A STUDY OF THE NEEDLE AND CONE TISSUE OF ALPINE FIR (ABIES LASIOCARPA (HOOK.) NUTT).

by

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

MASTER OF SCIENCE

IN THE DEPARTMENT

OF

BIOLOGY AND BOTANY

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

May, 1966

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Date April 28th 1966

ABSTRACT

Alpine fir(<u>Abies lasiocarpa</u>(Hook)Nutt.) needles and cones were studied in natural stands to determine the variability of several traits such as needle length, width, stomatal distance in a row line on the abaxial surface, difference between cone scale and bract lengths, seed-wing areas, etc. Additional histological characteristics of needle, cone scale and bract are presented. Sixty-five stands, located on the West Coast of North America, were sampled. Continuous distribution of variable characteristics has not been found in the 65 stands.

Correlation analysis shows that stomatal distance is directly associated with precipitation.Therefore, stomatal frequency increases with higher precipitation.Analysis of variance shows that the difference between cone scale and bract lengths is highly significant between the different stands. These differences indicate actual variations in the cone collection.

Varieties and clines are suggested to exist in the natural range of alpine fir.

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ACKNOWLEDGEMENT

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I wish to express my appreciation to the National Research Council of Canada and the Canada Department of Forestry for granting me financial aid during the period in which this study was conducted.

Thanks are due to my advisors, Dr. A.H. Hutchinson and Dr. T.M.C. Taylor professors of Botany at the University of British Columbia for much assistance and suggestions on many phases of the study.

I owe a special debt of gratitude to Mr. H. Sweet for helping to prepare microslides in 1960 and 1961.Appreciation is also expressed to many persons, too numerous to mention, for much help in locating study areas, for provided transportation and for direct assistance in the field and with office records.

INTRODUCTION.

In November 1958, the Forest Genetics Research Foundation, Berkeley, California, published its first survey of forest genetics research on the West-Coast.None of the ninety-four current projects was concerned with the Genus <u>Abies</u>. However, increasing demands from industry for good quality true firs for lumber and other purposes emphasize the need for such research.

In British Columbia little attention has been paid to the research of true firs. A.H.Hutchinson(1924) has done some work on the embryogeny of amabilis fir (<u>Abies</u> <u>amabilis</u> (Land) Forbes) and R.L.Schmidt published a paper on the silvics and plant geography of the Genus <u>Abies</u> (1957). Moreover, some scattered data were available from several authors concerning the different species of <u>Abies</u> occuring in British Columbia but a comprehensive study has not yet been published. For this reason and in response to the increasing interest in the use of this species for different silvicultural and industrial purposes, Dr.Hutchinson suggested that the writer undertake a project on alpine fir (<u>Abies lasiocarpa</u> (Hook.)Nutt.)

There are four species of <u>Abies</u> in British Columbia: amabilis or silver fir, (<u>Abies amabilis</u> (Land) Forbes); grand or white fir, (<u>Abies grandis</u> Lindl.); balsam fir, (<u>Abies balsamea</u> (L) Miller) and alpine fir, (<u>Abies</u> <u>lasiocarpa</u> (Hook.)Nutt.). Commercially amabilis fir is the most important species. Alpine fir is less important but it has by far the greatest altitudinal and geographical distribution in British Columbia.Since amabilis fir had been studied by Hutchinscn, the present study was undertaken to study the species of second greatest importance, the alpine fir.

The author began the problem in the fall of 1959 and continued studying it during the following years. The field work was carried out in the summers of 1960 and 1961.However,since 1961, more specific objectives,designed to learn as much as possible about the alpine fir in the West Coast,extended the investigation to Washington,Oregon and northern California.

The main purpose of this study was to determine the extent of the variation in alpine fir with respect to several histological and morphological characteristics and to develop procedures for further studies which might lead to some research in tree improvement.

Obviously, it would take a team of specialists to obtain all possible data in the morphology of alpine fir, so the problem becomes a matter of arbitrary selection based on the different traits obtained during the period of field and laboratory examination in the first three years. The following needle and cone characteristics have been considered: length, width and arrangement of needle; anatomical structure of the needle, cone scale and cone bract; distance between stomata in a row line on the lower surface of the

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needle; difference between cone scale and bract length, and size of the seed-wing.

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There were three primary objectives to this study:

1. to determine the variability of needle and cone characteristics for two morphological traits: distance between stomata in a row line and difference between cone scale and bract length,

2.to become familiar with other traits,

3.to ascertain whether alpine fir is essentially one population and whether in its phenotypic variations it follows certain environmental gradients.

ABIES LASIOCARPA - BACKGROUND.

Alpine fir belongs to the genus <u>Abies</u> in the family <u>Pinaceae</u>. Ten species are included in the flora of North America, eight of which are scattered through the forests of the West (Harlow and Harrar, 1950).

GEOGRAPHY:

Alpine fir is endemic to the western coast of North America and to the Rocky Mountain areas from Arizona to Alaska as far north as 62° of latitude. It grows under various ecological conditions in different habitats where the precipitation is from 10 to 140 inches. It exhibits a wide range of tolerance to light and occurs sometimes under the canopy of other species (Engelmann spruce, mountain hemlock and Douglas fir) in protected valleys or in open stands and pure groups at timberline. Its altitudinal distribution is from sea level to 3,000 feet in Alaska; 2,000 to 7,000 feet in British Columbia; 2,000 to 8,000 feet in Washington and Oregon and 3,500 to 9,500 feet in the Rocky Mountains (Harlow and Harrar, 1950). The distribution of alpine fir is broken up by lowlands, and stands are thus isolated from each other in some regions of its natural range. The segregation of stands may have brought about some inherent variation of characteristics within the species during the geological eras.

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SITE REQUIREMENTS:

Trees of largest dimension have been found by the author on fairly deep, loose podsolic soil at about 4000 feet elevation at Willson Creek,near New Denver B.C. and the poorest trees on bedrock covered by a thin mantle of soil at high elevations in the Rocky Mountains.Trees of moderate size were sampled on a sandy beach at Bear Lake,north of Prince George B.C., on well-drained loamy soil around Babine Lake, B.C. and on glacial tills on the Cascade Mountains and at Crater Lake,Oregon.

According to Harlow and Harrar (1950):"This species is rarely ever found on heavy clays but not in -frequently grows on soils too wet for Engelmann spruce." This quotation indicates that the alpine fir commonly occupies moist soils and occurs often in alpine meadows and along lakeshores at high elevations.

Schmidt (1957) pointed out that, on Vancouver Island, alpine fir is most abundant on well-drained, shallow, rocky soils. In addition to growing on these soils in the northern coastal forest, it grows also on soils characterized by impeded drainage and with a standing water-table near the soil surface during the growing season.

In summary: alpine fir is adapted to a wide variety of sites between elevations of 3,000 to 9,500 feet. However in the North the extension of its range into higher altitudinal zones is lower than in the South.Under poor con-

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ditions at high elevation it may be a pioneer on rock outcrops, as for instance on the sterile lava bed at McKenzie Pass, Eastern Oregon.

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Its adaptability to different ecological conditions makes alpine fir a very worthwhile species for silviculture and emphasize its role in the mixed forests of the spruce-balsam type regions in the northern and southern Interior of British Columbia, which areas form one of the principal timber reserves of the Province.-

TAXONOMIC DESCRIPTION:

Species of <u>Abies</u> are distinguished mainly by two characteristics:

(a) smooth twigs with circular needle scars

(b) the erect disintegrating cones.

Native Trees Of Canada (1961).

Alpine fir has spirally arranged acicular leaves which appear to be two ranked on the twigs, those on lower branches crowded and directed upward; upper crown needles directed forwards, often appressed on leading shoots (Harlow and Harrar 1950). The length of needles varies between 2 to 4 centimetres. The sunken stomata are both dorsal and ventral. The resin canals, usually two, are medial. The hypoderm is highly variable, uniform or multiform; the thick wall of the endodermis and the double fibrovascular bundles are characteristic of this fir.

According to Fulling (1934), presence or absence

of stomata on all surfaces of the needles, number of stomata per square unit, contrast in shape of cross sections of needles, fused, slightly separated or distincly separated nature of the two vascular strands - are all heritable, although the variability of species of <u>Abies</u> is very high in their morphological and anatomical characters.

Stover (1944) finds that the size of needles varies from year to year. The mesophyll shows palisade-like cells, and relatively large air spaces.Epidermal cells are thickwalled except those of the current growing season;xylem and phloem are separated into two bands within the vascular bundle; there is a difference in the size of the resin canals not only in different needles but also in those from different habitats, being smaller on the more mesic habitat.

Laing (1956) warns that the form of needle tip is often an uncertain character and has to be used with discretion. The apex of needle may be acute,rounded or marginate. He also stated that the cross section of the needle is important because often it has to be decided whether the resin canals, of which there are usually two, are at the edge of needle (marginal) or some distance from the edge (medial). It has been noted that the resin canals in the needles on non-coning shoots are sometimes in a different position to those on coning-shoots.

Alpine fir is monoecious and has separated staminate and ovulate cones on the same tree. The staminate cone is dark indigo blue, the ovulate cone is dark purple in the initial stage of development.

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Both the staminate and ovulate cone are borne on twigs of the previous year. The first occurs on the lower branches in the axil of the needles, the latter stands erect on the top branches of the crown (Collingwood and Brush 1955).

The ovulate cone matures during a single growing season.When mature it is from three to five centimetres long, (Fig.8 and 9), cylindrical and purplish grey to nearly black. The cone frequently drips with silvery resin. When mature its seeds are released and the scales are shed. The cone axis remains on the tree for some seasons.Bracts are shorter than the scale.The bract is mahogany-red and has erose,rounded shoulders and a long,black, spinelike tip (Harlow and Harrar 1950).

Boivin (1959) emphasizes that there is a constant ratio between scale length and bract length within certain variations of alpine fir. This ratio is discontinuous between different variations and species. The bract/scale ratio is about 5/10 - 6/10 for the alpine fir.

Seeds are ivory brown, from four to six millimeters long, with a large lustrous purplish or violet-tinged wing (Sudworth 1908). Figure 15 and 16.

Winter buds are rounded, consisting of light orange-brown scales more or less covered with resin.

Twigs are fairly stout, orange-brown, and when immature are covered with a fine rusty-red pubescence. The bark of the trunk is usually grey, but some-

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times chalky white. The blister-like resin pockets on the bark are characteristic of all the firs or "balsams". On large trees the bark is little broken, and usually narrow shallow cracks are present near the base of the trunk.

VARIETIES AND HYBRIDS.

Some color differences of the foliage are noted and described by several authors: Collingwood and Brush (1955), Sudworth (1908), Duffield (1962). However color differences of the foliage are difficult to distinguish since they vary with season, site, health of trees and with the age of foliage. Figure 11,12 and 13.

An alpine fir hybrid was reported in a personal communication by Heimburger to Klaehn and Winieski(1962). He had observed a natural hybrid with balsam fir in northern Alberta.

Harlow and Harrar (1950)list a variety as corkbark fir, (<u>Abies arizonica</u> (Merr.) Lemm.). This has thick, corky bark which is free of resin blisters. Furthermore, in alpine fir the cone scale are mostly wedgeshaped while in corkbark fir they are often halberdlike at the base. The corkbark fir occurs in the southern Rocky Mountains at elevations from 8,000 to 10,000 feet.

Dallimore and Jackson (1961) mention another variety of alpine fir, (<u>Abies lasiocarpa</u> var. <u>compacta</u> (Beissner) Rehder). This is a dwarf form of compact habit occuring on poor rocky soil. The irregular arrangement of the foliage, the pointed needles of the terminal shoot, and the conspicuous stomatic lines on the upper surface of the needle are its distin-

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guishing features.

Klachn and Winieski (1962) and Chiasson(1960, 1962) reported an easy crossability for female balsam fir and male alpine fir.

Three successful artificial pollinations were carried out by Mergen et al. (1964) on female <u>Abies procera</u>, <u>A. Koreana</u> and <u>A. sachaliensis</u> with alpine fir pollen. The resulting hybrids have been set out for progeny test in the Research Forest at Yale University.

BIBLIOGRAPHY.

The first bibliography of the true firs was published in 1963 by Lanner and Krugman and includes 373 articles. The author of this paper intends to bring this bibliography up to date and a further exploration of articles on the Genus <u>Abies</u> is underway; about 1200 articles have been aggregated.

METHODS, MATERIALS AND PROCEDURES.

Most of the field work for the project was carried out in the summers of 1960 and 1961, although a few specimens were sampled in the following years, when opportunities allowed the collection. Intervening periods were utilized in making laboratory and statistical analyses. All research and analyses were completed by June, 1964.

It was considered that specimens should be collected for investigation in some specific areas where alpine fir stands were known to be present. In addition the collection of specimens was sometimes partly casual and partly determined by accessability of some areas during the field trips.

Sampling was most intensive in the northern areas where it was desirable to include a number of prominent outlier stands and others having overlapping areas with balsam fir. The location of all sampled areas is shown on the map in Figure 1. The names and code number of the locations of the areas are given in Table 1.

Sampling procedures were carefully considered with a statistician concerning the number of samples desirable from a certain area and appropriate statistical methods for analyses. It was suggested that trees be selected for specimens at random from each stand as follows: trees to be sampled must be distributed equally in the area and located in uniform position as much as possible. It means uniform shade, density and mixture of other species. This way, the extraneous variability

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of needle characteristics which could jeopardize the confidence of the statistical analyses, can be avoided.

It was decided that ten trees per stand should be selected for sampling. These provide sufficent data to calculate mean values of needle characteristics for statistical analyses. The number of trees were limited by the available time and funds because of the wide range of alpine fir from Oregon to the Yukon Territory.

In a given stand the distance between the trees to be sampled was 150-250 yards, depending upon the extent of the sample-stand. However, the size of a sampling area was purposely left flexible to accommodate local differences in stand conditions which could not be predetermined.

Where alpine fir trees occupied a larger area at different altitudes or various slopes and aspects, two or more sample-divisions were made and ten trees were sampled from each division, e.g. Mt.Rainier and Olympic N.P. This method of sampling was followed where both the mixed and pure stands formed a continuous forest area.

At timber line where the trees form small isolated clumps on the alpine meadows, the method of collection was modified and needle samples were taken from the scattered groups following the same isobar and so contur line in the middle belt of the meadow.

Sometimes, alpine fir, mixed with other species was found in long strips beside the highways and roads. Trees were

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selected from the strip about 200 yards from each other along the road.

The total number of selected stands was 65 and 650 trees were sampled.

Needle samples were collected from healthy, sexually mature trees. This means 20-40 years of age in alpine fir. Needles were picked from 3 year-old shoots of branches on the south side of the tree and at a height of 150 centimeters. It was found that a 3 year old needle has a well-differentiated tissue complex in its cross-section but it can still be cut easily.

The number of needles collected was limited by the 16 milli-liter capacity of vials used as containers for their storage. FAA preservative was used for fixing and storing materials in vials.

NEEDLES; MORPHOLOGY.

