VARIATION IN LODGEPOLE PINE AND ITS ROLE IN THE GENETIC IMPROVEMENT OF COASTAL FORMS

by

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THE INLAND FORM OF PINUS CONTORTA

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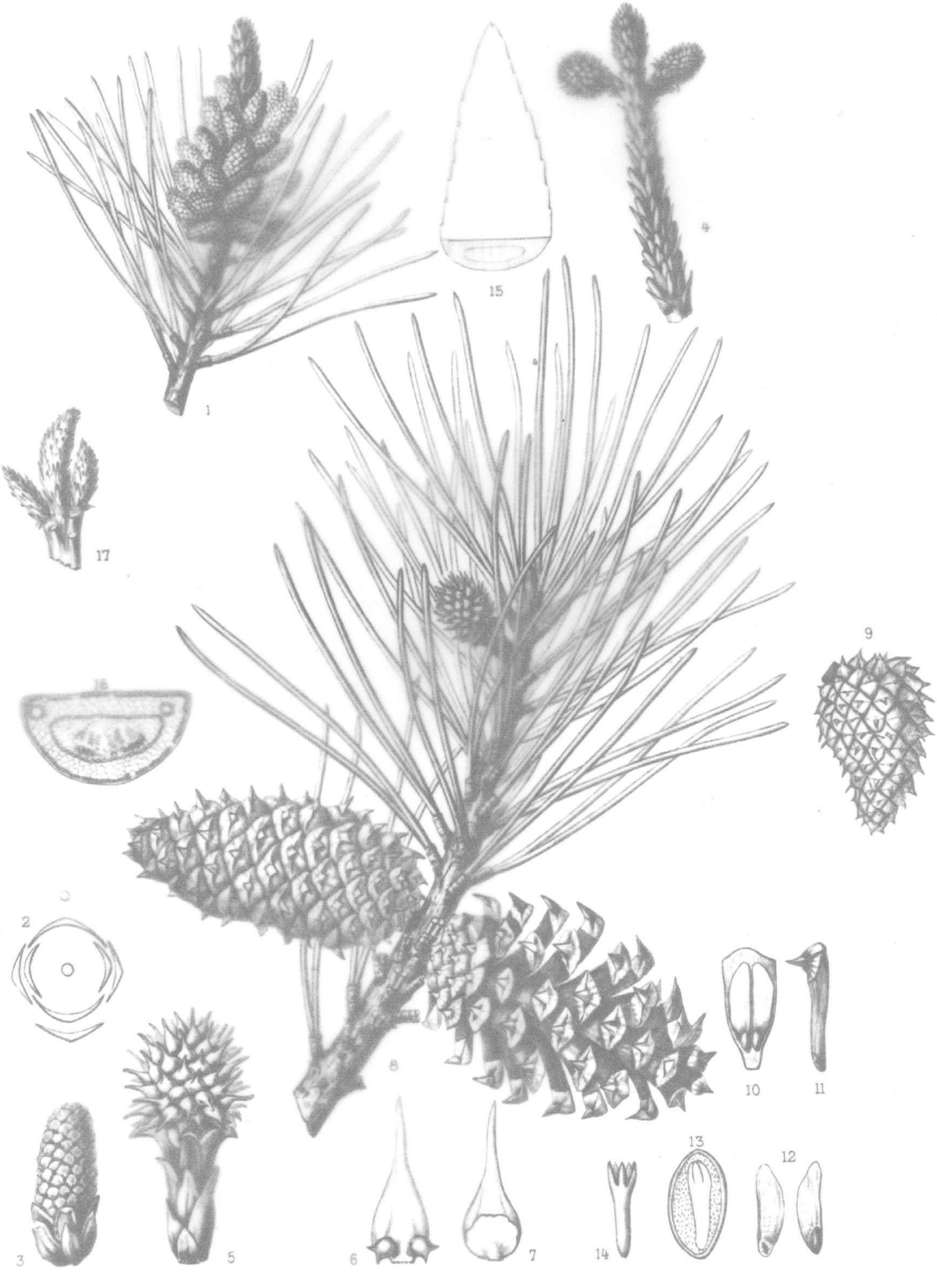
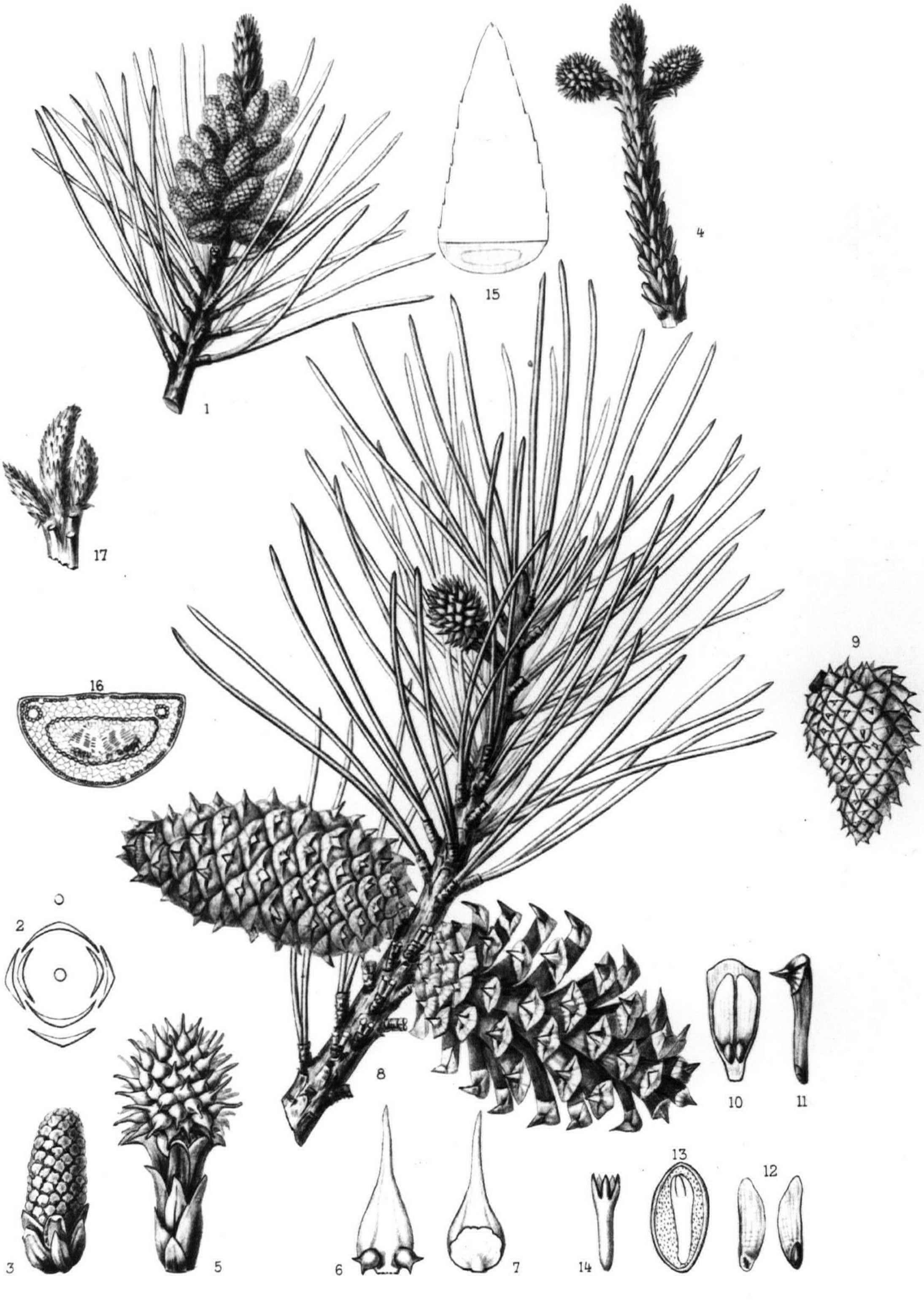


THE INLAND FORM OF PINUS CONTORTA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ABSTRACT

The thesis is divided into two parts. Part one deals with variation in a number of important silvicultural and taxonomic characteristics of Pinus contorta. Variation in bark and growth habit was studied in the field and recorded by means of photographs. The data obtained in this manner are supplemented by information concerning variation in both these characteristics in Lodgepole pine plantations in Europe.

It is concluded that the Shore form of Lodgepole pine is extremely intolerant of shade, and is not inherently a scrub tree, or inferior in form to the Inland variety of the species. The geographical position of some superior coastal stands is given.

The field study further showed that because of its shade intolerance the Shore form is restricted to the forests' edge, to ocean cliffs, sand dunes and muskeg. There its potential growth habit and form are obscured by extremes of environment, and observed only when grown in plantations, or in its natural habitat when competing species are eliminated by fire. Under the latter conditions the Shore variety of Lodgepole pine is a rapidly growing tree, with normal growth habit and form, and is seldom contorted either in bole or branch.

The Shore form has a characteristic bark type which is

inherently different from the Interior form.

A study of variation in needle morphology was made on material obtained from trees of the Lodgepole pine provenance trial at The Institute of Forest Genetics, Placerville, California. Needle width and length were measured, and it is demonstrated that a correlation between these two measurements exists. Because of this correlation the Shore and the Interior populations cannot be distinguished by either leaf width or length alone. Therefore the mean ratio of width to length is used to separate the variation in leaf morphology due to the place of origin of the trees from which the needles were collected. Analysis of variance shows that the mean ratio does not differ significantly between trees representing a particular site, between sites the difference is just significant, and between geographic regions highly significant. The Duncan multiple range test showed that the three major regions (Rocky Mountains, Sierra Nevada, Coastal) differed significantly from each other, but that there was no significant difference between the mean ratio of the Coastal and the Mendocino White Plains material.

Data concerning the growth rate of the trees at Placerville, supplemented by data from European plantations, suggest that coastal Washington and Oregon provenances show the most rapid growth rate in North Temperate regions.

Specimens of seed and foliage collected from natural populations show morphological differences between the Coast and Interior forms.

A method of distinguishing Coast and Interior seed is demonstrated.

Germination tests show that under standard conditions of temperature and humidity the rate of germination of the Coast seed is significantly different from Interior sources. Morphological differences in seed characteristics, can, therefore, be supplemented by germination data to effectively separate the Interior and Coast forms of Lodgepole pine.

Part two of the thesis deals with the selection and breeding of the Shore form. The proposed breeding program takes into account the theoretical and practical objections to the Scandinavian method of tree improvement. Nevertheless, it incorporates this method insofar as it is designed to produce large quantities of seed which is not inferior in several desirable characteristics, while simultaneously working for the genetic improvement of the species.

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VARIATION IN LODGEPOLE PINE AND ITS ROLE IN THE GENETIC IMPROVEMENT OF COASTAL FORMS

PART I

INTRODUCTION

In recent years there has been increasing interest in the Lodgepole pine resources of the Pacific Northwest. In the United States in particular this interest has been stimulated by increasing profits from the utilization of the species. Lumber production in 1956 was sixteen times greater than that in 1933, and Rocky Mountain area stumpage prices between 1950 and 1956 increased by over 200 per cent (McMahon 1957). It is obvious, therefore, that if present trends towards the utilization of small timber continue, Lodgepole pine, which in acreage is the third largest timber type in the West, will in future years achieve the status of an important commercial species, and will fall within the scope of a tree improvement program.

Before a tree improvement program can be initiated for any species it is first necessary to study its variation both in nature and in plantations. The variable characters studied may be purely taxonomic, or they may be characters which are principally of interest to the silviculturist.

The systematic botanist's objective is to classify the species, and his approach is, therefore, taxonomic. The forester, on the other hand, is interested in the species in relation to its environment, and the edaphic, climatic and biotic factors which influence it. He is also interested in the vigour of the species, and in its general form, and his approach to the study of variation, therefore, will not be purely taxonomic, but also genecological.

This thesis will describe variation in Lodgepole pine primarily from a silvicultural point of view. The approach is, nevertheless, a synthesis of taxonomic and silvicultural observation which seems, at this early stage in the development of forest genetics, to be the approach which yields the most useful information to the practical tree breeder.

Growth habit and bark variation were studied in the field during the summer of 1961, principally on the Coast of British Columbia, Washington and Oregon, but also in the Interior of these areas. Parts of Nevada, Idaho and California were also visited.

Stebbins (1950) pointed out that variation in some characteristics of a plant species is best recorded by means of photographs. This is the method used in the present study to record variation in growth habit and bark type.

In order to determine that provenance of Lodgepole pine which shows the most rapid growth rate in North Temperate regions a survey was made of the behaviour of the species in plantations and provenance trials in Europe; and particularly in England and Ireland. Height measurements were made on the provenance trial of the species at The Institute of Forest Genetics, Placerville, California.

The trees at Placerville were grown from seed collected in twenty areas scattered throughout the range of the species.

Intraspecific variation in needle morphology was determined from needles collected at Placerville from each of four trees representing twenty provenances of Lodgepole pine. The needles were two years old and collected from the lower crown on the south side of each tree. The mean width and length of ten needles from each tree were obtained, and the ratio of width to length used in determining the pattern of variation associated with the place of origin of the trees.

Foliage and seed specimens were collected in the field during the summer of 1961. Seed, bark and foliage specimens were also obtained from the British Columbia and Alberta Forest Services during the winter of 1961-62.

Germination tests were carried out on seed from nine different provenances of Lodgepole pine including four coastal sources in order to determine whether significant differences in germination rate existed between the Coast and Interior forms.

LITERATURE REVIEW OF VARIATION IN PINUS CONTORTA AND OTHER PINE SPECIES

Though P. contorta was discovered and named as early as 1825 there still exists considerable uncertainty concerning its taxonomic classification. For a short time it was known as P. inops (Mirov 1954), and in 1852 the Sierra Nevada form was collected and named Pinus Murrayana. This form is still considered a separate species by some American and European botanists.

Sargent (1897), after considerable study of the species in the field, concludes that the inland form (P. contorta var. Murrayana, Engelm.) is a variety of the shore form (P. contorta, Loud.). The drawings of the foliage, flowers and cones, of both inland and shore varieties included in Sargent's work are extremely accurate, and in respect of foliage density clearly illustrate the difference between the two types.

A few years later Jepson (1907) had this to say - "P. Murrayana is treated by many authors as a variety of Beach pine (Shore pine) of the coast. ..... On the contrary the typical forms of the two are not only very distinct and their habitats widely different, but the typical form is in each case the only form throughout the main geographical region of that species." He classified the inland form and shore form as distinct species, P. Murrayana Balf., and P. contorta Loud. respectively.

The following year Sudworth (1908) considered that differences in thickness of bark, size of cones and leaves, or size and form of the tree, are not too great to be merged in one polymorphous species. He described the Pacific form as a tree 20 to 40 feet high and from 6 to 20 inches in diameter, and the Inland form as a tree 50 to 100 feet high and from 12 to 24 inches in diameter.

In 1917 Davidson (1927) planted a single transplant of the Inland form and one of the shore form in the arboretum at the University of B. C. Writing in 1927 he stated that for the first few years minor points of difference could be demonstrated, but after ten years the trees were identical in foliage, habit, and rate of growth. He concluded that the Inland variety is nothing more than an environmental form.

The present writer has examined both these trees in the University arboretum. They are now approximately 45 years old. The following characters were studied: leaf length and colour, cone size, closed cone habit, and bark type. The results show that, with the exception of bark type, the two trees are distinctly different from each other in respect of all other characters. There is no noticeable difference in the bark type of the two trees.

Kalela (1937) stated that the Inland and Shore forms are separate species, respectively P. Murrayana and P. contorta, the former constituting a continued series of climatic races within which a variability similar to that in Scots pine can be observed. He considered the shore form to have a more rapid growth; wider, firmer and more twisted needles than the Inland form. However, Bowers (1942) agreed with Sudworth that P. contorta is a single polymorphous species.

Harlow and Harrar (1958) considered P. contorta a dimorphic species. The coastal form was described as a small tree, with a contorted bole and dense irregular crown of twisted branches, 25 to 30 feet high and 12 to 18 inches in diameter. The Inland form is a medium-sized tree 70 to 80 feet high and 15 to 30 inches in diameter, with a long, clear, slender bole and short, narrow, open crown.

Bulletin 61 of the Canada Forest Service (1956) treated Shore pine as a species, and the Inland form as a variety of it. Shore pine was described as a small, usually shrubby tree 15 to 50 feet high and 12 to 18 inches in diameter, with a crooked, often twisted trunk, and an irregular, open crown of large, twisted, generally much-forked branches. The Interior form was described as a tree with a narrow crown, 50 to 100 feet tall and one to two feet in diameter at breast height.

Generally speaking, the description of the growth habit of the Coastal form of P. contorta as given in the literature is in conflict with the evidence now being obtained from many

European plantations of this form, and with the observations of the present writer. Sudworth (1908), however, noted that in close stands the Coastal form develops a tall, clean, slender bole, with a short, small-branched crown.

P. contorta has been planted extensively in England and Ireland and its use is increasing rapidly in current planting programs. The climate over both these islands is relatively uniform in contrast to the extremes of climate which exist throughout the range of the species in North America. Many different seed sources have been used and there is considerable natural variation which is readily observable under plantation conditions and the fairly uniform climate. In England seven subtypes are distinguished, and in Ireland three (Lines 1957). They are listed as follows:

ENGLAND

1. North coastal
2. South coastal
3. Alaska
4. Alberta
5. Skeena river
6. North Interior
7. South Interior

IRELAND

1. South coastal
2. North Interior
3. Rainer Forest

Each type is distinguished by its branchiness, bark colour and thickness, leaf colour and length, density of foliage, and growth rate.

Lines' classification is to a great extent arbitrary, for many intermediate forms are found; nevertheless, it is useful to the practising forester and tree breeder, for the characters used to distinguish the different provenances are important silviculturally. To date there is no major work which attempts to classify natural forest types of P. contorta in this manner.

Wood (1957) considered P. contorta a polymorphic species, differentiated into ecotypes which may form ecoclines ranging from the coast to the continental zone east of the Rocky Mountains, and from 36 degrees north to 64 degrees north latitude.

Critchfield (1957) has carried out a major survey of variation in P. contorta. His approach was almost entirely taxonomic, for his conclusions were based on an analysis of several quantitative characters, in samples of natural and cultivated populations of the species, such as leaf width, presence or absence of leaf resin canals, cone angle and density. Macdonald (1958) in a review of this work was severely critical; considering it to be of little value to the forester. Insofar as

Critchfield's work was an attempt at systematic classification of the species this criticism is invalid. Nevertheless, the fact that it could be made demonstrates the necessity of evolving a method of studying variation in forest trees in which the genecologic rather than the purely taxonomic approach is used.

The forester must be interested not only in those characteristics which are relatively certain clues to the identity of a species. He must also amplify descriptive systematics by additional data on the characters of forest trees which are important economically, such as growth rates and branching habit and taper.

Critchfield concluded that P. contorta exists in several regional forms, exhibiting geographic unit and heritable differences, and meriting recognition as four subspecies, which are listed below:

1. Coastal region:

   P. contorta Douglas ex Loudon ssp. contorta

2. Mendocino white plains:

   P. contorta ssp. bolanderi (Parl.) stat. nov.

3. Rocky Mountains:

   P. contorta ssp. latifolia (Engelm. ex Wats.) stat. nov.

4. Sierra Nevada:

   P. contorta ssp. Murrayana (Balf.) stat. nov.

Critchfield stated that he found no variation within the

Shore variety of Lodgepole pine, which ranges from Southern California to Alaska. No single morphological character studied showed a clear-cut association with latitude. This is a surprising conclusion for such a wide-ranging form, and may be due to his limited sampling. For example between Baranof, Alaska and Newport, Oregon, only three trees were sampled, two of which were in the same area. This is a distance of approximately 1,000 miles, and includes almost the total range of the Coastal form of P. contorta.

From a silvicultural point of view it would not be possible to assume homogeneity in the Coastal form, for gradation in growth rates, and other important characters, almost certainly exist (Macdonald 1954). In this instance Huxley's remarks may apply: "When gradation exists within a group, the mere conferring of a subspecific name gives a false impression of the geographical homogeneity of the group." (Huxley, 1939.)

Langlet (1957) stressed the importance of estimating the relationships between certain characteristics (e.g., winter hardiness, growth rate, etc.) of a species and the factors to which adaptation has occurred and still occurs. "The risk of a seed transfer from a native stand to a site with a different temperature must be judged in relation to the variability of the species. Taxonomic subgroupings are then not only valueless, but downright harmful, since they suggest a non-existent homogeneity within conventional units which are in reality mere abstractions."

The taxonomic classification of forest trees without prior investigation of the broad pattern of variation, and the relationship of that variation to the locality and habitat in which the tree grows, has led to considerable confusion, and to strong disagreement between different authorities. For example, Wright and Baldwin (1957) appear to have used previously described taxonomic varieties of *Pinus silvestris* as an aid for grouping the species into geographic ecotypes. But as Langlet (1957) pointed out, "ecotype" is not a taxonomic but a geneco-logic term, and demonstrated conclusively that discontinuous variation does not exist in *P. silvestris*, which - "*A priori* may be expected to characterize any species with a large range which shows evidence of inherited adaptation to the climate or other continuously varying natural conditions."

