

The University of British Columbia

FACULTY OF GRADUATE STUDIES

PROGRAMME OF THE

FINAL ORAL EXAMINATION

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

of

LAURENCE ROCHE

B.Agr.(Forest.), B.A., University of Dublin,
Trinity College, 1960.

M.F. University of British Columbia, 1962.

MONDAY, DECEMBER 18, 1967 AT 2:00 P.M.

ROOM 256, MacMILLAN BUILDING

COMMITTEE IN CHARGE

Chairman: I. McT. Cowan

V.C. Brink	G.G.E. Scudder
P.G. Haddock	O. Sziklai
D.P. Ormord	T.M.C. Taylor

External Examiner: Dr. H. Nienstaedt
Institute of Forest Genetics
Rhineländer, Wisconsin, U.S.A.

Research Supervisor: O. Sziklai

GEOGRAPHIC VARIATION IN PICEA GLAUCA
IN BRITISH COLUMBIA

ABSTRACT

The study is divided into two parts, one of which is a genecological investigation of 150 spruce populations grown from seed in a relatively uniform environment during a period of two years. The second part is an investigation of geographic variation in mature populations of spruce, and refers principally to a biometrical investigation in cone scale morphology which was carried out on a mass collection of spruce cones collected in 157 areas throughout the range of spruce in British Columbia.

On the basis of the results obtained in both parts, zones of putative hybridization between white spruce and the other spruce species of British Columbia are demarcated, and the following general conclusions are made.

In regard to the white-Engelmann spruce complex in British Columbia, the environmental pressures which result in microevolution, i.e. speciation.

The faculty for normal development and survival of white spruce and its related forms in British Columbia, is conditioned by the cessation of growth and initiation of dormancy.

The genetic constitution of a natural population of white spruce, in any one region, is predominantly determined by the photothermal regime prevailing in that region.

On the basis of these general conclusions, recommendations are made in regard to the silviculture of white spruce and its related forms in British Columbia, and also in regard to the field testing of the 150 spruce populations subjected to genecological investigation in the nursery.

GRADUATE STUDIES

Field of Study: Forest Genetics

Advanced Plant Genetics:	V.C. Brink
Responses of Plants to Controlled Environments	D.P. Ormrod
Organic Evolution	G.G. Scudder
Problems in Forest Genetics	O. Sziklai
Forest Tree Seed	O. Sziklai
Taxonomy of Vascular Plants	T.M.C. Taylor

PUBLICATIONS

- Roche, L. The Lulu Island provenance of Pinus contorta. Irish Forestry, 18:50-56 (1962).
- Roche, L. The shore variety of Pinus contorta. Baileyana 11: 11-14 (1963).
- Roche, L. Variation in lodgepole pine with reference to provenances planted in Great Britain and Ireland, Forestry 39: 30-39 (1966).
- Roche, L. Spruce provenance research in British Columbia Proceedings of the tenth meeting of the committee on Forest Tree Breeding in Canada. Part II, 107-121 (1967).
- Roche L. The value of short term studies in provenance research. Commonwealth Forestry Review, in press (1968).

GEOGRAPHIC VARIATION IN PICEA GLAUCA
IN BRITISH COLUMBIA

by

LAURENCE ROCHE

B. Agr. (Forest), MA (Dublin) 1960
M.F. University of British Columbia, 1962

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

DOCTOR OF PHILOSOPHY

in the Department

of

FORESTRY

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

March, 1967

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and Study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Country

The University of British Columbia
Vancouver 8, Canada

Date Oct. 15, 1967

ABSTRACT

The principal objective of the study is the determination of geographic variation in white spruce in British Columbia. Since variation within this species in British Columbia is greatly influenced by hybridization with other spruce species, an attempt is made to demarcate zones of hybridization, and evaluate its effect on variation in white spruce.

In a preliminary chapter the literature pertaining to principles and concepts of taxonomic and genecological investigation is critically examined in relation to infraspecific variation in tree species. The conclusions of this chapter constitute the assumptions of the investigation.

A second chapter summaries the literature pertaining to the phylogeny and distribution of the spruce species of British Columbia. Photoperiodicity in forest trees is discussed in the third chapter.

Following the chapters referred to above the study is divided into two parts, A and B. Part A is a study of the growth behaviour of 150 populations of spruce grown in a relatively uniform environment during a period of two years. The seed, which was collected throughout the spruce complex of British Columbia, was sown at the British Columbia Forest Service research nursery on Vancouver Island in the spring of 1965. Detailed measurements were made during the growing seasons of 1965 and 1966. In the laboratory seed samples of the same populations were X-rayed to determine embryo development and subsequently germinated at 25°C. Further seed samples were germinated at 15, 20, and 30°C.

Part B is a study of geographic variation in mature populations of white spruce, and refers principally to a biometrical investigation of variation in cone scale morphology which was carried out on a mass collection of spruce cones collected in 157 areas throughout the range of spruce in

of spruce cones collected in 157 areas throughout the range of spruce in British Columbia during the summers of 1963 and 1964.

On the basis of the results obtained in parts A and B the following general conclusions are made:

- (i) In regard to the white-Engelmann spruce complex in British Columbia the environmental pressures which result in microevolution, i.e. infraspecific variation, differ only in degree rather than in kind from the environmental pressures which result in macroevolution, i.e. speciation.
- (ii) The faculty for normal development and survival of white spruce, and its related forms, is conditioned by the cessation of growth and initiation of dormancy.
- (iii) Time of initiation of dormancy in a population in any one region where the species occurs naturally is conditioned by its genetic constitution.
- (iv) The genetic constitution of a natural population is predominantly determined by the photothermal regime prevailing in that region.
- (v) In so far as there is a difference in the photothermal regime between any two regions the genetic constitution of the spruce populations occupying those regions will differ.
- (vi) One of the most important external manifestations of this difference is the time of cessation of growth and initiation of dormancy.

On the basis of these general conclusions, recommendations are made in regard to the silviculture of white spruce and its related forms in British Columbia, and also in regard to the field testing of the spruce populations referred to in part A of this study.

GEOGRAPHIC VARIATION IN PICEA GLAUCA

IN

BRITISH COLUMBIA

BY

LAURENCE ROCHE

ACKNOWLEDGEMENT

The writer is primarily and especially indebted to Dr. Oscar Sziklai of the Faculty of Forestry who is chief adviser and chairman of the examining committee, and who, since January 1961, has been his mentor in all matters pertaining to forest genetics.

Acknowledgement is also due to Dr. P.G. Haddock of the Faculty of Forestry, Dr. V.C. Brink and Dr. D.P. Ormrod of the Division of Plant Science, Faculty of Agriculture, Dr. G.G.E. Scudder of the Department of Zoology, and Dr. T.M.C. Taylor of the Department of Botany, all of whom directly contributed to the development of the ideas presented in this study. Special acknowledgement is given to Dr. A. Kozak of the Faculty of Forestry who gave major assistance with respect to statistical analysis, and also to Dr. J.H.G. Smith.

In regard to the distribution of the spruce species in British Columbia, the writer, in numerous discussions, availed of the long experience of Dr. B.G. Griffith of the Faculty of Forestry, and Mr. E. Garman of the British Columbia Forest Service (now retired). To both these men the writer extends his thanks.

The writer wishes to thank the University of British Columbia which, through the Faculty of Forestry, provided substantial financial assistance during the academic year 1965-66. Without this financial assistance it would not have been possible to undertake post-graduate training.

This study could not have been undertaken without close cooperation between the Faculty of Forestry of the University of British Columbia and the Research Division of the British Columbia Forest Service which, apart from the academic studies of the writer, financed the entire investigation. The writer, therefore, wishes to acknowledge his indebtedness to the British Columbia Forest Service, and to its personnel in general, but particularly to those of his colleagues, who by direct assistance in statistical matters, or by

constructive criticism contributed to the investigation.

Therefore acknowledgement is particularly due to Mr. R.H. Spilsbury, head of the Research Division of the B.C. Forest Service, who fully supported the writer's relatively untested ideas in regard to provenance research, and provided the financial assistance for their implementation. Acknowledgement is also due to Mr. G.C. Warrack, who supervised the technical aspects of the work during the writer's absence, to Mr. A. Bamford who provided the experimental material for Part A of the study, and to Mr. J. Revel who provided miscellaneous cone collections for part B. The writer is especially grateful to Mr. M. Kovats and Mr. A. Frazer for constant assistance in all aspects of statistical analysis. Special thanks is also extended to Mr. R. Bowden-Green who provided technical assistance throughout the course of this study, to Miss S. Lindley for her assistance in the laboratory, and to Miss E. Lemon for her unfailing help and good will over a period of 4 years in all matters pertaining to bibliography.

Miscellaneous cone collections for part B of the study were also provided by Mr. H. Bunce of Columbia Cellulose Co. Ltd., who, together with Mr. W.H. VanHeek, assisted the writer in sampling in the Nass and Skeena river areas of the province.

Finally, the writer wishes to acknowledge the indispensable help and encouragement provided by Dr. L. Daviault, Regional Director of the Federal Forestry Research laboratory at Quebec City during the winter of 1966-1967 when this thesis was being written. To all members of this laboratory who provided technical assistance in the preparation of the manuscript, especially Miss E. Poisson, Miss L. Lepage, Mr. R. Keable, Mr. R. Gagnon, and Mr. R. Charuest, the writer extends his thanks.

TABLE OF CONTENTS

	Page
ABSTRACT.....	I
ACKNOWLEDGEMENT.....	III
TABLE OF CONTENTS.....	V
LIST OF TABLES.....	VII
LIST OF FIGURES.....	IX
LIST OF ILLUSTRATIONS.....	XII
FRONTISPICE.....	XIII
Caption for frontispiece.....	XIV
INTRODUCTION.....	1
SYSTEMATICS IN RELATION TO GEOGRAPHIC VARIATION IN FOREST TREES: A STATEMENT OF ASSUMPTIONS AND OBJECTIVES OF THE PRESENT STUDY.....	3
DISTRIBUTION AND PHYLOGENETIC RELATIONSHIPS OF THE SPRUCE SPECIES OF BRITISH COLUMBIA.....	17
PHOTOPERIODICITY IN FOREST TREES: A LITERATURE REVIEW.....	23
MATERIALS AND METHODS.....	28
RESULTS PART A: GEOGRAPHIC VARIATION IN IMMATURE POPULATIONS OF WHITE SPRUCE.....	51
DISCUSSION.....	79
The ecological significance of photoperiodic adaptation in white spruce.....	83
The relative importance of flushing and dormancy in the microevolution of white spruce.....	89
Germination behaviour in the laboratory.....	95
RESULTS PART B: GEOGRAPHIC VARIATION IN MATURE POPULATIONS OF WHITE SPRUCE.....	99
DISCUSSION.....	106
The pattern of variation in the white-Engelmann spruce complex..	108
The pattern of variation in the white-black spruce complex..	113
The pattern of variation in the white-Sitka spruce complex..	118

THE RELATIONSHIP BETWEEN PATTERNS OF VARIATION IN IMMATURE AND MATURE SPRUCE POPULATIONS.....	121
THE TAXONOMIC SIGNIFICANCE OF GEOGRAPHIC VARIATION IN WHITE SPRUCE IN BRITISH COLUMBIA.....	125
THE SILVICULTURAL SIGNIFICANCE OF GEOGRAPHIC VARIATION IN WHITE SPRUCE IN BRITISH COLUMBIA.....	134
GENERAL CONCLUSIONS.....	149
LITERATURE CITED.....	157
APPENDIX: FIGS. 9 to 46.....	170

LIST OF TABLES

Table		Page
1	Embryo and endosperm classes corresponding to those shown in Illus. 2.....	31
2	Measurements of germination and growth made on 150 spruce provenances.....	37
3	Geographic origin of 150 spruce provenances.....	38
4	Geographic origin of 12 provenances sown in the Cowichan research nursery.....	39
5	Geographic origin of 157 spruce cone samples arranged in order of increasing elevation.....	44
6	Cone scale morphology of black, white, Engelmann and Sitka spruce.....	47
7	Comparison of means of cone scale morphology of white and Sitka spruce.....	48
8	Seed characteristics of 150 spruce provenances arranged in order of increasing embryo development.....	62
9	Growth behaviour during the first year in the nursery.....	63
10	Growth behaviour during the second year in the nursery.....	64
11	Dates of flushing of 150 spruce provenances during the second year in the nursery.....	65
12	Dates of dormancy of 150 spruce provenances during the second year in the nursery.....	66
13	Dates of flushing and dormancy of 12 spruce provenances on two soil types both inside and outside plastic greenhouse.....	67
14	Relationship between germination behaviour and seed quality at 15°C.....	68
15	Relationship between germination behaviour and seed quality at 20°C.....	69
16	Relationship between germination behaviour and seed quality at 25°C.....	70
17	Relationship between germination behaviour and seed quality at 30°C.....	71
18	Relationship between germination behaviour and factors of the environment.....	72

Table		Page
19	Relationship between flushing and factors of the environment	73
20	Relationship between growth rate during second year and factors of the environment.....	74
21	Relationship between growth and dormancy during first and second year and factors of the environment.....	75
22	Correlations between variables included in the principal component analysis.....	76
23	Weighing for original variables in computed components.....	77
24	Percentage of variation accounted for by four principal components.....	78
25	Percent of provenances in each of 5 elevational groups with a germination value of less than one at 15°C.....	98
26	Average germination capacity of Engelmann spruce in comparison with other species.....	98
27	Means of foliage samples from 60 trees and geographic origin of each sample.....	105
28	Percentage of 2-year-old seedlings of 13 spruce provenances dormant by August 22 at a southern and northern nurseries in British Columbia.....	137