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The following measurements and observations have been made in the laboratory from material that was collected in the field. All measurements were made on preserved needles selected at random from the vials.

LENGTH.

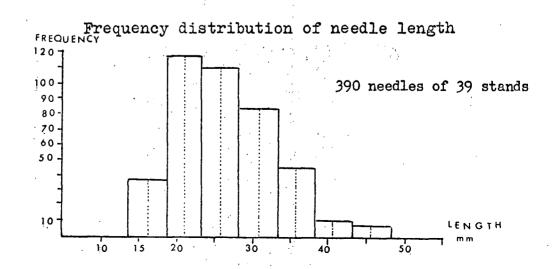
The length of needles is highly variable and different lengths are commonly found on the same tree. According to several authors (Collingwood and Brush 1955, Boivin 1959) those of the lower branches are relatively longer than those on the higher limbs and branches.Stover (1944) finds that the needles are longer on mesic and shorter on xeric habitats. The following needle lengths are reported by

various authors:

Boivin(1959) Collingwood and Brush(1955) 2.5 - 4.0 centimeter Fulling(1934) Harlow and Harrar(1950) Knuchel(1954) Native trees of Canada(1961) 2.5 - 4.4 centimeter

The authors have not made any notes about the position of branches, except Harlow and Harrar (1950) who chose needles for measuring from sterile side branches. However, the data of the quoted authors are very similar.Perhaps, they used the same source for the lengths of the needles.

The author of this paper measured the length of needles on sterile branches at the south side of the trees. The measurements were based upon the lengths of 10 needles, selected at random from thirty-nine stands' specimens. The lengths range from 0.9 to 4.3 centimeters. The diagram below shows the frequency distribution of needle lengths with a mean value (\overline{X}) of 2.13 centimeter and the standard deviation (S₋) 0.25 centimeter. This mean length is shorter than the minimum, reported by the above authors. The explanation of the significant differences between those of the quoted authors and of the authors of this paper might be the following: As it was mentioned above, needle length is strongly affected by habitat, aspect and the position of branches along the stem. In this project, the aspect and the position and location of branches were identical therefore it could be assumed that the habitat was chiefly responsible for the higher means and the larger range limits of the needle lengths. This theory is supported by the fact that the stands sampled are very widely distributed in their natural range and soil, climate and elevation also varied remarkably at the different locations.



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The change of needle lengths is discontinuous in the series of observations on different habitats. Therefore the obtained data are not appropriate for statistical analysis of continuous variations and no conclusion can be drawn as to the cause of the needle length differences between the specimens. However, it could be noted here that the longest needles were found at Wallowa Lake (43), the shortest were collected at Aleza Lake (28) and beside Giscome Road (15).

WIDTH.

Ten needles per stand were measured at three points of each needle:

5 1/4		1/4

The average value of these three measurements give the data for the computer.The results of computing are shown under X_3 in Table 1. In Table 2. under the column of X_3 , the following values of needle-width are listed: average width of needles of 65 stands, $\overline{X} = 1.76$ millimeter,standard deviation .17 millimeter and range: 1.35 - 2.20 millimeter. Table 3. presents the correlation coefficients with precipitation (X_2), altitude (X_5), and latitude (X_6).The coefficient of altitude has the highest numerical value among the other factors analysed although it does not indicate a significant correlation between the needle width and altitude. APEX.

Four hundred needles, selected at random from the vials, were used for testing the variability of the apex form. One half of the needles were notched, one fourth were acute and one fourth were rounded. This ratio of distribution of the different apex form is casual, although it shows that the apex is usually notched on the sterile, shaded branches.

Another observation was made on the form of needle apex.Needles were collected from different areas of the crown, i.e. upper,middle and lower areas. It was found that needles were acute or pointed on fertile branches from the upper crown at high elevation and rounded at low elevation. Trees at lower elevations have pointed needles only on the leading shoots.

A general statement could be drawn from the above observations: Needles are acute or pointed in the upper crown and on the leading shoots while notched and rounded in the lower crown.

GROOVE AND RIDGE.

The upper surface of the needle is deeply grooved at the base and slightly grooved at the apex. The lower surface is ridged along the midrib.These characteristics are common on/ some true firs which have flattened needles in cross section, e.g. balsam,silver and grand firs.It was observed that groove and ridge appear more sharply on the needles at high elevation than at low elevation.

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COLOR.

Colour of the needles varies from dark green to yellow green. Those collected on lava beds or from high elevations on bed-rock which had arisen from volcanic deposit, are yellowish green, Figure 10 and 12 ; those of understorey trees, located in well-drained, podzolic soil, are darker green, Figure 11 and 13.

STOMATA.

Two bands of stomata are on the abaxial surface of the needle consisting of 10-15 regularly distributed stomatal rows, Figure 18.

One band of stomatal rows follows the midrib from the tip to the base on the adaxial surface of the alpine fir needle. The band forms a thin stripe of two or three rows of stomata. Sometimes, this stripe disappears before it reaches the base of needle. The distribution of stomata is irregular in this band, and the number of stomata in a square unit is highly variable.

Stomata on both adaxial and abaxial surfaces is a unique feature of the alpine fir among the true firs of British Columbia. While species associated with alpine fir in the Province do not have stomata generally distributed on the adaxial surface of needles, they may have a few at the apex which do not extend beyond the upper quarter of the needle.

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This feature provides a good basis for distinguishing the alpine fir from other true firs occurring in the Province, but it cannot be used in Washington,Oregon and California where several species of true fir possess needles that are stomatiferous on both sides.

The irregularity and high variability of stomatal appearence on the adaxial surface of alpine fir needle led the author to examine the stomatal distance on the abaxial surface. Distances between two neighbouring stomata were measured on 20 needles per stand. Ten measurements on each needle give 200 data per stand.Needles were selected randomly from each vial which represents a stand.

The measurements were made in a one millimeter wide stripe crossing the centre point of the upper half of the needle where the stomatal distribution and the constancy of stomatal number proved to be fairly regular. A unit, equal to 0.2 millimeter was used for measuring the stomatal distances. The array of data has been consolidated by grouping measurements into unit classes. The classes were summarized to determine the total value of Y, called "distance index". Two separated measurements were made on each stand: Y_1 and Y_2 , to test the variability of stomatal distances within the stand. The average of Y_1 and Y_2 was used as distance index(Y) of a sampled stand for computing and analysing the data in different ways as presented in the following pages.

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Scoring system of 100 measured data Y₁ for Mount Rainier (25):

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Units 3 4 5 6 7 Frequency 4 26 48 15 7 Total Y_1 12 104 240 90 49 equal to 495 units.

This distance index (Y) shows more about the distribution of stomatal distances within a stand than the average value of measurements, and different stands can be distinguished from each other by the different values of"Y".

ANALYSES OF DATA ON STOMATA.

To analyse the interrelationships among the traits measured more data would have been needed. But there are sufficient measured data to find variations of the stomatal distances in the different stands and show relationships between the distance indices (Y) and some independent variables which affect the appearence of stomata on the needle surfaces.

The mean (\overline{X}) of the stomatal distances (based on the data in Table 1) is 0.104 millimeter in the 65 alpine fir stands sampled and the average number of stomata 9.21 per millimeter in a single row line. The average number of rows is 12 and so the average number of stomata is 115 in a 1 millimeter wide stripe which lays on the lower needle surface perpendicular to the needle axis, Figure 18. The details of analysis of variance for the distance index (Y) are the following:

Source	Df	Sum SQ	Mean SQ	F	
Stand Residual	64 65	2.64564E+05 6.99200E+03	4.13381E+03 1.07569E+02	38.429	
Total	129	2.71556E+05			

The F value exceeds the value for F = 1.80 indicated in the body of the table for the 0.1 % level with 64 an 65 degrees of freedom and shows that differences between the distance indices are highly significant. This result indicates that there are significant differences between the sampled stands and the differences are not a matter of chance. While the analysis shows that the means of stomatal frequency in the investigated 65 stands are not equal, it does not imply that all the stand means differ significantly from each other.

In order to determine which of the 65 stand means are significantly similar and which are different, <u>Duncan's</u> multiple range test was used as employed by <u>Li</u> (1959) as the "least significant difference" between two stand means. In this case LSD (Least Significant Difference) at the 1 % level is

$$\begin{split} \mathrm{LSD}_{(01)} &= t_{\mathrm{r}_{01}} \sqrt{S^2/f} \text{, in which} \\ t_{\mathrm{r}_{01}} &= \text{the tabulated 't' value from Duncan's Table(1955)} \\ \mathbf{f} &= \text{number of observation for each stand that is equal} \\ &= to 2, \text{i.e. } Y_1 \text{ and } Y_2 \text{ are the observations.} \\ S^2 &= \text{the error mean square of the analysis of variance.} \end{split}$$

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Since more than two stands are compared the quantity corresponding to the LSD is called the shortest significant range,(SSR).

The workings of the new multiple range test is given in Figure 3. To perform this test the means of the 65 stands are necessary and these are then arranged according to their magnitudes.

The standard error of the mean is needed in computing the SSR.

The standard error of the means of Y is: $S^2/n = 107.6/2 = 7.3$. The 1% significance level was chosen, the values of t were obtained from Duncan's Table.Each of the tabulated values was multiplied by the standard error to form the SSR, which are given in Figure 3 and in the table of Figure 3. In order to create groups within the series of stands sampled which are as close as possible to each other the smallest limit of each group was determined so that the corresponding SSR value was subtracted from the highest means (\overline{Y}) of the 65 stands one after the other. The means (\overline{Y}) , which fall into the intervals between the smallest limits and the corresponding means represent identified groups and the difference of stomatal frequency is not significant between the samples within each group. On the other hand, those of the means which fall outside an identified group differ significantly from each other. For instance, the mean value of the 65th sample is 646, after subtracting the SSR value 34, there

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will remain 612, which is the smallest limit of this group and includes the 620,644 and 646 distance indices as identified samples.

Figure 3 illustrates the associated samples with the 65 stands, represented by horizontal lines.Any two means and all the intervening means underlined do not differ significantly but the remaining means which are not underscored by the same line are significantly different. For example, the stomatal frequency of Nos.63, 64 and 65 differs significantly from the frequencies of No.1 to No. 62 stands. From Figure 3 it can be seen that the difference is highly significant between the first and last groups in the series of stands tested. The significance of differences increases gradually from one side towards the other of Figure 3.

The number of the samples in the identified groups varies from two to twenty eight. The largest group of identified samples falls into the middle part of the figure and includes populations which occur at various habitats from the Yukon Territory toward South Oregon. The range of the distance indices of these stands extends from 480 to 514. This group represents the most frequent stomatal number on the abaxial surface of alpine fir needle. Each group underlined deviates from it.

To explain the occurrence of such variations further statistical analysis has been made. Several factors were analysed by regression to test their relation to the stomatal frequency and distribution. The basic elements of these

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components are represented in Table 2. These are the only factors available for analysis,other desirable data such as humidity,radiation,soil quality,et cetera are lacking. The components in Table 2, such as precipitation,elevation and latitude generally characterize the ecological condition of the habitats where the samples were collected from. For example, the humidity of soil and air are controlled by the precipitation; the range of temperature and the radiation by the elevation; and latitude indicates some change of precipitation and temperature in British Columbia.

It was assumed that one of the components mentioned above may have some relation to the stomatal frequency represented by the stomatal distance (Y), and the regression analysis promotes to detect it.

At first, the means (\overline{X}), covariences ($S_{\overline{X}}$) and standard deviations (S) were calculated for each of the above mentioned components in order to obtain the correlation coefficients between them. The latter are given in Table 3.

The correlation between the various factors at 1 % level is found to be as follows (the meaning of the symbols used is given in the legend of Table 1 .):

X, correlate	signi:	ficantly	with		X.,	X_{4} and	Y
X_2	do			X,	X,	X_{δ} and	Y
X	do	•		. I	5	X, and	·Υ
X ₅	do				X.,	X,	
X ₆	do	•			X_2^{-}	X ₅	
Y	do	. "	N	_ X,	\mathbf{X}_{2}^{-}	X ₄	

After the evaluation of correlation between

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the distance index and tested factors it was found that there are highly significant negative correlation between Y and X,, X_2 and X_4 . The correlation of Y to X_2 confirms the first analysis of Duncan's multiple range test and proves that there are significant differences between the distance indices of the various stands. The distance index is in inverse ratio to the stomatal frequency (X_1) . On the other hand, this produces a positive correlation between stomatal frequency and precipitation both having negative coefficients in the regression equation.

Figure 2 shows that the stomatal frequency is the highest and distance index the lowest in those regions where the average precipitation is high over about 95 inches.

For example: Code No. Location	Prec. Inch	Freq.	Y
l Garibaldi Lake,B.C.	120	95	451
4 Black Tusk,B.C.	140	118	466
7 Arrowsmith Mt., V.I.	100	127	468
14 Boulder Lake,Olympic N.P	.,Wash. 100	107	485
19 Mount Rainier,Wash.	120	91	488
20 Forbidden Plat., V.I.	140	92	488

Where precipitation is low(under 25 inches), low stomatal frequency was found on the needles with the exception of the samples collected in the Yukon Territory. Lakes and swamps surround the mixed alpine fir stands in that region and keep the soil moist in spite of the low precipitation in this region which probably accounts for the high stomatal frequency.

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Code No.	Location	Prec. Inch	Freq.	Y	_
40 43 44 49	Pendelton Bay, B.C. Pine Lake,Yukon Wallowa Lake, Ore. Alaska Hwy.,Mi.852, Yukon Mt. Bonaparte, Wash. Divide Cr.,Glacier N.P.,Mont. Graves Mt.,Wash.	20 8 20 12 20 17	62 110 90 99 74 68 75	514 526 529 521 540 543 561	

The data from the analysis of variance can be treated to regression analysis by computing the regression equation.

> \overline{c} a + b, x, 66.86-0.367-0.387+0.611+7.866+0.002-0.025

The analysis was employed for the distance index as a trait and the six variables presented in Table 1 and 2. The result of the computation is given in Table 4. In Table 4, the variables have been ranked in accordance with their importance, i.e. their R^2 values.

The sum of the sample regression coefficients , $R^2 = 0.712$, reflects a fairly close association between the tested trait (Y) and the five independent variables (precipitation, stomatal frequency, needle width, latitude and elevation). Moreover, Table 4 shows that precipitation has the highest value of R, 57 of the total 71 percent, against the other variables, 14%. This result was obtained after omitting the other variables one after the other during the computation. Used Snedecor's (1956) Table for the 1% fiducial limit of R, it was found that the value of R equal to 0.331 in the row of 63 degrees of freedom with 2 variables.Since the computed R value is 0.570 that considerably exceeds 0.331, the association of stomatal distance with precipitation is considered to be highly significant.

A diagram in Figure 2 expresses visually the relation of Y with precipitation. The dots are lieing along the regression line (O-P) in a relatively narrow band extending from the positive upper left to lower right, not scattered widely over the whole field. This "significant relationship" means that as the precipitation varies, so the stomatal frequency varies directly. The variation pattern may be an example of a type of clinal variation and indicates a non-adaptive value, i.e. a physiological character to which stomatal frequency is linked. The analysis appears to prove that specific effects on stomatal differentiation can be obtained by different ecological conditions and that probably there are some possibilities of controlling stomatal distribution over the epidermal surface of the needle.