Stebbins (1950) stated that the best example of clinal variation within plant species are those described by Langlet (1934, 1936) in *Pinus silvestris*. Langlet measured percentage dry matter content of the needles at beginning of dormancy in 582 Swedish provenances of Scots pine, and, in a smaller number of Swedish provenances, the chlorophyll content, length of mature leaves, hardiness, and rapidity of shoot development in spring. He pointed out (1957) that dry matter content is a very good measure of the plant's readiness for hibernation, and shows a remarkably close correlation with latitude, the duration of the period of vegetation, and the length of the first day of the year with a normal average 24-hour temperature of plus 6 degrees C. at the place of origin of the material examined.

It will be seen that Langlet's approach to the study of variation in P. silvestris is very different from that of Critchfield (1957) in his study of P. contorta. Langlet's study was designed to yield as much information as possible which could be utilized by the silviculturist. On the basis of his results seed-collecting recommendations were drawn up for Scots pine. These recommendations are in common use in Sweden at the present time (Arnborg, 1960).

Fielding (1953, 1960) studied variation in Monterey pine in Australian plantations. This study, like Langlet's, was designed to assist the silviculturist and tree breeder, rather than the systematic botanist. Variation in the following important characteristics of the species was examined:

1. Rate of growth
2. Insect attack and disease
3. Wood properties
4. Form of the trunk
5. Straightness and verticality of the trunk
6. Crown characteristics
7. Flowering
8. Cones and seed
9. Ability to grow from cuttings

On the basis of the information thus obtained, Fielding was able to draw up recommendations for the selection and breeding of *Pinus radiata*.

From a survey of the literature dealing with variation in *P. contorta* it must be concluded that there is little uniformity of opinion regarding the systematic classification of this species. Despite Critchfield's suggested classification the most recent publication dealing with the genus *Pinus* classified the interior form of Lodgepole pine as *P. Murrayana* (Geussain, 1961), and Macdonald (1957) stated that the classification of recognisable features distinguishing important forest types of *P. contorta*, both in nature and in plantations, has yet to be done.

The literature also indicates that this classification is best achieved by a synthesis of silvicultural and taxonomic observation, amplified by climatic and geographic data in respect of the place of origin of the material studied.

GROWTH RATE

Much information concerning the growth rate and habit of the Coastal form of Lodgepole pine is now available from European plantations. This information was not available to earlier workers writing of this form, and is, perhaps, a further explanation for many of the contradictory opinions noted in the literature.

A systematic classification of a tree species should not be based only upon studies of variation in the field. The variable characteristics measured in natural populations should also be measured when a representative sample of the species is grown under uniform conditions, such as in provenances trials or plantations when the seed source is known. Only then is it possible to separate out the effects of environment, and to measure, with some accuracy, the extent of genetic variation.

In 1934 an experiment to test the value of seven seed lots of Lodgepole pine of different origins was laid down at Clocaenog forest in Great Britain. The collection included four lots from inland regions of British Columbia at medium elevations, one from Alaska and two lots from the coastal belt of the United States of America at elevations below 500 feet. The site of the experiment is exposed moorland at an elevation of over 1,000 feet. Edwards and Pinchin (1952) recorded that the growth and appearance of the two coastal lots were very good and were, in general, superior to the inland origins on this site.

Langlet (1934, 1938) carried out a small experiment in Sweden involving three provenances: Ocean Beach, Washington; Summer Lake, Oregon; Klamath County, Oregon. At the age of five years the mean height of the coastal provenance was greater than the inland provenances.

The importance of the coastal provenances of Shore pine in Irish silviculture was noted as early as 1928. Even at that relatively early date in the plantation history of this country the Shore form had in several situations in a plantation in County Wicklow reached a height of 60 to 70 feet (Forbes 1928). Forbes stated that trees planted side-by-side at Avondale clearly depict the characteristics and relative growth of the Shore and Inland forms, the former being 50 per cent higher than the latter in the course of 10 years.

Mooney (1957), writing of Lodgepole pine in Ireland, gave growth details concerning two 25-year-old plots of Inland and Shore forms growing on the same site. The Inland form, grown from seed supplied by the Associated Foresters of Canada, is 8 to 18 feet high on the higher, and 20 feet on lower, ground. Ground vegetation is unchecked and woody Calluna is waist-high. The Coastal form is 16 feet from the Inland form described above.

This plot has a closed canopy which ranges from 25 to 30 feet, in height. Mooney stated that this is not an isolated case, and went on to say... "From what one can observe most South Coastal types of Pinus contorta give a sufficiently high percentage of trees of good form and refined branch in the stand to form a final crop, whilst at the same time giving far greater yields than the Inland type of Pinus contorta, and, of course, it is capable of suppressing the competing ground vegetation - particularly Calluna - at an early stage."

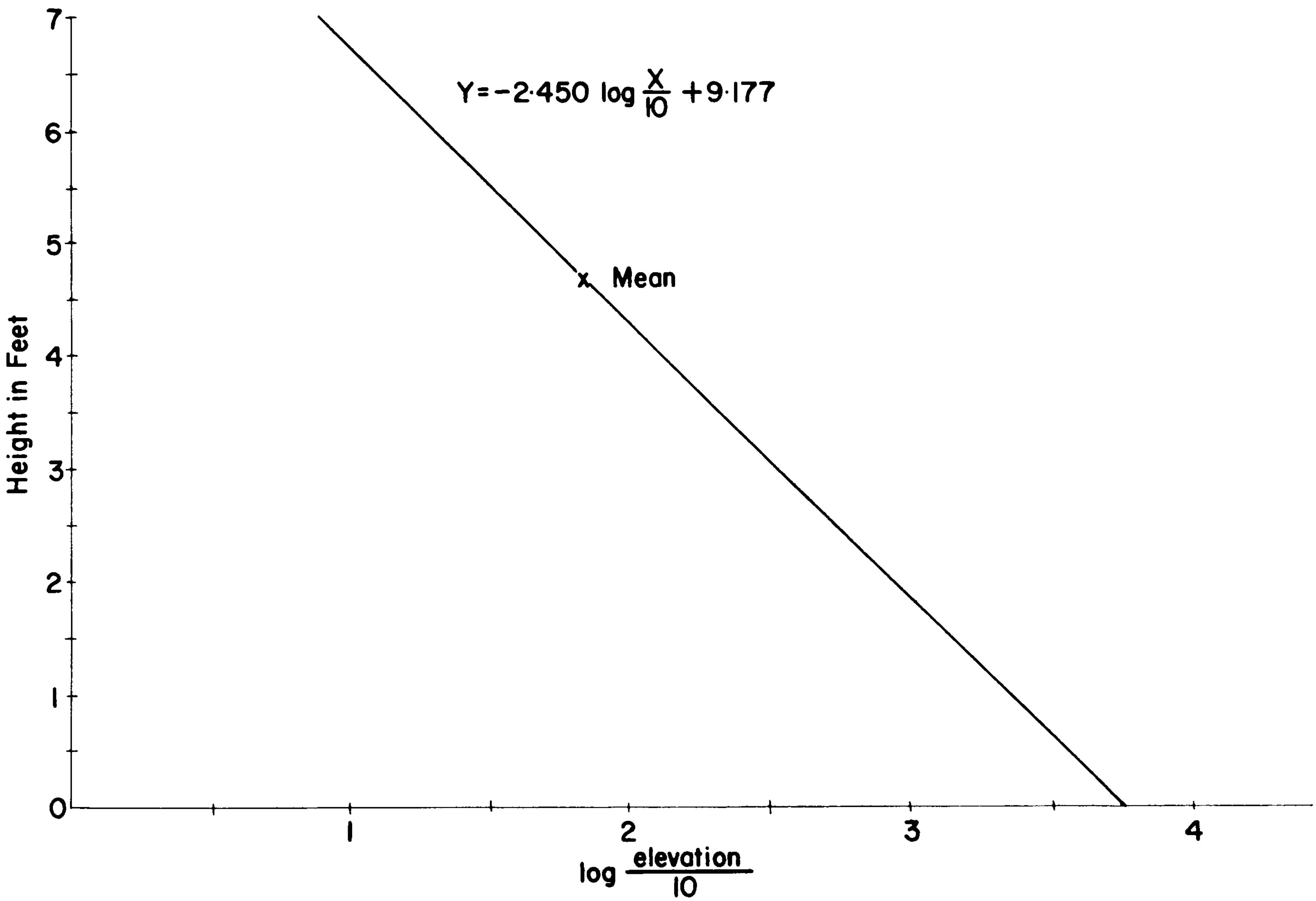
Mooney's conclusions concerning the South Coastal provenance of Shore pine are supported by Macdonald (1954), who said... "Assessments of provenance collections in Britain indicate that as far as height growth is concerned the coastal lots from Oregon and Washington are the tallest, and, at 14 years, even under wretched moorland conditions, have grown faster than quality class 1 Scots pine could have grown on a completely suitable site. Although the evidence does not all appear on these particular assessments it is almost certain that the height growth of coastal types increases from North to South."

During the summer of 1961 the writer measured the height of all the trees in the Lodgepole pine provenance trial at Placerville. The mean height for each of the provenances measured, and the elevation of each seed source, are given in Table I. The elevation of the seed source was obtained from Critchfield (1957). The data were subjected to regression analysis to determine the correlation, if any, between elevation of seed source and the height of the progeny at Placerville. A strong correlation was fonnd to exist (Figures 1, 2).

TABLE I

MEAN HEIGHT OF TWENTY PROVENANCES OF SEVEN-YEAR-OLD *PINUS CONTORTA* GROWING AT PLACERVILLE

Site No.	Elevation of Seed Source in Feet	Height of Progeny in Feet
	Rocky Mountain and Intermountain Region	
1	3,000	2.65
2	8,650	2.43
3	4,250	2.05
4	6,500	2.00
5	8,000	2.12
6	7,000	1.82
7	3,000	4.17
	Cascade Mountain Region	
8	4,700	2.26
9	8,250	1.70
10	5,550	2.50
	Coastal Region	
11	100	6.38
12	350	5.45
13	50	7.68
14	50	6.70
15	100	5.78
16	50	7.70
17	50	6.93
	Mendocino Region	
18	200	8.23
19	200	6.98
20	200	7.00



Fig· I Regression of height on elevation for 18 different provenances of <u>Pinus</u> <u>contorta</u> growing at Placerville

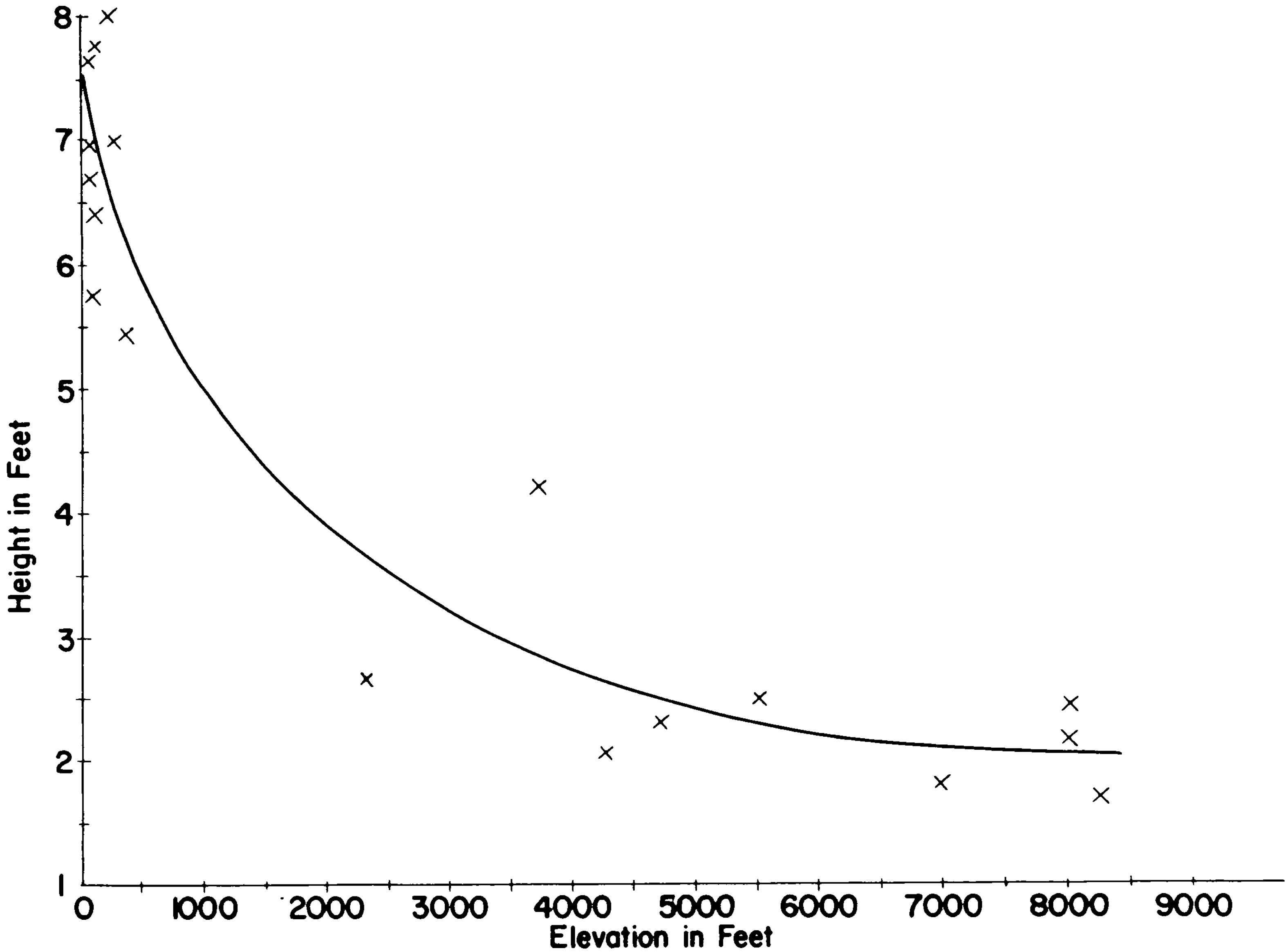


Fig. 2 Relationship of total height and elevation for 18 different provenances of *Pinus contorta* growing at Placerville

It must be noted that the relationship between the height of these trees and the elevation of the seed source is complicated by the fact that all the low elevation sources are of coastal origin. Therefore, while a correlation between height and elevation may exist, the principal conclusion is that on this particular site at Placerville the Shore pine is much faster growing than any Inland provenance of the same age.

The site on which these trees are growing is located between Sacramento and the summit of the Sierra Nevada at an elevation of 2,700 feet. It is approximately 170 miles from the Pacific Coast, and has, during the growing season, a relatively low rainfall. Aspect is south and southwest, and the soil is a deep, Aiken clay-loam (Liddicoet and Righter, 1960).

This environment cannot be considered optimal for growth rate of the coastal provenances from British Columbia, Washington and Oregon. For example, the Reedsport and Newport, Oregon seed sources have an average summer temperature, and an average annual rainfall, of 57 and 54 degrees F., and 73 and 66 inches respectively. The average summer rainfall is 14 and 17 inches. Placerville has an average summer temperature of over 70 degrees F., and an annual rainfall of 34 inches, 86.5 per cent of which falls between November and April. Less than one-half inch falls between July 1 and October 1. Yet these coast provenances are superior in height growth to all inland forms, including those seed sources relatively close to Placerville. For example, the Victoria, British Columbia; Umpqua, Washington, and the Newport, Oregon seed sources - respectively 800, 700, and 500 miles from Placerville - are more than twice as tall as those samples from Lower Dinky Meadow, California; Huntington Lake, California; and Mineral, California, respectively 220, 200 and 115 miles from Placerville.

This rapid growth rate of the Coast provenances cannot be explained in terms of a "transfer effect", for in general pines show a decrease in growth rate when transferred from a northern to a relatively southern provenance (Arnborg, 1960).

It is certain that in the maritime climate of Britain and Ireland the Coast form maintains its superior growth rate over the Interior form. However, the same superior growth qualities are maintained in the Shore form, at least in the juvenile stage, when it is grown in an alien environment. It is suggested, therefore, that the superior growth rate of the coast form is genetically determined, and that within this form the South Coastal provenances of Washington and Oregon are best adapted for growth in the North Temperate regions.

LEAF MORPHOLOGY

Much of the literature dealing with the taxonomic classification of forest trees is concerned with leaf morphology and anatomy, and many attempts have been made to delimit geographic ecotypes or clines within a species according to variation in leaf length, width, or thickness, and presence or absence of resin canals. Schotte (1905) found that northern sources of Pinus silvestris, growing in Sweden, had shorter needles than other areas. This is confirmed by Jaccard and Frey-Wyssling (1935) and Langlet (1938). Races of Pinus pinaster have been distinguished by needle length, number of resin canals per needle and foliage colour (Perry, 1940), (Rycroft and Wicht, 1948). Schwarts (1934) stated that resin canal number cannot be used to distinguish Scots pine, but that the number does increase with increase in elevation. Duffield (1951) found that stomatal structure, and resin canal number, will distinguish sources of Pinus muricata.

Difference in leaf width was one of the principal variable characters measured by Critchfield (1957) in his systematic classification of Pinus contorta. Because of the importance of this work it will be discussed separately and in some detail. The conclusions of other workers with respect to variation in leaf morphology of this species were that the Coastal form is narrower than the Inland variety, which includes the Rocky Mountains and the Sierra Nevada forms (Sargent, 1897), (Sudworth, 1908), (Laing, 1954); and also shorter (Lines, 1957), (Macdonald, 1954).

Critchfield sampled a maximum of 12 trees in each of 40 sites. Approximately 60 per cent of the sampled areas are confined to the Sierra Nevada region, and the coast of Oregon and California. Some samples were obtained from plantations in Britain and New Zealand, and others from the arboretum at Placerville. Ten needles were collected from each tree, each needle being obtained from a different branch. The trees sampled varied in age from 6 to 600 years, and in elevation from sea level to 10,000 feet. The tip and basal portions of the needle were removed, and the mid-portion, between one-half and one inch long, was preserved. Width was determined by measuring the mid-section of the retained portion.

Leaf length was also measured, but for a separate sample. Needle length was not considered a reliable characteristic in delimiting subtypes: "Only a brief survey of geographic variation in needle length is included in this study because of the probable influence of non-genetic factors on the expression of this characteristic; in particular because of the doubtful comparability of needles collected in different regions at different seasons." (Critchfield, 1957.)

On the basis of leaf width Critchfield found it impossible to separate the coastal and inland populations: "The range of leaf width in the coastal region coincides rather closely with the range of this feature in the Intermountain-Rocky Mountain region. Further, none of the samples from this part of the inland region has a mean leaf width significantly greater than that of the wider-leaved coastal samples. These facts emphasize the absence of any valid taxonomic distinction in leaf width between the inland region as a whole and the coastal region" (Critchfield, 1957). He concluded that the most important regional difference in leaf width within Pinus contorta is the difference between the Sierra-Cascade group and the remainder of the species.

There is no clearly defined pattern of variation in leaf length observable from Critchfield's data. Plantation samples representing inland sources are longer than coast plantation samples, but the former are represented by 8 samples and the latter by 4, and many of the inland, high elevation samples from natural populations are shorter than the coastal samples.

For the purpose of the present study of variation in leaf morphology of Lodgepole pine needle samples were obtained from 84 trees representing 23 provenances growing on the same site at Placerville, California.[1] The geographic location of 20 of

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1 This provenance trial was established from the seed samples collected by Dr. Critchfield. The trees are even-aged.

the provenances is given in Table V. Three major and one minor geographic region are represented: these are the Rocky Mountains, the Sierra Nevada and the Mendocino White Plains, and the Coastal region from British Columbia to Northern California. The Mendocino White Plains is the minor region, being only a few square miles in area. Ten, two-year-old needles were randomly taken from the lower crown, on the south side of each tree.

The width and length were determined for each needle, the former by ocular micrometer, and the latter by hand ruler scaled in millimeters. It was therefore possible to determine whether a correlation between width and length of needle existed. Needles from two trees representing each site were first measured (Lot 1). A preliminary analysis showed that a correlation between width and length existed in the needle samples representing the Rocky Mountain region. The measurements were then repeated for two more trees representing the same sites (Lot 2). The complete data for each geographic region was processed separately by Alwac III-E computer. The results of this analysis are given in Figure 3, and in Table II.

A correlation between width and length of needle was found for the three major geographic regions, but not for the Mendocino White Plains region.

