termed "site heterogeneity." The experimental trees outgrew this brush in the last few years. Table 8 shows the height increment of the last three growing seasons (1964-1967) before the measurements for this thesis were taken. This difference was calculated in an attempt to eliminate, in theory, the effect of brush competition on height growth. It would be incorrect to assume that once the trees are taller than the brush, they grow completely unimpeded.

Vaccinium spp. is definitely still competing for soil moisture and nutrients. Nevertheless, the height increment in those three years shows a slightly different ranking for many plots where some trees obviously suffered from brush competition. It

		Ranking of Provenances					
		Block					
Provenance #	Origin	I	II	III	IV	Average	Range
1=C	Sugar Loaf Mountain, Vancouver Island	11	3	1	10	6.2	10
2=B	Courtenay area, Vanc. Island	12	1	10	13	9.0	12
3=D	Robertson Valley, " "	2	5	12	8	6.8	10
4=A	Nimpkish Valley, " "	6	7	2	14	7.2	12
5=H	Elbe area, Washington	8	12	8	7	8.8	5
6=G	Shelton area, "	3	6	6	4	4.8	3
7=I	Tillamook area, Oregon	7	8	16	3	8.5	13
8=L	Salem area, "	9	10	9	6	8.5	4
9=J	Molalla, lower elevation "	13	9	7	11	10.0	6
10=K	Molalla, higher elevation "	4	16	11	2	8.2	14
11=M	Corvallis area, "	10	11	15	15	12.8	5
12=N	Oakridge, lower elevation "	14	14	4	12	11.0	10
13=O	Oakridge, higher elevation "	15	4	14	5	9.5	11
14=P	Butte Falls, "	16	15	13	16	15.0	3
15=E	U.B.C. Research Forest, British Columbia	1	2	3	1	1.8	2*
16=F	Snoqualmie area, Washington	5	13	5	9	8.0	8

Table 8 Height performance between the years 1964-1967. Ranking is from tallest (1) to shortest (16).

is true, however, that the provenance x block interaction is still significant in the analysis of variance, meaning that *Vaccinium* cannot take all the blame for the heterogeneity in site.

*The local provenance.

The Local Provenance

In terms of height increment for the years 1965-1967 inclusive, the local source (University of British Columbia Research Forest) all of a sudden ranks second tallest in block II where it held a meager tenth position for total height, when brush was not taken into account. In block III it moves from fifth to third position. Of all provenances tested, it shows the narrowest range (from third position in block III over second in block II to first in blocks I and IV). One is tempted to call it the best of all provenances as to overall performance if it were not for the harsh laws of statistics forbidding this conclusion against the background refrain of a significant block x provenance interaction. The performance of the local source at this stage might indicate that several years from now the effects of temporary "juvenile handicaps" such as brush competition, for instance, will disappear and inherent differences that the co-operative study set out to test, will appear. It may also be speculated that the ill effects of soil compaction caused by logging, as illustrated by Pearse (1958), may gradually fade as the roots loosen the soil.

In tables 4 to 7 this "upwards" trend of the local source can be followed for the years 1960-1964-1967.

In block	I	it moves from	4th	position to	1st
" "	II	" " "	15th	" "	10th*
" "	III	" " "	15th	" "	5th
" "	IV	" " "	3rd	" "	1st

In blocks I and IV the local source (University of

*Brush competition is still a problem in this plot.

British Columbia Research Forest) is significantly different from (i.e. superior to) all other sources after the 1967 growing season. Table 6 also shows that every British Columbia provenance ranks at least once, first or second tallest. If any provenance can be rated as inferior it will be Butte Falls. This is not surprising considering the difference in climate between Butte Falls and the University of British Columbia Research Forest where the temperature regime differences are more pronounced than in southern Oregon. The Butte Falls provenance is doing poorly in every block, even in block C, where it can be said to profit from a slight amount of seepage water.

How do These Results Compare with Earlier Results?