To confirm this statement only one reference needs to be mentioned here. Zucker(1963) emphasized that environmental conditions existing at the time of stomatal differentiation in the embryonic leaf bud greatly affect this process. Availability of water, light intensity, and temperature have all been shown to be important factors. Leaves of sunflower grown on a wet soil possess 20 times the number of stomata as do corresponding leaves from plants grown under very dry conditions.

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EXAMINATION OF NEEDLE CROSS-SECTION .

Preparation of cross-section for examination was adapted from the technique described by Johansen (1949) with some modification by Sweet (1960) and the author. The modification involves an acceleration of dehydration.Johansen (p.132) used a close series of dilutions of ethyl alcohol for dehydration. The author used only 5, 50, 70 and 95 % dilutions for two hours of each. Furthermore, the author used a mixture of Parowax, Fisher tissuement and bees wax, in(48:48:4) percent ratio respectively for embedding the needles instead of rubber-Parowax used by Johansen.

Usually it is necessary to soften the embedded needles of alpine fir for sectioning. So, the blocks were soaked in water for 48 hours or more.

The transections and longitudinal sections were cut 10 microns thick using a rotary microtome. Sections were stained with safranin and fast green and mounted in balsam.

The cross-section of alpine fir needles shows the following characteristics:

EPIDERMIS has one layer. Cells are cube shaped with very thick cell walls. Both surfaces of the needle usually are heavily cutinized which is a xeromorphic character, nevertheless needles have been collected at Bear Lake, Aleza Lake, Summit Lake and on Mount Idaho in British Columbia which show only a thin cuticle layer rarely visible under the misroscope.High moisture content of soil and air may be the reason for this lack of cuticle.

STOMATA are deeply embedded in the epidermis even apparently into the hypodermal layers. There are some differences in shape of guard cells in the sections observed due to the degree of opening of stomata at the moment of collection. The arrangement of cells surrounding the openings is always constant and the guard cells are overtopped by the sudsidiary cells, Figure 17. The term 'subsidiary cell' is used in the sense of Esau (1960).

HYPODERMIS shows several patterns under the epidermis. There are discontinuous and continuous layer or layers. One can infer that well-developed hypodermis usually indicates dry habitat and severe climate. It is assumed that the role of thickened hypo dermis is to strengthen the needles against wind and snow pressure on upper branches at high elevation. On dry habitats, the continuous layer, or layers, of hypodermis control the rate of water-vapor loss and reduce the injurious effect of wilting. It was found that needles collected from high mountains had continuous and often doubled layers while needles from lower elevation have discontinuous hypodermis, Figure 4.

MESOPHYLL tissue is differentiated into palisade-like and spongy parenchyma cells in the alpine fir needle. The feature of 'palisade like' cells departs from the common palisade in form and size.

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Palisade cells are elongated and quadrilateral-shaped. Those of alpine fir needle are shorter and more rounded and usually form one layer between the hypodermis and the spongy parenchyma, Figure 25. Grand fir has typical palisade among the true firs while palisade cells of the balsam fir are usually similar to those of alpine fir.

Irregularly distributed parenchyma cells are located under the palisade layer. The parenchyma cells have particularly large numbers of chloroplast and numerous air spaces were found between them in the three year old needles sampled for measurements. The air spaces are continued as intercellular spaces in the spongy parenchyma. The appearance of the intercellular spaces is usually irregular in the cross-section although in the longitudinal section they appear regularly arranged. Spongy parenchyma cells occupy all the abaxial region of the needle and include the resin canals medially located between the stele and epidermis sheath. It was observed during the investigation that the spongy parenchyma appears more compact in the young needles than in the three year old needles, Figure 26.

ENDODERMIS SHEATH lines the different tissue elements of bundle or stele. The sheath is made up from well differentiated large parenchymatous cells. The nucleus and Casparian strips are not visible and the latter actually are lacking. The absence of Casparian strips is not unusual in the secondary needles of true firs (Esau 1960). Sometimes the cell walls of the endodermis

sheath are pitted like primary pit fields. Bundle sheath extensions occur at both the adaxial and the abaxial side of the bundle as a narrow channel whose cells are packed with starch.

Within the endodermis sheath some thick-walled parenchyma cells line the transfusion tissue. These cells create a discontinuous sheath, very rarely continuous, around the inner part of the stele and are filled with starch.

The complex of parenchyma and tracheid cells in the bundle of needle is called transfusion tissue. Large transfusion tissue is characteristic for the alpine fir needle in contrast to the grand fir and Douglas fir which have limited transfusion tissue. The finding of a larger transfusion area inside the endodermis of the alpine fir needle may confirm Takeda's statement (1913) that the parenchyma cells of transfusion tissue are water storage cells occurring in xerphytes. The same extension of transfusion tissue was found by the author in the needle of red fir and silver fir collected from dry habitats, on the Sierra Mountains, California, and the Eastern slope of Mount Arrowsmith, Vancouver Island, respectively. In other samples, both red fir and silver fir have restricted transfusion tissue in needles collected from moist soil and climate. For example, needles of silver fir collected in the western valleys of Manning Park, British Columbia, have small transfusion tissue.

The vascular bundles are separated by parenchyma cells oriented obliquely, Figure 27 . As is usual in <u>Pinaceae</u>, the xylem is adaxial and the phloem is abaxial and both are ar-

ranged in 8-10 horizontal rows. Tracheids have helical thickenings or bordered pits in secondary walls. The helically thickened tracheids are in the adaxial side of xylem. The bordered pit membranes have a torus in a central position which is characteristic of <u>Abies</u> species (Esau 1960). Both in the xylem and in the phloem there are some parenchyma cells with crystals. The cells filled with crystals are usually in connection with each other and form a vertical column of cells in the xylem and phloem. The albuminous cells which are parallel to this column are easily seen beside the vascular bundle in Figure 27.

In another project, research has been done by the author concerning the location and tissue arrangement of vascular bundles in needle of balsam, red, Shasta and white fir. It was found that distinction can be made by these qualities for several sympatric species. For example, alpine fir needle has more enlarged stele and more vertical columns of xylem and phloem than balsam fir; transfusion tissue occupies more space in alpine fir than in balsam fir; white fir has one bundle in the stele, red fir forms two bundles with a well-developed extension sheath between them.

Detailed information on the above is to be published in collaboration with Eugene Parker of Medford,Oregon, who is working with the author on the distinction of some true fir species occurring on the west coast of North America.

RESIN CANAL. A paper Roller(1966a) concerning the number and position of resin canal of alpine, balsam and Fraser fir is

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in press. The evidence is given there and so only the conclusions quoted here.

Sixty needles were picked at random from the selected needle material of trees included in Table 6, and the same number of needles from the seedlings planted in the nursery at Chalk River, Petawawa Forest Experiment Station. For examination, free-hand sections were made and lightly stained in safranin.

Features of resin canals in true fir needles are taxonomic characters of well-established value. Their number and location have been regarded as only slightly less reliable characteristics, and many taxonomists have used these features with others to distinguish species in the genus <u>Abies</u>.

A more detailed study of this matter led the author to believe that the position and number of the canals seem to be highly variable in several stages of needle development. This research confirmed the thesis that resin canal position in alpine fir and its sympatric species varies from peripheral to medial depending on the age of needle and tree, and in certain cases on the height of branch. In the seedlings of alpine fir, resin canals were found in peripheral location, while needles of mature trees were characterized by resin canals in medial position. In some mature trees, needles picked from the lower crown had from none to two or more resin canals partly peripheral partly medial. Examples are shown in Figures 23 to 26.

Table 6 presents the measured and evaluated data of some selected specimens of alpine fir. The analysis of these data resulted in the following:

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The difference in the 'height' of resin canals in the mesophyll is highly significant between the needles collected from adult trees located in various regions.

A regression analysis of resin canal position on latitude and elevation shows very slight effect of latitude and no effect of elevation. The regression equation is

 $Y = 7.23 + 0.0196 X_1 - 0.00000586 X_2$

X, equal to latitude and X_2 =elevation.

The observations and analyses described in the quoted paper confirm the thesis that the change of resin canal position with age, i.e. in seedling and adult stage, is under genetic control, while the position of resin canals is modified by environmental factors in adult age.

SUMMARY OF OBSERVATIONS ON ABIES LASIOCARPA NEEDLES.

When in due course differences between the needles of various <u>Abies</u> species are examined, the following observations were made in this paper:

The surface of both sides of the needle is heavily cutinized; the thickness of the cuticle is variable and thicker on the surface of the upper crown needles at high elevation than low elevation.

The epidermis has one layer.

Sunken stomata are embedded into epidermis (Figure 19). The first collenchyma cells arise under the adaxial epidermis. The number of hypodermal layers increases with altitude and many layered hypodermal lines are located at the two margins of needle (Figure 4).

The mesophyll tissue differentiates into palisade-like and spongy parenchyma cells. The palisade-like cells are not true palisade cells (Figure 21).

Endodermis is usually broken at the adaxial side of stele(Figure 28). The inner bundle sheath gradually becomes visible during aging. A higher number of tracheids than parenchyma cells are in the transfusion tissue complex (Figures 28,29).

Vascular bundles are poorly developed in the juvenile stage (Fig.26). Two separated bundles are formed in the adult stage(Figure 25). In the seedling's needle, there are two peripheral resin canals joining the abaxial epidermal layer.While, in the needle of an

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adult tree, there are two medial resin canals embedded in the mesophyll (Figure 21).

Histological characteristics of thirteen samples are presented in Table 5. These samples were selected at random from the groups formed in Figure 3. These groups exhibit a series of stomatal distances from the lowest to the highest value of Y. The arrangement of samples in Table 5 follows the arrangement of samples in Figure 3 in order to obtain consistent variations of histological characteristics according to the increasing values of the stomatal distances.

Continuous distribution of variable characteristics has not yet been found during the investigation.Only one observation can be noted here, i.e. needles from Garibaldi Lake(1) have high stomatal frequency and an enlarged area of tracheid cells in the bundle(Figure 29). Contrary to this however needles from the Wallowa Mountains (65) exhibit low stomatal frequency and an enlarged parenchymatous area within the endodermis sheath (Figure 30). The former occurs on moist habitat with 120 inches annual precipitation, the latter on dryer habitat with 35 inches annual precipitation.

The inverse relation of stomatal distance with the parenchymatous area and direct relation with the enlarged tracheid elements seem to be casual because the changes are discontinuous in the intermediate samples although the stomatal distances increase gradually from the top to the bottom of the column in Table 4.

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<u>CONES</u> : FIELD PROCEDURES, TECHNIQUE OF PREPARATION AND MEASURING OF CONE PARTICLES.

Cones for examination were collected from 40 stands. Most of the samples were collected from the same trees as the needles discussed above and attempts were made to obtain as uniform a sample of cones as possible. When cones were not available from the same trees as the needles, other trees were used for collection of cones in the same stand, care being taken to obtain them from similar trees. Sometimes the cones were more than one year old remaining on the trees over the season and sometimes collection was made in the end of August when seeds were still immature. The distribution of samples and the measured data are given in Table 7.

SEED. Only a small quantity of sound seeds was available for examination of seed viability and weight. The location of the stands and the result of the analysed data are presented in Table 8.

To separate viable from empty seeds ethyl ether was used. The sound seeds sink while the empty seeds float. This was the method used to select viable seed samples for further test.

Cleaned seeds were put into a desiccator for 48 hours to equilibrate the moisture content of the different seed stock. Weighings were made by micro-analytical balance in grams per 1000 seeds, Table 8.

One portion of the seed specimens was used for

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germination test. For stratification, seeds were embedded in sand and kept in refrigerator under 37°F temperature for 60 days. Soundness and per cent of filled seeds were tested by germination test and cutting test respectively.

The largest seed was found in the cones from Mt. Idaho(24), Figure 16. The sample standard deviation (S) is equal to 1.678 gram/1000 seeds. A t-test shows that there are probably significant differences between the mean value of No.24 and the individual means of samples, because the calculated t - value does not exceed the value given by the 1 % probability level for 3 degrees of freedom in the Ficher's Table. The smallest seeds were collected around Aleza Lake, Figure 15.

SEED WING. To test the variability in form and size of the seed wings as many as available were prepared for investigation, also included were the wings of some empty seeds. In this way, eleven of 40 samples were obtainable. Thirty wings were taken out from the middle part of the cones of each sample. The wings were soaked in water for 24 hours then pressed on drawing paper to flatten them. The shape of wings was outlined in full size on the drawing paper and the area of each wing was measured with a planimeter in square centimeter, Table 8.

The standard deviation of sample means is equal to 0.344 sq.centimeter which indicates some significant differences between the individual means. There are conspicuous extremes such as 0.15 for No. 9, 0.18 for No. 5 and 1.40 for No. 18,

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and 1.05 for No. 38 . These data were tested for differences by the t-test and highly significant differences were found between the means of each individual and the sample mean.All the t values exceed the value given by the 0.1 % probability level for 10 degrees of freedom.

Trees growing on dry,rocky and even on cool sites have the smallest wings. For example, the sample taken from Mt. Rainier (No. 9) occurring at 7500-8000 feet has the smallest wings, Figure 5 . At that locality, the trees are small and stunted. In contrast to them, trees that are growing on good podzolic soil, as in Willson Creek (No. 38) or beside the Alaska Highway at 160 mile (No. 18) have the largest seed wings, Figure 5.

CONE AXIS. Unbroken axes, 40 of each stand, were selected, Table 8. The axes were measured from the tip to the bottom at the joint of the twig. The measurement was made in millimeter.

The standard deviation of means is equal to 15 millimeters. The difference between the sample mean and individual means is probably significant for No. 12,26 and 35 samples. The values for these do not exceed the value of "t' given by the 1% probability level for 6 degrees of freedom. The 't' value for No. 38 falls between 1 % and 0.1 % probability level in the Fisher's Table and so indicates significant difference.

The correlation between the length of the cone axis and the environmental factors is evident. With better habitats there are longer cone axes and bigger cones. There seems to be

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some increase in the development of the cone with higher precipitation. It should be noted that the measured data of cones collected in Willson Creek, in the eastern part of the Interior of British Columbia No. 38, differ from the data of other samples in all the three characteristics tested. However, the trees also differ in crown form, color and growth rate from the other stands. The distinction of these characteristics may allow one to suppose that the stand in Willson Creek involves variations which can be either genotypic or ecotypic, Figures 9,13,16.

CONE SCALE AND BRACT. Twenty scales with bracts were picked randomly from forty stand samples. Both the scale and the bract were measured separately. The result of the measurements is presented in tenth of millimeter in Table 7, under X_4 and X_5 , respectively. The difference of the lengths is given under Y. Theoretically Y is equal to $(X_4 - X_5)$. Actually, Y was found in a different manner as follows: Ten of the twenty scales with bracts were picked at random. These were measured and the ten length differences were totaled to obtain Y in hundredth of millimeter. Then, Y was introduced into computer to have the analysis of variance for the differences of the individual stand means and make regression analysis for the factors that may affect the development of the scale and bract. Tenth and hundredth of millimeter were used as a unit of measurement to avoid the decimal without loosing the accuracy of the data in the tables and the computer records.