The curves for the Rocky Mountain and Coastal samples clearly illustrate the difficulty of separating the two populations by width alone; the mean width being almost identical for

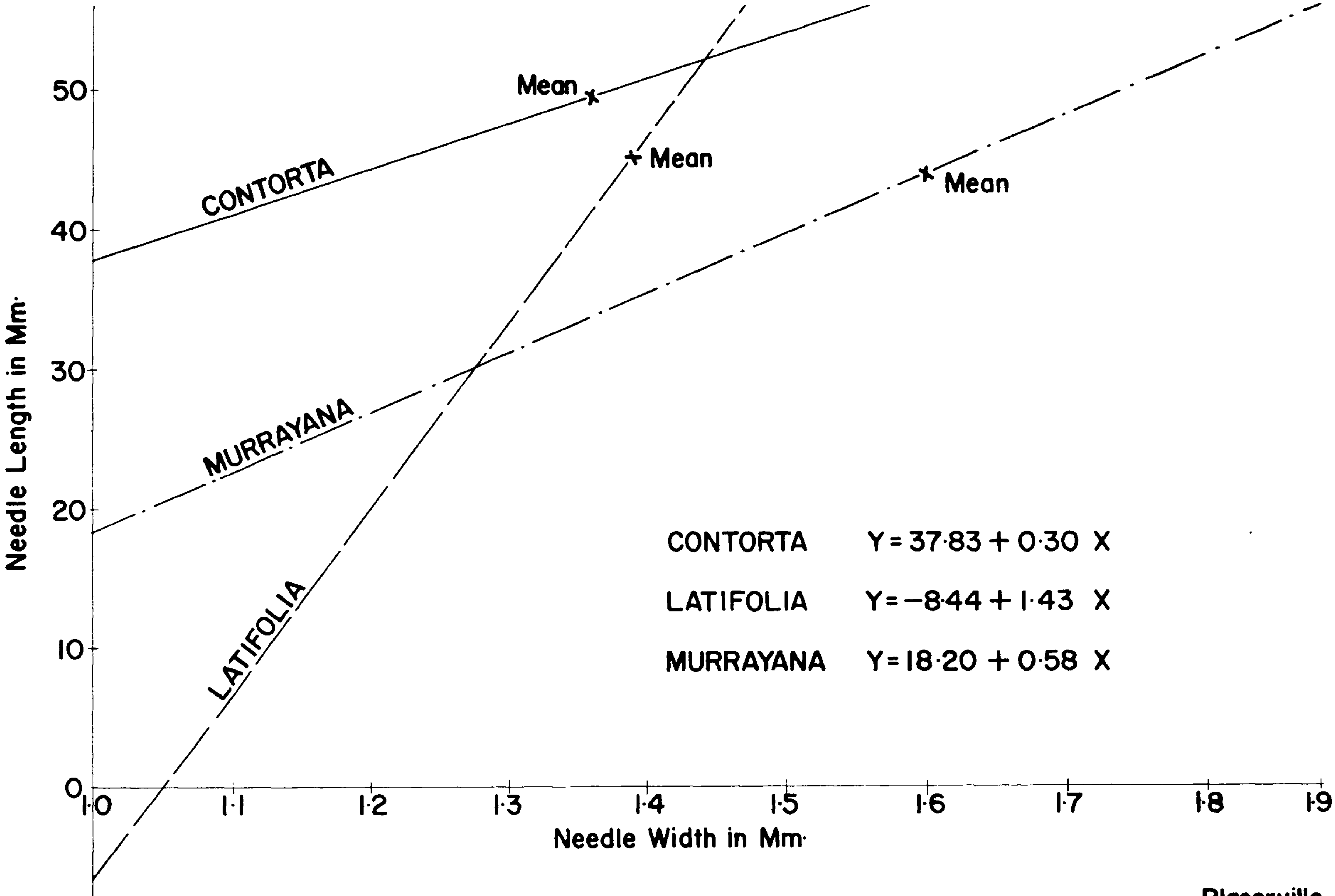


Fig. 3 Regression of length on width of *Pinus contorta* needles from 22 different provenances growing at Placerville

TABLE II

STATISTICS OF REGRESSION ANALYSIS OF NEEDLE LENGTH (Y) ON WIDTH (X) FOR FOUR REGIONAL VARIETIES OF *PINUS CONTORTA*

Variety	$\bar{X}$	$\bar{Y}$	No. of Samples	SD_x	SD_y	b	r	SE_E
Latifolia	1.39	48.04	279	0.015	10.6	- 8.4	0.5713**	8.74
Murrayana	1.64	43.34	142	0.014	7.6	18.2	0.2935**	7.34
Contorta	1.36	48.85	301	0.016	7.5	37.8	0.1800**	7.41
Bolanderi	1.34	54.93	121	0.012	11.8	51.3	0.0248	11.85

** Highly significant

All measurements are in millimeters

both regions. It is also clear that the nature of the relationship of width and length is different for the two populations.

The Sierra Nevada samples are sufficiently different in width to be able to distinguish this population from the Rocky Mountain and Coast forms by width alone. Nevertheless, because of the correlation of width and length, the populations are more precisely distinguished by the use of the ratio.

Table III gives the means of needle length and width, and the ratios for the four regions. Critchfield's data for both measurements for the same regions, excluding the Intermountain samples, are also given in this table. The Intermountain samples are excluded for the purpose of comparison, as only two sampled sites of this group are represented in the Placerville material.

It will be seen that there is considerable uniformity in the ratios representing the three major regions, although there is a distinct difference in length and width between each separate group of measurements. For example, Critchfield has a mean width for the Rocky Mountain group of 1.57 mm. This is much higher than the mean of the Placerville material for the same area, which is 1.39 mm. for both Lots one and two. However, the length for the same geographic group, as given by Critchfield, is 50.80 mm., which is also greater than the Placerville data, and thus the ratio of width to length for the two measurements is the same.

The ratios for the Mendocino White Plains group are quite different for each set of measurements. This same population showed no correlation between length and width of needles. However, it is not unlikely that such a relationship does exist. For example, when all three means for width and length are taken into consideration (Table III) it is obvious that even for this population the longest leaves are also the widest.

TABLE III

MEANS OF NEEDLE WIDTH AND LENGTH AND RATIOS FOR FOUR GEOGRAPHIC REGIONS OF PINUS CONTORTA

Width m.m.	Mendocino White Plains	Coastal Region	Rocky Mountains	Sierra Nevada
Lot 1	1.30	1.32	1.39	1.64
Lot 2	1.38	1.41	1.39	1.54
Critchfield	1.28	1.41	1.57	1.76
Length m.m.				
Lot 1	47.08	48.04	46.31	44.88
Lot 2	62.16	49.66	44.63	39.76
Critchfield	35.00	48.76	50.80	48.78
Ratio				
Lot 1	0.028	0.027	0.030	0.036
Lot 2	0.022	0.028	0.031	0.038
Critchfield	0.030	0.028	0.031	0.036

Using the mean ratio calculated for each sampled site an analysis of variance was carried out to determine differences between trees, sites and regions. No significant difference between trees was found. Difference between sites was just significant, and between regions highly significant (Table IV). When these data were subjected to the Duncan Multiple Range Test (Steel and Torrie, 1960) it was found that the three major regions differed significantly from each other, but there was no significant difference between the Mendocino White Plains and Coastal forms. The difference between sites is concentrated principally in the Coastal and Mendocino forms (Figure 4). For example, in the former group the mean ratio for sample 14 (Bandon, Oregon) is significantly different from sample 17 (Mouth of Noyo River, California); and in the latter group the mean ratio for sample 18 (Fort Bragg, California) is significantly different from sample 19 (one mile east of Mendocino White Plains).

The foliage of the interior sources at Placerville is yellow green in colour, while the coast is dark green. A similar difference in colour was observed in the coast and interior foliage samples collected in the field and obtained from the British Columbia and Alberta Forest Services.

The establishment of a correlation between width and length does much to explain the very large discrepancies in the estimations of both measurements for Lodgepole pine needles as given by different authorities. It is often stated that leaf length is more prone to environmental influences than width, which is under stronger genetic control (Critchfield, 1957). There is little doubt that leaf length does vary considerably with changes in environment. Nevertheless, leaf length, at least in Lodgepole pine, will positively influence leaf width, and because of this the ratio of the two measurements is a much more reliable comparative measurement. It is likely that a similar relationship between width and length exists in other pine species.

The results lend support to Critchfield's view that the coastal form is a separate subspecies, though, as already noted, Critchfield did not find any significant differences in length or width of needles between the coast and interior forms. However, the results do not support his conclusion that the Mendocino White Plains form is a separate subspecies. This population was subdivided principally because of the absence of resin canals. But some authors state that there are no resin canals in the shore form (Keng and Little, 1961), and it is certain that they are absent in the southern regions (Critchfield, 1957). Finally, resin canals are present in one of the Mendocino White Plains leaf samples measured for the present study.

It is suggested that the Mendocino White Plains population is merely the southern extremity of the distribution of the Shore form of Lodgepole pine, for neither leaf morphology nor absence of resin canals support the view that it is a separate subspecies.

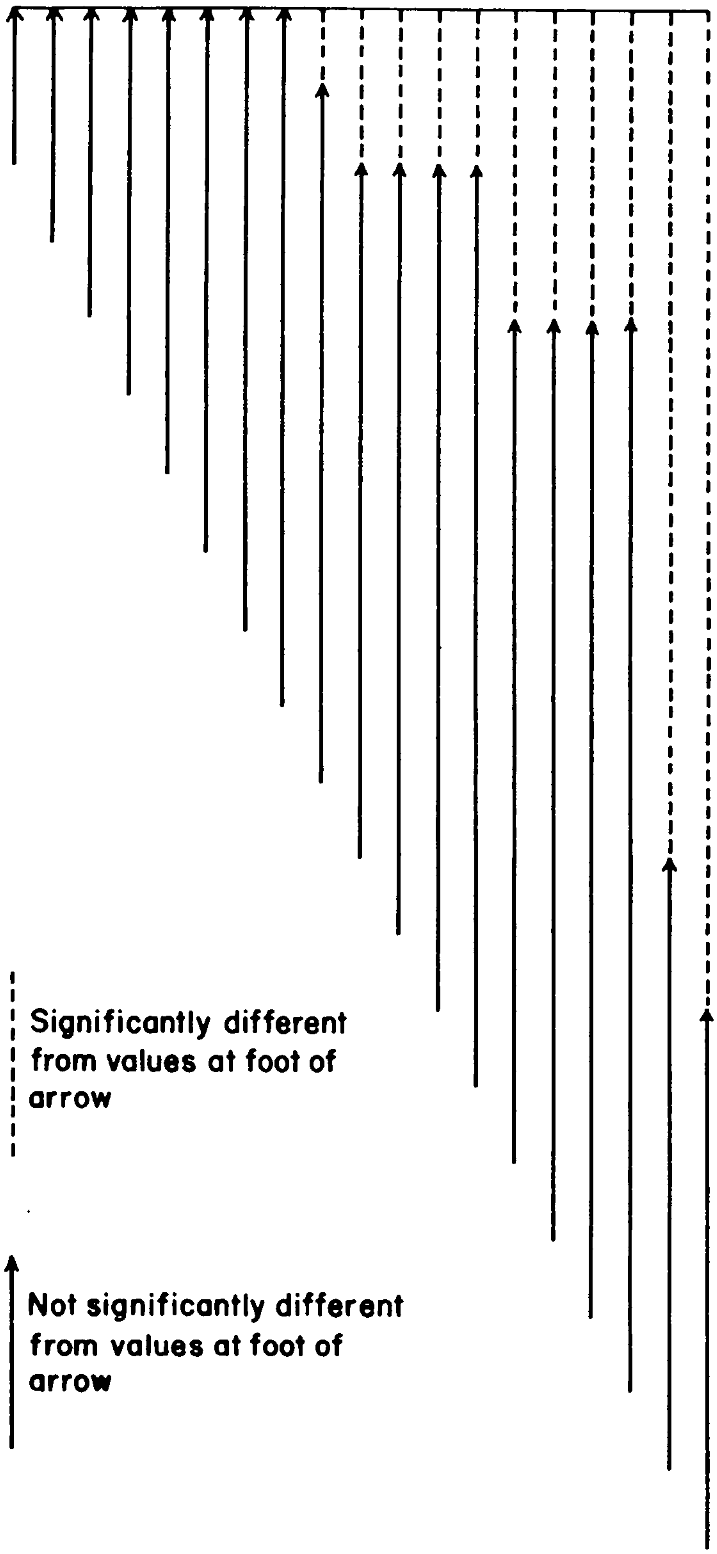
TABLE IV

ANALYSIS OF VARIANCE FOR DIFFERENCE IN LENGTH/WIDTH RATIO OF *PINUS CONTORTA* NEEDLES BETWEEN TREES, SITES AND REGIONS

Source of Variation	DF	SS	MS	F	F(table) 0.05	F(table) 0.01	Remarks
Region	3	.001092	.000364	16.55	2.78	4.16	**
Within Region	16	.000803	.000050	2.27	1.83	2.35	*
Trees	3	.000126	.000042	1.91	2.78	4.16	NS
Error	57	.001272	.000022				
Total	79	.003293					

** significant at 0.01 probability level

* significant at 0.05 probability level



Mean Ratios for Each Sample	Sample Number
·021	18
·023	17
·024	20
·024	13
·027	7
·028	12
·028	16
·028	2
·029	15
·030	19
·031	11
·032	8
·032	14
·032	3
·033	6
·033	5
·034	4
·034	1
·039	10
·040	9

Fig· 4 Differences in ratio of needle width to length for 20 provenances of *Pinus contorta* sampled at Placerville

TABLE V

GEOGRAPHIC ORIGINS OF TWENTY PROVENANCES OF

<u>PINUS</u> <u>CONTORTA</u> SAMPLED AT PLACERVILLE

Sample No.		Elevation in Feet
	R_1 Rocky Mountain and Intermountain Region	
1	6 miles NE of McLeod Lake, British Columbia	3,000
2	Fraser, Colorado	8,000
3	Exshaw, Alberta	4,250
4	2 miles North of Basin, Montana	6,500
5	Georgetown, Colorado	8,800
6	3 miles NE of Gardiner, Montana	7,000
7	Meacham, Blue Mountains, Oregon	3,000
	R_2 Cascade Mountain Region	
8	Mill Creek, Mineral, California	4,700
9	3 miles East of Huntington Lake, California	8,250
10	Precise origin unknown	
	R_3 Coastal Region	
11	15 miles West of Victoria, British Columbia	100
12	Maltby, Washington	350
13	Umpqua Lighthouse, Reedsport, Oregon	50
14	Bandon, Oregon	50
15	Newport, Oregon	100
16	Crescent City, California	50
17	Mouth of Noyo River, California	50
	R_4 Mendocino Region	
18	2 miles East of Fort Bragg, California	200
19	1 mile East of Mendocino, California	200
20	1 mile East of Mendocino, California	200

GROWTH HABIT

The original Shore pine was first described from coastal areas in the southern part of the entire range of P. contorta (Edwards, 1957), where it is scrub-like in appearance. Thus at a very early date it became known as Scrub pine (Sargent, 1897), and practically all subsequent literature, even the most recent, follows the early description, which is summed up by Tackle (1959), who stated that it is a "low scrubby tree of the Pacific coast".

The early description of Shore pine from the contorted scrub phenotypes of its southern extremity has been extended to the whole coastal form of the species. This has occurred, not merely because of reiteration in the literature of the early account, but also because of the refuge status of Lodgepole pine west of the Coast Mountains. If the species is studied in the field it is immediately clear that it is the most shade-intolerant tree of the major coast species. Thus it is relegated to sites which cannot support any other competing species, and is found in abundance on muskeg, rocky, coastal outcrops (Illus. 1, 2), and on poor, dry sites where fire is frequent. The severity of the environment of these areas greatly modifies its form, and its scrub-like appearance, though environmentally determined, is then frequently considered to be an inherent characteristic of the species.

Occasionally the incidence of fire will enable Shore pine to become established on Douglas fir-hemlock sites. Its rapid early growth, and precocious flowering give it the advantage in such areas. On these better quality sites Shore pine will grow rapidly, and can reach a height of 70 feet in a little over 50 years (Illus. 6). In form it will compare favourably with the Interior variety of the species.

There are extensive stands of this kind on the east coast of Vancouver Island, along the coast of Oregon and on the Kitsap Peninsula in Washington (Illus. 3, 4).

This capacity for height growth on good sites has been noted by some botanists who have had the opportunity to study the species both in its natural habitat, and in arboreta and plantations. Elwes and Henry (1910) stated that the coastal form will grow to 70 feet on good sites, and Dallimore and Jackson (1923) described it as "a tree varying greatly in stature and habit according to situation, from a stunted bush, or a small tree 10 - 30 feet high, with short, twisted branches, to a tree 70 - 200 feet high".

As with all tree species, inferior phenotypes, genetically determined, will be found, both in the Shore and Inland forms (Illus. 5, 7, 8). Though growing on relatively good sites they produce heavy, fastigiate branching and frequently a short bole. On inferior, isolated sites, where the species has been established for a long time, there may be some selective pressure for fitness to exist under extreme environmental conditions. Selection which will adapt the species for growth on bog could produce an ecotype unsuitable for commercial planting. The Lulu Island Lodgepole pine, which is an ancient population (Hansen, 1947), appears to be such an ecotype. In extensive planting in England and Ireland the strain has shown itself inferior to other provenances of the Shore form.

Unfortunately the Lulu Island stands, and similar stands at Long Beach, Washington, and near the village of Rainer, Washington, have long been the source of seed supplied to Britain and Ireland because of the accessibility and abundance of cones. However the progeny of such seed sources, though they vary considerably in desirable silvicultural characteristics, have not shown the scrub-like growth of Shore pine as described in the literature.

Studies by Heusser (1960) and Hansen (1947) of post-glacial forest succession in the Pacific Northwest support the conclusion that Lodgepole pine is the most shade-intolerant of the coniferous coast species, and clarify its present status in the ecology of the Pacific Slope forests.

Lodgepole pine was the predominant species over most of the Pacific Coast during early post-glacial times. Its advance was favoured by its ability to persist under conditions of physiographic instability following glaciation. However, following land stability, the proportion of pine greatly declined, and occupied only those locations "where survival was not endangered by competition for light by other conifers" (Heusser, 1960).

During the latter part of the post-glacial period there was a climatic change to wetness and coolness. The species which were competing with Lodgepole pine were unable to survive, and the pine, free of competition for light, again spread over vast areas.

The climate in historic times again favours species other than Lodgepole pine, and once again it is relegated to the forests' edge, to ocean cliffs, sand dunes, and muskeg. There its potential growth habit and form are obscured by extremes of environment, and are observed only when grown in plantations, or in its natural habitat when competing species are eliminated by fire.[1] Under the latter conditions the Shore variety of Lodgepole pine is a rapidly growing tree, with normal growth habit and form, and is seldom contorted either in bole or in branch (Illus. 9, 10).

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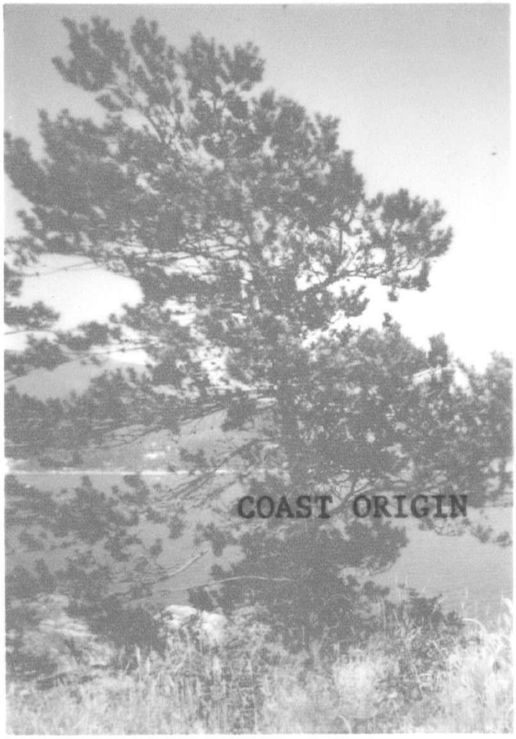
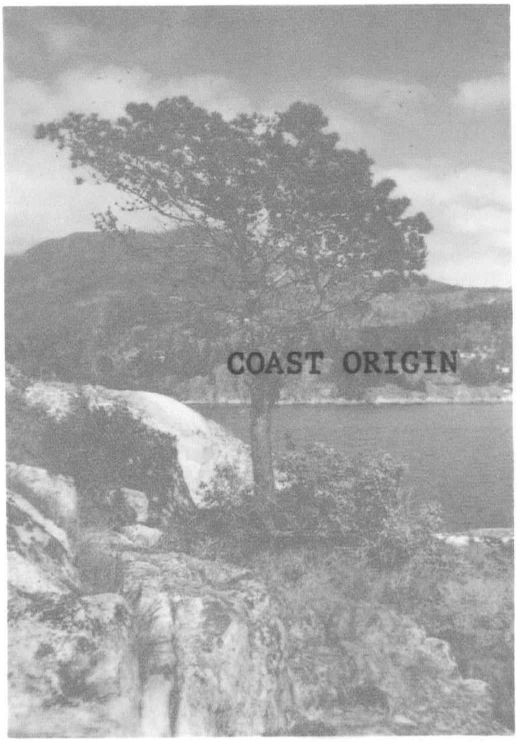
1 Seed collected from "dwarf" Lodgepole pine growing on the Mendocino White Plains in California, and planted with 22 other provenances at Placerville, has produced the tallest trees in the plantation.