LIST OF FIGURES

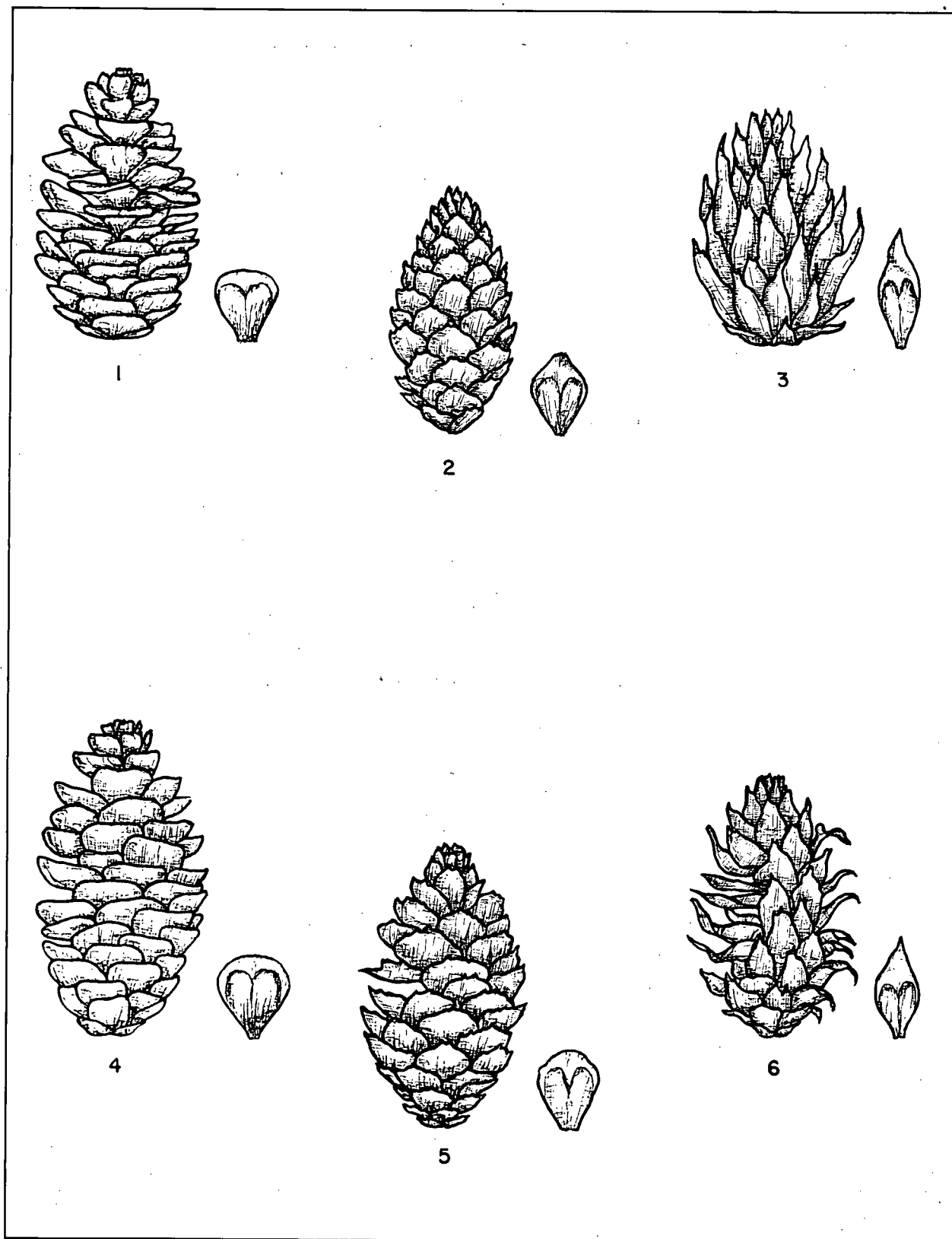
Figure		Page
1	Diagrammatic representation of spruce scale and bract showing five basic measurements.....	45
2	Characteristic curves obtained when cone scale morphology of populations from allopatric zones of white, Engelmann and Sitka spruce is compared by line of shape method.....	49
3	Characteristic curves obtained when cone scale morphology of populations from allopatric zones of white and Engelmann spruce is compared by line of shape method.....	50
4	Variation in embryo development in a number of provenances from two spruce seed crops.....	57
5	Relationship between degree of dormancy at the Cowichan nursery on July 15 and altitude at place or origin of each provenance.....	58
6	Relationship between growth of 12 spruce provenances in a uniform environment and elevation at place of origin.....	59
7	Second years growth of 12 spruce provenances in 4 environments.....	60
8	Relationship between altitude at place of origin and degree of dormancy of each provenance on July 14 at the Cowichan nursery.....	61
9	The relationship between continentality and temperature regime for representative climatic stations in British Columbia.....	170
10	The relationship between altitude and temperature regime for representative climatic stations in British Columbia...	171
11	The relationship between photoperiod and temperature at the Cowichan nursery and at Vavenby in south central British Columbia.....	172
12	The relationship between temperature and photoperiod at the Cowichan nursery and at Babine Lake in central British Columbia.....	173
13	The relationship between temperature and photoperiod at the Cowichan nursery and at Barkerville in east central British Columbia.....	174
14	The relationship between temperature and photoperiod at the Cowichan nursery and at Terrace in northwestern British Columbia.....	175

Figure		Page
15	The relationship between temperature and photoperiod at the Cowichan nursery and at Aleza Lake in east central British Columbia.....	176
16	The relationship between temperature and photoperiod at the Cowichan nursery and at Prince George in central British Columbia.....	177
17	The relationship between temperature and photoperiod at the Cowichan nursery and at Allison Pass in southern British Columbia.....	178
18	The relationship between temperature and photoperiod at the Cowichan nursery and on Old Glory Mountain in southern British Columbia.....	179
19	Degree of correlation between factors of the environment and flushing and dormancy.....	180
20	Curves of flushing for Sitka, white and Engelmann spruce....	181
21	Curves of dormancy for Sitka spruce and provenances from sympatric zones of white and Sitka spruce.....	182
22	Curves of dormancy for provenances from sympatric populations of white and Sitka spruce, and low elevation allopatric spruce provenances.....	183
23	Curves of dormancy for spruce provenances from elevations between 2000 and 2300 ft.....	184
24	Curves of dormancy for spruce provenances from elevations between 2300 and 2700 ft.....	185
25	Curves of dormancy for spruce provenances from elevations between 3000 and 4000 ft.....	186
26	Curves of dormancy for spruce provenances from elevations between 4000 and 4500 ft.....	187
27	Curves of dormancy for spruce provenances from elevations between 4600 and 5000 ft.....	188
28	Relationship between elevation and spruce cone scale-seed wing ratio. 1963 collection in the white-Engelmann complex.	189
29	Relationship between elevation and spruce cone scale-seed wing ratio. 1964 collection in the white-Engelmann complex.	190
30	Pattern of variation in a single measurement of cone scale morphology. 1963 collection.....	191
31	Pattern of variation in a single measurement of cone scale morphology. 1964 collection.....	192

Figure		Page
32	Pattern of variation in a single measurement of cone scale morphology. Miscellaneous collections.....	193
33	The pattern of variation in spruce cone scale morphology along a longitudinal transect from coastal Sitka spruce to montane white spruce forest.....	194
34	The pattern of variation in spruce cone scale morphology along an altitudinal transect at Stone Creek, South of Prince George, British Columbia.....	195
35	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 138.....	196
36	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 139.....	197
37	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 140.....	198
38	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 141.....	199
39	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 142.....	200
40	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 143.....	201
41	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 144.....	202
42	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 145.....	203
43	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 146.....	204
44	Variation in cone scale morphology in a sympatric population of white and black spruce. Sample 147.....	205
45	Sympatric and allopatric spruce populations as indicated by discriminant function analysis of cone scale data. 1963 collection.....	206
46	Sympatric and allopatric spruce populations as indicated by discriminant function analysis of cone scale data. 1964 collection.....	207

LIST OF ILLUSTRATIONS

Illustration		Page
1	Layout of seedbeds at the Cowichan nursery.....	35
2	The X-ray assessment of embryo development in spruce seed.....	36
3	The cone scale morphology of Engelmann, Sitka, white and black spruce.....	46
4	The differential growth behaviour of spruce populations from different elevations when grown in a plastic greenhouse on regular nursery soil.....	56
5	Cone scale morphology of white and Engelmann spruce, and intermediate form.....	101
6	Cone scale morphology of sympatric populations of white and black spruce in the boreal forests of northern British Columbia.....	102
7	The variation pattern in cone scale morphology along a longitudinal transect from coastal Sitka spruce to montane white spruce forest.....	103
8	Cone scale morphology of Sitka and white spruce and intermediate form.....	104
9	The subalpine Engelmann spruce forest.....	128
10	The white-Engelmann spruce complex in the Rocky Mountain Trench.....	129
11	The white-black spruce complex of the Alaska highway.....	130
12	The characteristic branching habit in high and low elevation spruce in British Columbia.....	131
13	Variation in branching habit in spruce in British Columbia....	132
14	Variation in spruce bark type in British Columbia.....	133



EXTREMES AND INTERMEDIATE FORMS OF THE SPECTRUM OF VARIATION IN
 CONE MORPHOLOGY IN THE WHITE-ENGELMANN SPRUCE COMPLEX IN BRITISH
 COLUMBIA. DRAWN TO SCALE FROM SAMPLES IDENTIFIED OVER LEAF

PLACE OF ORIGIN OF THE CONE SAMPLES ILLUSTRATED IN FRONTISPIECE

	Sample No.	Lat.	Elev.(ft.)	Locality
1	13	54°26'	2400	3 miles W. of Fort St. James
2	49	49°07'	2800	40 miles W. of Trail
3	50	49°11'	3300	31 miles S.W. of Princeton
4	64	52°12'	2700	6 miles N. of Williams Lake
5	63	50°00'	3300	13 miles S. of Merritt
6	111	50°47'	5200	52 miles N.E. of Kamloops

The differences between trees of the same kind have already been considered. Now all grow fairer and more vigorous in their proper positions; for wild, no less than cultivated trees, have each their own positions, some love wet and marshy ground, as black poplar, white willow and in general those that grow by rivers; some love exposed and sunny positions; some prefer a shady place. The fir is fairest and tallest in a sunny position, and does not grow at all in a shady one. The silver-fir on the contrary is fairest in a shady place, and not so vigorous in a sunny one.

Yew, pados and joint-fir rejoice exceedingly in shade. On mountain tops and in cold positions odorous cedar grows even to a height, while silver-fir and Phoenician cedar grow, but not to a height, - for instance on the top of Mt. Cyllene; and holly also grows in high and very wintry positions. These trees then we may reckon as cold-loving; all others, one may say in general, prefer a sunny position. However, this too depends partly on the soil appropriate to each tree; thus they say that in Crete on the mountains of Ida and on the White Mts. the cypress is found on the peaks whence the snow never disappears; for this is the principal tree both in the island generally and in the mountains.

Again, as has been said already, both of wild and of cultivated trees some belong more to the mountains, some to the plains. And on the mountains themselves in proportion to the height some grow fairer and more vigorous in the lower regions, some about the peaks.

THEOPHRASTOS OF ERESOS (380-287 B.C.).

INTRODUCTION

Depending on the objectives of the investigation, a study of geographic variation in a widespread coniferous species may take several forms. Therefore, it is particularly important for the investigator to make clear, at the outset, the objectives of the study he has undertaken. Ambiguity in this regard can result in considerable misunderstanding as to the silvicultural and/or genecological implications of the results of the investigation. For example, Critchfield's study of geographic variation in lodgepole pine (Pinus contorta Dougl.) (Critchfield 1957) and McDonald's criticism of this study (McDonald 1958) is a case in point. Wright and Baldwin's assessment of a large scale provenance trial of Scots pine (P. sylvestris L.) in New Hampshire (Wright and Baldwin 1957) and Langlet's detailed rebuttal (Langlet 1959) of both their premises and results even more clearly illustrates the validity of the above statement. There is, then, considerable diversity of opinion in regard to the purpose, methods and scope of studies of geographic variation in tree species. For this reason, and rather than discuss the problem in a general introduction, the matter is treated separately, and in some detail, in the following section.

The purely technical problems associated with an assessment of geographic variation in white spruce in British Columbia are enormous in scope. There is for example the major problem of sampling - which has not been satisfactorily solved in the present study. The species has a vast range throughout the province. It is sympatric with other spruce species in numerous areas, and introgressive hybridization is known to occur extensively. The problem facing the forest geneticist in this instance, therefore, is analogous to that of the geographer who, going into a very large, rugged relatively unexplored territory must first plot the approximate location,

height and breadth of mountain peaks, the depth and direction of major valleys, and the location of major rivers and lakes (see p. 28 Stebbins 1950). Races, ecotypes, clines, and hybrid swarms are the "gross topography" of genetic variation within the white spruce complex of British Columbia, and it is this variation with which the present study is principally concerned.

This study, therefore, by no means exhausts the possibilities for further study of variation in white spruce in British Columbia. On the contrary it is hoped that its results will lead directly to more detailed studies, particularly below the population level, in controlled and partially controlled environments. These studies can be conducted simultaneously with the long term assessments of the performance of experimental stock outplanted in diverse environments.

In accordance with the tenets established by Anderson (1949), and in the belief that long tables of statistics do not satisfactorily illustrate patterns of variation in natural populations, a special effort is made to present the data in graphic form wherever possible. For convenience of reference, and to avoid extensive divisions of the text, these graphs (Figs. 9 to 46) are placed in the appendix.

SYSTEMATICS IN RELATION TO GEOGRAPHIC VARIATION IN FOREST TREES: A
STATEMENT OF THE ASSUMPTIONS AND OBJECTIVES OF THE PRESENT STUDY.

INTRODUCTION:

Any student engaged in a study of geographic variation in a coniferous tree will soon realize, if his interest extends beyond the establishment of reciprocal plantations, that is, the provenance trial, that information relevant to his study may be gleaned not only from the silvicultural literature but also from the literature of taxonomy - classical, ^xexperimental and numerical - and genecology. This is so because the silvicultural problem of infraspecific variation in a tree species, though not generally recognized as such in the silvicultural literature, is in fact a problem of microevolution, and therefore cuts across several branches of botanical science. It is not particularly surprising that Darwin's major thesis was completely anticipated in 1831 in a book entitled "On Naval Timber and arboriculture".

A high percentage of the studies of geographic variation in widespread coniferous species reported in the literature takes the form of field trials, generally referred to as provenance trials, of untested progenies, and without reference to the variation patterns in mature populations in the wild. The principal objective of provenance trials in this sense is "to compare the growth of crops of trees from different lots of seed in terms of their ability to produce forests and timber" (Edwards 1956).

In general such trials are initiated by foresters. The characteristics assessed are silvicultural characteristics, and a provenance is frequently referred to as "good" or "bad" depending on whether it exhibits rapid or slow growth during development. For example: "The fact that one provenance does badly in the nursery is a matter of importance, but it

vitiates the future of the experiment and its interpretation in relation to normal practice if provenance experiments carry forward deficiencies which normally would be obliterated before the end of the nursery stage"(Edwards 1956). But the terms "good", "bad" or "deficient" when applied to total height growth in the nursery - or any other measurable characteristic - are meaningless in regard to the genecology of the species, and are not of much value as silvicultural terms either, since, depending on the environment in which they are outplanted, height growth may be reversed between any two provenances at a later date (Roche and Revel 1966).

There are many exceptions to these generalizations concerning provenance trials. Nevertheless, they hold good for a significant number of experiments which have as their objective the assessment, in silvicultural terms, of the effects of variation in tree species but ignore its causes. For example, nowhere in Edwards' publication is there any indication that the results of assessment of within species variation in forest trees have any significance outside the field of practical silviculture.

There is, however, no real reason why the assessment of variation in tree species should be conducted as if it were only a silvicultural problem and the broader implications of within species variation ignored. On the contrary, it is the writer's belief that the failure to place the problem of infraspecific variation in forest trees in its botanical context is a major reason why the results of a large number of provenance trials are not commensurate with the time and expense incurred during their establishment, maintenance and assessment.

What follows, therefore, is an attempt to place the problem of infraspecific variation in a tree species against the broad background of Post-Darwinian systematics. It is hoped that by so doing, unity and coherence will be given to the subject as a whole; and the objectives of the

present study brought into clearer perspective. The need for such an attempt is, perhaps, indicated by the extent of the divergence of viewpoint expressed in regard to various aspects of subject by Melville 1940; Edwards 1956; Wright and Baldwin 1957; MacDonald 1958; Wright, Bingham and Dorman 1958; Barber and Zobel 1959; Callahan, 1959; Nienstaedt 1960; Langlet 1959, 1962, 1963a; Stern 1964.