Some selected bracts from the measured specimens

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were photographed. The picture of these is given in Figure 14. Sometimes the scale and bract were crooked and twisted. In this case they were soaked in water for 24 hours, then pressed until they became dry and flat, thus making for easier measuring.

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For histological examination, scale and bract were used in immature stage after the tissues had been slightly differentiated. For this examination specimens were collected in the Coast Region at Lake Garibaldi, and on Vancouver Island after April, depending upon the elevation where the trees were located. At high elevation the cone tissue differentiates at the end of May or some days later, at low elevation it usually happens early in May.

The same laboratory method was used for preparation, dehydration and staining of material of scale and bract as had been done to the needles mentioned above.

EVALUATION AND ANALYSIS OF THE DIFFERENCE BETWEEN SCALE AND BRACT LENGTH.

The length of scale and bract can be measured easily giving adequate data for statistical analysis. Therefore, many taxonomists use it to discriminate the natural hybrid of two closely related species or different variations within one species. Boivin (1959) suggested a new classification within the species of balsam fir, on the basis of the ratio of cone scale and bract. He places alpine fir as a subspecies of balsam fir. Myers and Bormann (1963) adopt Boivin's method and use it to distinguish balsam fir from the Fraser fir in some southern regions of North America.

The statements and methods of these two authors led the writer to examine the ratio of the cone scale/bract length in the alpine fir variations. The examination has given a clear picture of the diversity of the scale/bract ratio and confirmed that a wide range of variations could exist within this species. A preliminary trial was made on some reduced specimens, taken from the 40 stands to prove the confidence of the scale and bract length difference against the scale/bract ratio. Both the scale - bract length difference and the scale bract ratio gave the same result in the discrimination of alpine fir variations. Because the calculation of length differences (Y) is quicker, it was used to measure all the samples collected from the 40 stands.

Hypothesis for analysis was the following: There are no significant differences between the value of 'Y' between the sampled stands.

In connection with this hypothesis it is assumed that the scale and bract have constant proportion in size. Both the scale and the bract may change symmetrically in size under various environmental effects, and during different growing periods, but the ratio between their length remains relatively constant. If not, the difference between them should not be due to chance alone.

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RESULT OF THE ANALYSIS OF VARIANCE. The range of Y, from 0.5 to 8.9 millimeter, shows high variability. It was supposed that there are significant differences between the stand samples and an analysis of variance was computed to prove it. The model of analysis of variance is the following:

Source	Df	Sum SQ	Mean SQ	F
Distance Residual		3.97049E+04 3.09500E+02	1.01807E+03 7.73750E+00	131.57
Total	79	4.00144E+04		

The F value exceeds the value for F indicated in the body of the table for the 0.1% level with 40 and 39 degrees of freedom.

The F test shows that the difference of the value of Y, i.e. the length distances between the scale and bract are highly significant between the different stands. As a conclusion of this analysis it can be stated that there are actual variations in this cone collection. Some of the samples are closely related to each other, and others are less so.

The relation between the stand sample means can be determined through the Duncan's method by the test of least significant differences (LSD). This method was described above in connection with the analysis of stomatal distances of needles (pp 21 - 23).

 $LSD_{(.01)} t_{.01} \sqrt{S^2/f} \quad equal to \quad t_{.01} \times \sqrt{7.7375/2}$ $LSD_{(.01)} t_{.01} \times 1.97$

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The expression of analysis in diagram is given in Figure 7. This illustrates the associated samples as groups underlined by continuous horizontal lines. Since the method of reading of this diagram had been explained in pages 21 and 22, it is only necessary to state the conclusions here.

The sample means (\underline{x}) of stands are highly variable and the arrangement of groups, underlined by the same horizontal lines, is not consistent concerning the location of stands in the field. The group which has the smallest values of Y, No.1 and 2, are located at Garibaldi Barriers, British Columbia and on the northern slopes of the mountains in the Olypic National Park, Washington, respectively. Between the two stands and close to them, in the field, there are many other stands, Mt. Arrowsmith (21), Forbidden Plateau (32), both in Vancouver Island; Mt. Rainier, Washington, (8 and 9), all located at about the same elevation apparently under the same environmental condition on intrusive rocks. But these samples are placed far from the low range limit in the diagram. They are closer to those groups which were diagrammed in the opposite side and occur under better conditions on gray-brown podzolic soils in the eastern regions of British Columbia and northern Washington. The highest group of (Y) involves: Alder Trail, Montana, (40), East Slope of the Glacier National Park, Montana, (39), and Willson Creek, British Columbia. (38).

The stands, diagrammed in the middle portion of Figure 7 and underlined by the same continuous horizontal line,

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are widely distributed in the alpine fir range and located on different habitats.

In Table 7, the data are increasing more or less proportionally with the values of Y except those of the bract lengths which change irregularly in the series of observations from No.1 to 40. It is obvious that the mean of stand samples (X_o) and the length differences (Y)exhibit parallel increase because both were calculated from the same measurements. Nevertheless, the proportional increase of the scale lengths (X_o) and length differences (Y) and the irregular change of the bract length (X_o)need further explanation and analysis to reveal the associations between the variables mentioned above. In the regression analysis, some ecological

factors are introduced as independent variables. Precipitation (X_i) , latitude (X_2) and altitude (X_3) are the only factors available for regression analysis. The results are given in Tables 9, 10 and 11. The sample regression coefficient, R^2 -0.993, reflects close association between Y and the variables mainly because the values of Y involve the individual means of samples (X_3) . However, omitting the corresponding variables one after the other it is possible to exhibit the relations between them. Herbert and Raymond Tables (1950 p. 140) of 1% points for R should be used to evaluate the associations of variables. The computed value exceeds the value in Table for 34 degrees of freedom and 6 variables. It is assumed that significant associations exist between Y and the variables.

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Table 10 presents these associations and allows one to conclude the following:

Precipitation correlate with latitude, altitude and bract length

Scale length correlate with individual mean of samples and Y

Bract length correlate with precipitation and scale length

Precipitation has an effect on bract length but does not affect the scale length. The bract may need a longer period for growing than the scale.Higher precipitation indicates a longer growing period for the bract and lower precipitation does the opposite.

There is correlation between scale length and Y but no correlation between bract length and Y. It should be necessary to analyse the relation of Y to the scale and bract length, separately. Two linear equations of X_4 and X_5 on Y are made up to find correlation between X_4 , X_5 and Y using a graph to show the two regression lines of these variables.

Equation of scale length: $Y = 42.213 + 0.573 X_4$ Regression coefficient equals to .573 and an estimated value of Y = 50, the value of $X_4 = 148.25$.

Equation of the bract length: $Y=55.919+0.335X_s$. Regression coefficient: .335, estimated value of Y = 50, then $X_5 = 105.60$.

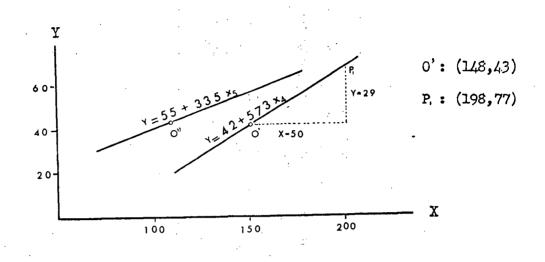
The divergency of the two lines indicate a poor correlation between the length of scale and bract. On the other hand the value of Y depends rather on the scale length than the bract length as the steeper slope of scale line exhibits.

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The graph of the lines X, and X, should be the





The explanation of the relation of X_4 and X_5 to the sum of the difference between the length of scale and bract can be purely numerical i.e. summarizing a large and a small figure the larger will increase the sum proportionally higher than the smaller figure. On the other hand, a biological explanation, if it is exists, would be more interesting, but it is beyond the scope of this study.

HISTOLOGICAL CHARACTERISTICS OF SCALE AND BRACT. The origin of the scale and bract as organs of the plant has been debated for a long time; to try to reconcile the various concept is more difficult than important.

Coulter and Chamberline (1910) present a brief account of the history of the concept of the ovuliferous scale: 'The ovuliferous scale of <u>Pinaceae</u> has been regarded successively an open carpel, a placenta, a flattened axillary shoot, the first two leaves of an axillary shoot, the first and only leaf of an axillary shoot, a ligule, fused outer integuments and a chalazal outgrowth'(pp. 244-248).

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Schoute (1913) gives some points about the development of cone scale including bract and assumes that at the growing point, bud forming materials may be present which have a restricting influence on leaf-formation. Every part of the vegetative cone in which the influence of the bud forming material ceases, can form a leaf primordium insofar as other influences do not prevent it. The leaf primordium is not visible through naked eye.

Jeffery (1922) calls the cone scale a reproductive foliar organ and points out that the view that the ovuliferous scales in the <u>Abietineae</u> consist of a fused pair of foliar structures has little evidence to support it. It is as clearly a single leaf as is the microsporophyll.

Büsgen (1929) considers the cone scale as a leaf which later in the developmental phase becomes leathery or woody.

Foster and Gifford (1959) emphasize that doubts have been repeatedly expressed by morphologists regarding the foliar nature of the ovule-bearing structure in gymnospermous plants. The evidence from ontogeny and vascular anatomy indicates that this ovuliferous structure is a highly condensed short shoot and not a simple megasporophyll.

The following observations confirm Foster and

Gifford's statement and show that the arrangement of tissue elements in the cone-scale are more similar to the stem than to the needle. The author observed that the cross-section of the cone bract has a needle-like structure in inverse arrangement, related to the position of bundle xylem and phloem.

The different structure in the cone scale and bract may allow one to assume a different derivation of these organs with a subsequent adherence during the development of the strobilus. However, final conclusions have to await further investigations.

SCALE. The hairy and resinous scale consists of epidermis in the cross-section which lacks stomata, but has mesophyll or cortex, numerous strands of vascular bundle, and various forms and numbers of resin canals, Figure 22.

The <u>epidermis</u> is multiple in the structure having 1 to 3 layers of cells and lacks chlorophyll. The cells of outer layer are thick-walled without cuticle on its surface. The scale is covered with resin when the cone matures and dries out. The epidermis is composed of regular epidermal cells and trichomes. Trichomes are built up of one to three cells. They are actively secretory having dense protoplast elaborating resin. Trichomes cover the surfaces of scale on both sides except in those regions where the seed wings and the bract attach to the surface. The author had the opportunity to make some observations on different species of <u>Abies</u> and found that the length of trichomes differs in various species: red fir has longer, silver fir has shorter

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trichomes on the scale surface than the alpine fir.Usually the mature scales have longer trichomes in all cases.

The <u>mesophyll</u> does not differentiate into palisade and spongy parenchyma. The tissue complex is relatively homogeneous in its features, being similar to the cortex in having hypodermal cells in the outer portion. Intercellular spaces, like subepidermal chambers in the needle mesophyll have been found under the epidermis at the adaxial side. The contents of cortex cells are starch and resin. Leucoplasts were found in the medial cells of cortex. The young parenchyma cells are located in the horizontal middle sheath rather than in the marginal region in the cross-section of the scale.

In a longitudinal section, elongated parenchyma cells are found immediately under the epidermal layers and have simple pits in the wall of the cells located in the outer layer of the parenchyma tissue.

The <u>vascular strands</u> are arranged horizontally in transection. Eighteen to twenty-two strands are present, distributed regularly in one plane parallel with the main axis of the scale. A diagram of scale venation pattern is given in Figure 6. The longitudinal strands converge at the base and diverge at the apex of the scale. These terminate in the cortex and are enclosed in transverse parenchyma cells. The parenchyma cells have simple pits on their side walls. The vascular bundles are not separated, so form one strand. The xylem element of this united bundle is located on the adaxial side of the scale and the phloem tissue on the abaxial side. The xylem consists of tracheids

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with annular and helical thickenings and parenchyma cells with simple pit fields on the side walls. The sieve cells alternate with parenchyma cells and abundant albuminous cells appear to be located at each side of the phloem.

The <u>transfusion tissue</u> consists of thick walled parenchyma cells and some tracheids. The latter are closer to the bundle than the former.

An ill-defined <u>endodermis</u> sheath lines the vascular and transfusion tissues. The sheath is interrupted by the extension of parenchyma cells which interconnect the strands laterally throughout the scale.

The <u>resin canals</u> are arranged mostly parallel with the vascular strands. It is possible to distinguish both large canals and some narrow canals. The larger ones are located in the adaxial half of the scale, close to the strands and more or less of the same number as the strands. The resin canals have an inner sheath that lines the cavity of the canal. This consists of thickwalled and large secretory epithelial cells filled with resinous material. The thin outer sheath is made up of small parenchyma cells which have a large nucleus. These cells appear to be intermediate between the secretory and cortex cells.

The smaller canals are distributed irregularly in the region of the vascular strands and are usually between two neighbouring strands. Their structure is much like the large canals but the cavity diameter is less and looks like a gap or an intercellular space in the center of a group of epithelial cells.

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BRACT. The bract consists of epidermis with stomata, hypodermis, mesophyll, vascular bundles and resin canals, Figure 20.

The <u>epidermal layer</u> is not covered by cuticle. On the adaxial surface stomatal openings interrupt its continuity. The wall thickenings of the epidermal cells are uneven and sometimes only the outer walls are thickened. The bract does not show xeromorphic characteristics as does the needle with their sunken stomata and cutinized epidermis. Probably the scale protects the bract from drying up. There are no chloroplasts in the cell of the epidermis, not even in the young cones of alpine fir.

Stomata are arranged in 8-10 parallel rows along the full length of the midrib in one narrow band. The stomatal cells i.e. guard cells and subsidiary cells are located lower than the epidermal cells around the opening but not sunken as in the needle. The occurrence of stomata on the bract surface has not been mentioned in the literature used for references. Their presence here may be evidence, that the bract and scale have the different origins.

Several specimens of <u>Abies</u>, <u>Picea</u>, <u>Pseudotsuga</u> and <u>Pinus</u> have been examined for stomata on the adaxial surface of their cone-bracts. It should be noted that the pines have several too many spirally arranged bracts each subtending an ovuliferous scale. With the exception of <u>Pseudotsuga</u>, all the genera mentioned have stomata on their bract surface, and each has the same arrangement of rows as alpine fir.

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<u>Hypodermal cells</u> are located under the epidermal layer of the adaxial surface in a discontinuous row. The fiberlike lamellar hypodermal cells are uneven in size and all of them have strongly thickened-walls. Sometimes they form two rows toward the edges of the two wings of the bract. There are conspicuously large hypodermal cells in the second row. Above the midrib the hypodermis occurs in one row, consisting of small cells with well-thickened walls. Under the epidermal layer of the abaxial surface, no hypodermal layer is formed. This side of the bract is soft and smooth and adheres to the seeds thus protecting them in the developmental phase.