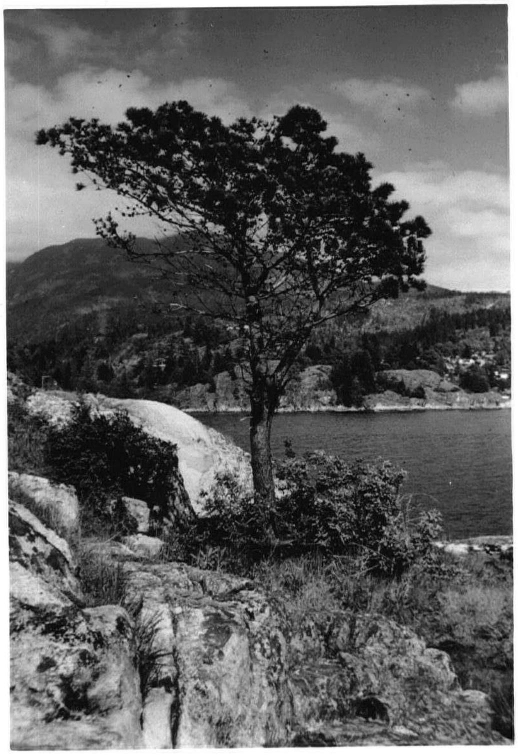


Illus. 1. P. contorta, Passage Island, Howe Sound, B. C.

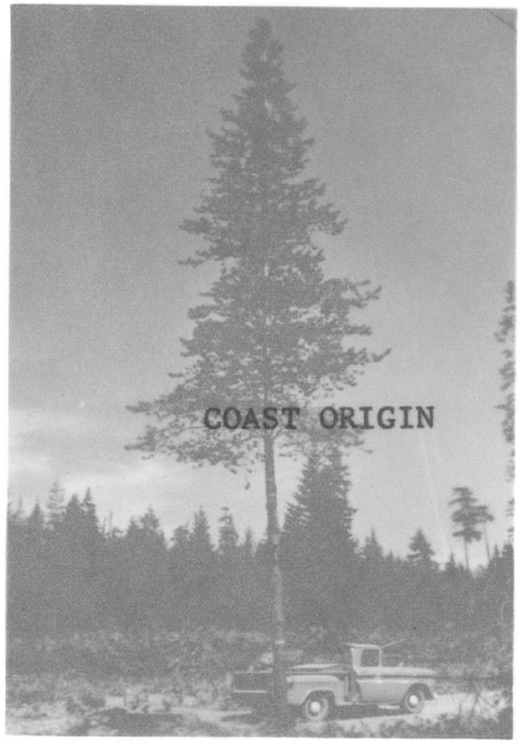


Illus. 2. P. contorta, Whytecliff, near Vancouver, B. C.

Illus. 1. P. contorta, Passage Island, Howe Sound, B. C.



Illus. 2. P. contorta, Whytecliff, near Vancouver, B. C.

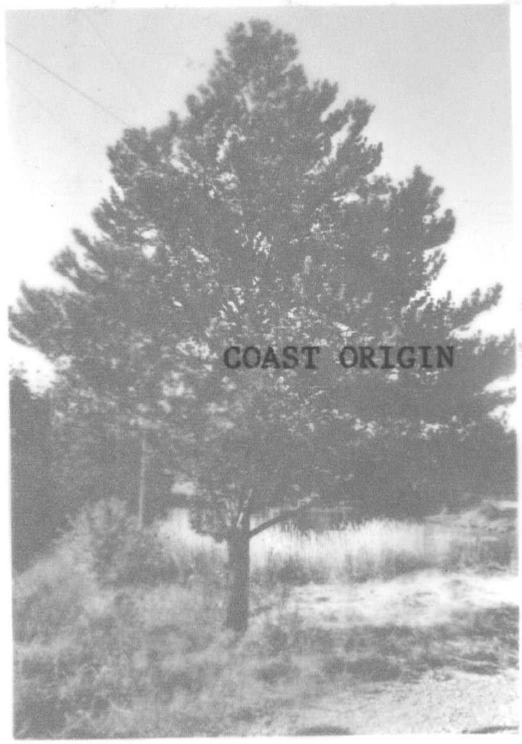


Illus. 3. _P. contorta_, Kitsap Peninsula, Washington

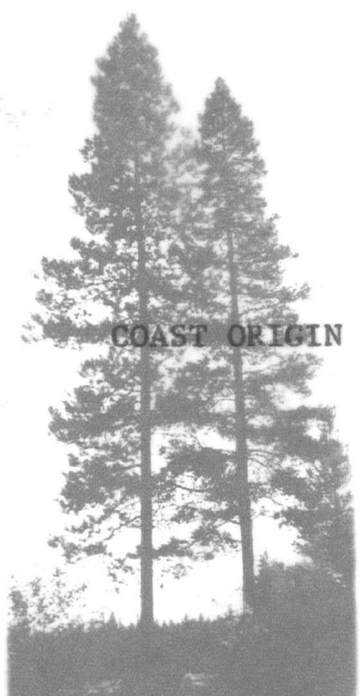
Illus. 4. _P. contorta_, Kitsap Peninsula, Washington

Illus. 3. P. contorta, Kitsap Peninsula, Washington

Illus. 4. P. contorta, Kitsap Peninsula, Washington



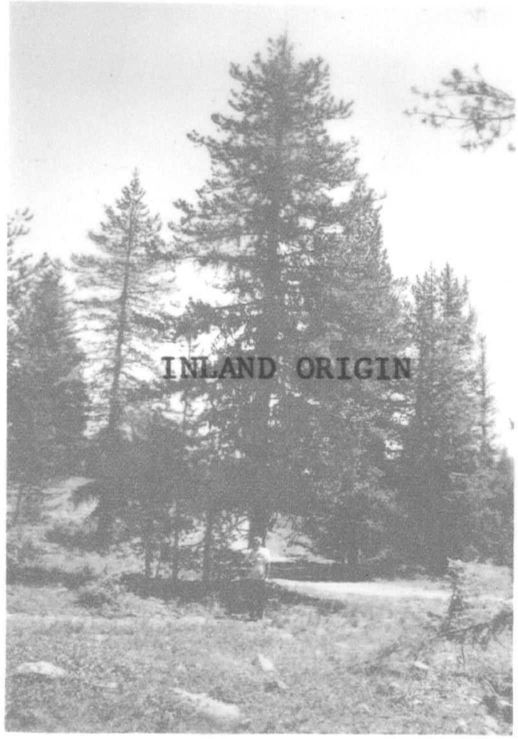
Illus. 5. P. contorta, 4 miles west of Olympia, Washington



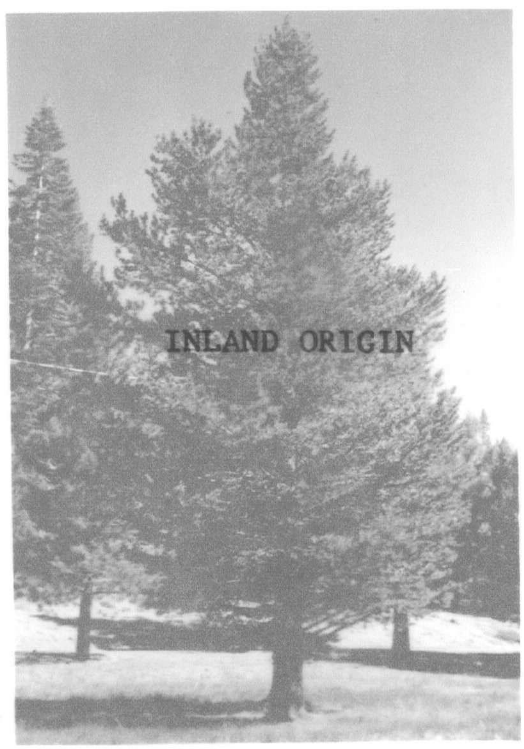
Illus. 6. P. contorta, 5 miles south of Olympia, Washington

Illus. 5. P. contorta, 4 miles west of Olympia, Washington

Illus. 6. P. contorta, 5 miles south of Olympia, Washington



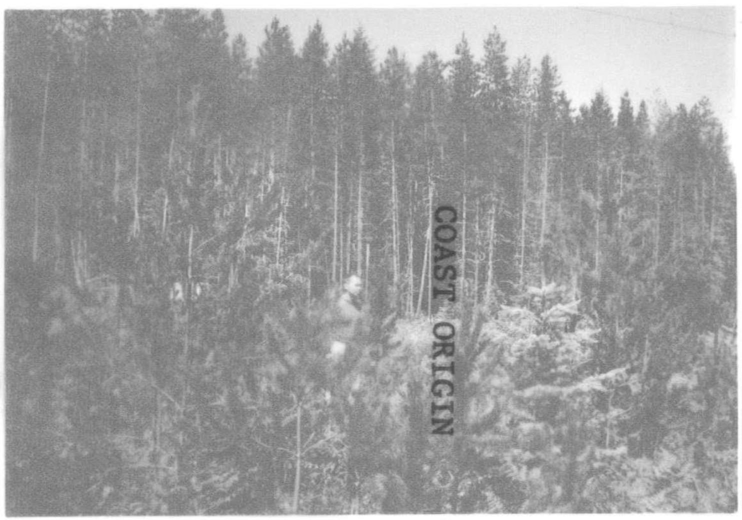
Illus. 7. P. contorta, Blue Mountains, Oregon



Illus. 8. P. contorta, east side of Lake Tahoe, Nevada

Illus. 7. P. contorta, Blue Mountains, Oregon

Illus. 8. P. contorta, east side of Lake Tahoe, Nevada



Illus. 9. P. contorta, Olympic Peninsula, Washington

Illus. 10. P. contorta, Ladner, near Vancouver, British Columbia

Illus. 9. P. contorta, Olympic Peninsula, Washington

Illus. 10. P. contorta, Ladner, near Vancouver, British Columbia

VARIATION IN BARK

Bark Thickness

There are extremely few studies concerning variation in bark within a forest tree species, and of these most are concerned with determining bark thickness in relation to the volume of the tree. To the writer's knowledge there is no major study which attempts to relate variation in bark thickness, texture and colour to ecotypic or clinal variation within the principal coniferous species.

In order to check the applicability of existing Lodgepole pine volume tables, Parker (1950) measured bark thickness of Lodgepole pine on four one-tenth-acre plots at Kananaskis Forest Experiment Station, Alberta. This study showed that bark thickness varies with age and site quality, being thicker on poor sites than on good ones, and on older trees than on young ones; though the ratio of thickness to the diameter of the tree decreases with increasing age.

Irish volume tables for the Shore form of the Lodgepole pine express bark as a percentage of over-bark volume (Joyce, 1961). It is clear from these tables that the ratio of bark thickness to diameter of the Shore form also decreases with increasing age.

Jentsch (1954) examined bark thickness in five interior and one coastal source of Lodgepole pine growing in Germany. Measurements, which were conducted on eighteen-year-old trees, failed to show any distinction in thickness between the coastal and interior forms.

Bark Texture and Colour

Sudworth (1908) stated that Shore pine bark is rough, furrowed and ridged, and purplish red brown in colour; though older trees have smooth, fined scaled bark, pale brown with a greyish tinge, which is also typical of the Interior form. According to Harlow and Harrar (1958), the Shore form is deeply furrowed and transversely fissured, and the bark of high elevation trees consists of thin, loosely appressed scales, orange-brown to grey in colour.

In Ireland the Shore form of Lodgepole pine is distinguished from the Interior form by bark texture. The bark of coastal trees is rough and dark, and vertically fissured; while the Inland form has smooth bark which is pale grey in colour.[1] However, Lines (1954), writing of Lodgepole pine in Ireland, stated that bark is not a good diagnostic feature. This is also the opinion of Critchfield (1957).

In 1955 and 1957 an investigation was carried out in England to determine the general properties of the timber from

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1 Communication from the Irish Forest Service.

Lodgepole pine plantations. The 1955 investigation was carried out on the Shore form and the 1957 on the Inland. The bark of the trees was examined in both years. It was recorded that there is a distinct difference in both types (D.S.I.R. 1960). The nature of this difference is clearly illustrated by photographs in the progress reports relating to this study. The Shore form is deeply fissured and dark in colour, the Interior form is light-coloured and smooth in texture.

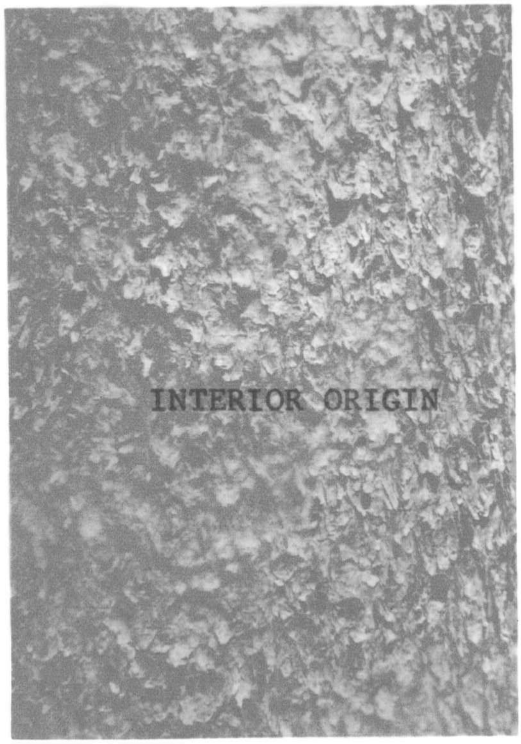
It is apparent from the literature that there is considerable variation in thickness, texture and colour of Lodgepole pine bark. There is also considerable evidence to show that variation in bark thickness in this species, both in the Shore and Interior form, is to a large extent influenced by such environmental factors as stand density and site quality, and also the age of the tree. It must be concluded that thickness is not a very reliable variant for precisely delimiting intraspecific variation. However, this latter consideration does not apply to bark texture and colour, on the contrary, evidence from plantations in England and Ireland suggests that major differences in both these characteristics of bark are associated with the principal regional forms of Lodgepole pine.

The present study deals primarily with the texture and colour of the bark, and was carried out with the object of determining to what extent the differences in these bark characteristics in plantations are paralleled by similar differences in natural populations. No measurement of thickness was made at any of the sites visited.

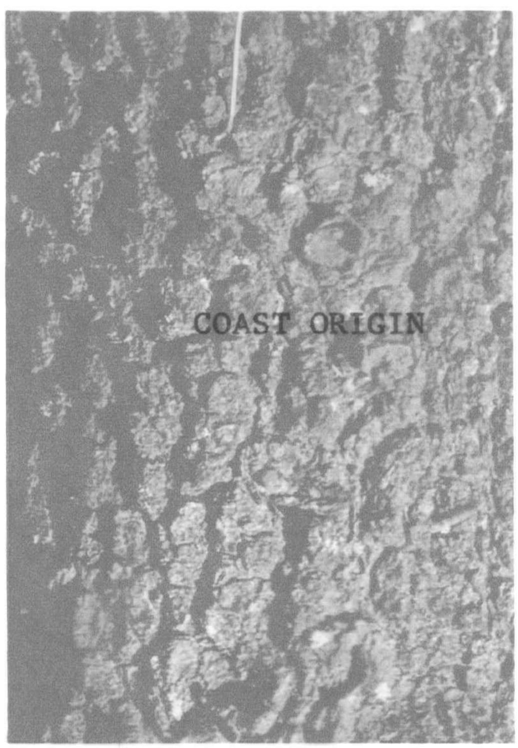
The study showed a distinct difference in bark texture and colour between the Inland and the Shore form of Lodgepole pine. Differences in bark texture are given in Illustrations 11 to 18, which are representative of each stand visited. Illustration 18 depicts the bark of a Lodgepole pine tree grown at Placerville, California from seed collected on the coast. The bark of the Shore form is fissured vertically and horizontally, and is dark in colour. The Inland form is fine-scaled and light grey or cinnamon in colour. No deeply fissured, black bark was observed on any of the Inland trees, though on occasion fairly thin, very lightly fissured bark was observed in coastal areas, particularly on young trees. However, no old trees of the Shore form had bark even remotely similar to that of the Inland form.

There is considerable variation within each major geographic region, for example, the high elevation sources from northern Alberta are much lighter and smoother than the bark from lower elevations in Alberta. Nevertheless, this variation is slight compared to the obvious, and consistent, distinction between the Inland and the Shore form.

The difference in bark texture and colour, sometimes observed in plantations, between the Inland and the Shore form of Lodgepole pine is paralleled in natural populations. It is suggested, therefore, that this characteristic is heritable and can be legitimately taken into consideration in classifying intraspecific variation.

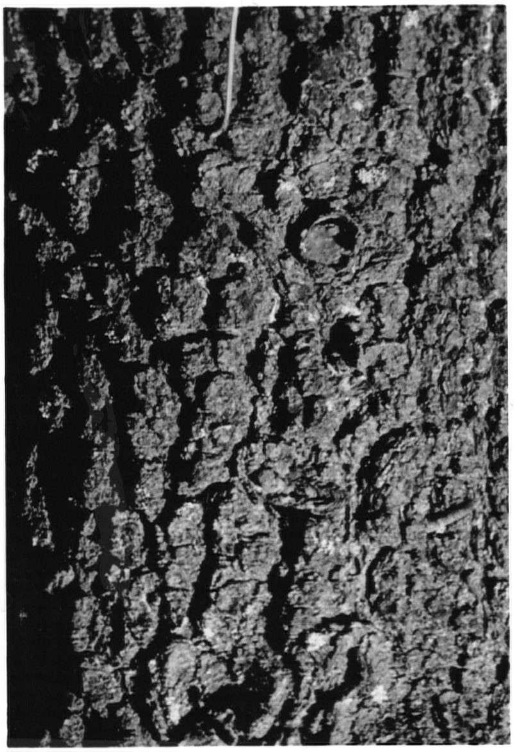


Illus. 11. P. contorta, Chinook Pass, Washington

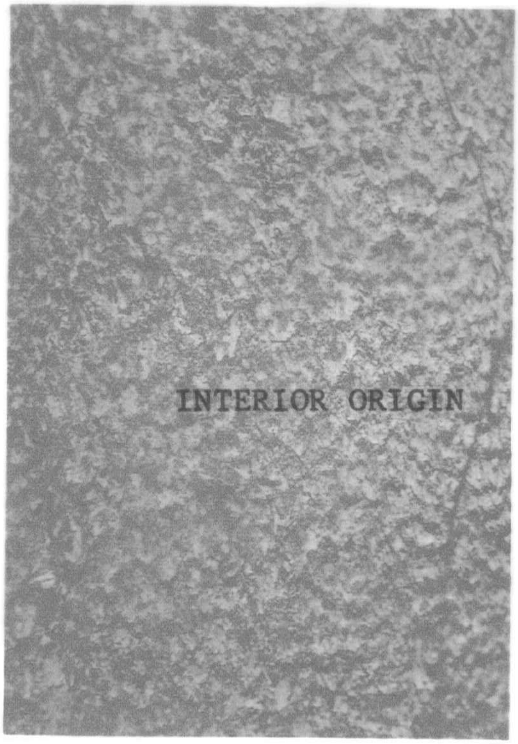


Illus. 12. P. contorta, 4 miles west of Olympia, Washington

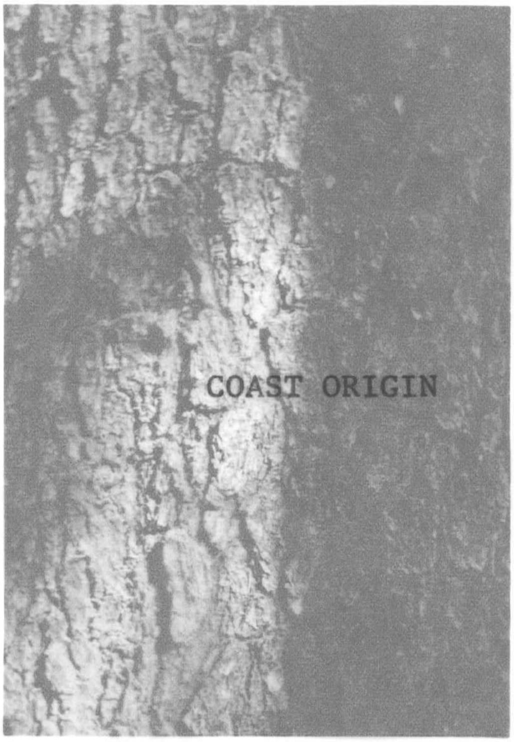
Illus. 11. *P. contorta*, Chinook Pass, Washington



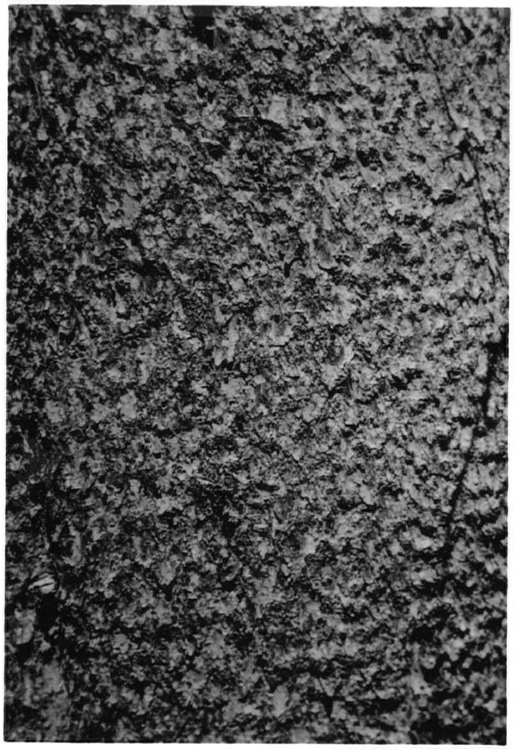
Illus. 12. *P. contorta*, 4 miles west of Olympia, Washington