To facilitate presentation, the subject matter is discussed under the following headings (1) Classical taxonomy (2) Experimental Taxonomy (3) Numerical Taxonomy (4) Genecology.

CLASSICAL TAXONOMY

Classical taxonomy was a well established discipline before the development of evolutionary theory. Plants were classified on the basis of morphological characters, and, after Linnaeus, a binomial was given to all plants so classified. The publication of Darwin's "Origin of Species" destroyed the prevailing ideas concerning the fixity of species and argued that many species may have common ancestors. Since then attempts have been made to group plants on the basis of evolutionary relationships, or phylogeny. Even, the very great advances in genetics, cytology and paleobotany since the publication of "The Origin of Species", have not resulted in any radical change in the methods of plant classification followed since the time of Linnaeus. Classical Taxonomy, therefore, which is based to a considerable extent on the intuitive determination of affinities, is still the predominant method of classification in use at the present time. A very clear statement of the methods of classical taxonomy has been given by Sprague (1940), and it is of interest to note that it appeared in Huxley's "The New Systematics" (Huxley 1940), the book which to a considerable extent accelerated the development of biosystematics or experimental taxonomy.

Good examples of the application of the methods of classical

taxonomy to a tree species, and the great importance of nomenclatural and bibliographical studies in this method of classification, are given by Fernald (1945) in his study of Betula in Eastern North America, and Dugle (1966) in her taxonomic study of Western Canadian species of the same genus.

The practicing forester is seldom appreciative of the activities of the classical taxonomist, and frequently fails to understand how taxonomic investigations, when applied to a tree species, can have any bearing on silvicultural problems (MacDonald 1958). Yet, as Wright et al. (1958) have pointed out, "the taxonomic and horticultural literature is a largely neglected source of information about genetic variation in forest trees even though it contains scores of examples for every example contained in the forestry literature". Furthermore, as Melville (1940) has shown, the taxonomists are not unaware of the silvicultural implications of their work when applied to a tree species.

Wright and Baldwin (1957) used the data from a 17-year-old, replicated provenance test of Scots pine in New Hampshire as a standard against which to compare 19th century provenance studies. "They found that herbarium studies made by leading 19th century taxonomists led to a better insight into the pattern of variation than did many low-precision provenance tests" (Wright 1962).

Constance (1957) has compared the system of classical taxonomy to a repository for the totality of all kinds of evidence. This is a valid comparison, and the forester engaged in provenance research would be unwise to neglect such a potential source of information in regard to the species he is studying. For example no forester initiating a genecological investigation of a western Canadian birch species could afford to ignore the methods and results of Dugle's taxonomic investigations (Dugle 1966), however applied his aims, and though nomenclature per se is not his interest.

EXPERIMENTAL TAXONOMY

A general statement of the purpose, principles, and results of the experimental method in taxonomy has been given by Clausen, Keck and Hiesey (1940, 1945, 1948) and Clausen and Hiesey (1958). These authors state that though morphological comparisons are of first importance in classification, cytological and genetical tests are the more conclusive indicators of relationships. Consequently the taxonomic units derived by the methods of experimental taxonomy are defined almost exclusively in genetic terms. White (1962), having described the biosystematic units recognized by Clausen and his co-workers stated, "Although no group can be considered to be fully worked taxonomically until its components can be arranged in biosystematic units similar to those of Clausen, Keck, and Hiesey, it is doubtful whether such a classification will be entirely acceptable to practical taxonomists (those who write and use monographs) without modification.--- For most of the world's flora, and particular for slow growing tropical plants of little economic importance, it is unlikely that experimental data will ever be available in sufficient quantity to provide a basis for a biosystematic classification".

According to Good (1964) there are at least 250,000 or more species of angiosperms alone in the world. Clausen and his co-workers have spent many years in assessing genetic relationships in a relatively minute number of species which were specially selected for their amenability to the methods employed. From a knowledge of both these facts, it is not possible to completely disagree with White's conclusion. However, there is no doubt that the methods of experimental taxonomy will continue to be applied on an ever-increasing scale, particularly by the genecologist, though his objective differs from that of the experimental taxonomist. Callahan's advocacy

(Callaham 1959) of biosystematic methods in the study of variation in forest trees was, at the time of publication, symptomatic of this general trend.

NUMERICAL TAXONOMY

In a discussion concerning the classification of plant communities Webb, as early as 1954, had this to say:

For a scientific taxonomy it is not enough to assure one's critics that with sufficient experience one can learn to recognize the units; there must be some means of defining them. Without this plant sociology can only be a craft to which one is apprenticed, and not a science which one can learn. It is as if organic chemistry were conducted without analysis, simply by relying on the sense of smell. Not only is such a procedure uncommunicable; it is also unreliable (Webb 1954).

Webb goes on to recommend a system of multifactorial recording, which, if necessary, is capable of being carried on punched cards, as a basis for the classification of plant communities. Since the publication of this article there has been a veritable flood of proposals in regard to numerical methods of classification of species and plant communities. Most of these publications are represented in the bibliographies of Sokal and Sneath (1963), which is the first book devoted to numerical taxonomy, and in Greig-Smith (1964) which deals with the numerical classification of plant communities.

The development of numerical taxonomy cannot be ignored by anyone engaged in the study of natural variation, and since it is the writer's opinion that Webb's remarks apply not only to classification of plant communities but also to problems of classification either above or below the species level, the question remains as to the bearing of numerical taxonomy

on investigations of infraspecific variation in long lived plant species such as the coniferous tree.

At the outset it is necessary to make the distinction between "numerical taxonomy", and the "numerical method in taxonomy". Because of this, and in view of what has been said above, the following must not be construed as adverse criticism of numerical methods in taxonomy. Nor is it an analysis of the methods of numerical taxonomy, for the writer is qualified neither by training nor interest to make such an analysis. In any event it has already been done (Heywood and McNeill 1964, Seal 1964, Williams and Dale 1965, McAllister 1966). What follows then, is an attempt to relate some of the basic assumptions of numerical taxonomy to problems encountered in genecological investigations of forest trees.

An excellent summary of some of the basic assumptions of numerical taxonomy is given by Ehrlich and Holm (1962), and is here quoted in full:

In summary, then, we would like to suggest that in broad investigations of the patterns of interaction and relationship among organisms the artificial and stultifying fragmentation of population biology into divisions such as taxonomy, population genetics, and ecology should be ignored. Care should also be taken to scrutinize current concepts such as 'species', 'niche', and 'community'. If some emergent patterns seem to correspond to a degree with these concepts, then the concepts may be given operational definitions and the labels should be retained. If there is no such correspondence, then the concepts will have outlived their usefulness and should be discarded.

The basic units of population biology are not communities, species, or even populations but individual organisms. In populations, variation, growth, genetic equilibria, selection,

behaviour and so on are not 'things' but relationships. Therefore, what is of interest in population biology is the pattern in which organisms are related in space and time.

Since these assumptions of Ehrlich and Holm have been critically examined in some detail by Stebbins (1963) no attempt will be made here to discuss, their validity at length. However, it is important to note that according to these authors the various branches of botanical science which have a bearing on systematics should be ignored in investigations of relationships among organisms. In other words taxonomic relationships are evaluated purely on the basis of resemblances existing in the material at hand, and a total ignorance is presupposed concerning the ecology of the species or variety requiring classifications.

It is also clear that Ehrlich and Holm (1962) think of evolution in terms of individuals rather than populations, but as Hardy (1965 p. 170) has pointed out, it is the populations which are evolving not the individuals. Any forester who has closely studied within and between population variation in coniferous tree species will have no difficulty in agreeing with Hardy.

The emphasis on descriptive morphology as the principal criterion of assessing relationships between organisms places the numerical taxonomists in the tradition of classical taxonomy, and Stebbins' rhetorical question posed with regard to Ehrlich's paper may equally be asked of numerical taxonomy as a whole: "In essence, does Ehrlich's apparently new approach to classification and species relationships represent anything more than an elaboration of old-fashioned morphological taxonomy, dressed in a shiny new algebraic suit of cloths, and given additional allure by means of that largest and most costly of modern scientific status symbols, the digital computer?" (Stebbins 1963).

In reviewing the second edition of Huxley's "Evolution: the modern Synthesis" (Huxley 1963), De Beer (1963) stated:"---Although it has been known since 1859 that evolution by natural selection was a unifying concept for all biology, it is only now becoming clear how all-embracing it is, and how closely it unites together the numerous and ever-increasing branches and experimental disciplines of biology". This is a statement of the synthetic theory of evolution, and it is this theory (held not only by De Beer and Huxley, but also by Stebbins (1950) and Mayr (1963)) that is implicitly, if not always explicitly, denied by the protagonists of numerical taxonomy.

However, in general it may be said that the literature of numerical taxonomy (Sokal and Sneath 1963) is less a rebuttal of the synthetic theory of evolution than a demonstration of the belief that biology is a sub-division of physics. For example the work of Charles Darwin is referred to on five pages of Sokal and Sneath's book, whereas the work of T.T. Tanimoto (a mathematician in the research division of International Business Machines) is referred to on no less than twenty-two pages.

It is difficult to avoid the conclusion that numerical taxonomy has been designed to fit the computer rather than to cope with the biological facts of variation and evolution. It is true that these facts are frequently inadequate. It is, however, also true that in the past many of the most brilliant discoveries in biology have been made by imaginative men who exercised their judgement on inadequate facts - a faculty which, perhaps fortunately, is not yet the prerogative of the computer.

In conclusion it is necessary to state that, in regard to the assessment of infraspecific variation in a tree species, numerical taxonomy is rightly considered a valuable contribution to the numerical method in taxonomy - an important distinction. For there is a numerical method in taxonomy which is evolving within the framework of the science. The objection

to numerical taxonomy, therefore, does not lie in the fact that it uses numerical methods but in the fact that its basic assumptions preclude the application of other methods and the utilization of much knowledge of species - environment interaction which followed the development of post -Darwinian systematics. Therefore, no synthesis is possible. However "---for the understanding of an important phase of microevolution the synthesis is indispensable, in the same way that a synthesis - on a broader canvas - was essential in the development of the argument of the 'The Origin of Species' (Heslop - Harrison 1964);" and, as already pointed out, the problem of infraspecific variation in forest trees is a problem of microevolution.

GENECOLOGY

As stated above, though the methods of the genecologist are similar to those of the experimental taxonomists, his objectives are different. The genecologist is primarily interested in determining habitat-correlated, genetically-based variation within the species (Turesson 1923), whereas the principal objective of the experimental taxonomist is classification. "Thus, ecological data and observations on genetic system, are a sine qua non of genecology, although by no means an essential part of taxonomy. Conversely, the nomenclatural, and biographical studies which are an obligatory part of any taxonomic study are not necessarily significant for a genecological investigation of a species". (Heslop - Harrison 1964).

The publication referred to above is a detailed and lucid review of 40 years of genecology, and since it contains an extensive and up-to-date bibliography no attempt will be made here to survey the literature of genecology. The important point is that although classification is not the objective of genecological studies, such studies, particularly of plant species, continue to elucidate some important evolutionary principles, and consequently

genecology has a definite, though indirect, bearing on phylogenetic classification.

Genecology is essentially a synthetic science. It incorporates in modified form the approaches of the several disciplines outlined above. Its basic propositions have been stated succinctly by Heslop-Harrison (1964), and are quoted below:

- 1) Wide ranging plant species show spatial variation in morphological and physiological characteristics.
- 2) Much of this infraspecific variation can be correlated with habitat differences.
- 3) To the extent that ecologically-correlated variation is not simply due to plastic response to environment, it is attributable to the action of natural selection in moulding locally adapted populations from the pool of genetical variation available to the species as a whole.

A provenance study is rightly considered an investigation of infraspecific variation in a plant species in relation to its environment. Therefore, in purpose, methods, and scope it is a genecologic investigation, and its basic propositions are those stated above.

Timofeef-Ressovsky (1940) has made the clear distinction between macro- and micro-evolution, and has pointed out that while the classical methods which gave a picture of macroevolution (the synthesis of palaeontological, morphological, embryological and biogeographical data) now seem more or less exhausted, little has been done in the field of microevolution. He defined microevolution as the evolutionary process taking place within shorter limits of time, smaller groups of organisms, and lower systematic categories, and concluded that the main phenomenon of microevolution is geographical variability.

If the main phenomenon of microevolution is geographical variability then it is clear that studies of geographical variability in forest trees, if rightly designed, could contribute substantially to the general understanding of microevolution.

Stebbins (1950) has pointed out that the dominant evolutionary processes are different at each of the three levels of variation in natural populations: "Individual variation is dominated by gene mutation and genetic recombination, microevolution by natural selection, and macroevolution by a combination of selection and the development of isolating mechanisms...." Therefore, it is the population which is characterized by its environment, for, as already pointed out, it is the population which is evolving and not the individual - an important distinction often not observed in studies of variation in forest trees. Hence the unrewarding search for populations which are endowed with characteristics randomly occurring in individual trees; and the not infrequent attempts to relate variation in individual trees, or very small numbers of trees, of different populations to factors of the environment at their place of origin.

In the highly heterozygous coniferous species many desirable silvicultural characteristics are most frequently the result of genetic segregation and recombination, and, therefore, are rightly studied at the level of individual variation. These are not, generally, the result of selection and adaptation. For example, as Langlet (1963) has pointed out, from an ecological point of view, increment in forest trees is only of secondary importance since it does not directly condition survival or reproduction.

The emphasis, therefore, on silvicultural characteristics in provenance trials, especially during the early phases of the test, is misplaced.

What is of principal interest is the growth rhythm of each provenance at the test site in relation both to the environment at the test site, and the environment at its place of origin. In this respect careful measurements of flushing and dormancy, for example, are of greater significance than increment measurements. It is only when some understanding of genetically-based, habitat-correlated variation has been obtained that the silvicultural potential of a provenance is known. Furthermore, such an understanding can be obtained from carefully designed studies of the growth rhythm of diverse populations at the juvenile stage in controlled and partially controlled environments (Wareing 1950, a, b, c; 1951, 1956). Increment measurements have greater importance in field tests, and are especially significant at the level of individual variation.

The assessment of genecological differentiation within a tree species need not be confined to physiological studies on progenies grown in a uniform environment. As pointed out by Heslop-Harrison (1964 p. 217) there is no direct evidence that habitat-correlated variation in morphological features is non adaptive, and that if populations in one type of habitat are regularly found to differ from those in another in any characteristic whatever, those differences have adaptive significance, and are due to the differential effect of selection in the two environments. Therefore, biometrical studies on mass collections of field specimens of cones and foliage can in many instances also yield valuable information concerning the genecology of the species under study, as already indicated in the discussion of classical taxonomy. Such studies are likely to be of especial value in, for example, the forest regions of Canada where relatively little is known of the distribution, taxonomy and degree of introgressive hybridization of many coniferous species (Roche 1964).