The mesophyll is not well-differentiated in the specimens collected at the period of examination. The cell walls seem to be thickened and fully perforated with primary pit fields. There are shizogenous intercellular spaces between the cells. The cells cling closely together forming outer ridges from their walls which press the wall of the neighbouring cells into the cell lumina. The content of the cells is homogeneous and no plastids appear to be inside the cells.

The <u>Vascular bundles</u> are separately lined by an illdefined endodermis sheath. There is no difference between the cells of the mesophyll and endodermis in the structure of walls and the shape, but only in size. The endodermis cells are smaller than the needle endodermis and turn their tangential walls towards the vascular bundles, apparently having no Casparian strips in their side walls. Some of the walls are pitted.

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Inside the endodermis, the <u>transfusion tissue</u> consists of living parenchyma cells and tracheids as does the transfusion tissue complex of the needle. Both the tracheids and the parenchyma form continuous system and the two system interpenetrate each other. Rarely, some sclerenchyma cells appear among them.

In the neighborhood of the vascular bundle, like a large many-layered sheath, albuminous cells are located at each horizontal side of the bundle with dense cytoplasm and prominent nuclei.

The separated vascular cells are oriented as in the needle, but the xylem complex points towards the adaxial side of the bract. The total number of radial rows are 8 to 10 together in the two separated parts of the bundle. Both the xylem and the phloem have thickened and lignified walls. Annular and helical thickenings are present in the xylem. The parenchyma cells, located between the two parts of the bundle and around the bundle, have primary pit fields and simple pits in their secondary walls.

Resin canals are two to three in number, embedded in the mesophyll in medial location as in the needle cross-section. The resin canals are lined with thin-walled secretory epithelial cells. Outside these cells, a sheath of parenchyma cells make contact with the mesophyll tissue.

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The author observed that the bract develops first during the growing season and reaches a slightly differentiated form and size earlier than the scale. Therefore, the bract protrudes beyond the scale in the early developmental phase of the strobilus. Some cones have been examined in early stages of differentiation of strobili and have been found to have the bract separated from the scale. This may be further evidence that the origin of scale and bract is not common.

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DISCUSSION AND CONCLUSION.

Ten of twenty traits were tested by 't' test and an additional two by regression analysis. Significant differences of several traits were revealed among stand samples located in various ranges of the alpine fir on the West Coast. But the traits tested do not give sufficient evidence to prove the existence of regional populations perhaps because an equal number of specimens was not available for all traits, e.g. cones were collected only from two-thirds of the stands sampled for stomatal distances, seeds were available only from four stands. Thus, the question of whether alpine fir is to be considered one general population or composed of several populations isolated during the geological eras is one that this study is unable to answer. The scope of this project has been too limited by time and opportunity to observe continuity and adaptability of quantitative or qualitative characters on a large scale which may indicate the existence of genotypically different or regional populations. The fact that there are significant differences between some specimens concerning the stomatal distance or scale and bract length does not indicate regional differentiation within the population of the alpine fir. A population can include groups of individuals of almost any phenotypes. Stebbins (1957) defines the population as a group of individuals among which a larger or smaller amount of interbreeding and gene exchange can occur. Studies in natural stands, i.e. the taxonomic approach,

have the major disadvantage that the method is purely descriptive and no precise distinction can be made of the environmental and genetic components of variations. And so, it is not possible to present evidence here for any variations between the stands sampled which seem to be solely under genetic control.

The author is convinced by numerous observations that there are natural hybrids between alpine and balsam fir in the overlapping areas (Roller 1966b). Several traits such as resin canal position and hypodermal tissue in the needle cross-section, thickness of the needle, distribution of stomata on the upper surface of the needle, size of the parenchyma extension in the bundle, length and number of the lenticels on the middle-age bark and finely the percentage of the β - pinene and β - phellandrene in the resin, show intermediate characteristics between alpine and balsam fir in the samples collected from northern Alberta and British Columbia.

However, the most difficult is to identify any hybrid by purely morphological characteristics. In the regions, where these putative hybrids occur, the different species and hybrids exhibit characters which increase or diminish in a given direction under the same environmental conditions and therefore the individuals of these different species show quite similar phenotypic characteristics. Some characteristics may vary on different parts and at various levels of the same tree. Sometimes, certain characteristics vary on the same part of a tree during the long period of tree development. Nevertheless, the length of period depends on the aspect, habitat, association etc. This consideration does not support the clari-

fication of the hybrids or the ecotypes which may exist in the different regions where habitat differences are found. Certainly, the geographical distribution of alpine and balsam fir is very wide and trees growing in various regions exhibit high variety in morphological characteristics which sometimes must be due either to natural selection or other mechanisms such as mutations, introgression or genetic.

In most cases, it is almost impossible to define that the characteristics, selected for testing, are variations or the result of a higher tissue differentiation in the aging of the plant. Most parts of the inner tissue in the needle follow this pattern, particularly those which take part intensively in the building up of the tree. For instance, the stele of the needle has a very high variability in the arrangement of conducting elements, Figures 23-30 while the mesophyll cells do not vary significantly during the development of the needle either within or between the samples collected, except the chlorophyll content in the palisade cells. The needles of understorey trees and seedlings have conspicuously higher chlorophyll content in the palisade cells than the needles sampled from trees in open grown stands, or needles from cone-bearing branches which are in a more developed stage.

On the basis of observations and measurements, and after considering the high variability of characters within stand

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and between stands, two variation patterns have been revealed.

Those stands which include variations such as the stomatal distances, scale and bract length differences, and different size of seed wings are distributed horizontally in different regions of the natural range of alpine fir and separated by geographical barriers.

The other groups of the variation patterns involves those stands which are distributed vertically in the same region, being located at different altitudes and related to ecological gradients within a restricted area. They occur in characteristics such as height, crown and bark color, needle form, cone size and color, stomatal frequency on the adaxial surface of needle, etc..

In the first case, regression analysis confirms that the variability of stomatal indices and scale-bract length differences are under environmental control. Although there is no evidence against the hypothesis that the stomatal frequency may be adaptive, the analysis has not shown any genetic control of the formation of the stomatal distribution. Obviously, that distinction between environmental-induced modification and genetic variation could not be made.

Stomatal distance in a row line was inversely correlated to the precipitation, elevation and latitude. This means that the environment is largely resposible for the stomatal distance and that changes in the environment affect changes in trait values.

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All the traits concerned are discontinuous and divergent in the series of sampled stands. Thus, it is not possible to establish a systematic classification, at least according to two characteristics like stomatal distance and difference between scale and bract lengths.

The horizontally distributed variation pattern should be illustrated by some examples. The extreme stands, which are the ends of this variation pattern, constitute samples at Garibaldi Lake (No. 1) and on Wallowa Mts. (No. 65) . The data of these two extremes are presented in Figure 3. Significant difference between the sample means is proved by analysis of variance, (p. 20), but the trees in both stands show similarities in their character combinations. Habitat is different in both regions. Garibaldi Lake is located in the coastal forest region occupying a zone between Douglas fir, hemlock-cedar forests, and the alpine tundra and snow fields. This forest type is characteristic of both the Subalpine and the Coast Regions. High precipitation and true podzol predominate. Wallowa Mountains are located in the Mountain Forest region of the United States characterized by lower precipitation and fairly deep and loose podzolic soil.

The two regions are far enough from each other to be quite separate. It is concluded that the difference between needle characteristics from these areas arose after their regional isolation and might be due to adaptation during the past geological eras. Between the two regions, which are almost

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the western and eastern range limit of alpine fir occurrence, there are several intermediate types of alpine fir and the value of stomatal distance shows some decreasing tendency from east to west. But the decrease of stomatal distance is irregular and discontinuous, not constant, therefore, it would not be reasonable to draw conclusions for introgressive populations.

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However, in many instances there are gradual changes in the stomatal distances from one stand to a distant one. A gradation of character occurs, called cline by Huxley (1933) who lists many of them. This cline may be classified as intra group cline because the mean values of character change gradually through the continuous population. The author does not consider the continuous variations of one trait to be sufficient to establish a cline even if they have been followed in the series of stands.

The author considers that the second variation pattern, i.e. the vertical segregation of different stands, is a cline and demonstrates it by an example. In the Glacier National Park, Montana altitude ranges from 3500 to 7000 feet on high mountain slopes. Trees located at the higher altitude around Logan Pass and at lower altitude along Alder Trail possess characteristics that change continuously from the high to the low elevation. These may be parallel the example of Clausen, Keck and Hiesey (1940) adopted from Stebbins (1957) in connection with two ecotypes of <u>Potentilla glandulosa</u> subs. <u>nevadensis</u>. The quotation is the following: 'It consists of two ecotypes, one is a dwarf, early-flowering alpine that occurs above 2600 m., while the other is subalpine and may be distinguished in garden cultures by its taller stature and later flowering.' The occurrence of the alpine fir from Alder Trail up to Logan Pass is analogous the existence of two <u>Potentilla</u> ecotypes at low and high elevations. Baur (1932) gives another similar example of <u>Antirrhinum glutinosum</u> which was found in the Sierra Nevada of southern Spain at altitudes ranging from 800 m. to 2800 m. on high mountain slopes. Plants taken from higher altitudes show different characters in frost resistance and habit from those grown at lower altitude.

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No doubt, two types of alpine fir occur in the Glacier National Park from Alder Trail to Logan Pass and their separation is due to the response of the selective effect of ecological and climatic differentiation. This means differences in the upper horizon of soils, growing season, radiation, annual average of temperature, humidity and number of frosty days. The annual average of precipitation does not differ significantly but the distribution of snow and rain fall do so. At high elevation, snow covers the slopes until June while along Alder Trail snow is usually melted in late April.

The question may be justly asked if these two types of alpine fir could be classified as cline. If Huxley's definition of the cline is taken into consideration i.e. 'internal intra group clines occur when the mean value of the characters changes gradually through a continuous population' the two types of alpine fir would be internal clines because the means of the tested traits, such as stomatal distance, scale/bract length difference, needle length and width, bark formation, crown color, height of tree, branch formation, etc. vary gradually from Logan Pass to Alder Trail. These two extreme types of <u>Abies lasiocarpa</u> might be called as 'high-alpine type' at high elevation and 'subalpine type' at lower elevation.

The taxonomical description of these two types is the following:

Mature bark:

High-alpine type: ashy grey or whitish, slightly fissured on the lower and smooth on the higher part of the trunk.

Sub-alpine type: dark, grey, furrowed and superficially scaly. Bark on the upper stem usually exhibit well-developed horizontal lenticels, Figure 33, which do not appear so definitely on the bark of high-alpine type trees.

Mature needle:

High-alpine type: cross-section slightly rounded, less than 2.5 cm. long and about 1.60 mm. wide, yellowish or light yellow green. Stomata on the adaxial side appear as a narrow band along the midrib but abundant at the apex, fully covered on the needles of top branches; on the abaxial side the mean of stomatal frequency in square millimeter is 103. Apex is acute and pointed, the latter occurs particularly on the leading shoot; slightly rounded in the lower part of the crown. The crown consists of ill-developed, short branches in its upper part.

Sub-alpine type: cross-section flattened, longer than 2.5 cm., and about 1.80 millimeter wide, long, dark blue and blue green to silvery green. Adaxial surface is covered by irregularly distributed stomata. On the abaxial surface, the mean of stomatal frequency in a square millimeter is 70. Apex is notched and marginate. The crown is dense and consists of well-developed, proportionally distributed branches.

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Cone:

High-alpine type: dark, slightly black with resin flows. Axis is 4 cm. long. The tip of bract short with unformed shoulder; seed wing shiny and purplish.

Sub-alpine type: dark purple, length of axis is 6 cm., the tip of bract is long,slender,pointed, seed wing yellowish brown.

The high-alpine type variation grows five to six meters in height with slender form and spire-like crown, but scarcely distributed branches, Figure 10. They occur in small pure groups dispersed along the timber line.

The sub-alpine type variation develops normally, reaching 25-30 meters in height and mingle with other forest trees forming continuous stands on well-drained mountain-sides, Figure 11.

Trees were found with similar habit to the highalpine type variation on dry sterile sites on the lava rock of Belknape Crater (61) and McKenzie Pass (30) Oregon and on Hurrican Hill, Washington (2). The trees have similar forms, colors and habits to the high-alpine type trees, but they are higher in growth and their stomatal indices (Y) on the lower surface of the needle are 607, 504 and 457 respectively. The needle collected at Logan Pass, Montana (3) show an index of 461. The habitat at Belknape Crater is very dry and nothing else, but lava outcrop covers the ground without any plant association. The alpine fir is pioneer here, where wind blown material has begun to accumulate and may exhibit an ecotypic variation different from the others.

The high stomatal index suggests a dry ecological condition and presents an essential distinction between the two variations located along Belknape Crater and at Logan Pass.

The observations on the sampled trees and the analysis of the measured data give a picture of the diversity of quality differences in the stands scattered on the West Coast. It is obvious, that the greatest diversity is expected between the extremes located in northern and southern limits of the natural range of alpine fir. If the traits in these extremes inherited and became aquired the finding of some genotypic variations in its natural range can be expected.

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SUMMARY.

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This is a morphological-anatomical study of natural stands of Alpine fir.

Its objectives were (a) to determine the variability of needle and cone characteristics for two morphological traits: distance between stomata in a row line on the abaxial surface of the needle and difference between cone scale and bract length; (b) to become familiar with other traits; and if possible (c) to ascertain whether alpine fir is essentially one population and its phenotypic variations follow certain environmental gradients.

Sixty five stands, located in the Yukon Territory, British Columbia, Washington, Montana and Oregon,were sampled.

Laboratory procedures involved: preservation of needles and young cones in FAA, needle and cone cross-sections by microtome, several sets of observations and measurements on needles, seed wings, cone axes, cone scales and bracts.

The following tree mean data were used as the basic units for the study of variation: needle length, width and apex form; presence of groove and ridge; color of foliage; stomatal distance on the abaxial needle surface; stomatal distribution on the adaxial needle surface; stomatal structure; seed wing area; seed weight; length of scale; length of bract; difference between scale and bract lengths; length of cone axis; histology of needle, scale and bract; and resin canal position. Mean. standard deviation and range were calculated from tree means, and stand means were computed. Correlation analysis and 't' test were used to show the association between several traits and environmental factors and prove significant differences between the stand means.

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The correlation was the highest between stomatal distances and precipitation. The stomatal distance in a row line is inversely related to the increase of precipitation, and so stomatal frequency increases with higher precipitation.

All traits show higher variability between stands than between trees sampled. The variability of traits is apparently largely due to the environmental factors. Nevertheless they sometimes suggest casual associations.

Eastern and western varieties, and high-alpine and sub-alpine fir have been described.

The major conclusion is that care must be exercised in describing trait variability. The particular environmental gradient must be specified because the same trait can show clinal, ecotypic and random relationship patterns, depending on the component with which the trait is compared.

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Table: 1. DISTRIBUTION OF DATA OF ABIES LASIOCARPA ON THE WEST COAST.