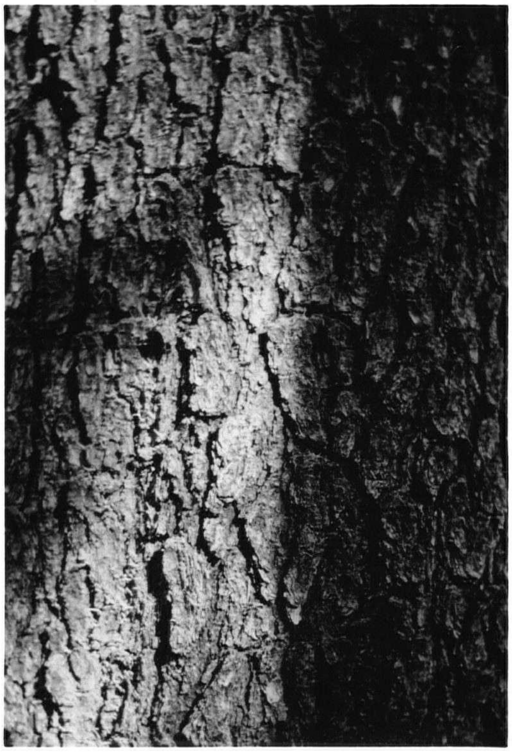
Illus. 13. _P. contorta_, 20 miles east of Placerville, California



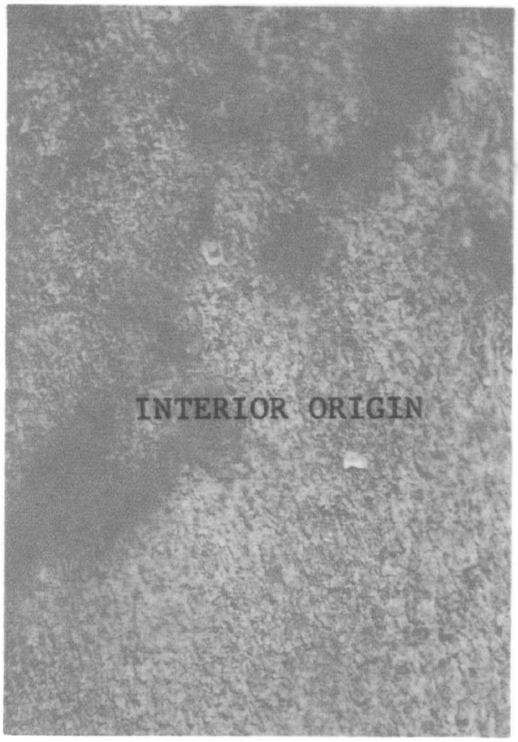
Illus. 14. _P. contorta_, 5 miles south of Olympia, Washington



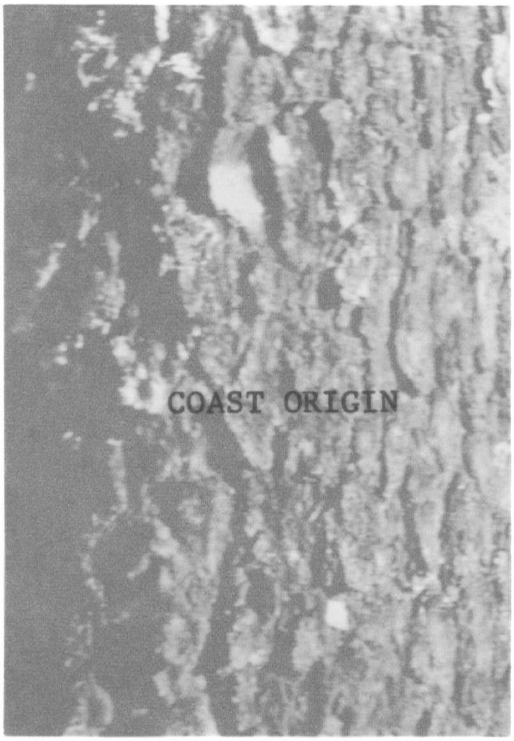
Illus. 13. P. contorta, 20 miles east of Placerville, California



Illus. 14. P. contorta, 5 miles south of Olympia, Washington



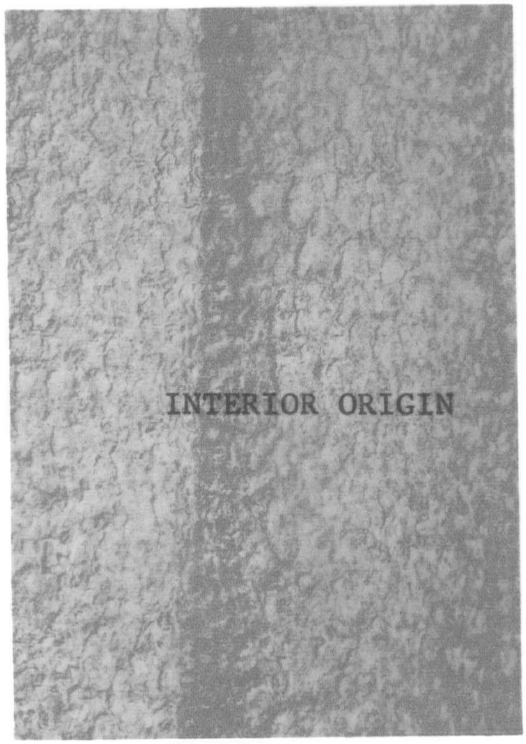
Illus. 15. P. contorta, east side of Lake Tahoe, Nevada



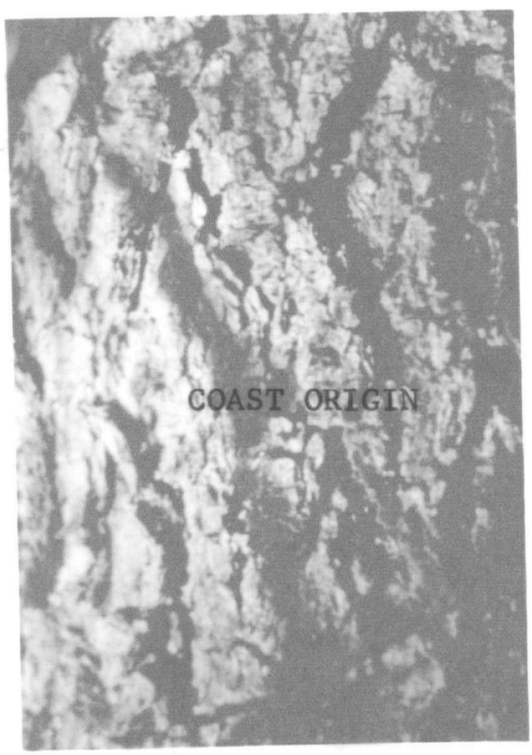
Illus. 16. P. contorta, 60 miles north of Vancouver, B. C.

Illus. 15. P. contorta, east side of Lake Tahoe, Nevada

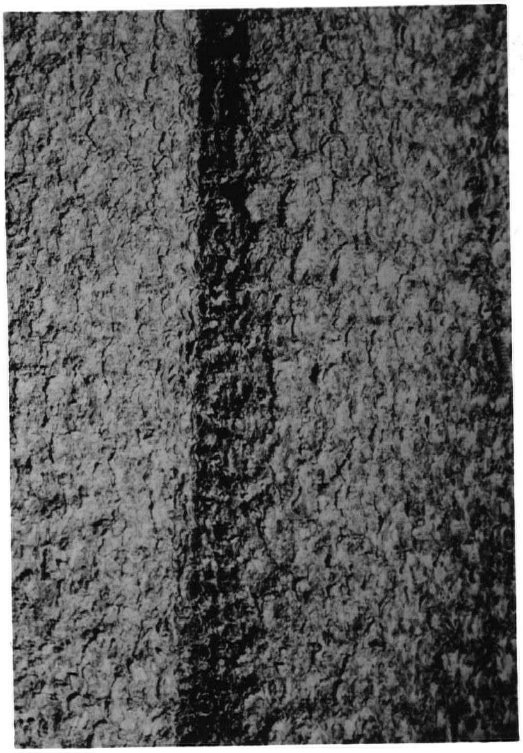
Illus. 16. P. contorta, 60 miles north of Vancouver, B. C.



Illus. 17. P. contorta, near Placerville, California

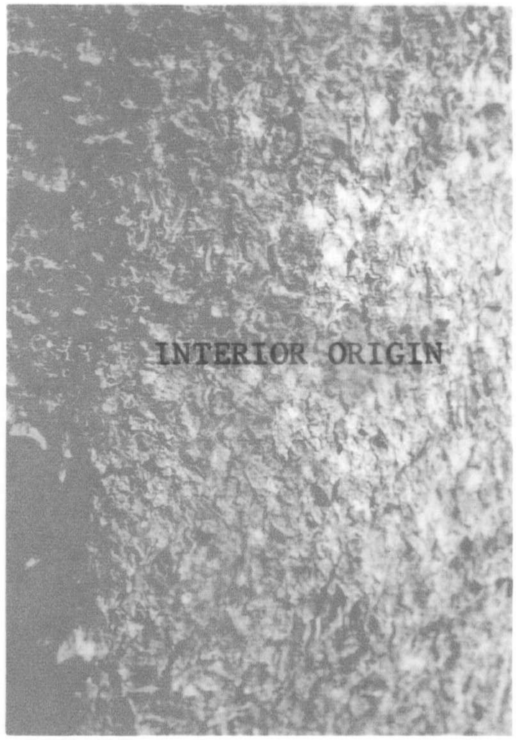


Illus. 18. P. contorta, Placerville, California
Seed origin - Samoa, California

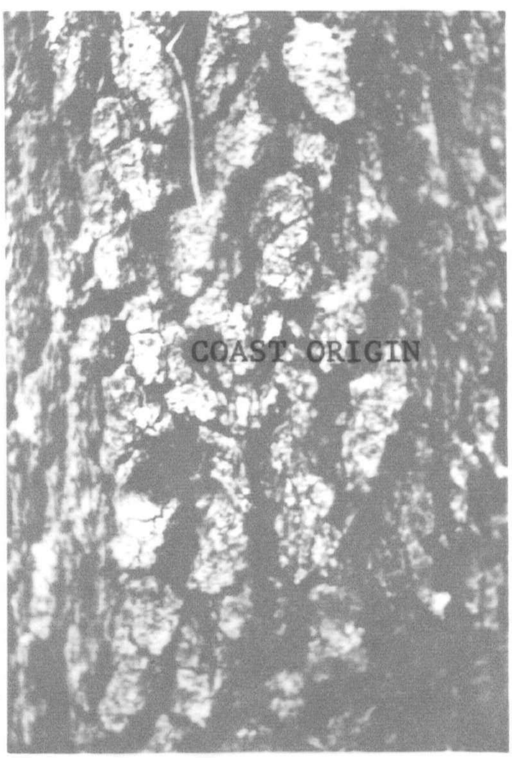


Illus. 17. P. contorta, near Placerville, California

Illus. 18. P. contorta, Placerville, California
Seed origin - Samoa, California



Illus. 19. P. contorta, Blue Mountains, Oregon



Illus. 20. P. contorta, East Coast, Vancouver Island

Illus. 19. P. contorta, Blue Mountains, Oregon

Illus. 20. P. contorta, East Coast, Vancouver Island

SEED CHARACTERISTICS

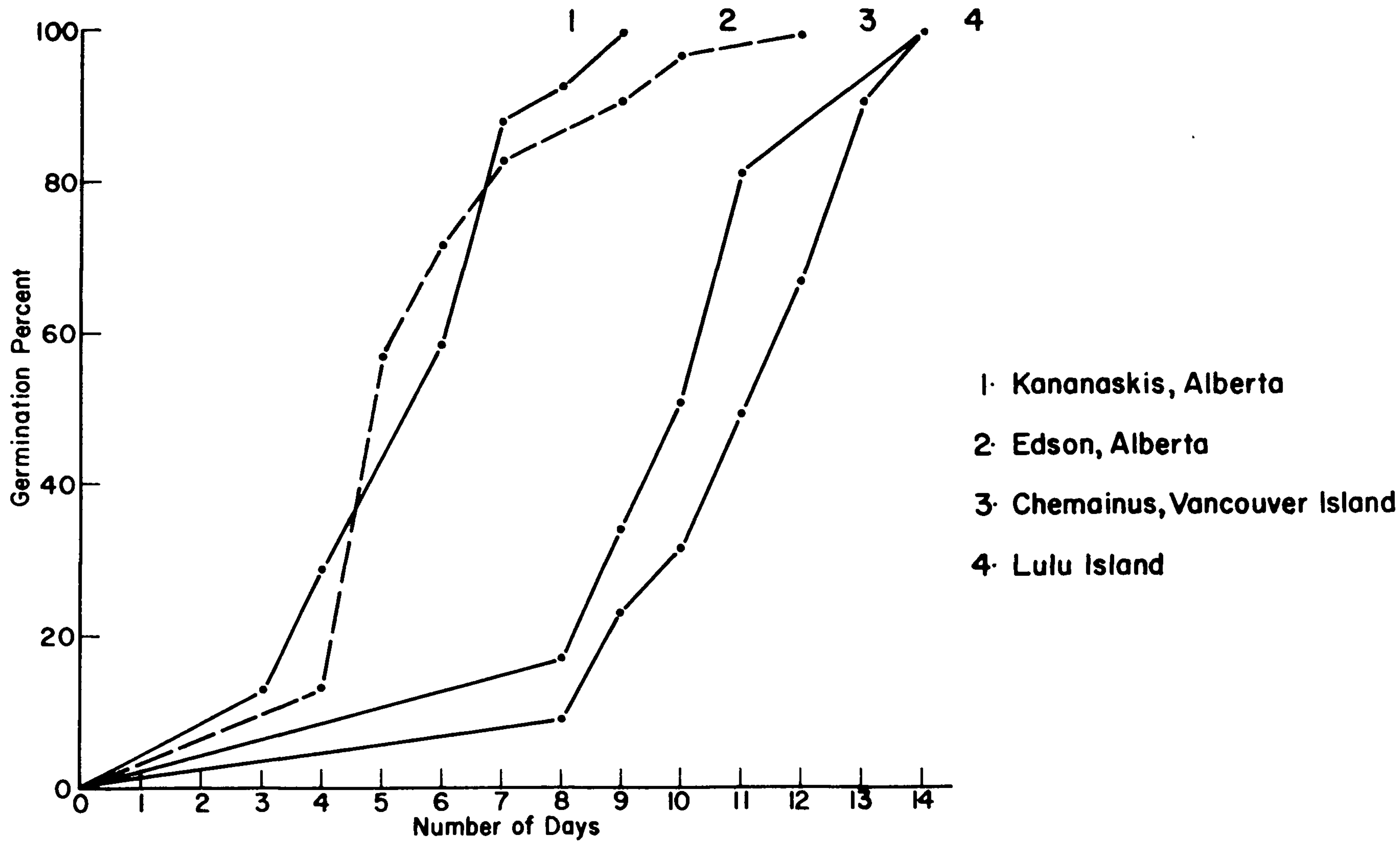
A microscopic study of interior and coastal Lodgepole pine seed, similar to that of Allen (1960) for Douglas fir, showed that certain morphological characteristics may be used to distinguish the seed from each source. These characteristics are illustrated in Figure 6.

A preliminary investigation was made to determine the behaviour of seed incubated without stratification. It was found that the Coast form is extremely sluggish in rate of germination relative to the Interior seed sources (Figure 5). Four sources, two Interior and two Coast, were then incubated following naked stratification as devised by Allen and Bientjes (1954), fifty seeds of each lot being incubated after two, four and six weeks' stratification. The results are given in Table VII.

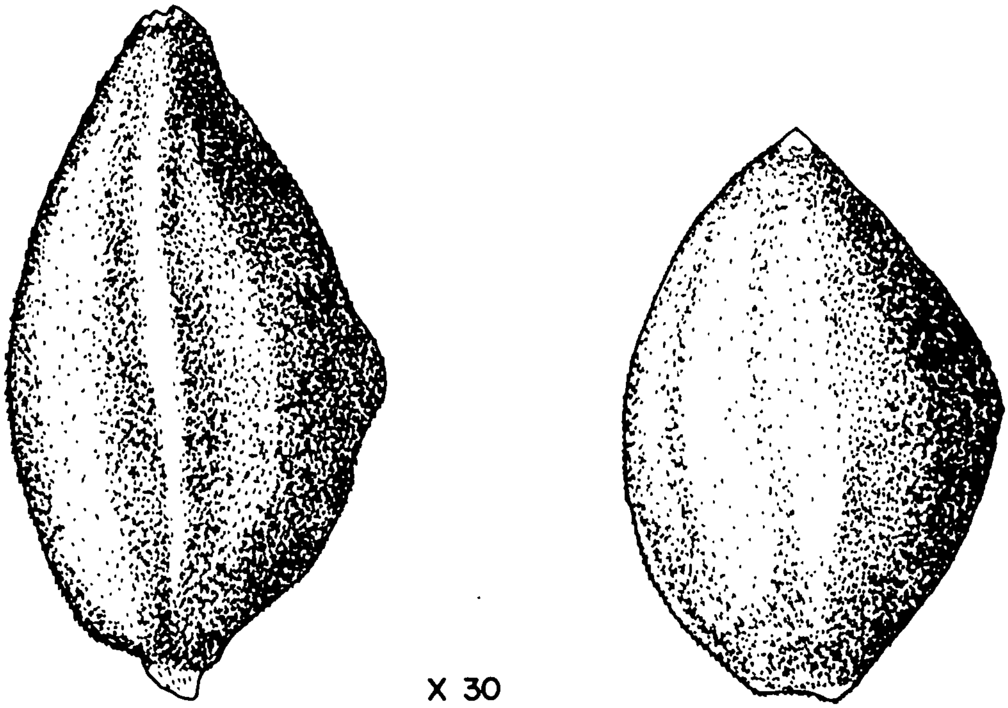
It will be seen that the longer the stratification period the more rapid the germination rate of the Coastal seed lots. Nevertheless, whatever the period of stratification, the Coastal lots are slower to germinate than the Interior. Increasing the period of stratification does not noticeably increase the germination rate of the Interior lots. After two weeks' stratification the germination per cent is almost as great in three days' incubation as it is for the same lots stratified six weeks.

In order to test the validity of the above results, nine seed lots, including four of coastal origin, were germinated following naked stratification for two weeks. The same pattern of variation was observed (Table VIII). (Lot A is taken from a tree of Interior origin growing in the arboretum of the University of British Columbia.) It is suggested, therefore, that interior and coastal seed lots may be rapidly distinguished by this method, and that the optimum period of stratification for such a test is approximately two weeks.

Following the practice of Haasis and Thrupp (1931) the germination percentage for all tests is calculated as a percentage of the total number of seeds germinated. The incubation temperature was 25 degrees C. in all cases.



Fig· 5 Differences in rate of germination at 25° C between coast and interior seed of Pinus contorta·



INTERIOR FORM	COAST FORM
Pointed protuberance at funicular end of seed	Protuberance usually absent
Usually over 3 mm in length	Usually under 3 mm in length
Prominant ridge on upper surface	Ridge not usually prominant

Fig. 6 Method of distinguishing interior and coastal *Pinus contorta* seed.

TABLE VI

GERMINATION RATE OF FOUR SOURCES OF *PINUS CONTORTA* SEED AT VARYING PERIODS OF STRATIFICATION

Period of Incubation - Days:	1	2	3	4	5	6	7
2 Weeks Stratification							
1. Lulu Island				8	16	72	100
2. Sechelt				35	73	78	100
3. Rocky Mountain House			64	100			
5. Lot A		13	77	100			
4 Weeks Stratification							
1. Lulu Island			28	70	85	100	
2. Sechelt			16	58	75	85	100
3. Rocky Mountain House			64	88	72	100	
4. Lot A		32	63	66	100		
6 Weeks Stratification							
1. Lulu Island		8	74	84	88	94	100
2. Sechelt			49	52	68	89	100
3. Rocky Mountain House		89	100				
4. Lot A		77	97	100			

1, 2 are of coastal origin

3, 4 are of interior origin

TABLE VII

GERMINATION RATE OF NINE SOURCES OF *PINUS CONTORTA*

SEED FOLLOWING TWO WEEKS STRATIFICATION

	Seed Lot	Elevation in Feet	Days 1	2	3	4	5	6	7
1	Chemainus	100					20	80	100
2	Lulu Island	25				8	16	70	100
3	Sechelt	100				34	70	100	
4	Mount Finlayson	1,000			14	79	100		
5	Edson	3,150		30	94	97	100		
6	Kananaskis	4,900		16	86	100			
7	Rocky Mountain House	3,245			62	100			
8	Lot A	-		13	91	100			
9	Grande Prairie	2,000		32	100				

1, 2, 3, 4 are of coastal origin

5, 6, 7, 8, 9 are of interior origin

SUMMARY OF CHARACTERISTICS DISTINGUISHING THE COAST FORM OF *PINUS CONTORTA*

Growth Rate and Habit

Normal tree-like growth habit on fair to good sites, reaching 70 to 80 feet in 50 years.

Foliage Characteristics

Dark green in colour. Ratio of needle width to length usually less than .03.

Seed Characteristics

Usually less than 3 mm. in length. Distinguished from interior seed by absence of pointed protuberance at funicular end, and indefinite ridge on upper surface. Germination rate for stratified or unstratified seed distinctly slower than interior seed.