Ching (1965) in his report on early growth, did not find any significant differences between provenances at the University of British Columbia Research Forest for 1960 and 1961. He listed the sources as to their overall performance, without mentioning the provenance x block interaction which was found to be significant in the present study. In his summary, Ching stated that " ... trees from the local seed source grew as well as did those from the best three sources." The results after the 1967 growing season at the University of British Columbia Research Forest certainly do not disprove that statement and it is felt that possibly the local source will maintain if not improve its position in future years. The findings of Ching that "trees from seed collected at northern and southern extremes of the study grew least in the three years" are supported by the present thesis for the southernmost provenance (Butte Falls), whereas the northernmost source (Nimpkish) is doing very well at least in one block. Seed source G (Shelton) has maintained its position as one of the very best. Ching and Bever (1960) as well as Heaman (1963) did not find any correlation between height growth and geographic variables such as latitude and altitude. Nothing was found in the present study to support such a correlation either.

VII. EVALUATION OF THE CO-OPERATIVE PROVENANCE TEST

Good Points

The initiative to convince a large portion of private and public forest industry in the Pacific Northwest, including British Columbia, of the importance of the provenance problem, to spend money, time and effort on the co-operative study, certainly deserves praise. The attempt to find an answer to practical and theoretical aspects of the provenance problem was honest. The mistakes made (see below) illustrate the complexity of the problem and help to make the task easier for investigation of future provenance tests.

Weak Points

The following evaluation is not meant to be critical of the originators of the study, but should be interpreted as a help for further provenance trials.

Since temperature and frost free period were to be the major criteria in determining the existence of distinct "races" of coastal Douglas-fir, more emphasis should have been put on the standardization of weather measurements (see Heaman's criticism, page 51). In such a mountainous region as the area covered by the co-operative provenance study, mere altitude and latitude, or their combination (see "hypotheses to be tested," page 39) cannot be expected to describe or to determine true climatic differences. Aspect, slope, local topography, proximity of the ocean, etc. are too influential in modifying the effects of altitude and latitude, especially within a limited area. The area covered was too large and the number of provenances included too small for meaningful clues on the nature of the variation within coastal Douglas-fir. The altitudinal sampling was not uniform, since no representative was selected from 750 to 1250 feet elevation, where much logging is being carried out. The cone collection radius of twenty-five miles was too large, areas of great climatic differences can be covered by a fifty-mile diameter, as illustrated by Heaman (1963) for the area around Lake Cowichan on Vancouver Island. Besides that, the cones were not collected according to the same standards by all co-operators. One could almost say that a provenance test is as good as the test sites. If these are heterogeneous (as the University of British Columbia Research Forest test site is, for instance) it is very difficult to test any hypothesis related to various provenances, although the difficulty in finding homogeneous sites, large enough to accomodate two three-acre plantations in the rugged topography on the Pacific coast, is fully appreciated. Damage by hare and deer could have been partly avoided through fences. The frost problem in the Robertson Valley could have been recognized by more careful study of existing weather data.

VIII. CONCLUSIONS AND RECOMMENDATIONS

Since the analyses of variance show a significant provenance x block interaction, no conclusion as to overall performance of any particular provenance can be drawn from the measurements taken at the University of British Columbia Research Forest when the trees were eleven years old. Because of this, none of the hypotheses that the co-operative provenance study set out to test can be accepted or rejected. Significant growth differences between provenances do show up within individual blocks, but the results are inconsistent and therefore not conclusive, due to the extreme site heterogeneity. Observed, but statistically not proven differences tend to indicate that the local provenance is by no means inferior to any other seed source tested, and in future years it might prove to be the best one of all in terms of height growth, as it could be shown to move up the ranks over the last years. Thus, the long-held view that local seed is safest, and probably best (e.g. Bingham, 1966), is still valid. The southernmost provenance is doing very poorly at the University of British Columbia Research Forest. It is possible that several years from now the effects of juvenile handicaps, such as brush competition and maybe soil compaction, will have faded away and genetic differences, if any, will show up statistically.