- X. :Stomatal frequency/sq.mm.
- X₂:Precipitation, inch

No

- X3:Needle width, millimeter
- X₄:Mean,distance in units between two stomata in one row line, 1 unit equal to 0.02 millimeter.
- X₅:Elevation, feet
- X_c:Latitude,degrees
- X₇:Longitude, degrees
- Y :Combined data of stomatal distances on twenty randomly selected needles. Explanation on page 19.

Location X, X_2 $X_3 X_4$ X_{5} Xő X, Υ

-	A A A A A A A A A A A A A A A A A A A	•								
	Garibaldi Lake Trail, BC.	95	120	1.74	4	4800	50.0	123.3	451	
2	Hurricane Hill, Olympic	740	80	7 06	A	EACA	417 1	107 0	A (** ** **	
. 7	N.P., Wash.	148	80	T-90	4	5464	47.05	123.8	457	
·)	Logan Pass, Glacier N.P.,		40	2 65		7000	40 -	77 0	467	
	Mont.	103	- 40×	T.+02	4	1000	40.2	113.8	401	
4	Black Tusk, Garibaldi		740	1.60	~	FCOO	50.0	307 7	ACC	
F	Prov.Park, BC.							123.3	466	
	Arrowsmith Mt., Peak, V.I.							124.5	466	
	Scott Lake, Ore.	95						121.9	468	
	Arrowsmith Mt.,V.I.							124.5	468	
	Manning Park, BC.	104		1.84				120.5	475	
-	Wood River, BC.	70						118.5	480	
	Siskiyou Mts., Ore.	125						123.6	481	
	Downie Cr., BC.	86 78						118.3	481	
	Azouzetta Lake, BC.	78 88						122.7	482 483	
	Ottauwau River, Alta.	. 00	- T 2	T+25	2	2500	22.U	110.0	40)	
74	Boulder L., Olympic N.P., Wash.		100	2.20	Ē	1500	47 E	123.9	AOE	
זה	Giscome Rd., Willow R., BC			1.40				122.5	485	
	Naver Cr., BC.	75		1.57				122.2	486	
	Arrowsmith Mt.,Hill, V.I.							124.5	487	
	Parsnip River, BC.	71		1.37				123.0	• •	
	Mt.Rainier, Timberline, Was	•						121.8	488	
	Forbidden Plat., V.I.							126.0	488	
	Pine River Valley, Alta.							122.5	490	
22	Alaska Hwy., Mi. 500, BC.	1/3	17	1.66	Ę	2300			491	
23	Bear Lake, BC.	- 49	25	1:58	5	2500	54.5	122.0		
	Hurricane Ridge, Wash.	105	80	1.71	5	5000	47.5	123.5	495	
	Mt.Rainier,Wash.	100	80	1.75	5	6500	46:3	121.9	495	
	Bear Lake, BC.	88						122.0	495	
	Alaska Hwy., Mi.356, BC.	- 74	-	1.60				122.3	498	
28	Aleza Lake, BC.	82		1.95				121.7	499	
	Mt. Hood, Ore.	81						121.4		
	McKenzie Pass, Ore.	95						121.8		
20		, c c			م ن	<i>,,,,,</i> ,	TT • /	~~~• `	207	

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Table 1. cont.

No	Location	Χ,	X 2	X3	X 4	X_{5}	X.	$X_{ au}$	Y
- 32 - 33	Willson Cr., New Denver, BC Champion Lakes, BC. Andimaul Nash, BC. Eagle Cap, Slope,	. 99	40 35 40	1.87 1.65 1.60	5 5 5 5	3000 3600 1600	50.6 49.2 55.3	118.5 118.5 127.5	505 507 510
35 36	Andimaul Nash, BC. Eagle Cap, Slope, Wallowa Mts., Ore. New Hazelton, BC. Pendleton Bay, BC. Kicking Horse Pass,	90 81 62	30 40	1.66	5	5500 3800	45°3 55°0	116.9 127.5 125.7	514 514
38 39	Yoho N.P.,BC. Alaska Hwy.,Mi.305,BC. Alaska Hwy.,Mi.160,BC. Pine Lake,Yukon	103	17 17	1.66 1.97	5	1100 3500	59.0 58.0	116.2 123.5 122.5 133.8	523 524
41 42 43	Alaska Hwy.,Mi.480,BC. Manning Park,BC. Wallowa Lake,Ore.	88 77 90	25 50 20	1.88 1.60 1.81	5 5 5 5	2800 4000 3000	59.0 49.1 45.3	126.8 121.0 116.9 133.0	527 529 529
45 46 47	Alaska Hwy., Mi.852, Yukon Mt.Rainier, Wash. Crater Lake, Ore. Slave Lake, Alta.	99	79 69 15	1.62 1.86 1.73	555	2800 7500 2000	46.3 43.0 55:3	121.8 122.3 115.0	532 539 539
49 50	Cirrus Mt., Banff N.P., Alta Mt.Bonaparte, Wash. Divide Cr., Glacier N.P., Mont.	74 68	20	1.62 1.81	5	4500 4500	48.7 48.5	115.3 119.2 113.5	540 543
52 53	Dixie Pass,Ore. Lava Camp Lake,Ore. Alaska Hwy.,Mi.720,Yukon Graves Mt.,Wash. Lake Louis,Alta.	78 87 83 75	40 25 17	1.75 1.89 1.80	555	5700 3200 5200	44.3 60.0 48.2	117.8 122.0 129:1 116:0	546 558 561
56	Lake Louis,Alta. Alder Trail,Glacier N.P. Mont. Mt.Idaho,New Denver,BC.	65 70 57	40	1.76	5	4200	48.3	116.3 114.0 118.4	574
58 59	Alaska Hwy.,Mi.735,BC. Mt.Edith Cavell,Jasper N.P., Alta. Upper Pine River Valley,	106	20	2.01	5	3000	60.0	128.0 112.0	580
61	Alta. Belknap Crater,Ore. Nagle Cr.,North Bend Hwy.		50 [.]	1.95	6	5300	44•3	122.8 122.0	607
64	BC. Nisqually,Wash. Beaverdell Range,BC. Wallowa Mt.,East Peaks,Or	67 75 63 e•67	45 25	1.82 1.89	6 7	1000 2500	46.5 49.3	118.5 123.2 118.3 116.9	620 644

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Table 2.

BASIC ELEMENTS OF STATISTICAL ANALYSIS

ON STOMATAL DISTANCE

	X ₁	x ₂	I ₃	×4	x ₅	x ₆	Ĭ,	¥2	$\frac{r_1 + r_2}{2}$
Ī	8.767692E+01	4.690769E+01	1.7610768+02	5.053846 E+ 01	4.095338E+03	5.1098460E+02	5.221999E+02	5.179230E+02	5.200615E+02
SD	2.015882E+01	3.330996E+01	1.7467078+00	3.657513E-00	1.624364E+03	4.8534750E+01	4.6846202+01	4.526736E+01	4.551996E+01
Range	sq.mm	inch		unit	feet	degrees	- C.D.	C.D.	C.D.
Max:	148	140	2.20	-6.5	8000	60.30	643	649	646
Min:	47	8	1.35	4.0	1000	42.00	448	449	448

	Stomatal frequency per sq.millimeter Precipitation Needle width Mean of stomatal distances Elevation Latitude	X: Mean of variables SD: Standard deviation l unit 0.02 millimeter C.D.:combined items,ex- planation on page 20.	Y1: Distance between two stomata in a row line, first measurement. Y2: Second measurement	
--	--	--	--	--

TABLE 3.

CORRELATION COEFFICIENTS OF STOMATAL DISTANCE.

Row	. x 1	.×2	X ₃	x ₄	x ₅	x ₆	Y
I II	-0- 0.3759 x	0.3759 x	0.1698 0.1121	-0.4447 x -0.2075	0.0444 0.4533 x	-0.0153 -0.4637 x	-0.5054 x -0.3933 x
III IV	0.1698 -0.4447 x	0.1122	-0- -0,0009	-0.0009	0.1825	-0.0715 -0.0694	0.1939 0.7550 x
V V IV	0.0444 -0.0152	0.4533 x -0.4637 x	0.1825	-0.0694 -0.7152	-0.6191 x	-0.6191 x -0-	-0.0436 -0.0127
VII	-0.5054 x	-0.3933 x	0.1939	0.7550 x	-0.0431	-0.0127	-0-

The correlation coefficients' values in the Table: r = .244

.05

.01

r = .318

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"-" indicates a negative slope

"+" indicates positive slope -O- the factors to which the other factors

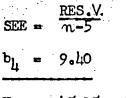
are correlated x significantly correlated at .01% level

TABLE 4.

REGRESSION COEFFICIENTS OF CLIMATIC FACTORS Elimination of Y, stomatal distance

The variable to be omitted	Constant term (a)	Residual Variance (SEE)	R ²	K
€ <u>,</u>	6.686142E+01	6 •5 77782E+02	•71231080	71.23
x 5	1. 059740E+02	6.578876E+02	•70730190	70.73
6 	6.185729E+01	6.565248E+02	•70295760	70.29
X 3	1.514535E+02	7.773202E+02	.64244240	64.24
1	9.328281E+01	7.943285E+02	.62867110	62.87
2	4.515440E+01	9.094479E+02	•57008730	57.01

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 $X_5 = 45.15 + 9.40 X_1$

EXPLANATION OF TABLE 5. ANATOMICAL CHARACTERISTICS OF NEEDLE

Epidermal tissues are categorized as follows:

A: well-developed hypodermal cells, two or more layers

B: developed, but thin, broken layers

C: ill-developed layers

- 0 : no hypodermal cells under the epidermis
- 1 : hypodermal cells are only under the abaxial epidermis
- 2 : hypodermal cells are at the angles of needle wings
- 3 : hypodermal cells are at the angles and under the abaxial epidermis
- 4 : continuous or alternately broken hypodermal layers line the mesophyll in two or more rows

<u>Mesophyll tissue</u> can be palisade-like formed quadrangular cells and closely attached to each other, and spongy parenchyma involved numerous intercellular spaces between them.

Size of resin canal is inticated as:

I	:	150-200	micron	large	cavity
II	:	100-149	•	do	
III	:	70- 99	•	do	

Endodermis: Inner sheath means the perycicle, which is illdefined in most cases

<u>Transfusion</u> <u>tissue</u>: Percentage means the ratio of parenchyma and tracheid elements in the abaxial part or half of the stele

1/2 - phloem and xylem band occupies the upper half of the stele

1/3 - the band occupies the upper one/third space of the stele

Toble 5. ANATOMICAL CHARACTERISTICS IN THE NEEDLE CROSS-SECTION OF SOME SELECTED ALPINE FIR SAMPLES.

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Samples are ranked as for the stomatal distance

No. of	LOCATION	EPIDERMAL	MESOPHYLL	RESIN	ENDO-	TRANS-	VASC	ULAR B	UNDLE	
or xampie	Y _S = stomatal distance Y _B = bract and scale	TISSUE	TISSUE	CANAL	DERMIS	FUSION		ROWS		NOTES
•	length difference					TISSUE				
	(hundredth of mm.)		,				cal	xylem	phloen	
1	Garibaldi Lake Trail, BC Y _S = 451 Y _B = 50	A'-4 3 layers	Rounded palisade spongy parenchi- ma	some times	conti- nuous	70% T 1/3 @	13	5	5	Xylem and ph located in the upper half of the stele.
3	Logan Pass, Glacier NP. Montana YS = 461 YB = 690	B - 3	Rounded palisade spongy parenchi- ma	l different cavity size one	cont, ili-de- veloped inner sh	60% T 1/3 @	17	5	7	
11	Downie Creek, B.C. Ys = 481 YB= -	C - 3	Palisade like layers dense tissue without air spaces	11	Broken	70% T 1/3	16	5	6	
20	Forbidden Plat., V.I. Y _S = 488 YB = 650	B - 3	Palisade like layers dense tissue	11	cont. ill-d. inner sheath	70% T 1/2	20	5	5	
29	Mt. Hood, Ore. $Y_S = 500 Y_B = -$	A - 4	Palisade like layers abundant chloro- phyll	li 3 epith. layers	cont. ili–d. inner sheath	70% T I/2	13	4	6	
37	Yoho NP., B.C. Ys = 515 YB= 480	C - 3	rounded palisade spongy parenchi- ma	II different cavity size	Broken	70% T /3	15	4	8	Conspicuous separated bundles
38	Alaska Hwy., Mi. 305, B.C. Y _S = 523 Y _B = -	C - 3	Palisade like layers dense tissue	n n	Cont.	70% Par. 1/2	11	5	7	
41	Radium Hot Spring, Alaska Hwy., Mi.480 BC Y _S = 527 Y _B ⊒ -	C - 0	Palisade like layers spongy parenchi- ma	11–111 O – 4 canals	Broken	80% Par. 1/2	12	4	8	Medial and marginal can. Sometimes on epithelial cel sheath only
54	Graves Mt., Wash. Y _{S =} 561 Y _B =340	B – 3	Palisade like layers spongy parenchi= ma	II outer sheath *	Broken large uneven cells	60% Par 1/2	17	5	6	* large
58	Alaska Hwy., Mi.735 BC Y _S = 580 Y _B = 170	A-4	Rounded palisade spongy parenchima	H	Cont.	80% T 1/2	17	6	7	1
59	Mt. Edith Cavel Jasper NP., Alta. Ys = 587 YB= -	C - 2	Palisade like layers spongy parenchi– ma	III one sheath ' only	Broken	80% T 1/3	13	5	6	
64	Beaverdell, B.C. Y _{S =} 644 Y _{B =} 550	B - 3	Palisade like layers spongy parenchi= ma	111 +	Broken	50% Par. 1/4	16	5	7	*Sometimes one additional epithelial sheath
65	Wallowa Mt., Ore. Ys = 646 YB = -	A – 4 2–3 alter– nated lay– ers	Rounded palisade cells spongy parenchi- ma	•	Cont.	80% Par. 1/2	13	5	6	*3 epithelial sheaths

- TABLE: 6 GEOGRAPHICAL DISTRIBUTION OF ALPINE FIR SAMPLED, AND SOME CHARACTERISTICS OF RESIN CANALS IN THEIR NEEDLES

סייינדי ג'ייינט אינט אינט אינט אינט אינט אינט אינט		\$*************************************				
No. of	Location	Lat. and	Elevation	Resin o		
sample	-	Long. (Degrees)	(feet)	Diameter Mic:		S x Micron
		(Degrees)		<u> </u>		I MICION
22	Crater Lake, Ore.	43°02,N - 122°04,W	7500	170.0	170.0	2.14
20	Siskiyou Mt., Ore.	42°02,N - 123°03,W	7400	235.0	163.0	2.66
53	Mt. Edith Cavell, Alta.	53°07,N - 115°24,W	6000	211.3	237.2	2.34
12	Mt. Tusk, Garibaldi, B.C.	50°05,N - 124°10,W	5600	188.8	195.0	1.43
7	Forbidden Plt., B.C.	49°24,N - 126°00,W	5100	187.0	151.3	1.53
13	Scot Lake Mt., Wash., Ore.	44°12,N - 115°48,W	4500	177.8	196.1	1.27
48	Liard Hot Spring, B.C.	59°05,N - 126°54,W	2800	96.3	186.3	3.87
60	Bear Lake, B.C.	54°42,N - 122°30,W	2500	128.8	181.3	0.93
47	Alaska Hwy. Mi.500. B.C.	59 ⁰ 12,N - 127 ⁰ 06,W	230 0	112.5	97.5	1.99
24	Hazelton, B.C.	55°12,N - 125°18,W	1600	106.4	144.4	1.52

Note: Each sample represents 60 needles from a sample unit of three trees. Total: 600 needles for entire table.