CONCLUSIONS

Intraspecific variation in a tree species is best considered as a problem in microevolution rather than a purely silvicultural problem. When so considered the problem is brought into clearer perspective, and objectives become more sharply defined.

Genecology, a synthetic science which embraces the ideas and methods of the several botanical disciplines discussed above, is the study of intraspecific variation of plants in relation to their environment. Thus its basic propositions and methods apply directly to studies of geographic variation in tree species.

A purely numerical approach to the study of intraspecific variation in the manner of the numerical taxonomists is precluded because of the synthetic nature of genecology. In this context numerical taxonomy is considered simply as a statistical technique which may illustrate certain aspects of genecological differentiation, for example morphological variation in mass collections of field specimens.

The synthetic theory of evolution as outlined by Hardy (1965) is the great unifying concept in biology, and it is this theory which both illuminates and provides the framework for interpretation of all phenomena relating to variation in natural populations, including populations of forest trees.

DISTRIBUTION AND PHYLOGENETIC RELATIONSHIPS OF THE
SPRUCE SPECIES OF BRITISH COLUMBIA

There are three species and one subspecies of spruce in B.C. which between them form a complex of sympatric and allopatric populations with a province wide distribution. These are Sitka spruce (Picea sitchensis (Bong.) Carr.), black spruce (P. mariana (Mill.) BSP), white spruce (P. glauca (Moench) Voss subsp. glauca) and Engelmann spruce (P. glauca (Moench) Voss subsp. engelmannii). The nomenclature follows that proposed by Taylor (1959). The taxonomic literature (Little 1953a) also recognizes the occurrence of two other varieties of white spruce in British Columbia. These are Porsild spruce (P. glauca var. porsildii Raup.) and western white spruce (P. glauca var. albertiana (S. Brown) Sarg.).

The distribution of the components of this great spruce complex is known only in very general terms indeed (see map 2, Stanek 1966) and literature references to distribution and taxonomic relationships are conflicting in the extreme. There are no detailed distributional maps available for British Columbia other than those published by Whitford and Craig in 1918. These distributional maps continue to be referred to in the literature. For example, Hansen (1955) interpreted the results of bog pollen analysis in British Columbia on the basis of the modern distribution of spruce species as given by Whitford and Craig. There are, however, a number of reports and studies dealing with the distribution and taxonomic relationships of white and Engelmann spruce in B.C. (McKinnon 1938, Griffith 1940, Garman 1957, Taylor 1959).

Whitford and Craig (1918) placed the northern limits of Engelmann spruce almost at lat. 58°00', and the southern limits of white and black spruce at approximately lat. 53°30'. These distributional limits, therefore,

in the absence of complete altitudinal segregation of species, indicate a very large sympatric zone of white, black and Engelmann spruce between latitudes $53^{\circ}00'$ and $58^{\circ}00'$. This zone, broadly speaking, corresponds to zone 9 (sub-boreal) of Krajina's classification of biogeoclimatic zones of British Columbia (Krajina 1965), though zone 8 (Engelmann spruce-subalpine fir) of this classification gives the Yukon border (Lat. $60^{\circ}00'$) as the northern limit of Engelmann spruce in B.C. However, a northern distribution of this extent for Engelmann spruce is not corroborated by the findings of Griffith (1940), Raup (1945) or Garman (1957).

In further contrast to the southern distributional limits of white, and the northern distributional limits of Engelmann spruce as given by Whitford and Craig, Garman (1957) has reported the occurrence of white spruce at lat. $49^{\circ}30'$ in the East Kootenay valley at altitudes of 2500 to 3000 ft. and Recknagel (1939) has stated that reconnaissance studies along the upper reaches of the Fraser river (along Lat. $54^{\circ}00'$ between longitudes $120^{\circ}00'$ and $123^{\circ}00'$) definitely determined that the prevailing species of spruce is white spruce and not Engelmann.

Raup (1945) has reported the extensive occurrence of sympatric populations of white and black spruce along the Alaska highway, particularly between Fort St. John and Whitehorse. Garman (1957), who sampled spruce populations along the Alaska highway north of Fort St. John, has also recorded the occurrence of a sympatric population of white and black spruce at Muncho Lake, lat. $59^{\circ}00'$. However, he considered that the association of these two species in this area was not common. Wright (1955) has stated that although the range of black spruce approaches that of Engelmann and Sitka it does not overlap them as does white spruce.

Raup (1945) has also reported the occurrence of Porsild spruce

(P. glauca var. porsildii) in northern British Columbia. However, Garman (1957) found only white spruce in northeastern British Columbia, and detected no trees having the smooth-bark, and broad-crown characteristic of Porsild spruce.

Most authors are in agreement that the variety P. glauca var. albertiana is the hybrid between white and Engelmann spruce (Little 1953, Wright 1955, Garman 1957, Taylor 1959); Garman (1957) is the principal authority in regard to its general distribution in the province of British Columbia.

There has been no detailed study of introgressive hybridization between the spruce species of British Columbia, though Taylor's (1959) and Garman's (1957) studies, and Horton's (1959) study in Alberta have provided considerable evidence of its occurrence in populations of white and Engelmann spruce.

The most important work in regard to crossability in spruce is that of Wright (1955). Wright crossed numerous spruce species, including those which are indigenous in British Columbia, and in addition surveyed the literature pertaining to crossability between the species. The data presented overleaf, summarize that portion of Wright's work which has a bearing on the problem in British Columbia.

Black spruce hybridizes freely with red spruce (Morgenstern and Farrar 1964) and, since the publications of Wright's findings, Little and Pauley (1958) have located and described a natural hybrid between black and white spruce. There is, then, evidence, both from studies of natural populations and artificial hybridization that there are no major genetic barriers to hybridization between white and Engelmann, white and Sitka, and Engelmann and Sitka spruce. The evidence is less conclusive for black and white spruce but, nevertheless, it appears that hybridization between both is also possible.

SUMMARY OF REPORTED CROSSES IN WHITE, BLACK, ENGELMANN
AND SITKA SPRUCE (FROM TABLE 2, WRIGHT 1955)

		Male parent			
		<u>glaucia</u>	<u>mariana</u>	<u>engelmannii</u>	<u>sitchensis</u>
Female Parent	<u>glaucia</u>	-	U	S	S
	<u>mariana</u>	F	-	-	-
	<u>engelmannii</u>	S	-	-	S
	<u>sitchensis</u>	S	-	S	-

S - successful cross, F - unsuccessful cross, U - results of cross uncertain.

In regard to white, Engelmann, and Sitka spruce Wright (1955) concluded that morphological, distributional and genetic data indicate a common, relatively recent, origin of these species, and that they are related to the Old World spruce species through P. jezoensis (Sieb. and Zucc.) Carr. of Japan. However, Fowler (1966) has recently published interesting results of artificial hybridization in a number of spruce species which led him to conclude that P. glauca and not P. jezoensis is the connecting link between Old World and Western North American spruces. Wright (1955) also concluded that P. mariana is closely related to P. rubens Sarg. and is a remnant of a more ancient migration than that which gave rise to the other three species.

Studies of post-glacial forest succession based on bog pollen analysis, which are relevant to the present discussion, indicate that all four spruces which occur in B.C. survived the pleistocene in southern refugia, and reinvaded northern regions following the withdrawal of the ice (Hansen 1947, 1955, Heusser 1960, Watts and Wright 1966). However, Hansen (1955) has suggested that spruce may also have reinvaded central and south central British Columbia from refugia along the eastern flank of the Rocky Mountains in Alberta and British Columbia, and in west central Yukon during the late Wisconsin.

It appears that the isolated stands of white spruce in Wyoming, Montana, and in the Black Hills of South Dakota are relics of the spruce populations of the southern refugia referred to above. The white spruce populations in the Black Hills are in association with ponderosa pine (Pinus ponderosa), dwarf birch (Betula glandulosa) and the shrub Shepherdia canadensis (Watts and Wright 1966).

Watts and Wright carried out pollen and seed analysis in an alluvia-

ted lowland 200 km. southeast of the white spruce stands in the Black Hills. Their results indicated that the Black Hills population is a relic of a semi-continuous distribution during late Wisconsin times, and that forests from Canada and the eastern Rockies were probably in contact in the Western Great Plains during Wisconsin. The late Wisconsin forest inferred from their results is described as xeric but cool spruce forest with dry openings. (see illus. 10).

Watts and Wright found a relatively high incidence of the herb Artemisia in their pollen counts, and explained its presence with spruce fossils by suggesting that there may have been a mosaic-type vegetation marked by Artemisia-dominated cover in dunes, and virtually pure stands of white spruce in hollows, resulting in the forest type described above. It was concluded that this forest type may have no modern analogue. However, in this regard it may be noted that Hansen (1955) has reported the occurrence of Artemisia tridentata on open slopes adjacent to a spruce stand on a bog two miles south of Clinton in British Columbia, and that there are sympatric populations of ponderosa pine and spruce in the Rocky Mountain Trench in British Columbia (Eastham 1949).

PHOTOPERIODICITY IN FOREST TREES: A LITERATURE REVIEW

There is now considerable evidence that photoperiod or day length exercises a major influence on the growth rhythm of a number of tree species.

Since the classic work of Garner and Allard (1920) it has been known that the development of many herbaceous² plant species is strongly influenced by photoperiod, and in recent years it has become evident that not only development but growth also is so influenced.

The increasingly sophisticated techniques of controlled environment studies have been applied in recent years to assessing photoperiodic response in woody plant species, and there is now considerable experimental evidence that photoperiod exercises a major influence on the growth rhythm of many woody plants including a large number of deciduous and coniferous trees of the montane, subalpine and boreal forest regions.

R. Van der Veen (1951) has studied the influence of day length on the dormancy of some species of the genus Populus by growing cuttings of several species in five different growth cabinets, and exposing them to different temperatures and photoperiods. His results showed that plants subjected to a short day treatment were the first to go dormant even though the temperature regime of the short day was higher than that of the long day treatment. Nevertheless, under the latter treatment all plants continued growth.

In a series of controlled experiments of considerable significance for foresters Wareing (1950a, 1950b, 1950c, 1951) showed that in a number of woody species dormancy is hastened by short day conditions, and that the cessation of cambial activity is also controlled by photoperiod, and takes place after the cessation of extension growth. Wareing's results also indicated that there was little evidence that the breaking of dormancy in the spring under natural conditions is photoperiodically controlled, for

as he points out, if plants have been previously exposed to low temperatures, dormancy is readily broken at any time regardless of the photoperiod, simply by transferring the plants to warm conditions. Wareing also observed that in the case of Scots pine there is often a reduction in internode length tending towards a "rosette" growth-habit under short days (Wareing 1951).

Pauley and Perry (1954) demonstrated that high latitude clones of Populus tricarpha Torr and Gray, when grown in the natural day regime at the latitude of Boston U.S.A. (ca. 42°N), cease height growth on or about the time of the summer solstice. However, if photoperiod is lengthened by artificial illumination they continue to grow. These authors concluded that photoperiod influences the onset of dormancy, but does not appear to be directly concerned with flushing.

In a detailed study of geographic variation in Tsuga canadensis (L.) Carr. in controlled environments, Olson et al. (1959) concluded that provenances from high latitudes and high elevations terminated growth before these from low latitudes and low elevations. These results suggested that there is a critical night-length for Tsuga canadensis of 8 to 9 hours at which there is a maximum change from active shoots to dormant buds.

Olsen et al. also concluded that the similarity in response of hemlock seeds and buds to photoperiod, temperature, and previous chilling requirements, suggest that the mechanism which regulates the germination of seeds is also related to such vegetative phenomena as the breaking of bud dormancy, growth and return to dormancy.

Vaartaja (1959) conducted numerous studies of photoperiodic response in tree species. He concluded that for most of the species studied, including Picea glauca, decreasing day length after midsummer appears to be an important factor in initiating the rest period. Vaartaja also concluded that the critical day length for continental trees should be longer than

that for maritime trees.

To illustrate photoperiodic reactions of trees under outside conditions Vaartaja (1959) constructed a table from the data reported by Heikinheimo (1954). The table gives the fresh weight of one-year-old seedlings of Picea abies (L.) Karst (Norway spruce) from different sources when grown at five different latitudes 47°00', 51°00', 55°00', 60°00', and 66°00'N. Allowing for nursery effects other than climate it is quite clear from the results presented that there is a strong interaction between growth and photoperiod at each nursery. Maximum differences between provenances occurred in the southern nursery at lat. 51°00' where provenances from high latitudes showed least growth, and provenances from southern latitudes maximum growth.

Besides the study of Olsen et al. it seems clear from the results of other investigations that provenances from high altitudes respond to photoperiod in a manner similar to that of provenances from high latitudes. In this regard Vaartaja's interpretation of Heikinheimo's data referred to above, and the results of investigations reported below are of considerable interest and relevance to the present study.

Karschon (1949) found that the lower the elevation of Scots pine provenances the greater the growth under a short day treatment. Vaartaja (1960) showed differences between high (6300 ft.) and low (500 ft.) elevation provenances in response to photoperiod. Under short days the high elevation source grew less vigorously than the low elevation source.

Special interest is attached to the studies of Irgens-Moller (1958) in that he investigated photoperiodic response in provenances of Pseudotsuga menziesii (Mirb.) Franco (Douglas-fir) from British Columbia. Provenances from Salmon Arm in the interior of B.C. (Elev. ca 2000 ft.) when grown in a nursery at Corvallis, Oregon, entered dormancy before provenances from coastal

British Columbia. When grown in controlled environments the same interior provenances grew more vigorously under a long photoperiod, and showed least growth under a short photoperiod. From similar investigations with the same species reported in 1962 Irgens-Moller concluded that differences in response to photoperiod do exist among seedlings of different origin independently of possible differences in chilling requirements.

In a recent paper Orr-Erwing (1966) showed the profound effect of the male parent on the time of cessation of growth and dormancy in the progenies of controlled crosses of coastal and continental Douglas fir. He thus indicated the degree of genetic control on this phase of the growth rhythm of the species.

One of the strongest correlations between factors of the environment at their place of origin and the growth behaviour of diverse provenances in a uniform environment is that demonstrated by Langlet for Scots pine (Langlet 1959). Stebbins (1950) has stated that this particular study is one of the best examples of a cline within a plant species. Langlet used as an index of the environment at the place of origin of each provenance the day length on that day of the year which first showed a temperature of plus 6°C. The correlation between this index of the environment and the dry matter content of 52 provenances of Scots pine was striking. The correlation coefficient was + 0.98. Thus approximately 97% of the original variance in regard to dry matter content in 2-4 year old seedlings, was removed by eliminating the influence of day length during the first + 6°C. day. More importantly, Langlet (1959) has also shown that the growth behaviour of 42 different provenances of Scots pine at 17 years is similarly correlated.

The investigations of photoperiodic response in tree species in controlled and partially controlled environments, reported above, provide

experimental evidence of the profound effect of photoperiod, and its interaction with temperature, in influencing the growth rhythm of tree species. The question remains as to what extent the growth behaviour of the diverse spruce provenances at Cowichan Lake has been similarly influenced.