Bark Type

Dark in colour and fissured both vertically and horizontally.

Tolerance

Extremely shade intolerant.

PART II

THE GENETIC IMPROVEMENT OF THE SHORE FORM OF *PINUS CONTORTA*

INTRODUCTION

Research in forest tree breeding is now proceeding at an increasing rate in many centers in Canada and the United States. However, a relatively small proportion of this research is applied to the actual commercial production of improved forest tree seed, and in no part of North America, except, perhaps, in the Southern United States, has this aspect of forest tree breeding reached the proportions it has in Sweden and Great Britain. In fact, remarkably little attention is given in the main centers of research to the study of the techniques involved in producing and marketing improved varieties of forest tree seed.

Forest tree breeding is essentially applied research, and its principal purpose is the economic and regular production of large quantities of seed superior in quality to that collected casually in the forest, which is often deficient both in quality and in quantity. The resources of British and Swedish tree breeders are directed primarily to this objective, with the result that in a relatively short period all the seed required for the planting program of some of the main species will be obtained from seed orchards. Britain is producing large quantities of hybrid larch (Larix eurolepis) in this way, and by 1963 will also have established the seed orchards required to produce its total annual needs of Scots pine (Pinus silvestris) seed, which is 2,000 pounds annually. Plans are now being drawn up to produce similar quantities of Lodgepole pine seed. Sweden has already established 350 hectares of seed orchards, which is half its total requirements for the whole country (Arnborg, 1960).

It is true that those countries have large planting programs. It is equally probable that within the next few years there will be a very rapid increase in planting in North America. If planting is to be the principal method of regeneration then it is simply a further rationalization of the regeneration program to supply the seed from seed orchards.

There are a number of reasons which explain why many North American tree breeders are reluctant to adopt fully what has now become known as the Scandinavian method of tree improvement, but the most important may be stated as follows: first, it is considered too expensive, and secondly, it is pointed out that trees selected and registered as plus trees in this manner, and propagated in seed orchards, will retain the status of plus trees permanently even though at a later date progeny trials will have proved them otherwise. Workers will be reluctant to reject them because of the very heavy expense incurred in the initial selection and propagation in seed orchards. Finally, there is a theoretical objection to the Scandinavian method of individual tree selection. It is stated that the amount of genetic gain obtained by individual tree selection is not worth the cost incurred. For example, J. W. Wright estimated that if heritability of a character such as height/increment is 25 per cent, then the selection differential would have to be one in ten thousand to obtain an increase of 2.2 feet in height growth at 25 years.[1] It is argued from examples such as this that the cost of inspecting 10,000 trees to obtain one tree with such a small increase in growth potential is much greater than the value of the genetic gain.

This argument is based on an equation drawn from the work of animal breeders, which may be stated as follows:

$$\text{Estimated genetic gain} = \text{Heritability} \times \text{Selection Differential}$$

$$\text{Heritability} = \frac{\text{Additive Genetic Variance}}{\text{Total Phenotypic Variance}}$$

$$\text{Selection Differential} = \bar{X}\text{ selected} - \bar{X}\text{ unselected trees,}$$

where $\bar{X}$ is the mean of a single character measurement of the selected and unselected trees.

It will be seen that if the heritability of a particular character is high there is less need for a high selection differential in order to obtain genetic gain.

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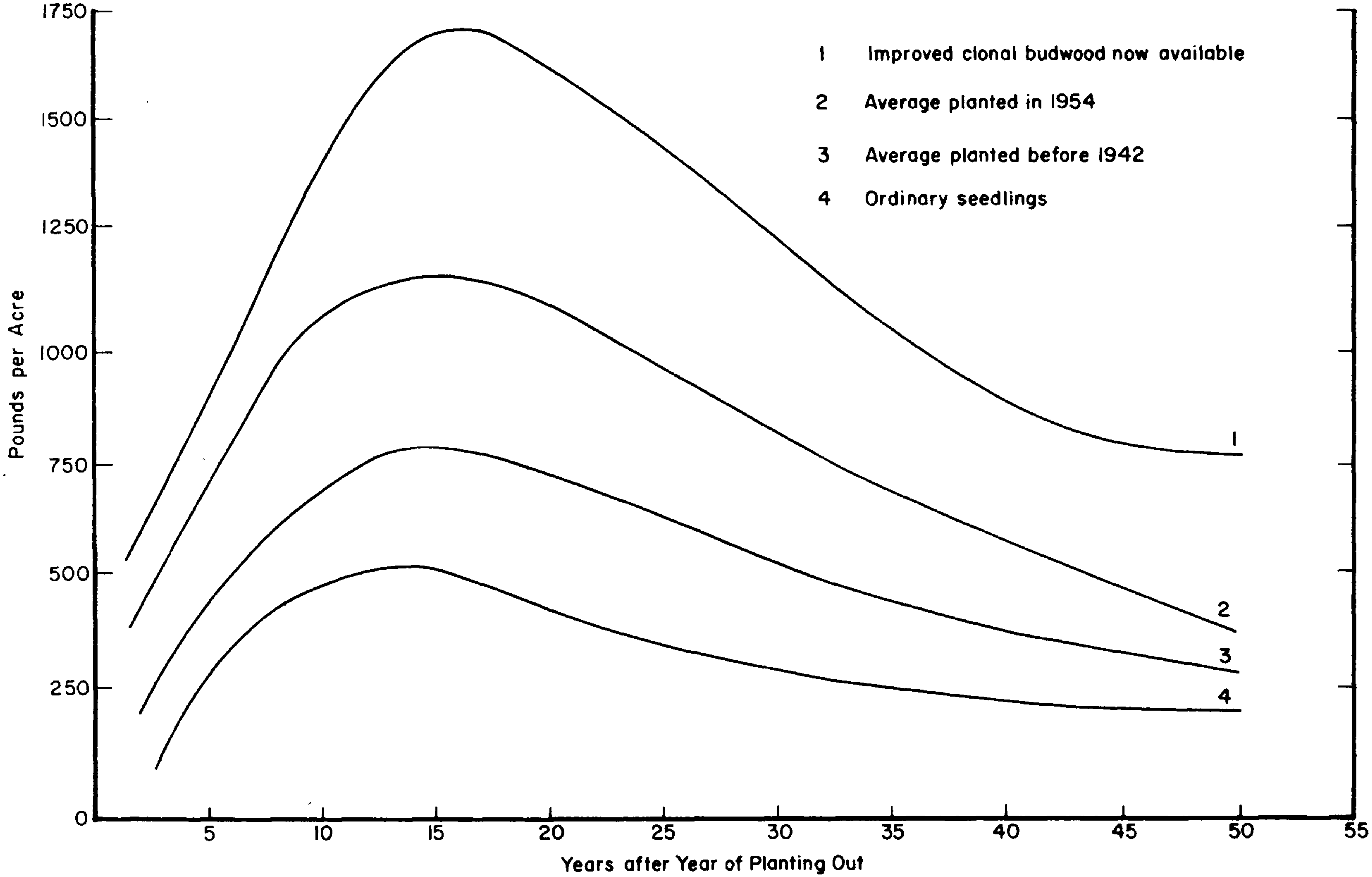
1 Unpublished material, Library, Faculty of Forestry, U. B. C.

In Australian Capital Territory, the techniques applied to obtain superior Pinus radiata are similar to those applied to Pinus silvestris and Picea excelsa in Sweden, and it is considered that a ten per cent increase in monetary returns in a rotation is a very conservative estimate. This increased expectation value allows an additional 21 Australian pounds per 1,000 plants to be spent to produce superior stock without any loss being sustained. The present cost of producing planting stock in Australian Capital Territory is approximately 2 pounds per 1,000 plants. Thus any expenditure less than 23 pounds per 1,000 plants (or 11 times the amount now spent) in producing such superior stock, would result in a financial gain (Fielding, 1957). Perry and Wang (1958) showed that a genetic improvement of as little as one per cent more than justifies the extra costs of programs of seed orchard establishment, or of harvesting seed from seed-producing areas, besides preventing severe losses due to the use of seed of improper geographic origin, or inferior genetic quality. Duffield (1962) estimated that an expected genetic gain of one-half of one per cent in Douglas fir will justify a 47 per cent increase in seed investment.

In the late thirties the natural rubber industry of Malaya realized that its position was about to be seriously menaced by the development of synthetic rubber. The leaders of the industry decided that, if the industry was to survive, production per acre must be greatly increased, and cost per pound of latex greatly reduced. An intensive drive aimed at the development of high yielding trees was launched. The results of that effort are shown in Figure 7. Production per acre was increased by no less than 260 per cent (Swan, 1955).

It must be concluded that the weight of the evidence justifies a program of forest tree improvement, and that genetic gains can be achieved by the full utilization of the knowledge already obtained by workers in this field.

In drawing up the proposed program for the breeding of Shore pine, the theoretical objections to the Scandinavian method of tree breeding, as stated, have been taken into account. Nevertheless, the program does incorporate certain aspects of the Scandinavian method insofar as it is designed to mass produce seed which is not inferior in certain important characteristics while simultaneously working for a genetically improved variety.



after Swan, 1955

Fig. 7 Increase in latex yields per acre by selection and breeding of superior stock

POLLINATION IN RELATION TO BREEDING

Natural Method of Pollination

In *Pinus*, ovulate strobili develop during a period of three to four weeks from a tiny bud to a conelet ready for pollination. Both the Institute of Forest Genetics at Placerville, and the North Idaho Forest Genetics Center find it useful to classify the various stages of female flower development as follows: (1) buds small, (2) buds large, (3) buds opening, (4) flowers partly open, (5) flowers maximum, (6) flowers closed, and (7) cones enlarging. Stages 1, 2, and 3 are determined by the size or condition of the bud. Stages 4, 5, 6, and 7 are determined by the position of the cone scales relative to the axis of the conelet. Stage 5 is the optimum period of receptivity. In Stage 6 the cone scales are tightly closed so that pollination is no longer possible (Cumming and Righter, 1948).

There is considerable variation in the time of shedding of pollen. Trees at higher elevations and latitudes will normally shed pollen later than those of lower elevations and latitudes. There is also genetic as well as annual variation in this characteristic. Thus it is always necessary to determine for specific areas the average period of pollen-shedding, besides the period of optimum receptivity of female strobili.

Duffield (1947, 1953) showed that at latitude 39 degrees N., longitude 120 degrees W., the mean date over a three-year period for the Inland form of *Pinus contorta* is June 22, for the Coast form at Point Arena, California, June 9.

In common with all the pines, Lodgepole is an anemophilous species. Wind carries the pollen to the upright female strobilus. The pollen grain rises through the droplet in the micropylar orifice and contacts the nucellus with the prothallial cell side of the grain away from, and the pollen tube side towards, the nucellus (Doyle and O'Leary, 1935). Fertilization, however, does not occur immediately, for the pollen tube ceases growth and lies quiescent over summer and winter. The following year the pollen tube again starts to grow and the egg is fertilized during early summer (Stanley, 1958). Thus it takes three seasons from the initiation of the floral primordia to seed maturation.

The Coast form will normally shed its seed at maturation, but the Inland variety tends to produce serotinous cones, and the seed is often retained until artificial heat is applied (Crossley, 1956). Seed from the Inland form is mature in August and September, that of the Coast in September and October (Publication No. 654, U. S. D. A.).

The Effect of Inbreeding

There is some evidence that several species of pines are self-compatible, and that selfing is accompanied by reduced fertility and loss of vigour in the progeny. Bingham and Squillace (1955) showed that self-pollination in *Pinus monticola* resulted in a 50 per cent reduction in seed yields, though cone yields were almost identical with the cross-pollinated control. Seed germination and seedling height for the first three years were also below that of the cross-pollinated seed. Mergen (1954) found a reduction in height growth in self-pollinated *Pinus elliottii*. Johnson (1945) recorded the results of selfing in *Pinus strobus*, *Pinus silvestris* and *Pinus resinosa*. In *P. strobus* eleven out of forty-six seedlings of selfed origin showed pronounced chlorophyll deficiency. *Pinus strobus* and *Pinus silvestris* were at four years of age significantly smaller than comparable seedlings derived from open and intraspecific cross-pollination. Selfing had also an unfavourable effect on seed set and seedling emergence in *P. silvestris*, and on seed set in *P. resinosa*. Similar results have been obtained when other coniferous species have been selfed (Orr Ewing, 1954), and in general it can be concluded that the selfing of Lodgepole pine will result in a loss of vigour, and a deterioration in other characteristics in the progeny. A full account, therefore, must be taken of this phenomenon in the breeding of the species.

Most agricultural plants are annuals, and many are difficult to reproduce vegetatively. Therefore, in order to produce a desirable hybrid type it is necessary to develop pure lines by selfing. These pure lines can be maintained indefinitely and crossed each year to produce the hybrid. Trees on the other hand are perennial and there is no need to develop a pure line in order to maintain a particular genotype as is necessary in the case of an annual. Furthermore, the most important coniferous species can be maintained indefinitely by grafting or from cuttings. Thus, if the progeny of a cross between two trees has proved desirable that same cross can be repeated indefinitely, and one of the major reasons for selfing in an agricultural crop does not apply in relation to forest trees.

It is sometimes suggested that several desirable characters may be incorporated in a single strain by crossing a number of pure lines, each homozygous for a particular character. There are three major objections to this practice. First, it would take a considerable length of time to achieve homozygosity in the highly heterozygous pine tree. Secondly, outcrossing the inbred lines, which will be greatly reduced in vigour, is likely to restore the vigour of the parental types only; heterosis cannot be expected. Very few of the thousands of inbred lines of agricultural crops, when outcrossed, show heterosis in a measure that makes them valuable commercially (Allard, 1960). Thirdly, in theory any variation that is obtained by inbreeding and outcrossing can be obtained by crossing alone.

It is concluded that the inbreeding of Lodgepole pine can have no direct application in the production of seed, or in the genetic improvement of the species. Selfing, however, can be a useful technique for evaluating the inherent qualities of the species (Orr Ewing, 1954). It will also be necessary to establish the degree and effects of self-compatibility in Lodgepole pine, and therefore a small experiment must be set up for this purpose.

Controlled Pollination Techniques

The method of controlled pollination in _Pinus_ was first developed at the Institute of Forest Genetics in Placerville, California, and gradually improved over a period of forty years. This method, which has proved itself satisfactory for controlled pollination of Lodgepole pine, was studied by the writer during the summer of 1961. It is proposed that this method, modified to include some recent technical developments, be used in the breeding program.

The Isolation of Female Flowers

It is necessary to isolate ovulate flowers before pollen flow. This is accomplished by covering them during the "buds small" stage with sausage casing, which is impervious to moisture. A strip of cotton is first wrapped around the branch at the point of attachment of the bag. Strong twine or other suitable material may be used to tie the bag to the branch.

The number of buds enclosed in each bag is recorded so that it is possible to ascertain whether a reasonable surplus of buds over the desired number has been bagged.

The Collecting of Pollen

As soon as the tree begins to shed its pollen, unopened male flowers are picked and brought indoors. If aceto-carmine smears show that pollen grains have completed second division in the development of the gametophyte, the male flowers will ripen after picking, whereas flowers collected prior that stage may not ripen.

A simple and effective way of extracting large amounts of pollen is to place the flowers in flat trays in a greenhouse. This is the method used at the North Idaho Forest Genetics Research Center. However, some contamination is liable to occur using this method, and the use of a pollen extractor is advisable. This consists of a pollen-proof bag fitting tightly over a funnel that empties through a rubber tube into a glass receptacle. The extractor is hung in a warm room and shaken vigorously before drawing off the pollen. The pollen should be processed before use in the manner devised by Worsley (1958).

Controlled Pollination

A hypodermic syringe is used for placing the pollen inside the bag which covers the female flowers. The hole thus made is then covered with gummed paper. When the ovulate flowers reach stage seven (conelets enlarged), the pollination bags are removed.

Hand-pollinated pine conelets of the previous season are protected from attack by insects by enclosing the cones in cloth bags.

NATURAL AND INDUCED MUTATIONS AND THE BREEDING OF PINE

In 1936 Nilsson-Ehle discovered a triploid aspen in Sweden which grew more rapidly than the diploid aspens. This finding generated great interest in the potentials of breeding polyploid trees. Efforts to induce polyploidy by physical means such as x-ray, heat, or ultra-sonic treatment are only moderately promising in trees, and require expensive equipment. However, it has been found that colchicine effectively doubles the chromosomes and is not costly. This accounts for the widespread acceptance of colchicine by forest tree breeders. Mergen (1959) and Hyun (1954) have both induced polyploids in the genus Pinus by means of colchicine. Mergen concluded from his study that the best results will be obtained if the germinating seed or seedling can be kept under conditions of optimum growth during the treatment. With pines at least, colchicine should be prevented from touching the radicle or root during the treatment period. With colchicine it is very easy to obtain polyploidy in dividing cells, but the problem is to devise a satisfactory method of isolating and perpetuating the polyploid tissue.

The doubling of the chromosomes, either during meiosis or during mitotic division of the gametophyte, has some potential. This method will shorten the waiting period needed to obtain reproductive structures with doubled chromosome numbers, and allow the production of both triploid and tetraploid plants with stable chromosome complements (Mergen, 1959).

Hyun induced polyploidy in several pine species (P. ponderosa, P. jeffreyi, X P. attenuradiata) with 0.2 per cent and 0.4 per cent colchicine, and produced tetraploids and mixoploids with 2n, 3n, and 4n tissues in various combinations. However, these individuals showed very poor growth. At six years they were only two feet high, and sickly in appearance, whereas the controls of the same age were nearly twenty feet tall.

Mehra (1960) pointed out that natural polyploids are exceedingly rare in conifers. The only cases so far known are the California Coast redwood (Sequoia sempervirens), which is a hexaploid; Juniperus chinesis, a tetraploid; and Juniperus synamata, also a tetraploid. He also pointed out that the occurrence of polyploid races within a species is unknown, but that there are records of stray polyploid individuals in some species. For example, a single tree of European larch (Larix decidua) of tetraploid constitution, has been found in Denmark; a tetraploid Norway spruce (Picea abies) in Sweden, and a triploid Juniperus virginiana in the U. S. A.

Richens (1945) and Gustafsson (1960) gave fairly complete accounts of most of the mutants, induced and natural, in the principal forest trees.

A survey of the work dealing with artificially induced mutations in Pinus shows that the mutations are always deleterious. It is suggested, therefore, that at the present stage in the development of forest genetics it would appear to be much more profitable to concentrate on selection and breeding of desirable commercial types of Lodgepole pine from the abundant variation found in natural forests and in plantations, rather than from random mutants, artificially induced. Mutation breeding must remain a minor adjunct to the above method, and will continue in this position until two important questions are answered:

1. Do artificially induced mutations differ in any way from natural mutations, or do mutagenic agents merely reproduce the aame spectrum of variability that occurs naturally?

2. Do mutations with phenotypically constructive expressions occur often enough to make the search for them profitable, and their incorporation into commercially acceptable varieties competitive with other methods of breeding (Allard, 1960)?

CYTOGENETICS AND THE BREEDING OF PINE

Buchholz (1945) investigated the embryological aspects of hybrid vigor in the embryos of the hybrid Pinus murraybanksiana. He stated that about two weeks longer was required for the embryos of the wind-pollinated control to reach the same mid-stages of development than for the embryos of the hybrid. He concluded that the set of observations indicated definitely that the embryos of the hybrids actually grow much more rapidly (though they do not reach a greater size than the control), and that the embryo enjoys a higher growth rate before the seed is mature as well as after planting.

The seed of the pine is full grown and has reached its ultimate size at the time of fertilization. This applies without known exception to the pine family, and to nearly all conifers. The seed coat becomes stony near the time of fertilization, and there can be no enlarging effect on the seed size due to the activities of the contained embryo, whether it be hybrid or otherwise. If fertilization fails, the seed coat remains fully as large as when fertilization has taken place. An abortive seed may be full grown, an empty shell complete with wing, but with the contents shriveled. Therefore it is not possible to distinguish hybrid seed by a morphological study, for the principal differences are physiological and biochemical

(Buchholz, 1945).

The pines are included in the family Pinaceae. All genera within this family, with two exceptions, show the haploid chromosome number of n = 12. The exceptions are Pseudolarix, which has n = 22, and Pseudotsuga, which has n = 13 (Mehra, 1960).

There are a number of major classifications of the pines; the best known being Shaw (1914) and Pilger (1926). However, from the point of view of tree breeding the most important is that proposed by Duffield (1952). The former classifications are based primarily on morphological, anatomical and biochemical differences, the latter gives equal value to the crossability of the species. Therefore much wasted effort, in attempting to cross uncrossible species, will be saved by following Duffield's classification rather than the older and better known systems of Pilger and Shaw.

SOURCES OF HEREDITARY VARIATION

Selection of Naturally Occurring Trees with Desirable Characteristics

Characteristics of a raw material which are considered desirable for one particular use may not be considered desirable in another. Branchiness, with its accompanying knots, is an undesirable characteristic in veneer manufacture, but, nevertheless, is of little importance to the pulp and paper manufacturer, who is more interested in fiber length and wood density. The complete rationalization of silviculture would entail the production of diverse types of forest trees each in its way best suited to a particular industry. This is not a practical proposition at the present time, nor is it really desirable, for the processing industries can be relied upon to develop techniques of utilizing the raw material that is available. For example, the pulp and paper industry of the Eastern United States is now utilizing the large hardwood forests of that area. It is usually much easier to develop techniques for the manufacture of a raw material than to attempt to change the nature of the raw material in order to accommodate a particular manufacturing process.