 $S_x =$ Standard deviation of the resin canal position with regard to the centre of stele and the edge of needle.

Table: 7. MEASURED DATA OF THE SCALE AND BRACT OF

ABIES LASIOCARPA.

 X_{μ} : Length of scale, average of twenty samples, tenth of mm. X_5 : Length of bract, average of twenty samples, tenth of mm. X_6 : Mean; difference of 20 scale and bract length, millimeter. Y : Sum of the differences in length of the scale and bract

of ten randomly selected samples. Hundredth of millimeter. Nos: Code number of stomatal specimens from Table 1.

	No	Nos	Location	X 4	X ₅	X 6	Y	
•	12		Garibaldi Lake Trail, BC.	109	102	l	55	
			Hurricane Hill, Olympic N.P., Wash.	115 :	106	l	90	
	3		Hurricane Hill,Olympic N.P., Wash.	123	112	, l	100	
	6 7 9 10 11 12	58 20 18 45 57 57 28	Hurricane Peak,Olympic N.P. Wash. Alaska Hwy.,Mi.735,BC. Forbidden Plat. V.I. Parsnip River,BC. Mt.Rainier,Wash. Mt.Rainier,Wash. Mt.Idaho,New Denver,BC. Arrowsmith Mt.,Peak,V.I. Aleza Lake,Lower Elevation,BC	105 81 128 106 104 105 102 136 •132	82 113	222222222222222222222222222222222222222	150 170 175 185 195 295 210 240 245	
	15 16 17 18 19	49 54 55 39 19	Black Tusk, Garibaldi Prov.P. BC. Black Tusk, Timberline, BC. Mt.Bonaparte, Wash. Graves Mt., Wash. Lake Louis, Alta. Alaska Hwy., Mi.160, BC. Mt.Rainier, Timberline, Wash. Aleza Lake, Higher Elevation,	143 130 135 157	110 110 96 101		300 315 320 340 340 360 380	
	21	17	BC. Arrowsmith Mt.,Hill,V.I.	135 223	93 183	2 4	380 400	r.
	23	••••	Hurricane Ridge,Olypic N.P. Wash. Arrowsmith Mt.,V.I.	154 158	115 115	5 4	435 443	,
			Mt.Idaho, New Denver, Lower Elevation, BC.	147	99	5	480	
	25	21	Kicking Horse Pass, Yoho N.P. BC.	' 145	95	5	485	
					. :		•	

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Table 7.Cont.

No Nos	Location	X4	Xs	Xo	Y
	Pendelton Bay, BC.		77	5	500
	Beaverdell Range,BC. Hurricane Ridge,Olypic N.P.,		103	5	550
	Wash.		115	6	555
29 -	Jackson Glacier, Glacier N.P., Mont.	751	92	6	620
30 23 1	Bear Lake, BC.		109	-	625
31 25 1	Mt.Rainier,Wash.	177	113	9	650
			136	•	655
	Black Tusk,BC. Hurricane Lodge,Olypic N.P.		121	7	660
	Wash.		103	6	665
	Kokanee Galcier Prov.P.,BC.	177	110	7	670
<u> 20 - 0</u>	Jackson Glacier,Glacier N.P.,Mont.	163	93	7	695
37 39	Alaska Hwy., Mi. 160, BC.		118	8	750
	Willson Cr., New Denver, BC.	180	99	7	805
39 50 1	Divide Cr.,Glacier N.P., Mont.	190	108	8	815
40 56 .	Alder Trail, Glacier N.P.,		T 00	Ŭ.	
	Mont.	218	130	10	890

Result of statistical analysis:

Mean of Y : 428 hundredth of millimeter Standard deviation: 32 hundredth of millimeter F = 131.576, greater than the F in the Table at 5 % and 39 DF.

The differences between the value of Y are highly significant in several cases which are expressed in the diagram of the Duncan's test. Figure 7.

Code		S	EED	AXIS
-		WEIGHT	WING SIZE	LENGTH
No	Location	GR/1000	لساءته والله المراجع	mm .
5	Alaska Hwy., Mi.735, Yukon	-	0.18xxx	61
7	Parsnip River, BC.		0.82	-
9.1	Mt.Rainier,Washington	-	0.15xxx	-
12	Aleza Lake, BC. Lower Elevation.	5.94	0.64	51
18	Alaska Hwy., Mi.160, BC.	-	1.40xxx	-
20	Aleza Lake, BC. Higher Elevation.	5.02	0.75	42 x
22	Hurricane Ridge, Olympic NP., Wash	-	0.50	-
25	Kicking Horse Pass, Yoho NP., BC.		0.82	<u> </u>
26	Pendleton Bay, BC.	6.21	0,•40	43x
35	Kokanee Glacier Prov.P., BC.	_	0.75	76x
38	Willson Cr., New Denver, BC.	8.93	1.05xxx	82xx

TABLE 8. MEASUREMENT DATA ON SEEDS AND CONES OF ALPINE FIR.

LEGEND:

x PROBABLY SIGNIFICANT does not exceed 1.0% probability level. xx SIGNIFICANT falls between 1.0 and 0.1% probability level. xxx HIGHLY SIGNIFICANT exceeds 0.1% probability level. Fisher's Table was used from SNEDECOR (1956)

)	· .									
•						TABLE 9.					4
				· · ·	BASIC ELEM	TENTS OF STATIS	STICAL ANALISIS	3		. •	
		• • •	• •	•	`.	ON SCALE AND F	BRACT		•	•	1
	X	X1 6.605000E+01	X2 5.032000E+01	X₃ 4.659100E+03	X 4 1.482500E+02	X ₅ 1.056000E+02	x ₆ 4.350000B-00	¥1 4.260000E+01	Y ₂ 4.292500E+01	$\frac{Y_1 + Y_2}{2}$ 4.276250E+01	
	SD	3.995763E+01	3.306113E+00	1.367355E+03	3.291617E+01	1.904757E+01	2.402456E-00	2.229039E+01	2.300210E+01	2.256187E+01	1
۰	Range	inch	degrees	feet	mm	mm	mm	1/100 mm	1/100 mm	1/100 mm	ت
	Max:	140	60,00	8000	22.3	18.3	10	890	890	890	
· : 	Min:		47.50	2500	8.1	6.4	1	70	40	55	• •
•••			· _				•				
		X1: Precipita X1: Latitude X3: Altitude X4: Length of	SI Scale	: Mean values the variable D: Standard dev	8	of scale	difference the length and bract asurement	<u> </u>	me as Y ₁ measurement		
•	· · · ·	X ⁴ : Length of X ₆ : Average of difference tween X ₄	of the ces be-		~ `	· · · ·			. •		
		4	5			-					
-								•		•	
ł		· · ·		· · · · ·	с.	· · · · ·					
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				· · ·		·					
1				· .							

TABLE 10.

CORRELATION COEFFICIENTS OF SCALE AND BRACT

	x 1	X 2	X 3	X 4	X 5	X 6	Y	
Ĭ	∞ 0 ∞	⊷•51238391 x	•52091683 x	•05976 233	•40767108 x	~_017 006502	⊷₀ 24360658	
II	•••51238391 x	= 0≈	⊶.66971426 x	09742801	19494580	-•06546816	~。0 0383624	
III	•52091683 _x	⊷.66971426 _X	ed) 600	∞₀0 5264150	•0896339 7	∞₀0266 8998	13810740	· · · · · ·
IV	•05976233	~.0 9742801	05264150	~ 0w	•75863036 x	•82373938 x	₀83568909 ×	•
V	•40767108 x	⊶.19494580	•08963397	•7 5863036	~ 0æ	•30683411	281034 59	
VI	~ •17006502	⊷•06546810	⊷₀0 2668998	•82373938 x	. 30683411	~ 0 ~	•96162277 ^x	
VII	∞₀24360658	-•00383624	⊷.13810740	•835 68909 x	28103459	•96162277 x	~0 ~	
· · ·			·					· · · · · ·
	"_" indicates a	a negative sl	ope	<u>.</u>	orrelation co	efficients: H	R = .312 .05	

-O- the factors to which the other factors are correlated

x significantly correlated at .01 level

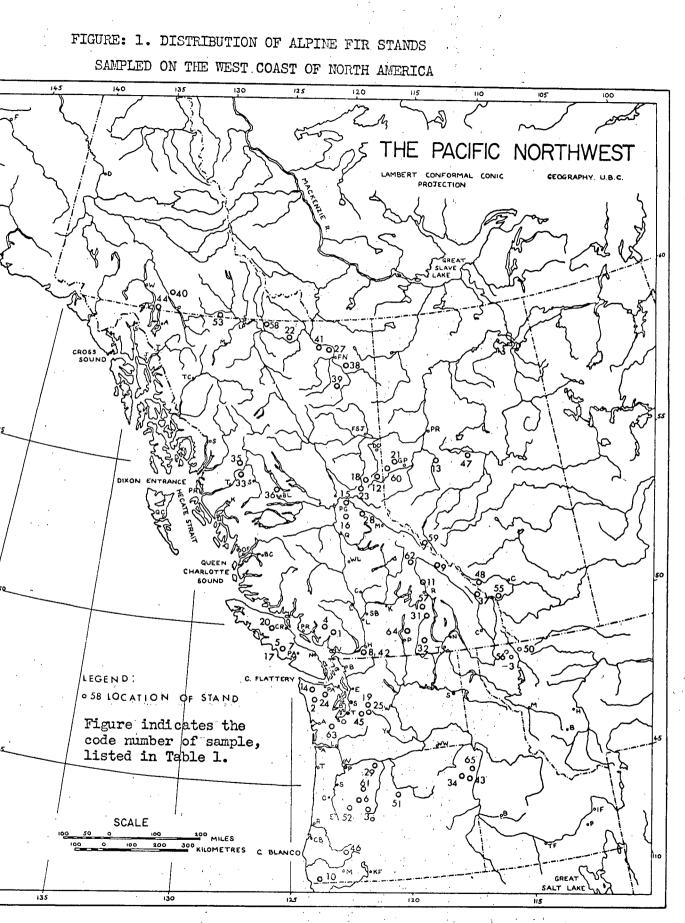
R = .403 .01

TABLE 11. REGRESSION COEFFICIENTS OF THE VARIABLES

Elimination of Y, difference

of the length between scale and bract.

The variable to be omitted	Constant term l a	Residual variance (SEE)	2 R	%	
х б	9,389189E+00	4.126255E+00	•99314110	99,3	
X 5	1.581377E+01	3.066287E+01	•9474 8580	94 , 7	·
X 2	-3. 536110 <i>E</i> -01	3.024501E401	•94667800	94,6	
X 3	-5.4 80186E+00	3.078240F401	•94418000	94,4	
X l	5₀73171 3E+00	3 . 722516E+01	•9 3062180	93.1	
X 4 REMARKS:	$3.478677E+00$ SEE = $\frac{\text{Res.Var.}}{n-4}$	3.932972E401 X ₁ - Precipitation, X_{2} = Latitude, degre X ₃ - Altitude, feet X ₄ = Length of scal X ₅ = Length of brac X ₆ = Individual mea	es e,mm	92.5	

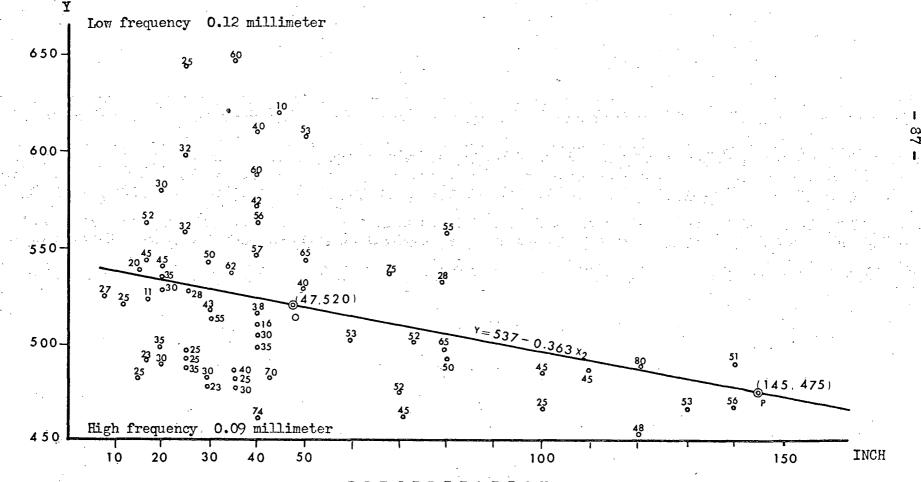


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FIGURE 2. REGRESSION LINE OF PRECIPITATION ON STOMATAL DISTA NCE

(Figures beside the dots indicate the elevation in hundreds. Y on the line represents the correlation equation.)

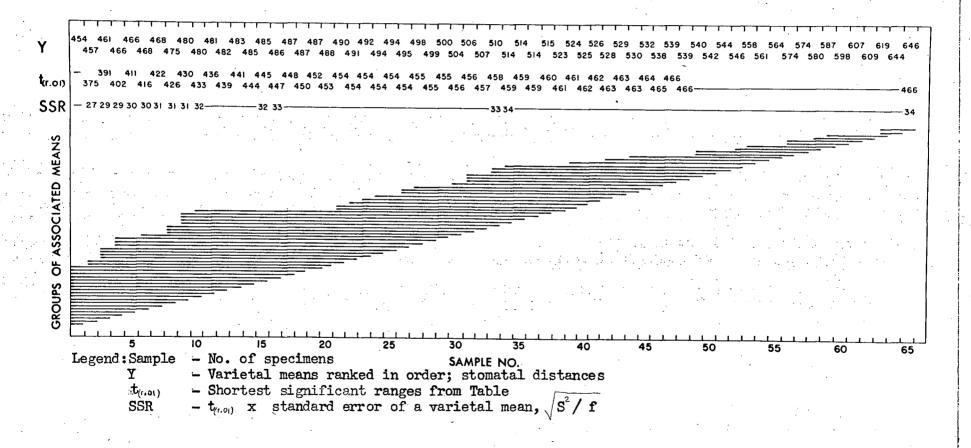
STOMATAL DISTANCE



PRECIPITATION

Figure 3. Comparison between means of the distances of stomata on the lower

surface of needles as Duncan's multiple range test, (LSD).