MATERIALS AND METHODS

To facilitate presentation the study is divided into two parts, A and B.

Part A is a study of geographic variation in immature populations of white spruce, and refers principally to a study of physiological variation of 150 different spruce provenances sown in a relatively uniform environment in the spring of 1965. Part A also incorporates references to a pilot investigation of variation in immature spruce populations. However, the data resulting from this investigation are ancilliary to the major study of physiological variation of 150 spruce provenances referred to above.

Part B is a study of geographic variation in mature populations of white spruce, and refers principally to a biometrical study of variation in cone scale morphology which was carried out on a mass collection of spruce cones collected in 157 areas throughout the range of spruce in British Columbia during the summers of 1963 and 1964. Part B also refers to other variable characteristics in mature spruce populations, for example foliage morphology, bark type, and branching habit. However, no detailed study was made of these characteristics, and as in part A, the data presented is purely ancilliary to the major study of variation in cone scale morphology.

PART A

Seeds from 150 spruce provenances were sown at the Cowichan Lake research station on Vancouver Island, British Columbia, in the spring of 1965 (illus. 1). Germination tests, which are referred to below, were conducted in the laboratory on a separate portion of each seed sample. Each provenance represents the bulked seed of a varying number of trees collected and registered under the supervision of professional personnel of the British Columbia Forest Service. Table 3 and fig. 5 give details of the geographic origin of each provenance. Fig. 5 also shows the location

of the Cowichan research nursery.

The provenances were randomized in each of six blocks and sown on a prepared soil mix (University of California 1957) in rows six inches apart and at right angles to the long axis of each bed.

Germination was facilitated by covering the beds with plastic-sheeted, fiberglass flyscreens. When germination was complete the plastic sheeting was removed from the flyscreens, and the seedlings thinned to approximately 2 cm. apart by cutting superfluous seedlings at the root collar. When growth had proceeded beyond the cotyledon stage the fiberglass screens were removed from the beds. During the winter the beds were again covered with plastic-sheeted, fiberglass screens.

To facilitate measurement on the same seedlings during the growing season 10 seedlings per row were selected by placing a board with 10 evenly spaced teeth alongside each row and selecting that seedling nearest each tooth. A coloured chicken ring was placed over each selected seedling.

At the end of the first growing season a sample of 10 seedlings was obtained for study from each row by placing a board with 10 evenly spaced teeth (so arranged as to lie between the permanently marked seedlings) and selecting that seedling nearest each tooth. The seedlings were cut at the root collar, and the following measurements obtained in the laboratory; (1) epicotyl length (2) root collar diameter (3) dry weight.

Flushing and dormancy assessments were made at the beginning and at the end of the second growing season by scoring permanently marked seedlings in each row. A seedling was considered flushed when the bud scales were ruptured and needles were visible. A seedling was considered dormant when the terminal needles of the epicotyl were stiff and whorled, and a terminal bud visible. Shoot length was obtained every two weeks during the second growing season by measuring permanently marked seedlings. At the

end of the second growing season the permanently marked seedlings were lifted by cutting at the root collar, and the following measurements obtained in the laboratory (1) shoot length (2) root collar diameter (3) dry weight.

Using X-ray techniques, Scandinavian workers have demonstrated that embryo development in spruce and pine seed is highly correlated with germination behaviour. It is also possible that embryo development may influence early growth in the nursery. Consequently provenance differences in germination behaviour and even early growth (differences which, unlike embryo development, are genetically based) may be obscured if no account is taken of this factor.

In order, therefore, to obtain a measure of seed quality (expressed as embryo development) which would allow a more accurate interpretation of the ecological significance of the results of germination tests, 4 replications of 100 seeds from each provenance were X-rayed. A X-ray unit producing soft rays was used for this purpose (Nippon super soft X-ray apparatus Type EM supplied by the Nippon Softex Co. Ltd. Tokyo), and the conditions of exposure were as follows (15 kV, 1.5 mA, f. 35 cm., 15 sec.). The quality of the radiographs thus obtained is shown in illus. 2. Using a Bausch and Lomb, Stereoscopic binocular microscope, embryo development and full seed percent were assessed from the resulting radiographs, and classified in the manner indicated by Table 1 and Illus. 2.

Germination tests were also conducted at 15, 20 and 30°C. 4 replications of 100 seeds each were germinated at each of these temperatures. In all germination tests conducted, the seed was unstratified and germinated on filter paper in petri dishes filled with vermiculite. Water was supplied only once, and at the beginning of each test. In all instances the indices of germination behaviour were calculated in the manner proposed by Czabator (1962), and the following table is from Müller-Olsen et al 1956.

TABLE 1

EMBRYO AND ENDOSPERM CLASSES CORRESPONDING TO THOSE SHOWN IN ILLUS. 2

Embryo class

- O - Neither embryo nor endosperm (empty seed).
- I - Endosperm but no embryo.
- II - Endosperm and one or several embryos, none of which is longer than half the embryo cavity.
- III - Endosperm and one or more embryos, the longest of which measures between half and three-quarters the embryo cavity.
- IV - Endosperm with one fully developed embryo completely, or almost completely, occupying the embryo cavity. Diminutive embryos rarely occur.

Endosperm class

- A - The endosperm almost fills the seed coat to capacity and absorbs the x-radiation well.
- B - The endosperm only partially fills the seed coat and is often shrunk or otherwise deformed. The X-ray absorption is inferior to that of class A.

The pilot investigation of variation in immature spruce populations refers to 12 spruce provenances sown on two soil types in the spring of 1964 at the Cowichan research nursery (Table 4).

In the fall of 1964 the 12 provenances were sampled by placing a board with 10 teeth alongside each row of seedlings and taking that seedlings which was closest to each of the 10 teeth to give 10 seedlings per row. Since there were 4 replications, each provenance was represented by 40 seedlings. Shoot length and root collar diameter were obtained for

every seedling and the mean of all measurements calculated for the 12 provenances.

During the early spring of the second year a plastic greenhouse was placed over two blocks, one of the artificial soil mix, and one of local soil. A sampling and measuring procedure similar to that referred to above was followed in assessing the second year's growth. In addition, however, shoot extension was measured every two weeks during the growing season. Dates of flushing and dormancy were also obtained.

All data were subjected to statistical analysis in order to determine the relation between the variation observed and factors of the environment at the place of origin of provenances. This included principal component analysis and multiple regression analysis.

Principal component analysis is a form of multivariate analysis which in recent years has found increasing application in genecological and taxonomic investigation. The mathematics of the technique have been discussed by Seal 1964 (pp. 101-122), and its application in regard to geographic variation and taxonomy of tree species has been demonstrated by Jeffers and Black 1963, and Gardiner and Jeffers 1963.

Jeffers 1965 has briefly summarized the objectives of principal component analysis, and his summary is given below in full:

1. Examination of correlations between separate variables.
2. Reduction of the basic dimensions of the variability to the smallest number of meaningful dimensions.
3. Elimination of variables which contribute relatively little extra information to the study.
4. Examination of the taxonomic groupings of the individuals
5. Determination of the objective weighting of the variables in the construction of taxonomic indices.

6. The identification of individuals of doubtful or unknown origin.
7. The recognition of misidentified specimens.

Since the objectives of the present study are genecological and not taxonomic, objectives 1 to 3 are of much greater importance than objectives 4 to 5. The value of the principal component analysis in the present instance, therefore, is that it enables the investigator to identify, from the many variables measured, those variables which contribute most to the total pattern of variation. Consequently the identification of variables of greatest genecological significance is facilitated.

Multiple regression analysis was used to determine the degree to which the variation observed is related to environmental factors at the place of origin of each provenance. In this way factors which exercise selection pressure on the species may be shown to have association with measurable geographic factors such as altitude, latitude or longitude.

Because of the extreme paucity of climatic information for the montane, and particularly the subalpine forest regions of British Columbia, an attempt was made to calculate the number of days in the growing season at the place of origin of each of the 150 spruce provenances from the known data of altitude and latitude.¹

¹ Data concerning forest regions in British Columbia, climatic data, and data concerning photoperiod have been obtained from the following sources:

Rowe, J.S. 1959. Forest regions of Canada. Bulletin 123, Canada Dept. of Northern Affairs and National Resources Forestry Branch. 71 pp.

1946. Tables of sunrise, sunset and twilight. Supplement to the American Ephemeris. Nautical Almanac office, United States Naval Observatory.

Climates of the states for, Washington, Idaho and Montana. United States Department of Commerce, Weather Bureau.

Climate of British Columbia annual reports. Department of Agriculture, British Columbia.

Climatic summaries for selected meteorological stations in Canada: Frost data. Meteorological Division, Canada Department of Transport.

The altitude, latitude and number of days in the growing season were obtained for each of 457 weather stations representing a wide altitudinal and latitudinal range in British Columbia and adjacent territories in the Yukon, Alberta, Idaho, Washington and Montana. These data were subjected to regression analysis, the independent variables being altitude and latitude, and the dependent variable being the number of days in the growing season.

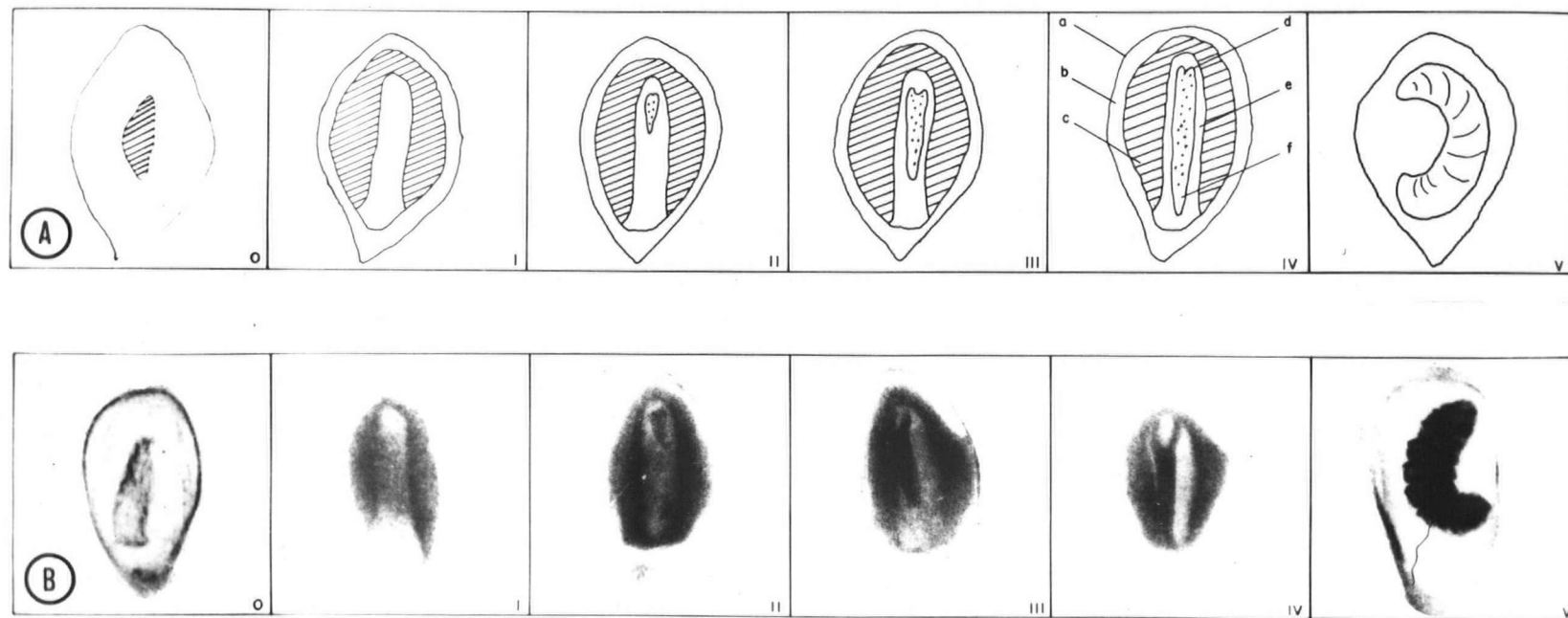
Using the regression equation thus obtained, and by inserting altitude and latitude at the place of origin of each of the 150 provenances, it was possible to obtain a measure of the number of days in the growing season at the place of origin of the same provenances. This measure is henceforth referred to as the index of the vegetative period.

The index of the vegetative period calculated in the manner described above has a relative value only. Nevertheless it is based on a body of data much more extensive than is obtainable in British Columbia alone, though at the same time obtained from territories on the periphery of this province. Furthermore the results obtained are in approximate agreement with results published in regard to European countries, in that they indicate that a displacement of one degree north shortens the growing season by 6 days, and that a displacement of 300 ft. upwards will have a similar effect (Wiersma 1963).

This index of the vegetative period is, therefore, used in the present study, since even as a relative value it has more biological significance than altitude or latitude.



Illus. 1. Upper photo gives general view of the layout of the nursery beds at Cowichan. Lower photo shows layout of seedlings in these beds.



Illus. 2. The X-ray assessment of embryo development in spruce seed.

A. Diagrammatic representation of spruce embryo classes and insect infested seed: a - seed coat; b - cavity between seed coat and endosperm; c - endosperm; d - cotyledons; e - embryo cavity; f - radicle.

B. Photographic representation (obtained from radiographs) of spruce embryo classes and insect infested seed corresponding to those illustrated in A. Note the polyembryonic condition of class II.

TABLE 2

MEASUREMENTS OF SEED QUALITY, GERMINATION, AND GROWTH MADE ON
150 SPRUCE PROVENANCES, AND MEASUREMENTS OF FACTORS OF THE
ENVIRONMENT AT THEIR PLACE OF ORIGIN.

MEASUREMENT

CODE

1	Altitude	A
2	Latitude	L
3	Index of the vegetative period	D
4	Day length of the first day of the year with average temperature of 43°C.	DL43
5	Percent of embryo development class III in each seed lot	ED3
6	Percent of embryo development class IV in each seed lot.	ED4
7	The rate of germination at 15, 20, 25, 30°C.	PV15, PV20, PV25, PV30
8	Mean daily germination at 15, 20, 25, 30°C	MDG15, MDG20, MDG25, MDG30
9	Actual germination percent	AGP
10	Germination value (FVXMDG) at 15, 20, 25, 30°C	GV15, GV20, GV25, GV30
11	Rate of germination at 25°C. adjusted for embryo development . . .	PVA25
12	Germination value at 25°C. adjusted for embryo development	GVA25
13	Shoot length in first year	SL1
14	Root collar diameter in first year	RCD1
15	Dry weight in first year	DW1
16	Shoot length in second year.	SL2
17	Root collar diameter in second year.	RCD2
18	Dry weight in second year.	DW2
19	Percent flushed on April 6, 14, 20, 27 in 2nd year	FL6, FL14, FL20, FL27
20	Percent Dormant on June 30, July 7, 14, 21, 28, August 4	DJ30, DJY7, DJY14, DJY21, DJY28, DA4.
21	Shoot extension May 10, 24, June 6, 20, July 4, 18 during the second year.	SM10, SM24, SJ6, SJ20, SJY4, SJY18.
22	Shoot extension May 10, 24, June 6, 20, July 4, 18 during the second year expressed as a percent of total growth	PM10, PM24, PJ6, PJ20, PJY4, PJY18.