The results found indicate the complexity of the provenance problem and the overwhelming influence of a heterogeneous site. Further provenance studies are necessary to investigate the nature and extent of variation within coastal Douglas-fir and to establish detailed seed transfer rules and seed collection zones. Based on the findings at the University of British Columbia Research Forest and on the weak points of the co-operative test, the following recommendations for provenance tests seem logical (see also Heaman, 1963):

1. General recommendations
   a) Standardization in all phases of a co-operative study is imperative. Controls are necessary and should be exercised by one co-ordinator, in constant personal contact with all co-operators.
   b) Intensive sampling of a smaller area than that covered by the co-operative study, is likely to yield more information.
   c) Cone collection areas should be clearly defined, based on a thorough local knowledge.
   d) Outplanting areas have to be thoroughly studied. Besides topography and vegetation, climatic data should be looked into, the soil should be analyzed in an attempt to have at least homogeneous blocks.
   e) More studies should be carried out to find one

criterion for soil fertility, or for site differences, so that better statistical results may be obtained.

f) Weather measurements should be supplemented with phenological observations.

g) Damage from animals and fungi has to be kept to a minimum.

2. Recommendation for management

Plant local seed. Collect it from selected trees during good crop years and store it. This way unpleasant surprises due to seed crop failures and purchase of seed of unknown origin, can be avoided.

IX. SUMMARY

Importance, scope and nature of the provenance problem are discussed in this thesis. Experience gained from major provenance trials with Douglas-fir in both Europe and North America is reviewed. From this, the complexity of the problem and the extreme genetic variability of Douglas-fir are apparent.

The "Co-operative Douglas-fir provenance test" is discussed in detail. It was started in 1957 and included sixteen coastal origins from Oregon, Washington and British Columbia, planted close to the seed collection areas, one of which is located on the University of British Columbia Research Forest, where height growth was measured when the trees were eleven years old. The objectives in analyzing these data were

to find whether significant differences between provenances show at an early stage and whether the University of British Columbia Research Forest test site is homogeneous.

The statistical analysis shows a significant provenance x block interaction, indicative of a heterogeneous site. The results are very confusing and no conclusion can be drawn yet as to overall performance of any individual provenance. After removing the effects of brush, randomly scattered over the test site, the results tend to become more meaningful. Although the interaction term is still significant, the following conclusions are drawn: The local provenance is by no means inferior, and it might prove to be the best one of all in a few years when brush competition will have become less important. The southernmost provenance from Butte Falls, Medford, Oregon, is inferior to all other origins tested.

It is hoped that the measurements taken after the 1970 growing season by all co-ordinators will yield more conclusive information than the measurements from the University of British Columbia Research Forest alone. The co-operative test is critically evaluated and recommendations for future provenance studies are included. It is felt that many more tests with Douglas-fir are necessary to answer the questions raised by this and by other studies.

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APPENDIX

Scientific and common names of species cited in the text

Abies amabilis (Dougl.) Forbes	Pacific silver fir
Acer circinatum Pursh.	Vine maple
Armillaria mellea (Fr.) Kumm.	Armillaria root rot fungus
Chamaecyparis nootkatensis (D. Don) Spach	Yellow cedar
Contarinia pseudotsugae Condrashoff	Douglas-fir needle midge
Epilobium angustifolium L.	Fireweed
Larix decidua Mill.	European larch
Picea abies (L.) Karst	Norway spruce
Picea sitchensis (Bong.) Carr.	Sitka spruce
Pinus monticola Dougl.	Western white pine
Pinus ponderosa Laws.	Ponderosa pine
Pinus sylvestris L.	Scots pine
Pinus taeda L.	Loblolly pine
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir
Rhabdocline pseudotsugae Syd.	Douglas-fir needle blight fungus
Rubus spectabilis Pursh.	Salmonberry
Thuja plicata Donn.	Western red cedar
Tsuga heterophylla (Raf.) Sarg.	Western hemlock