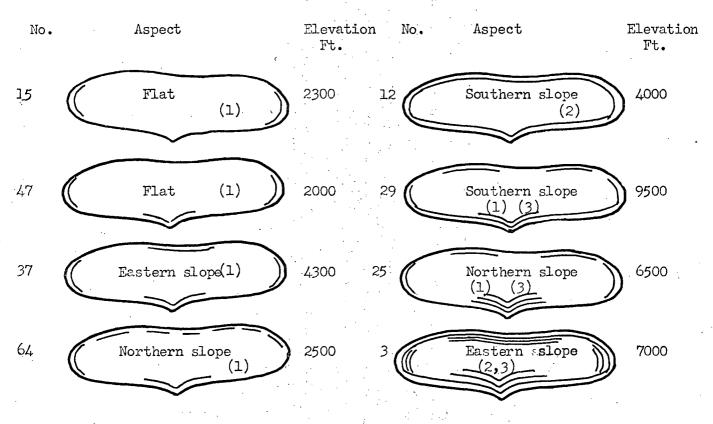


FIGURE, 4. DISTRIBUTION PATTERNS OF HYPODERMAL CELLS

UNDER THE NEEDLE EPIDERMIS OF THE ALPINE FIR

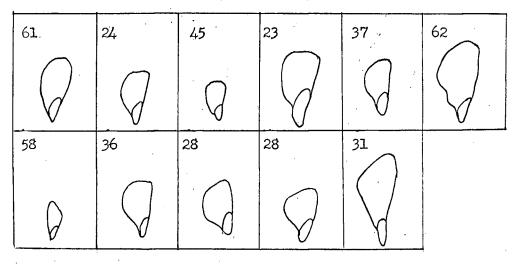
IN ITS CROSS-SECTION.

Each line in the needle cross-section represents a single hypodermal layer. There are discontinuous (1), continuous (2) and multiplied (3) layers.



Figures at the left of the cross-sections refer to the code number in Table 1. STANDS OF ALPINE FIRE

(life size)



Figures at the above left indicate the sample number as coded in Table 7.

Figure: 6. DISTRIBUTION OF VASCULAR STRANDS IN THE SCALE

OF ALPINE FIR . (front view, tangential section)

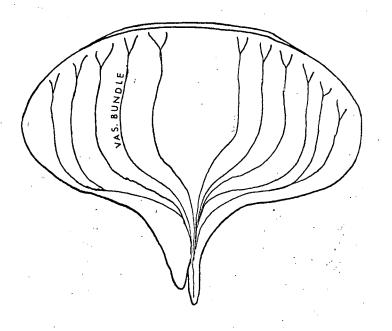


Figure 7. Comparison between means of the difference in the length of scale

and bract. Duncan's multiple range test (LSD).

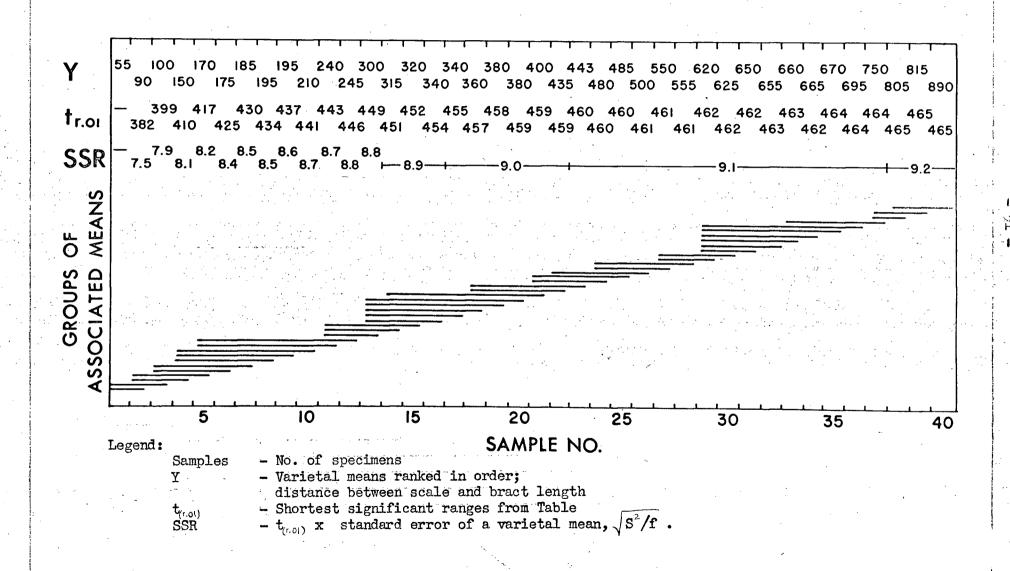




Figure 8.



Figure 9.



Figure 10.



Figure 11.



Figure 12.



Figure 13.



Figure 14.

Code No. from Table 7.

5,37,60, 7,26, 20,12,25,17,38,24 24,38, 3, 8,22, 2, 31,31,19, 9,31

x 1.5

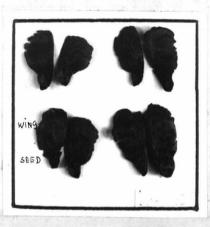


Figure 15.

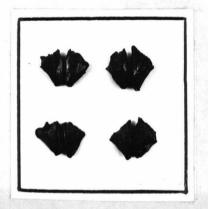
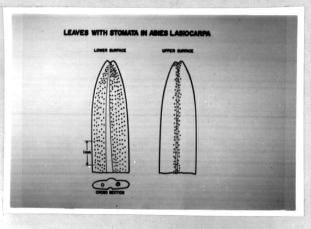


Figure 16.

- 95

Legend:

- E epidermis
- S subsidiary cells
- G guard cells
- CH substomatal chamber





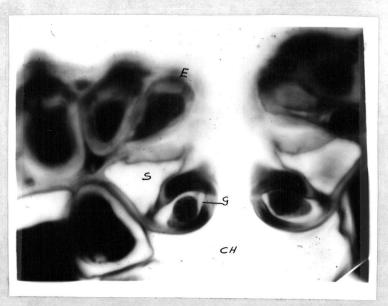


Figure 17.

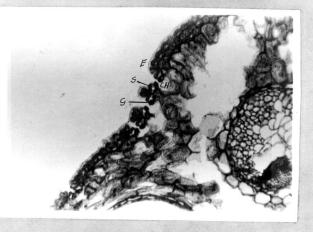
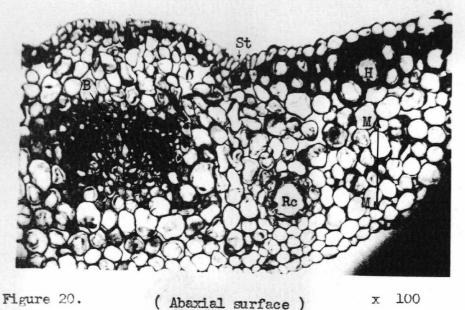


Figure 19.

- % -



St stomata hypodermis H resin canal Rc bundle B M mesophyll

Figure 20.

(Abaxial surface)



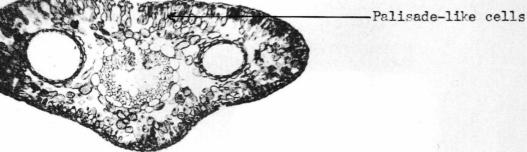
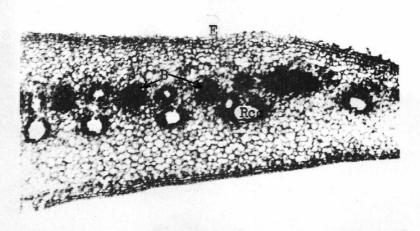
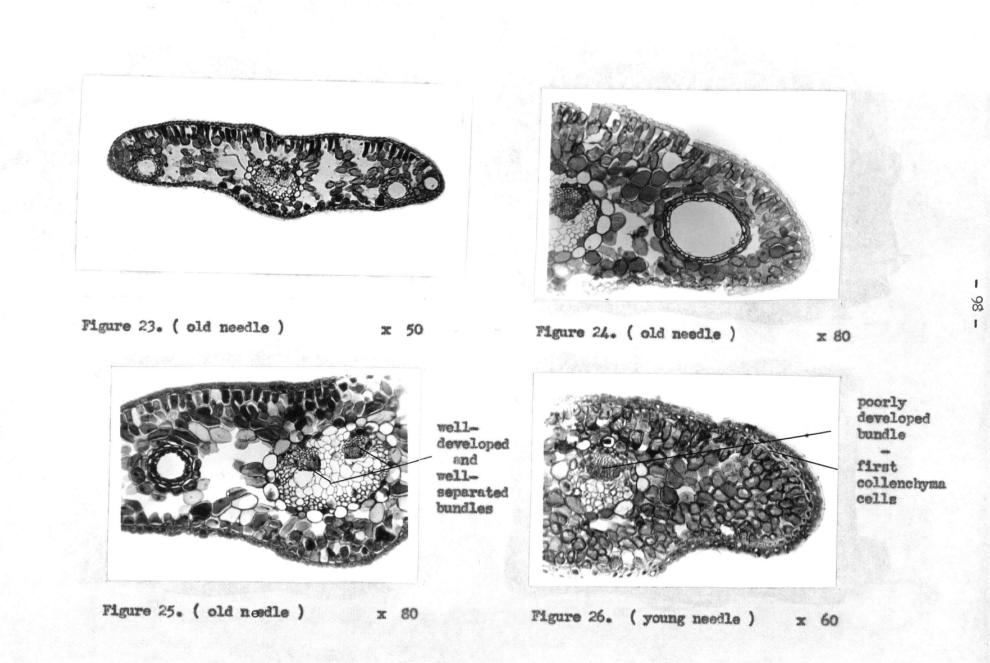
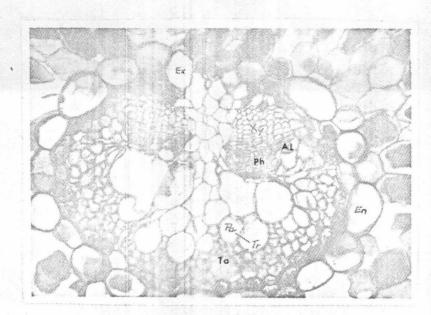


Figure 21. (Abaxial surface) x 50



E epidermis cells B bundle Rc resin canal





--- 99 ----





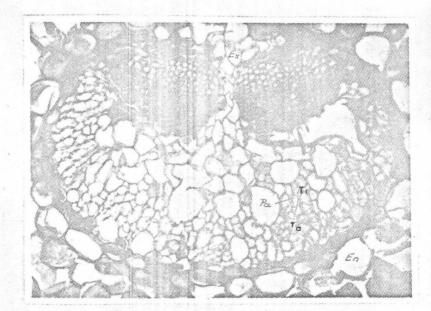


Figure 28.

x 350

- Legend: AL Albuminous cell
 - Xy Xylem
 - Ph Phloem
 - Tr Transfusion tissue
 - En Endodermis
 - Pa Parenchyma cells
 - Ta Tracheids
 - Ex Bundle sheath extension, through broken endodermis

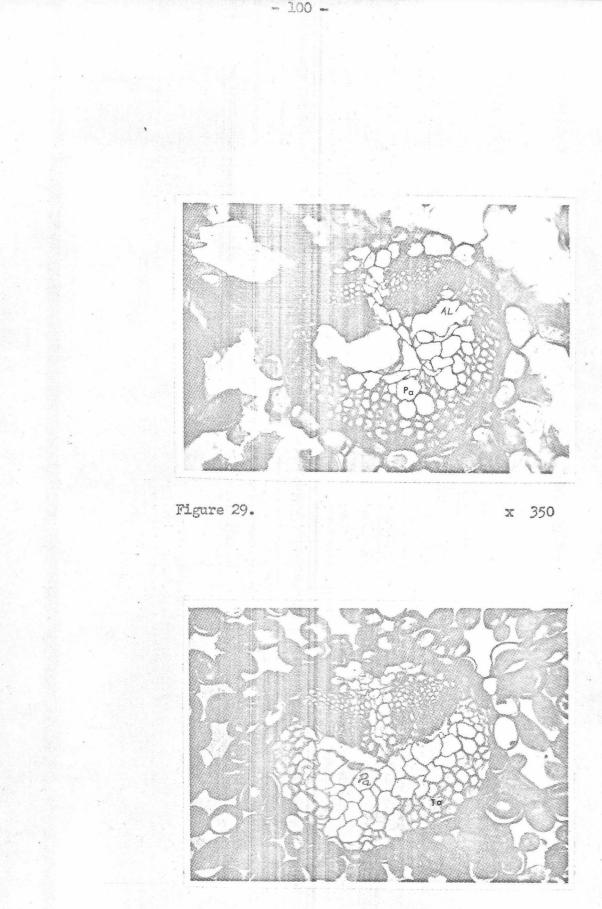
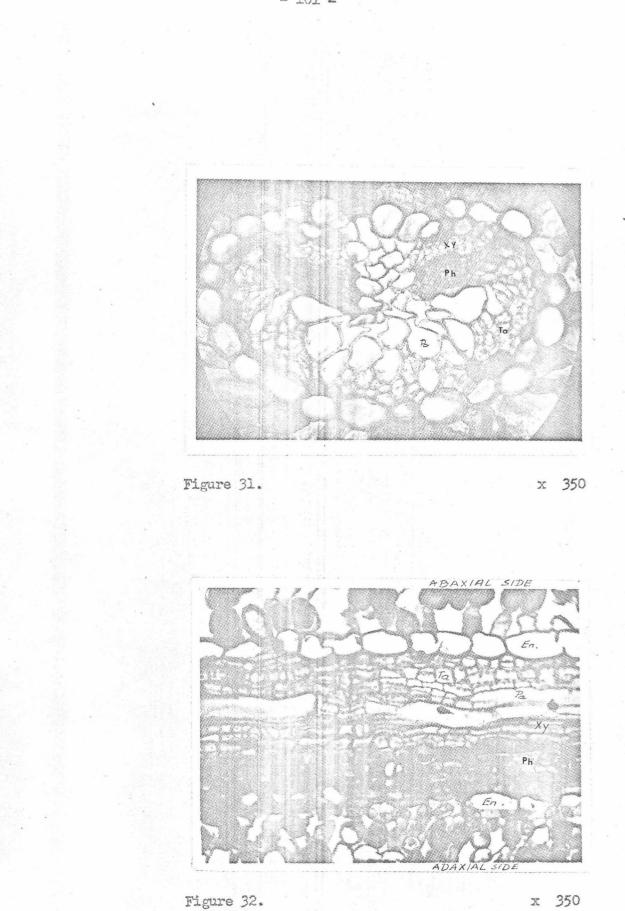


Figure 30.

x 400



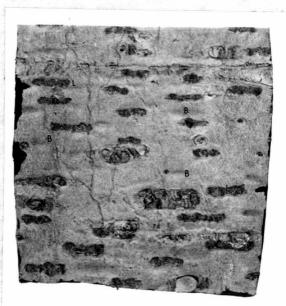


Figure 3 3.

x 0.5

Legend:

- L Lenticel
 - B Resin blister