For the reasons stated above, and because of the difficulties involved in selecting for a large number of characteristics, it is proposed that artificial selection in Lodgepole pine be confined to six basic characteristics which are always desirable irrespective of the final use to which the wood is put. These six characteristics are as follows:

1. Resistance to disease
2. Good seed production
3. Rapid growth rate
4. Wood of high specific gravity
5. Straightness of stem
6. Light branching habit

It is obvious that characteristics one and two are not only desirable, but essential. There is little value in selecting for three, four, five and six if the species cannot be propagated cheaply, and in abundance.

Heritability in the narrow sense for all these characteristics except number six is good (Zobel, 1960). There are few reliable studies with respect to branching habit, though Fielding (1953) reported that clones in general resemble their parent trees in important characteristics such as the number of whorls of branches produced annually, branching defects, the angle of branching and the relative size of the branches.

One of the most common diseases affecting the Shore form of Lodgepole pine is Western Gall Rust (Cronartium harknessii). The most noticeable result of rust infection is the stimulation of the host to abnormal tissue development resulting in malformed organs, or parts of the host, such as galls, swollen stems, stunting and leaf casting. It is found in stands lacking vigor due to poor growth on low quality sites. For example, in the stands growing on muskeg on Lulu Island almost every tree is severely infected. Where growth is more vigorous, as in Ladner and the east coast of Vancouver Island, the disease is much less prevalent. Nordin (1954) suggested that healthy trees of the Inland form are likely to be less prone to this disease. There is little doubt that selected, vigorous stock, growing on good sites, will be little affected by this disease. The European plantations of Lodgepole pine appear to be completely free of Western Gall Rust.

Lodgepole pine is an extremely early seed producer. It is not uncommon to find ten to twenty cones on a tree five years old, and though there is considerable variation in cone bearing ability, in general the species is a consistent, as well as a precocious, seed producer (Tackle, 1959). A study of flowering in the Lodgepole pine provenance trial stands at Placerville suggests that partial dioeciousness exists in some trees.[1] Therefore, before selecting trees for further propagation, both flowering habit as well as fertility must first be determined.

Height growth and straightness of bole are strongly heritable in the narrow sense in forest trees (Zobel, 1960). Both of these

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1 Personal communication.

characteristics are relatively easy to recognise, and trees of superior growth and form can be rapidly selected, both on the Coast and in the Interior. It has been shown that Shore pine is not a scrub tree, nor does it normally possess a contorted bole. Nevertheless, trees of inferior quality, genetically determined, do exist. Such trees are multinodal, and have heavy, fastigiate branches. They are often very good seed producers. Such trees, which at present provide the bulk of the Lodgepole pine seed being sent to Europe, should be avoided in the selection program. Shore pine stands of excellent form are common on the East coast of Vancouver Island, the coast of Oregon and in many areas in Washington, including the Kitsap Peninsula and in the vicinity of Olympia. The most desirable stands of the Northern coastline are near Terrace in the Skeena Valley (Wood, 1957).

The Shore variety of Lodgepole pine tends to have more branches and denser foliage than the Inland form (Report on Forest Research, B. F. C., 1955). Nevertheless, there is sufficient variation within the Coast form to be able to select for uninodal, light branching types.

Selection for the improvement of the extensive plantations of Lodgepole pine in England and Ireland should be carried out within those plantations for two principal reasons: first, outstanding trees are immediately observable, and selection can be rapid, for phenotypes which are well above the average condition of the stand in growth qualities or other desirable characteristics can be considered of superior genotype until progeny trials prove otherwise. Secondly, as the phenotype is the result of the interaction of environment and genotype, it is more desirable to carry out artificial selection of an introduced species in its new habitat rather than in the country of its origin. The genotypes most adaptable to the new environment will have shown in the phenotype which can then be selected for further propagation. Selection is purely visual, whether in natural stand or plantation, but if carried out in even-aged and well stocked stands, the selected trees will normally be those that have survived competition and are best fitted for that particular site (Mergen, 1959).

This type of selection will assure Lodgepole pine seed of known origin from good phenotypes at a cost competitive with that from commercial sources. Above all it will tend to counterbalance the dysgenic practices now common of collecting cones from isolated, deformed trees; for the characteristics that make a tree attractive to the commercial collector (extreme limbiness and a large crown combined with low, stunted growth) are those excluded by the tree improver. The method of individual "Plus" tree selection, with its accompanying high selection differential, is not advocated for Lodgepole pine. It is not necessitated by the proposed breeding program which is designed to produce a variety incorporating a relatively small number of desireable characteristics, of which the most important is rapid growth rate, while at the same time producing seed free of grossly undesireable characteristics. The selection criteria, therefore, will be applied to stands rather than to individual trees.

Recombination of Naturally Occurring Variation by Means of Hybridization

Inter-specific hybridization

Jack pine (*Pinus banksiana* Lamb.) is a North American species occupying an enormous range from Nova Scotia and Maine westward to British Columbia, and in Alberta crosses naturally with Lodgepole pine (Moss, 1949). This hybrid, known as *Pinus murraybanksiana*, has been produced artificially at the Institute of Forest Genetics, Placerville, California. It is fertile, and is distinctly superior in vegetative vigor to the Lodgepole pine while possessing the light branch quality of the Jack pine parent. The hybrid has attracted the attention of commercial lumber companies of the Pacific Northwest, and Duffield and Righter (1953) suggested that it should be tested in England and Ireland and those parts of Australia and New Zealand where Lodgepole pine has been successful.

Interspecific hybrids are now occupying an important position in the planting programs of many countries. The hybrid *Pinus attenuata* X *Pinus radiata* is now being planted by the U. S. Forest Service, and New Zealand, Australia and Spain have imported quantities of seed and scions from California. This remarkable tree can show a height increment of nine feet per annum. The hybrid *Pinus rigida* X *Pinus taeda* is supplanting the pitchpine (*P. rigida*) as the principal forest tree in South Korea (S. K. Hyun, 1956). It surpasses the pitchpine in volume growth by about 500 per cent besides having better form. In Europe the majority of poplar clones being propagated are cultivars of natural hybrids, e.g., *Populus* X *berolinensis* (Denmark, Germany, Norway, Sweden); *Populus* X *euramericana* (Holland, France, Belgium, Germany, United Kingdom); *Populus tremuloides* X *P. tremula*, and *Populus deltoides* X *P. trichocarpa* (Sweden, Denmark and Finland). In Britain selection and breeding of the larches (*Larix decidua* and *Larix leptolepis*) was begun in 1950, and seed of the first generation hybrid larch (*Larix* X *eurolepis* Henry) is now being produced on a large scale in seed orchards, while *Picea* X *lutzii* (*P. sitchensis* X *P. glauca*) from the Kenai Peninsula in Alaska, is an important tree in the reafforestation of Iceland.

There is little doubt, therefore, that a breeding program of any tree species is incomplete if it does not include the interspecific hybridization of the species to be genetically improved. Crosses between related species should always be attempted. For example, if *Pinus silvestris* and *Pinus contorta* could be crossed the hybrid would obviously be of greater value in Britain and Ireland than the *P. contorta* X *P. Banksiana* hybrid.

Intraspecific hybridization

The value of intraspecific hybridization as the principal means of improving the vegetative vigor of Lodgepole pine is effectively demonstrated by the results of experiments carried out at the Institute of Forest Genetics, Placerville. Crosses between geographic ecotypes of the species have been made, and the progeny of each cross then subjected to the Institute's standard progeny test. In each case the intraspecific hybrid has shown itself superior to the control in height and diameter increment. This result is not surprising for such hybrid varieties of agricultural crops make better use of heterosis than any other breeding procedure yet developed (Allard, 1960).

Matthews and McLean (1957) stated that intraspecific hybridization will be used to obtain genetic improvement of *Pinus silvestris* in Britain, and Bannister (1959) advocated the technique for the improvement of *Pinus radiata* in New Zealand.

M. V. Edward (1957) recommended selecting suitable provenances of Lodgepole pine to combine the vigor of the coastal, and the straight, narrow-crowned properties of the Inland form. There is little doubt that it is possible to combine these desirable characteristics in one strain, and such a combination is worth seeking. Nevertheless, it is certain that trees of suitable form can be found on the coast, and by far the greatest benefit to be obtained from such a cross is the increased growth rate of the progeny over the parental types.

Heterosis is seldom discussed in relation to "plus" tree selection, for the method of plus tree selection is not designed to achieve a heterotic effect in the progeny of the selected trees. On the contrary, if the selected trees are concentrated in a small area in a continuous population there is likely to be a deterioration in vigor at worst, and at best the maintenance of parental vigor.

In the proposed program for the genetic improvement of Lodgepole pine heterosis is directly sought. Therefore, intra-specific hybridization will form the basis of the breeding program.

The areas stipulated for selection must be sufficiently far apart to obtain genetic diversity. Nevertheless, it is necessary to avoid introducing a strain much more adapted to a continental climate than maritime. For these two reasons selection should be in the following areas:

A. North Coastal - The Skeena valley region

B. North Interior - Prince George region

C. South Coastal - Coast of Washington and Oregon

D. South Interior - Upper Fraser River and Shuswap Lake region

Denoting each region by its respective capital letter one can see that in the first generation six different combinations are possible:

	N. Coastal	N. Interior	S. Coastal
S. Interior	AD	BD	CD
N. Coastal		AB	AC
N. Interior			BC

In the second generation it would be possible to produce thirteen different hybrid populations, twelve incorporating three regions and one incorporating all four:

	BD	CD	AB	AC	BC
AD	ABDD	ACDD	AABD	AACD	ABCD
BD		BCDD	ADBB	ABCD	BBCD
CD			ABCD	ADCC	BDCC
AB				AABC	ACBB
AC					ABCC

This hybrid progeny, besides possessing greater vigor than the parental types, should also exhibit the desirable silvicultural characteristics peculiar to the different regional types. For example, it might be possible to select from the hybrid progeny a genotype possessing the rapid growth qualities of the South Coastal type, and the hardiness of the North Interior strain.

Trees will be selected in each of the four regions, and must incorporate at least the six characteristics already discussed. Scions should be taken from these trees and grafted on vigorous stock in an area sufficiently isolated from stands of Lodgepole pine to avoid contamination. Crosses can be made as soon as sufficient flowering has resulted.

If the four selected regions are represented in plantations which are not separated by great distances, then it may be practical to carry out the cross in the field and eliminate the necessity to graft. This is the technique used by Bingham in breeding rust-resistant white pine (Pinus monticola).

The trees selected will not necessarily be "plus" trees, for the intraspecific hybridization program does not entail the selection of trees in the manner necessary for the pedigree breeding of Coast Douglas fir (Pseudotsuga menziesii). Therefore, the pollen from grafts representing a particular region will be mixed, and used to pollinate all other grafts. The cross will be reciprocal.

Despite care during the selection of the trees, it will be found that some trees will have fewer female flowers than others. This is to be expected in the light of Critchfield's findings already referred to. In order to obtain the required number of bagged female flowers for each region it will be necessary to isolate more female flowers on some trees than on others. This will lead to a bias within the derived progenies in favour of the heavily flowering trees. To offset this bias the pollen collected from the trees representing each region should be weighted reciprocally on a volume basis before mixing. For example, if the proportions of female flowers on trees A, B, C, D, and E of the North Interior region were 1, 2, 3, 4, and 5, the proportion by volume of pollen used in the mixture representing that provenance is 5, 4, 3, 2, and 1 respectively. This practice, of course, assumes that the pollen from each tree has the same viability (Faulkner, 1961).

The layout and maintenance of the seed orchard will follow the procedures recommended by Matthews for Scots pine (Matthews, 1955, 1957).

The grafts should be topped and pruned in order to obtain a wide crown. If correctly pruned, seed-production will be enhanced, and cone collecting facilitated. Seed harvests can also be increased by soil fertilization.

IDENTIFICATION OF TREES WITH DESIRED HEREDITY

There is some evidence that desirable characteristics in a mature tree are correlated with observable characteristics in seedlings. Schmidt (1938) claimed that it is possible to determine whether a conifer is straight-stemmed on the basis of its phototrophic behaviour in the early stages of its growth. Schrock (1951) stated that it is possible to extrapolate the growth curve on the basis of observations of growth rate made during the first few years, and Callaham (1961) has shown a correlation between the height of a seedling at two years and its height at fifteen. Mitchell considered it possible to make selections in five-year-old hybrid larch (*Larix eurolepis*).[1] However, there is as yet no sound method of determining, by physiological and biochemical investigation, the existence in seeds, seedlings and saplings, of characteristics correlated with desirable characteristics in the mature tree.

By careful morphological study it is possible to correlate certain measureable characteristics in young plants with their future growth quality. These characteristics are growth rate, straightness of stem, and branching habit, and, to a considerable extent, resistance to disease. Therefore, attempts should be

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1 Personal communication.

made to select for those characteristics at an early stage in the progeny of the controlled crosses. If the artificial stimulation of flowering is successful it may also be possible to select for precociousness and fertility.

The present controversies concerning what one should select for in a forest tree should not be allowed to delay selection in the progeny of the controlled crosses of Lodgepole pine. More and more the demand from the timber-consuming industries (such as pulp and paper, hardboard and chipboard industries) is for maximum dry weight per acre per annum at minimum cost. It is the business of the tree breeder to work for this objective; and it is suggested, therefore, that the best method of attaining it with respect to Lodgepole pine is to select for the six characteristics stated.

It is assumed that selection of any one of these characteristics will not result in the exclusion of another. Light branching habit in the Shore form does not appear to be associated with slow growth. The relationship between rate of growth and wood density has been the subject of many studies, the most recent of which indicate that it is possible to develop high yielding strains without any significant reduction in wood density. Work conducted on Monterey pine (Pinus radiata) in the Australian Capital Territory by Fielding and Brown (1958, 1960) has shown that any correlation existing in this species between the inherent rate of growth of the individual tree and the density of its wood is so small as to be negligible.

Progeny trials

To evaluate and select that portion of the controlled crosses showing heterosis and other desirable characteristics the progeny must be planted out in a conventional experimental design embodying replication and randomization, both of which are essential to the calculation of the error term. Variables such as growth rate, wood specific gravity and degree of flowering are evaluated by t or F tests, including analyses of variance, and, when applicable, of covariance (Publication No. 30, U. S. D. A., 1960).

Those hybrids showing the desirable characteristics will be retained and the inferior ones eliminated. The remaining trees will then be allowed to inter-pollinate freely. Undesirable parental types will be eliminated from the original seed orchard, which will continue to be the source of F_1 hybrid seed.

The commercial hybrid

In breeding cross-pollinated crops, the basis of improvement lies in the controlled utilization of the heterosis that occurs in hybrids among certain genotypes. This controlled utilization can be achieved by the production of a synthetic variety. The term "synthetic variety" is used by plant breeders to designate a variety that is maintained from open-pollinated seed following its synthesis by hybridization in all combinations among a number of selected genotypes (Allard, 1960). Therefore, the hybrid progeny obtained in the manner described is analogous to the parental form of the synthetic varieties produced by the breeders of naturally cross-pollinated agricultural crops, and in theory will behave similarly when bred *inter se*.

SUMMARY OF BREEDING PROGRAM

1. Trees exhibiting certain desirable characteristics are selected in four areas which are sufficiently far apart to obtain genetic diversity.

2. Scions are cut from these trees and grafted on root stock.

3. When sufficient flowering results, the pollen from all trees representing a particular region is mixed and used to pollinate all other trees. The cross will be reciprocal.

4. The progeny of the intraspecific cross will be subjected to progeny tests. The resulting superior progeny will be allowed to interpollinate freely to produce a synthetic variety.

5. Undesirable regional forms will be eliminated from the original seed orchard, which will continue to be the source of F_1 hybrid seed for further propagation of the synthetic variety.

6. Stages 1 and 2 are eliminated if the four desired regional forms are represented in plantations or provenance trials within a limited area. Stage 3 is then carried out in the field.

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THE SHORE FORM OF PINUS CONTORTA


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THE SHORE FORM OF *PINUS CONTORTA*

1. A branch with staminate flowers
2. Diagram of involucre of the staminate flower
3. A staminate flower
4. An anther, side view
5. An anther, front view
6. A branch with pistillate flowers
7. A pistillate flower
8. A scale of a pistillate flower, lower side
9. A scale of a pistillate flower, upper side
10. A fruiting branch
11. A cone scale, lower side
12. A seed enlarged
13. Vertical section of a seed
14. An embryo
15. A cluster of young leaves
16. Tip of a leaf
17. Cross section of a leaf
18. A seedling plant

From Sargent (1897)

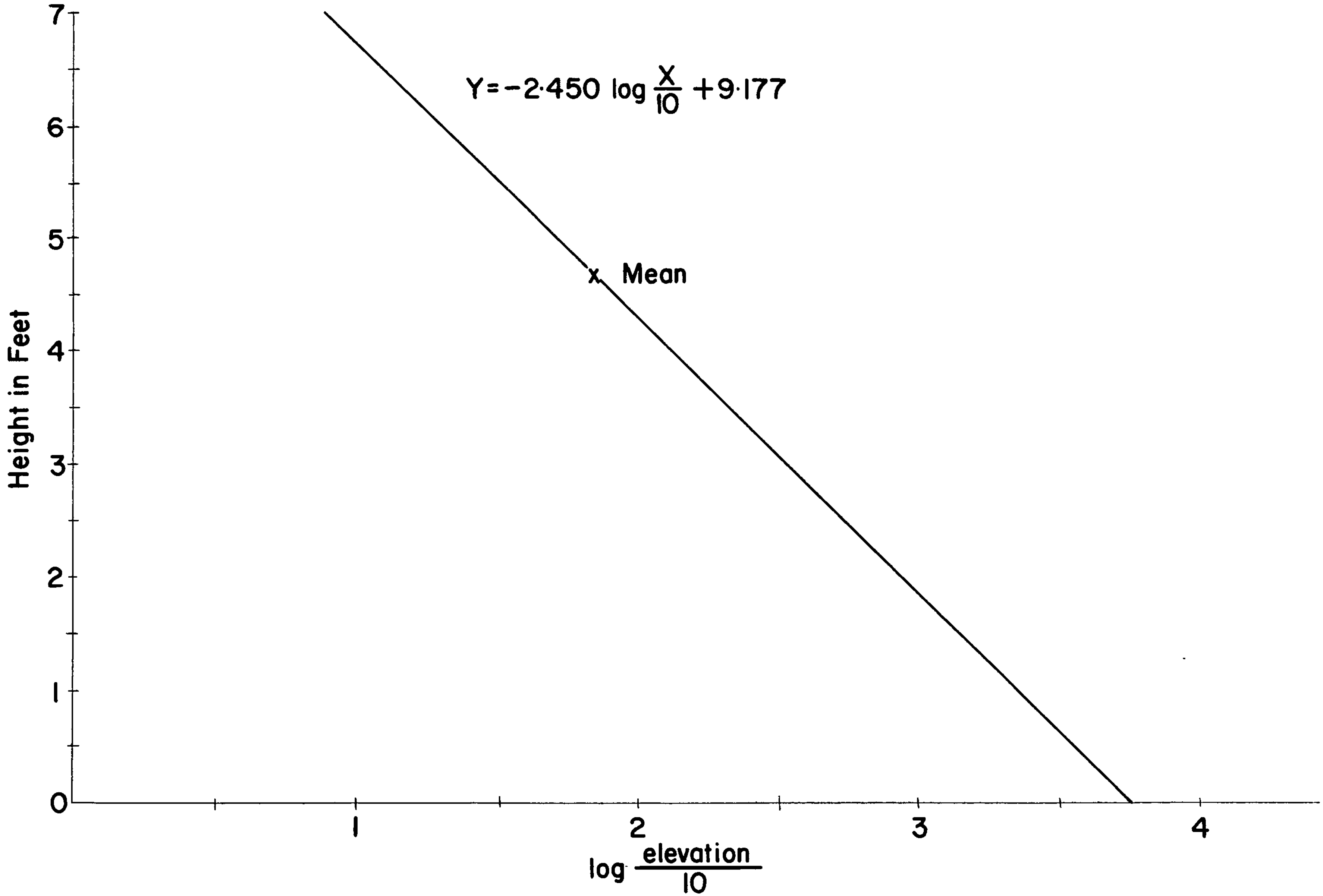


Fig. 1 Regression of height on elevation for 18 different provenances of *Pinus contorta* growing at Placerville