TABLE 3
GEOGRAPHIC ORIGIN OF 150 SPRUCE PROVENANCES ARRANGED IN ORDER OF INCREASING ELEVATION

No.	Prov. No.	Reg. No.	Lat.	Long.	Elev. in 1000 ft.	Location	No.	Prov. No.	Reg. No.	Lat.	Long.	Elev. in 1000 ft.	Location
1	94	529	53 40	132 20	0.1	Juskatla, Q. Charlotte Is.	76	113	623	58 10	121 50	2.7	Nig Creek N. of Fort St. John
2	96	692	52 22	126 45	0.1	Bella Coola	77	12	380	55 36	127 50	2.7	Kispiox River
3	103	748	50 03	127 03	0.1	Kaouk R. N.W. of Zeballos	78	17	374	54 27	126 54	2.7	N.W. of Barrett
4	131	840	55 05	129 25	0.1	S.W. Alayash, Nass River	79	69	359	54 04	121 30	2.7	12 miles N. of Sinclair Mills
5	132	464	54 03	128 39	0.1	7 miles N. of Kitimat	80	100	723	54 15	121 55	2.7	N.E. of Aleza Lake
6	101	742	49 08	125 25	0.1	Kennedy L.S.E. of Alberni	81	7	722	54 04	122 27	2.8	N.E. of Sinclair Mills
7	93	526	55 05	129 20	0.1	Nass R., S.W. of Alayash	82	113	789	54 21	125 26	2.8	Talispin L. N.E. of Burns Lake
8	104	766	48 50	124 45	0.3	Klanawa R. Vancouver Island	83	115	791	55 05	127 20	2.9	Morice Town
9	105	767	53 05	132 05	0.3	Pallant Creek, Q.C.I.	84	9	388	53 40	122 25	3.0	Stone Creek S.E. of Prince George
10	130	809	53 30	132 15	0.4	Gold Creek, Graham Is.	85	18	356	54 08	127 09	3.0	S.W. of Houston
11	63	281	53 06	132 03	0.4	Mosquito L., Moresby Is.	86	114	790	54 04	127 13	3.0	McBride L. S.W. of Houston
12	125	801	50 32	127 15	0.6	West of Port McNeill	87	53	240	50 10	116 00	3.1	Whatchan Creek, Upper Arrow Lake
13	85	426	54 40	128 45	0.7	Kitsum Kalum L., N. of Terrace	88	120	796	54 51	127 00	3.2	12 miles N.E. of Smithers
14	92	525	54 45	128 45	0.8	Kitsum Kalum L., N. of Terrace	89	74	371	54 06	127 12	3.3	Morice R. S.W. of Telkwa
15	64	284	54 11	125 34	0.9	Klinakiini R. Knight Inlet	90	42	773	53 20	122 10	3.4	Haverahou Rd. Prince George
16	116	792	55 08	127 24	1.0	Beaumont N. of Smithers	91	20	427	51 42	120 10	3.5	N. of Clearwater
17	117	793	55 18	127 42	1.1	7 miles N. of Hazelton	92	90	488	49 04	120 45	3.5	Manning Park
18	126	805	55 28	127 42	1.2	N. of Hazelton	93	102	745	52 12	119 15	3.5	Thunder R., N.E. of Blue R.
19	124	800	55 17	127 24	1.2	Suskuwa R., E. of Hazelton	94	21	448	51 10	120 15	3.6	S.W. of Barriere
20	25	740	51 35	119 51	1.4	N. Thompson R., Birch Is.	95	37	344	49 35	115 59	3.6	Perry Cr., N.W. of Cranbrook
21	62	905	51 35	119 51	1.4	N. Thompson R., Birch Is.	96	142	575	50 00	116 00	3.6	Shelter Bay Upper Arrow L.
22	127	806	54 54	127 15	1.5	Swelvin, N. of Smithers	97	28	334	49 00	116 45	3.9	Boundary Cr., S.W. of Creston
23	76	379	55 36	127 50	1.5	Kispiox R.	98	55	691	49 07	120 53	4.0	Gibson Pass Manning Park
24	77	382	55 36	127 50	1.5	Kispiox R.	99	146	644	50 38	116 00	4.0	Upper Arrow Lake of Arrowhead
25	51	44	53 25	122 40	1.7	Hixon	100	84	447	51 14	120 15	4.0	Peterson Creek W. of Barriere
26	13	358	55 28	127 50	1.7	20 miles N. of Hazelton	101	31	346	49 55	116 35	4.0	Kettle R., E. of Kelowna
27	121	797	54 46	127 11	1.9	B.C.F.S. Office, Smithers	102	23	147	49 10	120 35	4.0	Manning Park
28	122	798	54 45	127 11	1.9	Bigelow Lake, Smithers	103	22	150	49 55	120 35	4.0	S.E. of Merritt
29	106	769	54 40	122 10	1.9	Fraser R., N.E. of Newlands	104	30	393	49 55	119 46	4.1	W. of Kelowna
30	110	777	54 40	122 10	2.0	Fraser R., N. of Giscome	105	134	576	50 15	117 50	4.2	Upper Arrow L., S.W. of Nakusp
31	68	355	54 44	122 22	2.0	McBride L., Morice R.	106	135	856	49 00	116 40	4.2	Boundary Cr. S. of Creston
32	60	49	55 30	121 35	2.0	Peace R. Area	107	87	430	50 40	119 35	4.2	Fly Hills, Salmon Arm
33	47	779	54 06	122 03	2.0	Aleza Lake Exp. Station	108	86	428	51 44	120 05	4.2	N. of Clearwater
34	16	367	54 56	127 25	2.0	Doughty N. of Smithers	109	52	725	50 39	117 32	4.2	Trout Lake
35	2	48	55 40	122 12	2.0	Pine River, Peace River	110	33	747	49 20	117 15	4.2	S. of Nelson
36	70	364	54 56	127 25	2.0	Doughty N. of Smithers	111	26	738	50 42	119 30	4.5	Fly Hills, W. Salmon Arm
37	71	365	54 56	127 25	2.0	Doughty N. of Smithers	112	24	741	50 52	119 50	4.5	6 miles S.W. of McGillivray L.
38	72	366	54 56	127 25	2.0	Doughty N. of Smithers	113	136	868	49 03	116 58	4.3	Monk-mun Creek S.W. of Creston
39	73	369	54 56	127 25	2.0	Doughty N. of Smithers	114	40	709	51 08	117 05	4.3	Spillimacheen R., S.E. of Golden
40	89	454	54 56	127 25	2.0	Doughty N. of Smithers	115	15	737	51 07	118 15	4.3	Big Bend, Columbia R.
41	91	499	54 05	122 20	2.0	Fraser R., Giscome	116	54	715	49 29	117 14	4.4	Clear Creek, Nelson
42	98	718	54 11	122 07	2.0	N.W. of Aleza Lake	117	148	655	49 05	115 47	4.5	Spruce Tree Cr., Tahk Valley
43	99	719	54 11	122 07	2.0	N.W. of Aleza Lake	118	138	539	49 55	114 46	4.5	Line Creek, W. of Natal
44	111	780	54 05	121 53	2.0	Fraser R., S. of Hansard	119	67	340	50 32	115 55	4.5	Shushwap Creek, Radium
45	6	746	54 06	122 03	2.0	Aleza Lake Exp. Station	120	44	732	49 25	118 02	4.5	Deer Park, Lower Arrow Lake
46	8	353	54 56	127 25	2.0	Doughty N. of Smithers	121	29	343	49 49	116 16	4.5	St. Mary's R., W. of Kimberley
47	56	39	54 05	122 03	2.1	Aleza Lake Exp. Station	122	141	542	49 55	114 45	4.6	Line Creek, N. of Natal
48	107	770	54 15	122 20	2.2	Fraser R. of Giscome	123	83	446	50 51	119 52	4.6	2 miles W. of McGillivray Lake
49	108	771	54 15	122 20	2.2	Fraser R., N. of Giscome	124	61	66	51 40	120 10	4.6	Clearwater
50	109	772	54 10	122 15	2.2	Fraser R., N. of Giscome	125	39	345	49 05	116 45	4.6	Boundary Creek, S.W. of Creston
51	128	807	55 18	127 19	2.2	16 miles N.E. of Hazelton	126	36	701	50 08	115 26	4.6	E. of Canal Flats
52	55	37	54 05	122 03	2.2	Aleza Lake Exp. Station	127	34	740	49 22	114 35	4.6	S.E. of Fernie
53	65	296	54 10	122 10	2.2	N.E. of Newlands	128	19	429	51 46	120 10	4.6	N. of Clearwater
54	78	389	54 00	122 00	2.2	Aleza Lake	129	88	447	51 00	119 52	4.7	McGillivray Lake
55	79	390	54 00	122 00	2.2	Aleza Lake	130	82	395	50 07	117 42	4.7	N.W. of Kelowna
56	3	42	54 30	124 06	2.2	Fort St. James	131	80	392	50 04	119 41	4.7	N.W. of Kelowna
57	4	493	54 30	122 40	2.2	Davie L., N. of Prince George	132	43	898	51 07	117 15	4.7	S.W. of Golden
58	10	522	52 20	121 40	2.2	Antoine L. E. of Soda Creek	133	35	699	49 10	116 08	4.7	S.W. of Cranbrook
59	11	523	52 25	121 25	2.2	Horsety Lake E. of Soda Cr.	134	149	657	49 15	116 44	4.8	Kidd Creek S.W. of Cranbrook
60	50	431	54 07	121 50	2.2	6 miles N.E. of Upper Fraser	135	145	641	50 34	119 29	4.9	Spa Lake N. of Salmon Arm
61	1	50	56 30	121 06	2.3	N.W. Fort St. John	136	139	540	49 55	114 55	4.9	North Fork Pass, W. of Natal
62	5	494	54 20	122 40	2.3	Summit L., N. of Prince George	137	45	338	49 45	117 00	4.9	Cedar Creek S. of Kaslo
63	14	370	55 20	126 38	2.3	Fort Babine, Babine Lake	138	144	636	49 46	115 24	5.0	Summer L., S.E. of Skookamchuck
64	57	43	54 17	122 37	2.3	North of Prince George	139	137	888	50 05	117 45	5.0	McDonald Cr. South of Nakusp
65	58	46	54 05	122 05	2.3	Aleza Lake Exp. Station	140	133	545	49 03	114 40	5.0	Gouldrey Creek W. of Flathead
66	59	47	54 05	122 05	2.3	Aleza Lake Exp. Station	141	66	336	50 15	115 45	5.0	Upper Dry Creek, Columbia Lake
67	123	799	55 02	126 30	2.3	Smithers Landing, Babine L.	142	27	720	50 29	119 45	5.1	S.E. of Westwood
68	129	808	54 40	127 15	2.5	Telkwa R., W. of Telkwa	143	97	703	49 26	115 08	5.1	Perry Creek W. of Cranbrook
69	48	385	54 15	122 15	2.5	N. of Giscome	144	140	544	49 55	114 44	5.1	North Fork Pass N. of Natal
70	49	51	54 10	121 10	2.5	Salmon R., N.W. of Pr. George	145	46	335	49 20	116 08	5.3	Moyle R. S.W. of Cranbrook
71	118	794	54 38	127 12	2.5	6 miles S.W. of Telkwa	146	150	857	49 15	117 45	5.5	S.W. of Castlegar
72	32	387	54 22	122 30	2.6	5 miles N.E. of Summit Lake	147	38	341	49 18	116 00	5.5	Rabbit Pt. Cr., S.W. of Cranbrook
73	75	373	54 05	127 15	2.6	Morice R., S.W. of Houston	148	81	394	50 01	119 42	5.5	N.W. of Kelowna
74	112	784	54 53	126 44	2.7	Chapman L., N.E. of Smithers	149	147	654	49 06	114 40	5.6	Cabin Creek W. of Flathead
75	119	795	54 07	125 25	2.7	S.E. of Burns Lake	150	41	337	49 35	117 48	5.7	N. of Castlegar

Lat. - latitude; Long. - longitude; Elev. - elevation

TABLE 4

GEOGRAPHIC ORIGIN OF TWELVE PROVENANCES SOWN IN THE
COWICHAN LAKE RESEARCH NURSERY

<u>No.</u>	<u>RN</u> ¹	<u>Lat.</u>	<u>Long.</u>	<u>Elev. in</u> <u>1000 ft.</u>	<u>Locality</u>
12	779	54°06'	122°03'	2.0	Aleza Lake
2	522	52°20'	121°40'	2.2	Summit Lake
8	40	54°30'	122°40'	2.3	Antoine Lake, E. of Soda Creek
4	387	54°22'	122°30'	2.6	5 Miles N.E. of Summit Lake
6	388	53°40'	122°25'	3.0	Stone Creek S.E. of Prince George
7	773	53°20'	122°10'	3.4	Naverabu Rd. Prince George
1	334	49°00'	116°45'	4.0	Boundary Creek S.W. of Creston
3	343	47°49'	116°16'	4.5	West of Kimberly
9	702	49°14'	115°58'	4.7	Whitney Creek
10	338	49°45'	117°00'	4.8	Cedar Creek S. of Kaslo
11	335	49°20'	116°08'	5.3	Moyie River S.W. of Cranbrook
5	337	49°35'	117°48'	5.7	N. of Castlegar

¹ Registration number

PART B

During the summer of 1963 sampling was confined to the white-Engelmann spruce complex, and 57 samples were made. During the summer of 1964 sampling was extended north to the Yukon border and west to the Coast; 100 areas were samples. The 1964 sample, therefore, embraces elements of both black and Sitka spruce as well as white and Engelmann.

Cones were collected from the ground at the base of each of 5 trees, which were at least 100 feet apart, in all sampled areas. To avoid contamination from neighbouring trees, care was taken to collect cones as close as possible to the bole of the selected tree. At least 20 cones, which were kept separate by trees, were taken from the base of each tree at each sampled area. This gave a minimum of 100 cones per sampled area.

General ecological observations were made at each area visited, and any notable variation in gross morphology of the trees sampled was noted and permanently recorded by means of photographs. In areas where field observations indicated the presence of sympatric populations, sampling was more intensive and conducted along transects which passed from one broad ecological zone to another. Foliage samples were also taken in these areas. Table 5 gives the geographic origin of the 157 cone samples.

In the laboratory a single cone scale and bract were taken from the midpoint of each of 100 cones per sampled area, and photographed together with a ruler scaled in mm. (illus. 3). All subsequent measurements were made from these photographs utilizing the mm. scale cut from the photograph. A desk magnifier was used to facilitate measurement. Five basic measurements were made on each cone scale and bract and transferred directly to computer data sheets. Five further measurements were then derived from these basic measurements (Fig. 1). All statistical analysis were carried out by electronic computer.

Miscellaneous cone samples were supplied by the reforestation Division of the B.C. Forest service, by personnel of the Research Division and also by the Columbia Cellulose Company. These samples were measured in the manner described above, but the resulting data were not included in the main analysis.

In order to clarify the complex pattern of variation in cone scale morphology, and to facilitate interpretation, recourse was made to extensive graphing of data. A modified form of the "line of shape" method developed by Jentys-Szaferowa (1959) was used, and is explained below.

From the total number of trees sampled, 5 trees were selected from allopatric zones of white, Engelmann and Sitka spruce. Since no allopatric zone of black spruce was sampled it was necessary to select individuals known to be pure black spruce trees from different sympatric zones of white and black spruce. These trees, representing the pure form of each of the four spruces occurring in British Columbia, are henceforth referred to as standard samples. The cone scale samples of these trees were measured in the manner already described, and mean measurements obtained for each of the four species in its pure form (Table 6).

Table 7 is derived from Table 6 and the figures in column 3 of Table 7 may be graphed in such a way as to allow a visual assessment of the line of shape of one species in relation to another (Fig. 2). In Fig. 2:1 the straight line represents white spruce and is given the numerical symbol 1. The angular line represents Sitka spruce, and the figures on the horizontal line represent the number of times each measurement of the Sitka spruce scale deviates positively or negatively from the corresponding measurement of the white spruce scale (See Table 7). The angular line, therefore, is the characteristic curve obtained when pure Sitka spruce is graphed on pure white spruce. The figures on the vertical line represent the

10 measurements of cone scale morphology illustrated in Fig. 1. The other species are similarly represented in Fig. 3.

When a cone scale sample is from a sympatric zone, and is doubtfully or unknown as to species - the rule rather than the exception in respect of such samples - it can be graphed against the standard samples, using the means for the species represented in the sympatric zone. In this way it is possible to determine the degree to which the unknown sample represents a known standard sample, and to assess the degree of putative hybridization occurring in the sympatric zone.

A large number of samples have been graphed in this way. For example, the sampled area is represented by 5 trees, and if the area is a sympatric zone of white and black spruce, each tree is graphed against standard samples of white and black, and on the same figure the characteristics curves of white on black, and black on white (curves 11 and 12 on each figure) are also given (Figs. 35 to 44).

In addition to the line of shape method of discriminating species and intermediate forms in sympatric zones, all cone scale data resulting from the cone collections made in 1963 and 1964 were subjected to discriminant function analysis.

Jeffers (1965) has discussed the uses of discriminant function analysis in the study of variation. In this same publication he lists the relevant literature. In the present instance the principal objective of the discriminant function analysis is to indicate sympatric and allopatric zones of white and Engelmann spruce, white and Sitka spruce, and white and black spruce, on the basis of variation in cone scale morphology.

If for any sample of 5 trees the analysis indicates that two spruce species are present, then that sample is classed as sympatric for these species, even though it contains say four trees of one species and only one of another.

The sample is classed as allopatric if all five trees are of the same species according to the analysis.

TABLE 5
GEOGRAPHIC ORIGIN OF 157 SPRUCE CONE SAMPLES ARRANGED IN ORDER OF INCREASING
ELEVATION

Sample					Elev. in 1000 ft.	Location	Sample					Elevation in 1000 ft.	Location
No.	No.	Lat.	Long.	No.			No.	Lat.	Long.				
1	129	54 14	128 32	0.3	9 miles N. of Kitimat.	80	19	51 04	119 56	3.0	40 miles N. of Kamloops		
2	128	54 15	129 27	0.3	55 a. E. of Prince Rupert	81	149	56 25	121 09	3.0	40 miles N. of Kamloops		
3	126	54 15	129 48	0.4	32 miles E. of Prince Rupert	82	78	54 44	127 16	3.0	40 miles N. of Kamloops		
4	127	54 13	130 26	0.4	13 miles S.E. of Prince Rupert	83	136	54 27	126 45	3.1	40 miles N. of Kamloops		
5	125	54 15	130 8	0.5	14 miles E. of Prince Rupert	84	118	56 44	121 55	3.2	40 miles N. of Kamloops		
6	121	55 10	129 15	0.5	70 miles N.W. of Terrace	85	56	53 40	122 25	3.2	40 miles N. of Kamloops		
7	119	55 2	129 33	0.5	89 miles N.W. of Terrace	86	141	59 16	129 37	3.2	40 miles N. of Kamloops		
8	131	54 35	128 23	0.5	12.5 miles E. of Terrace	87	79	54 45	127 17	3.2	40 miles N. of Kamloops		
9	120	55 3	129 30	0.5	84 miles N.W. of Terrace	88	144	58 44	124 55	3.3	40 miles N. of Kamloops		
10	130	54 37	128 42	0.6	18 miles N. of Terrace	89	115	50 54	119 49	3.3	40 miles N. of Kamloops		
11	132	54 57	128 23	0.7	43 miles E. of Terrace	90	24	50 55	120 25	3.3	40 miles N. of Kamloops		
12	124	55 16	129 02	0.7	70 miles N. of Terrace	91	50	49 11	120 36	3.3	40 miles N. of Kamloops		
13	133	55 2	128 16	0.8	58 miles E. of Terrace	92	63	50 00	120 36	3.3	40 miles N. of Kamloops		
14	134	55 7	127 46	1.1	80 miles E. of Terrace	93	85	54 56	126 34	3.4	40 miles N. of Kamloops		
15	123	55 23	128 53	1.2	84 miles N. of Terrace	94	109	51 30	117 18	3.4	40 miles N. of Kamloops		
16	86	55 12	127 14	1.2	48 miles S.W. of Smithers	95	8	53 40	122 25	3.5	40 miles N. of Kamloops		
17	135	55 23	127 36	1.2	16 miles N. of Hazelton	96	25	50 55	120 25	3.5	40 miles N. of Kamloops		
18	31	51 28	120 10	1.3	15 miles N.E. of Little Port	97	80	54 46	127 17	3.6	40 miles N. of Kamloops		
19	139	57 55	131 11	1.3	Telegraph Creek S.W. of Watson Lake	98	87	50 42	119 23	3.6	40 miles N. of Kamloops		
20	122	54 28	127 47	1.4	104 miles N. of Terrace	99	9	51 18	122 08	3.7	40 miles N. of Kamloops		
21	117	51 35	119 53	1.4	91 miles N. of Kamloops	100	26	50 55	120 25	3.7	40 miles N. of Kamloops		
22	115	58 37	122 14	1.6	29 miles S. of Pt. Nelson	101	58	49 04	120 50	3.8	40 miles N. of Kamloops		
23	146	58 12	122 44	1.7	40 miles S.W. of Smithers	102	20	51 03	119 53	3.8	40 miles N. of Kamloops		
24	143	59 39	126 53	1.7	40 miles S.W. of Smithers	103	108	51 21	116 34	3.8	40 miles N. of Kamloops		
25	16	51 08	120 02	1.8	40 miles N. of Kamloops	104	147	57 17	122 45	3.9	40 miles N. of Kamloops		
26	66	52 46	122 26	1.8	58 miles N. of Williams Lake	105	27	50 55	120 25	3.9	40 miles N. of Kamloops		
27	74	54 50	127 14	1.9	6 miles N.W. of Smithers	106	57	53 40	122 25	3.9	40 miles N. of Kamloops		
28	144	58 14	127 08	2.0	10 miles S.E. of Smithers	107	49	49 39	119 50	3.9	40 miles N. of Kamloops		
29	67	52 55	122 27	2.0	69 miles N. of Williams Lake	108	141	50 52	119 50	3.9	40 miles N. of Kamloops		
30	32	51 50	120 03	2.0	100 miles N. of Kamloops	109	60	49 06	120 50	4.0	40 miles N. of Kamloops		
31	3	54 06	122 04	2.0	40 miles N.E. of Prince George	110	81	54 47	127 17	4.0	40 miles N. of Kamloops		
32	4	54 02	121 40	2.0	50 miles N.E. of Prince George	111	37	51 50	120 03	4.0	40 miles N. of Kamloops		
33	69	54 06	122 23	2.0	24 miles E. of Prince George	112	22	50 44	119 11	4.0	40 miles N. of Kamloops		
34	142	59 58	128 09	2.1	30 miles S.E. of Watson Lake	113	59	49 03	120 51	4.0	40 miles N. of Kamloops		
35	51	54 10	122 25	2.1	30 miles S.E. of Prince George	114	88	50 42	119 23	4.0	40 miles N. of Kamloops		
36	151	55 37	122 00	2.1	21 miles W. of Chetwynd	115	105	50 48	118 00	4.0	40 miles N. of Kamloops		
37	17	51 10	120 05	2.1	50 miles N. of Kamloops	116	91	49 6	116 54	4.1	40 miles N. of Kamloops		
38	65	52 21	122 20	2.2	24 miles N. of Williams Lake	117	40	50 08	118 34	4.1	40 miles N. of Kamloops		
39	12	53 00	122 30	2.2	2 miles N. of Quesnel	118	28	50 55	120 25	4.1	40 miles N. of Kamloops		
40	75	54 50	127 15	2.2	6.5 miles N.W. of Smithers	119	82	54 47	127 17	4.2	40 miles N. of Kamloops		
41	45	54 32	125 45	2.2	15 miles N. of Burns Lake	120	155	53 04	121 31	4.2	40 miles N. of Kamloops		
42	153	54 39	122 43	2.2	150 miles S. of Chetwynd	121	106	51 42	115 58	4.3	40 miles N. of Kamloops		
43	68	54 6	122 44	2.2	4 miles W. of Vanderhoof	122	29	50 55	120 25	4.3	40 miles N. of Kamloops		
44	71	54 1	124 6	2.3	4 miles W. of Vanderhoof	123	96	49 6	116 56	4.3	40 miles N. of Kamloops		
45	156	54 18	122 37	2.3	35 miles N. of Prince George	124	113	50 50	119 50	4.3	40 miles N. of Kamloops		
46	7	54 00	122 30	2.3	20 miles N.E. of Prince George	125	89	50 42	119 24	4.4	40 miles N. of Kamloops		
47	10	53 49	122 47	2.3	10 miles S.W. of Prince George	126	118	51 33	119 44	4.4	40 miles N. of Kamloops		
48	52	53 67	122 25	2.3	30 miles S.E. of Prince George	127	93	49 44	117 09	4.4	40 miles N. of Kamloops		
49	154	54 18	122 36	2.3	35.5 miles N. of Prince George	128	102	49 44	115 31	4.5	40 miles N. of Kamloops		
50	140	58 15	130 38	2.3	39 miles N.E. of Telegraph Crk.	129	104	50 39	116 00	4.5	40 miles N. of Kamloops		
51	47	49 17	117 13	2.4	20 miles S. of Nelson	130	36	51 50	120 03	4.5	40 miles N. of Kamloops		
52	5	54 20	122 37	2.4	30 miles N. of Prince George	131	43	49 03	117 00	4.6	40 miles N. of Kamloops		
53	13	54 26	124 21	2.4	3 miles W. of Ft. St. James	132	103	49 47	115 27	4.6	40 miles N. of Kamloops		
54	84	55 3	126 30	2.4	47 miles E. of Smithers	133	21	51 00	119 50	4.6	40 miles N. of Kamloops		
55	157	53 45	122 52	2.4	14 miles W. of Prince George	134	92	49 44	117 09	4.7	40 miles N. of Kamloops		
56	152	55 21	122 36	2.4	74 miles S. of Chetwynd	135	35	51 50	120 03	4.7	40 miles N. of Kamloops		
57	73	54 13	125 39	2.5	65 miles W. of Vanderhoof	136	23	50 46	119 27	4.7	40 miles N. of Kamloops		
58	76	54 44	127 11	2.5	5 miles S.W. of Smithers	137	30	50 55	120 25	4.7	40 miles N. of Kamloops		
59	50	53 40	122 25	2.5	30 miles S.E. of Prince George	138	48	49 12	118 00	4.7	40 miles N. of Kamloops		
60	1	53 45	122 30	2.5	20 miles S.E. of Prince George	139	116	50 33	119 30	4.7	40 miles N. of Kamloops		
61	11	53 41	122 55	2.5	20 miles S. of Prince George	140	110	50 59	119 33	4.7	40 miles N. of Kamloops		
62	46	49 02	117 10	2.5	40 miles W. of Creston	141	112	50 48	119 52	4.8	40 miles N. of Kamloops		
63	61	49 14	121 06	2.5	Manning Park	142	62	49 5	120 46	4.8	40 miles N. of Kamloops		
64	72	54 03	124 42	2.5	31 miles W. of Vanderhoof	143	90	50 42	119 25	4.8	40 miles N. of Kamloops		
65	33	51 50	120 03	2.6	100 miles N. of Kamloops	144	34	51 50	120 03	4.9	40 miles N. of Kamloops		
66	64	52 12	122 06	2.7	6 miles N. of Williams Lake	145	95	49 6	116 58	4.9	40 miles N. of Kamloops		
67	70	53 54	120 38	2.7	19 miles W. of Dawson Creek	146	101	49 17	115 58	5.1	40 miles N. of Kamloops		
68	54	53 40	122 25	2.7	30 miles S.E. of Prince George	147	98	49 24	116 10	5.1	40 miles N. of Kamloops		
69	2	53 45	122 15	2.7	30 miles S.E. of Prince George	148	42	49 03	117 00	5.1	40 miles N. of Kamloops		
70	150	55 45	120 38	2.8	19 miles W. of Dawson Creek	149	45	49 06	116 58	5.1	40 miles N. of Kamloops		
71	18	51 05	120 00	2.8	35 miles N. of Kamloops	150	39	50 05	119 40	5.1	40 miles N. of Kamloops		
72	49	49 07	118 35	2.8	40 miles W. of Trail	151	111	50 47	119 52	5.2	40 miles N. of Kamloops		
73	77	54 44	127 12	2.8	5.8 miles S.W. of Smithers	152	44	49 07	116 54	5.4	40 miles N. of Kamloops		
74	137	54 29	126 15	2.8	67 miles E. of Smithers	153	94	49 6	117 1	5.4	40 miles N. of Kamloops		
75	138	59 48	129 08	2.9	45 miles S.W. of Watson Lake	154	107	51 12	116 05	5.5	40 miles N. of Kamloops		
76	83	54 45	127 02	2.9	10.5 miles E. of Smithers	155	100	49 20	116 06	5.6	40 miles N. of Kamloops		
77	38	51 50	120 03	2.9	100 miles N. of Kamloops	156	41	49 15	117 22	5.8	40 miles N. of Kamloops		
78	55	53 40	122 25	2.9	30 miles S.E. of Prince George	157	97	49 29	116 08	6.7	40 miles N. of Kamloops		
79	6	54 07	121 44	3.0	60 miles N.E. of Prince George								