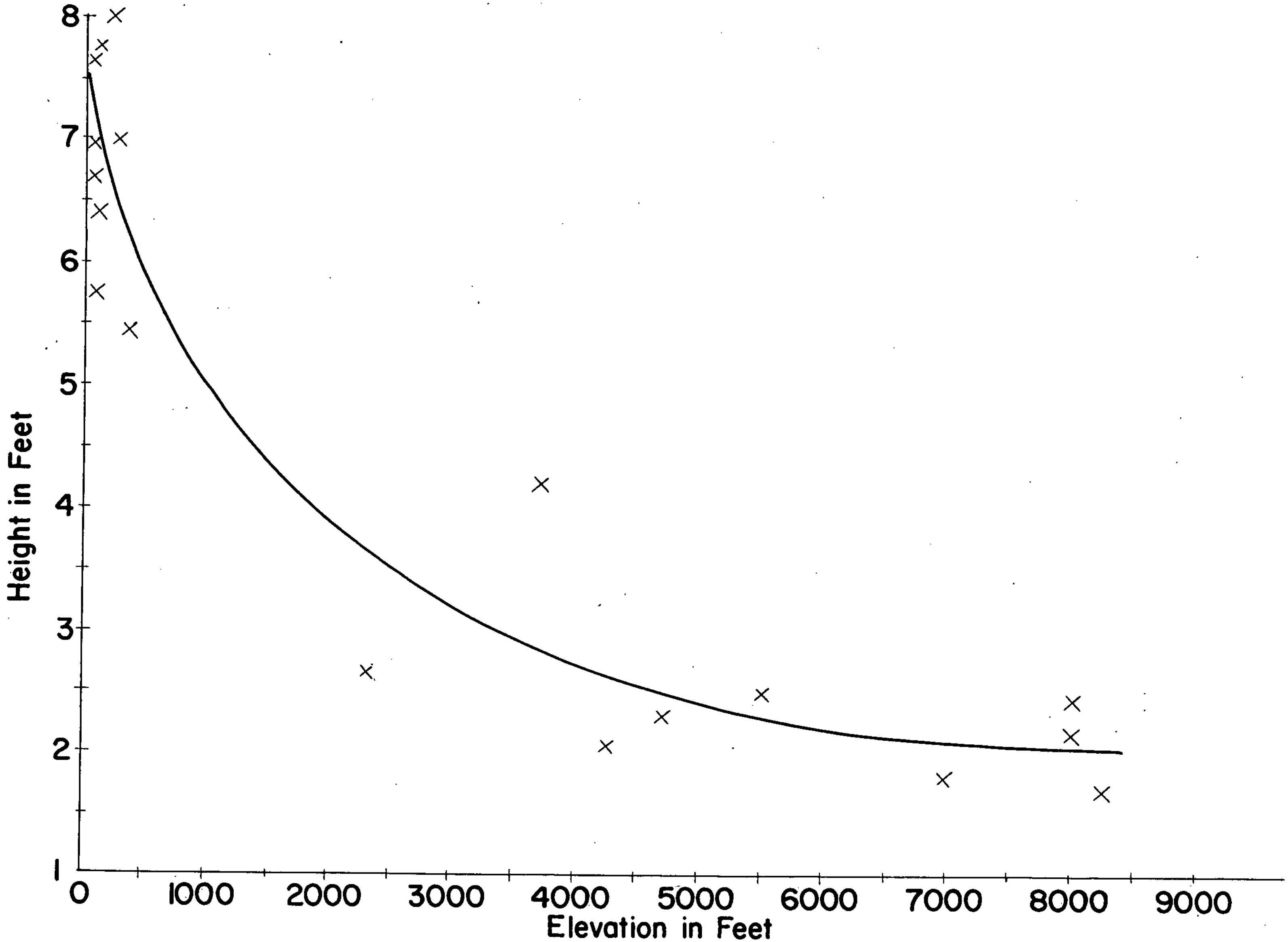
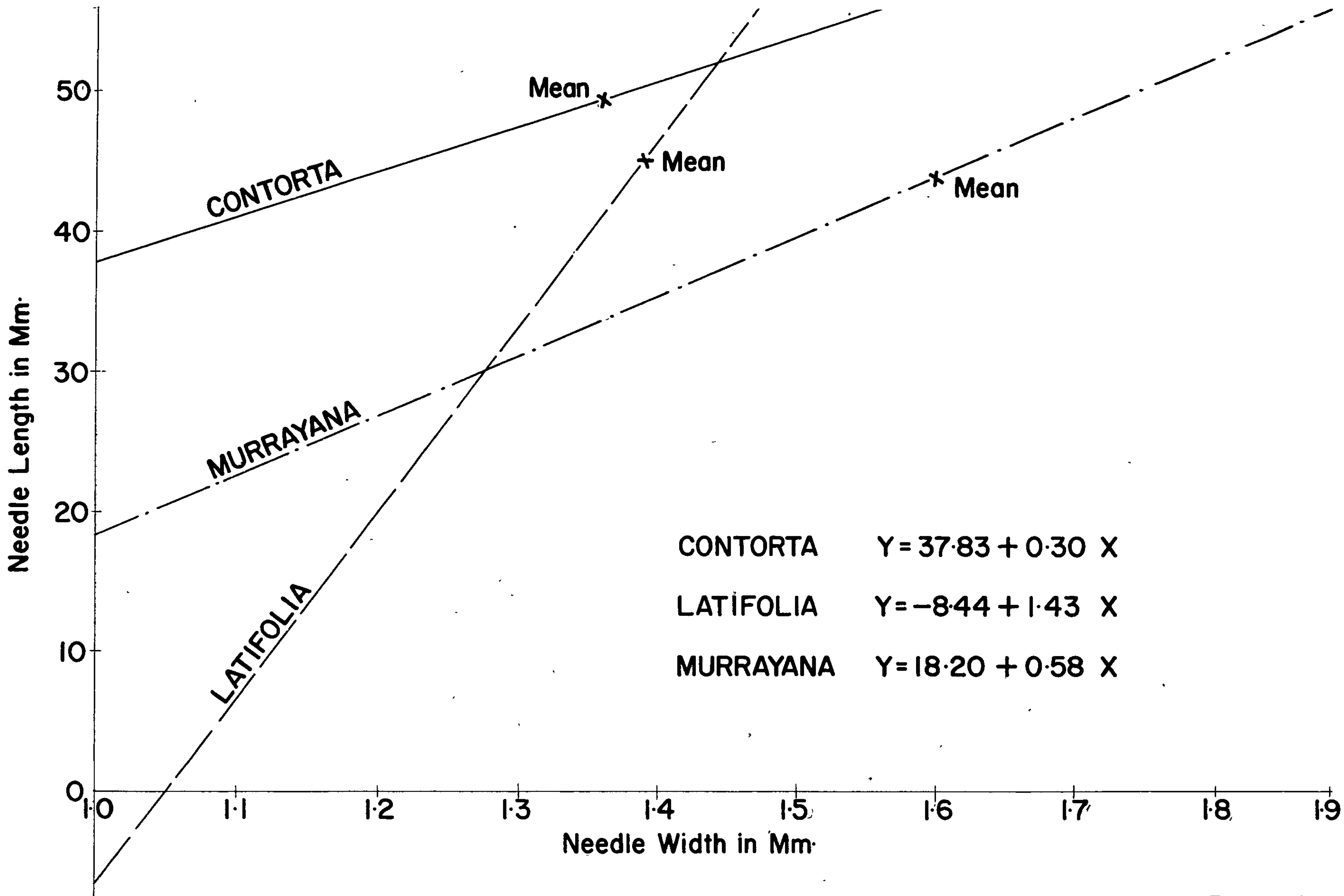


Fig. 2 Relationship of total height and elevation for 18 different provenances of Pinus contorta growing at Placerville



Fig· 3 Regression of length on width of <u>Pinus</u> <u>contorta</u> needles from 22 different provenances growing at Placerville

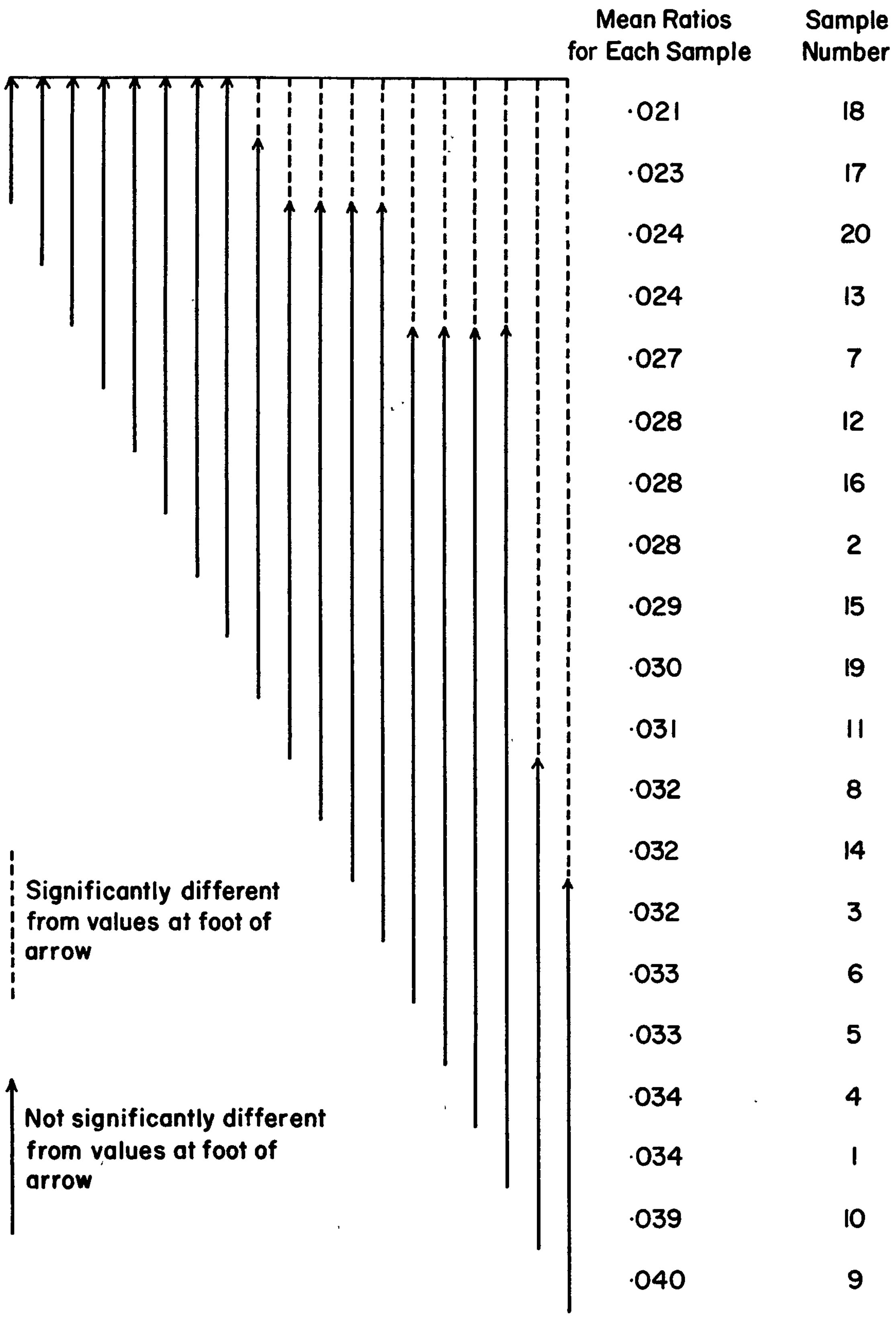
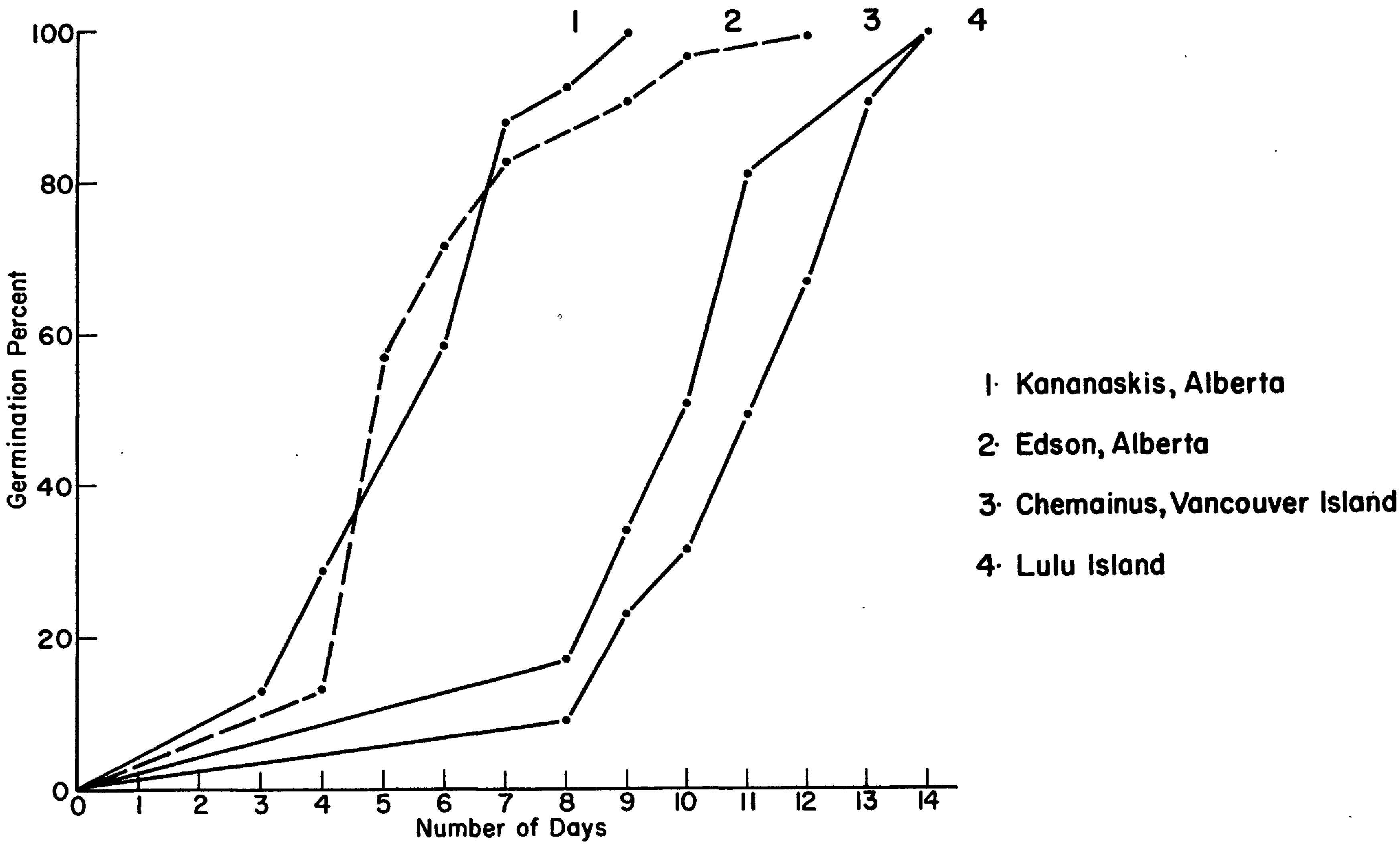
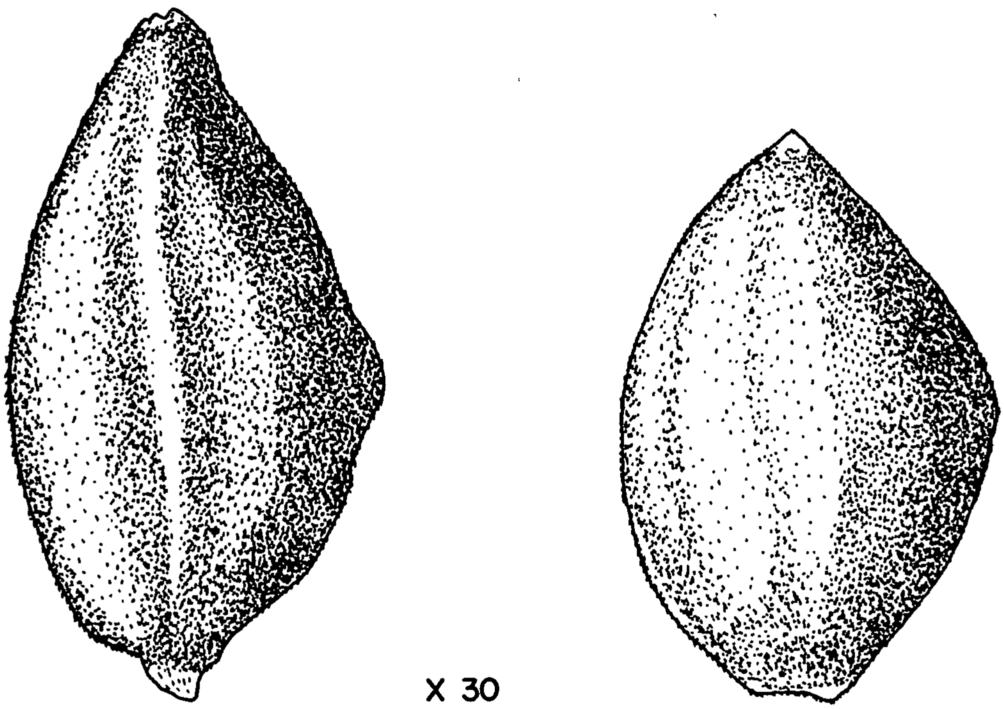


Fig. 4 Differences in ratio of needle width to length for 20 provenances of *Pinus contorta* sampled at Placerville

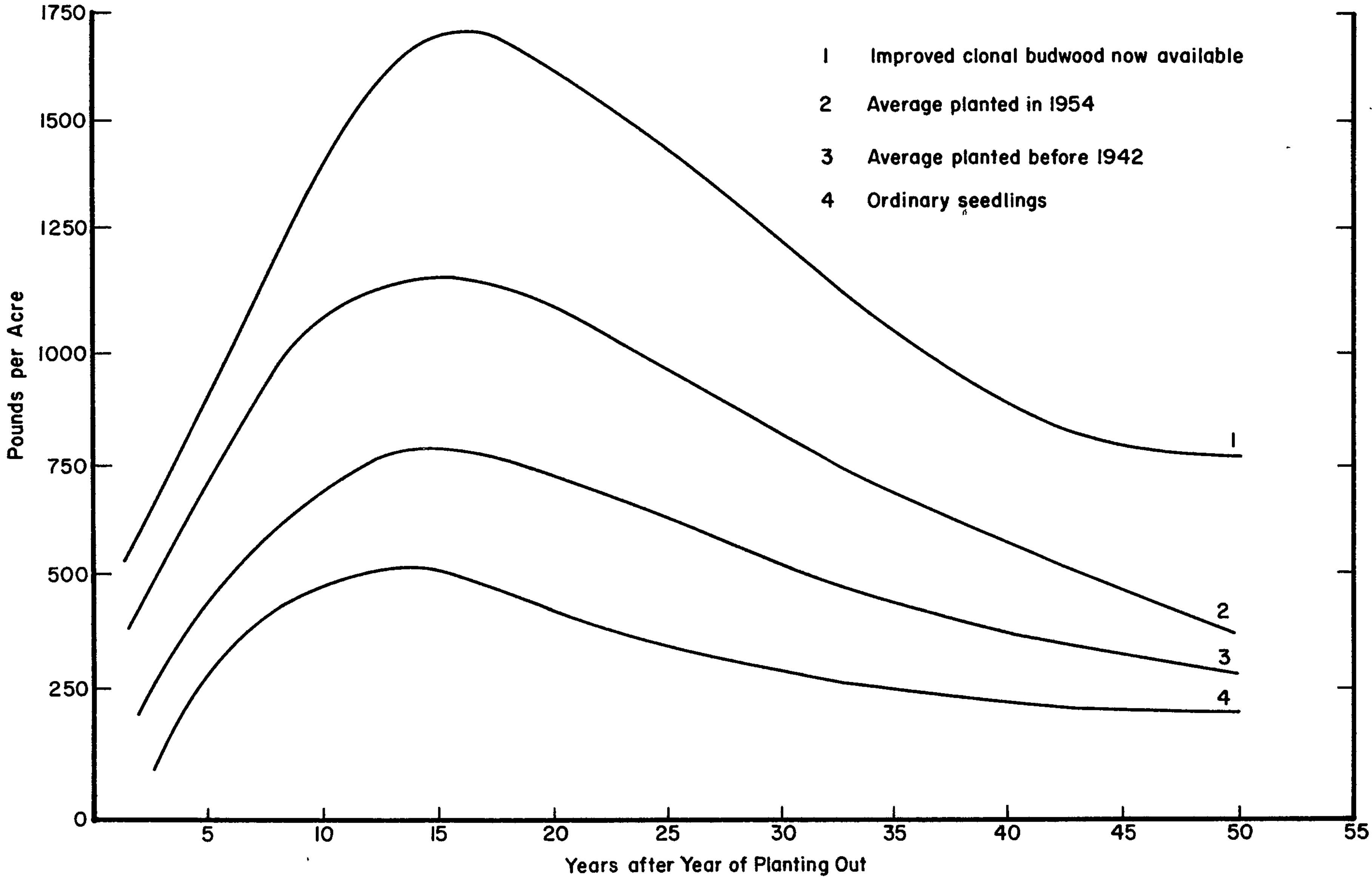


Fig· 5 Differences in rate of germination at 25° C between coast and interior seed of Pinus contorta·



INTERIOR FORM	COAST FORM
Pointed protuberance at funicular end of seed	Protuberance usually absent
Usually over 3 mm in length	Usually under 3 mm in length
Prominant ridge on upper surface	Ridge not usually prominant

Fig. 6 Method of distinguishing interior and coastal *Pinus contorta* seed.



after Swan, 1955

Fig. 7 Increase in latex yields per acre by selection and breeding of superior stock