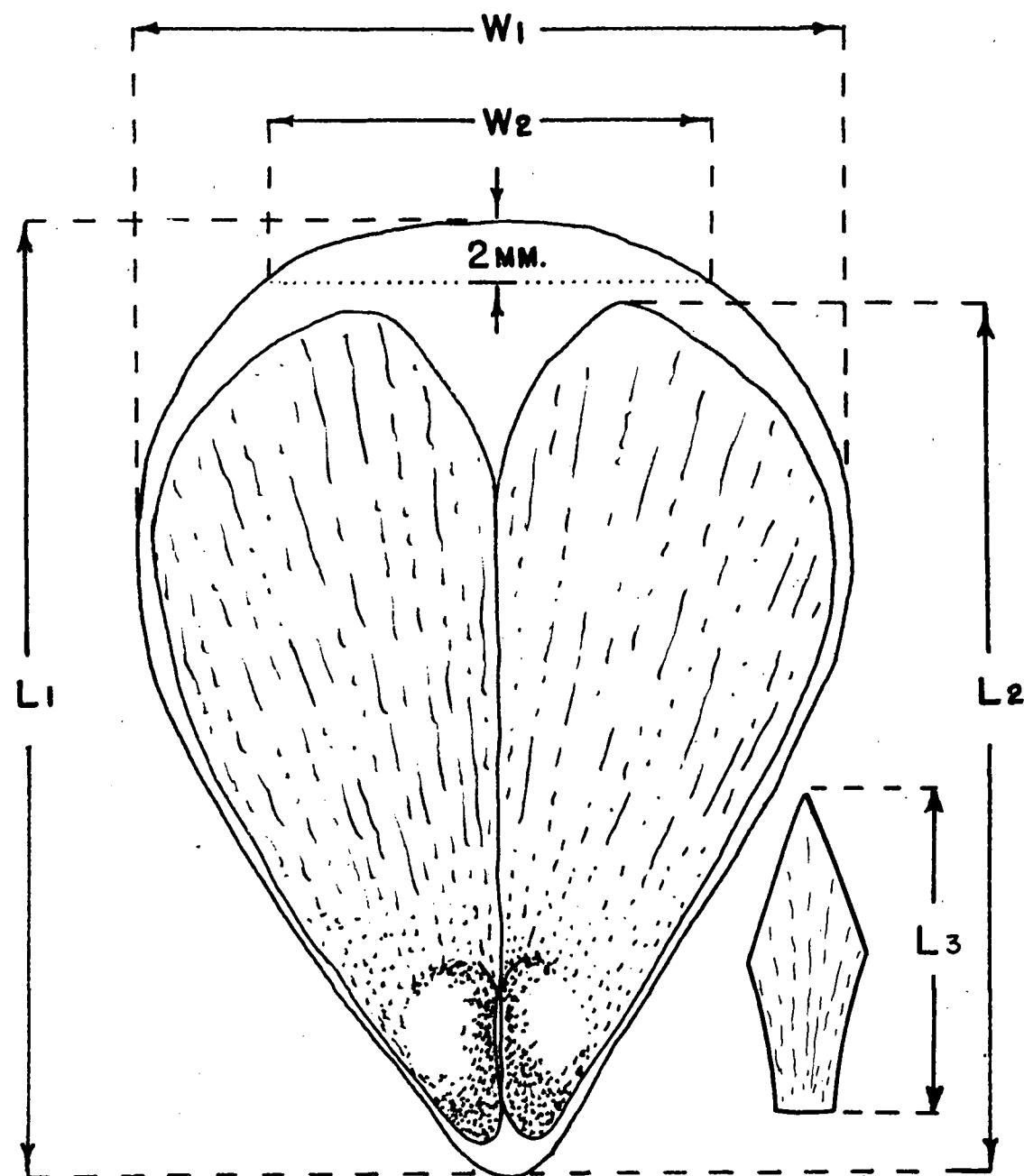
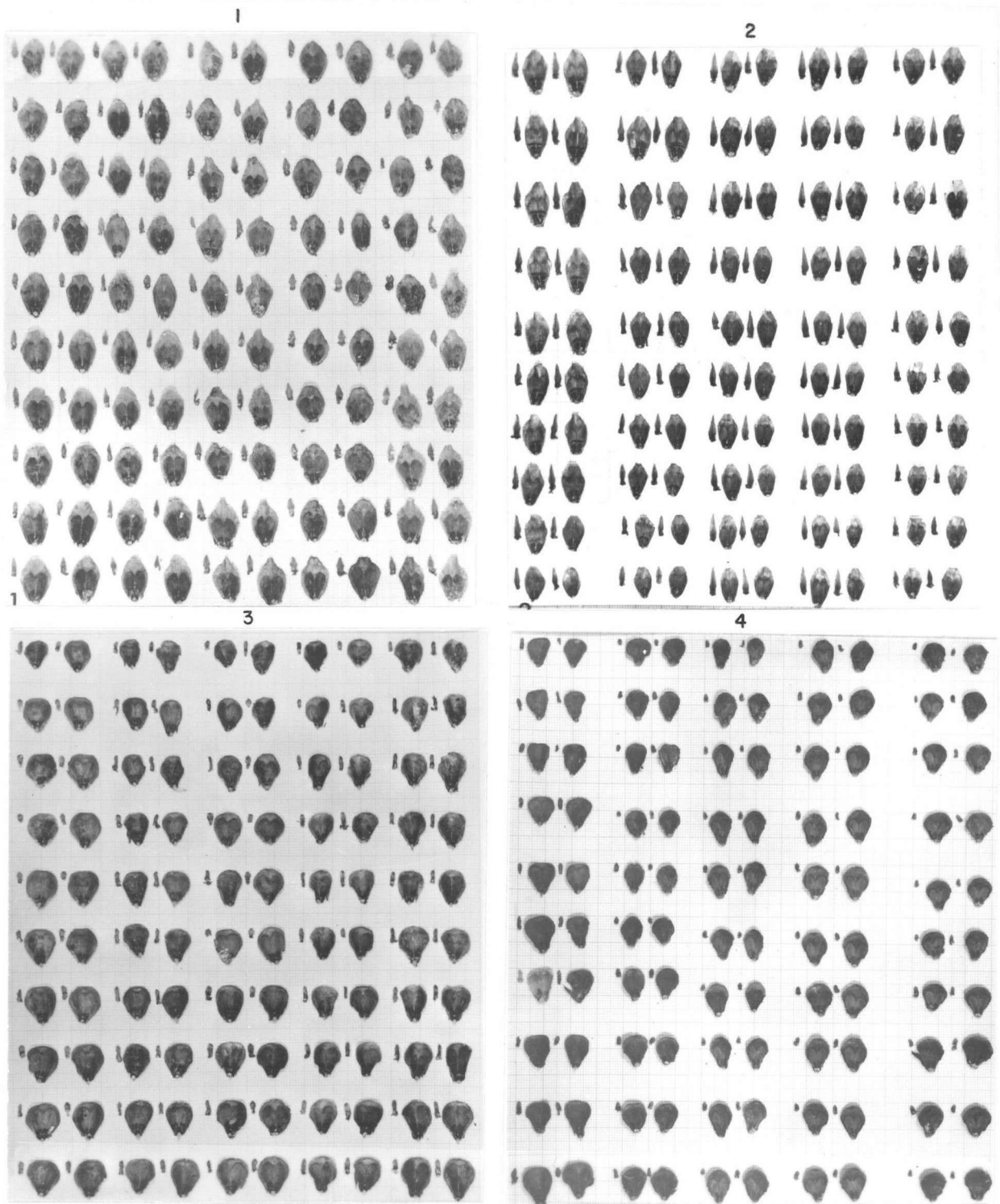


Fig. 1 Diagrammatic representation of spruce scale and bract showing five basic measurements. The five derived measurements are L_1/L_2 , L_1/L_3 , L_1/W_1 , L_1/W_2 , and $L_1/L_2 \times L_3$. The order of occurrence of these 10 measurements in all subsequent figures and tables is as follows:

1	2	3	4	5	6	7	8	9	10
L_1	L_2	L_3	W_1	W_2	L_1/L_2	L_1/L_3	L_1/W_1	L_1/W_2	$L_1/L_2 \times L_3$



Illus. 3. Cone scale morphology of Engelmann (1) Sitka (2) white (3) and black (4) spruce. The first column of scales in 4 are from a white spruce tree. The remainder are black spruce. Each column of 20 scales and bracts represents a single tree.

TABLE 6

CONE SCALE MORPHOLOGY OF BLACK, WHITE, ENGELMANN AND SITKA SPRUCE

S	P	L ₁	L ₂	L ₃	W ₁	W ₂	L ₁ /L ₂	L ₁ /L ₃	L ₁ /W ₁	L ₁ /W ₂	L ₁ /L ₂ × L ₃
BLACK	138-3	1.02	0.82	0.32	0.86	0.76	1.24	3.27	1.19	1.36	0.39
	143-3	1.09	0.82	0.30	0.92	0.75	1.33	3.67	1.19	1.46	0.40
	144-1	0.84	0.68	0.22	0.68	0.60	1.24	3.81	1.25	1.41	0.28
	145-5	1.13	0.83	0.31	0.97	0.80	1.37	3.80	1.17	1.46	0.42
	146-4	1.12	0.79	0.24	1.00	0.81	1.43	4.76	1.12	1.40	0.35
	\bar{x}	1.04	0.79	0.28	0.89	0.74	1.32	3.86	1.18	1.42	0.37
WHITE	64-1	1.16	0.99	0.45	0.91	0.82	1.18	2.63	1.29	1.42	0.53
	65-1	1.16	0.99	0.43	0.89	0.79	1.18	2.78	1.32	1.48	0.51
	70-1	1.17	1.01	0.46	0.93	0.82	1.17	2.60	1.27	1.44	0.54
	71-1	1.11	0.98	0.45	0.84	0.77	1.14	2.52	1.33	1.45	0.51
	72-1	1.20	1.00	0.42	1.05	0.92	1.20	2.96	1.14	1.32	0.50
	\bar{x}	1.16	0.99	0.44	0.92	0.82	1.17	2.70	1.27	1.42	0.52
ENGELMANN	93-1	1.21	0.86	0.59	0.92	0.67	1.41	2.09	1.32	1.92	0.82
	95-1	1.32	1.00	0.54	0.88	0.62	1.32	2.49	1.49	2.16	0.72
	99-1	1.51	1.15	0.64	0.97	0.59	1.32	2.37	1.56	2.60	0.84
	116-1	1.25	0.92	0.54	0.88	0.61	1.37	2.35	1.44	2.12	0.74
	118-1	1.34	0.99	0.59	0.83	0.57	1.35	2.28	1.61	2.39	0.80
	\bar{x}	1.33	1.00	0.58	0.90	0.61	1.35	2.32	1.48	2.24	0.78
SITKA	119-1	1.22	1.00	0.82	0.62	0.52	1.23	1.51	1.97	2.35	1.00
	120-1	1.48	1.06	0.87	0.76	0.51	1.40	1.73	1.97	2.97	1.21
	125-1	1.25	0.90	0.73	0.80	0.57	1.41	1.74	1.58	2.23	1.02
	128-1	1.62	1.11	0.98	0.89	0.52	1.46	1.66	1.83	3.15	1.43
	129-1	1.57	1.14	0.83	0.71	0.50	1.38	1.92	2.21	3.16	1.14
	\bar{x}	1.43	1.04	0.85	0.76	0.52	1.38	1.71	1.91	2.77	1.16

S - species, P - provenance, L₁ - etc. - measurements as indicated in fig. 1.

TABLE 7

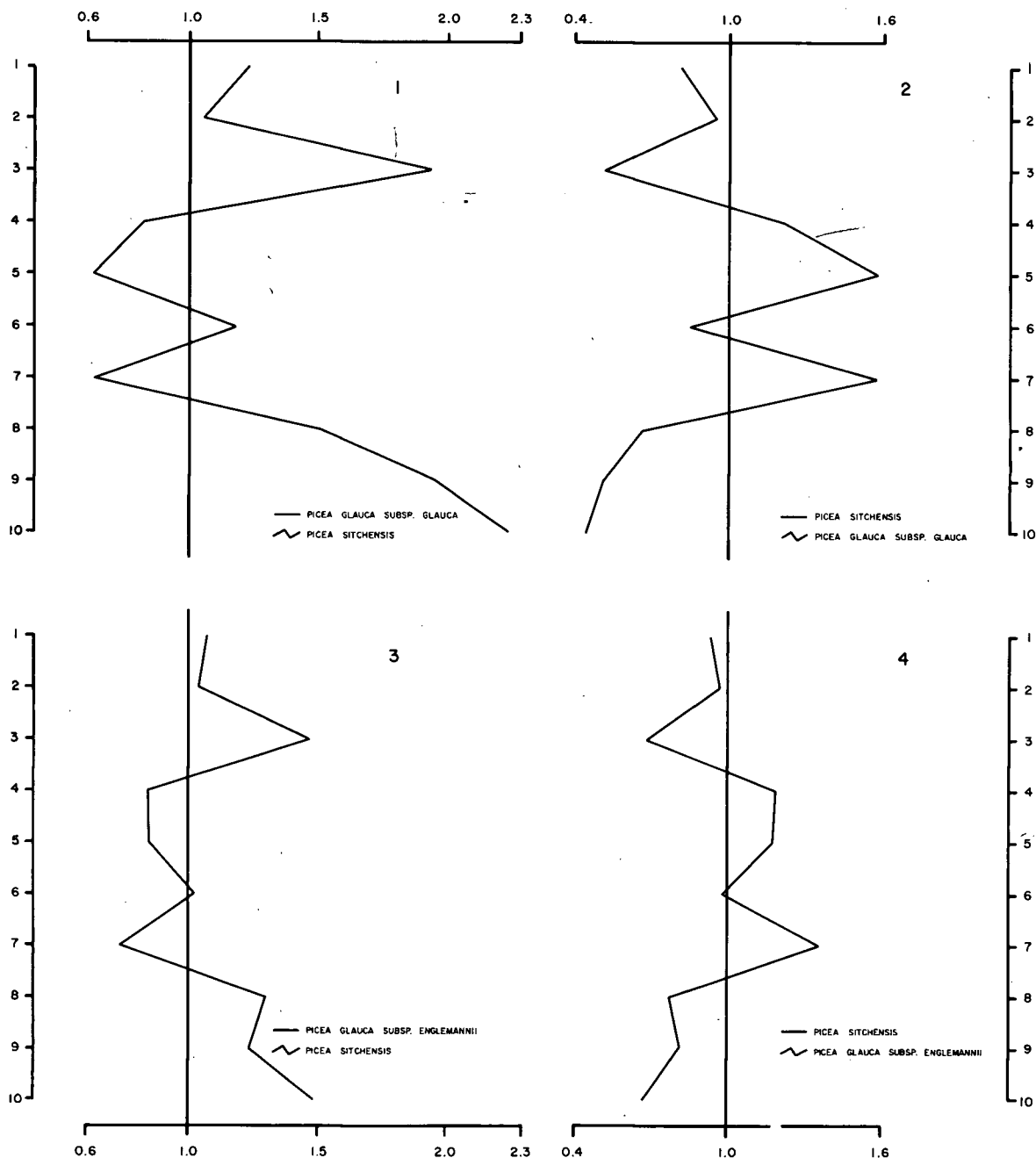
COMPARISON OF MEANS OF CONE SCALE MORPHOLOGY OF WHITE AND SITKA SPRUCE

M	1 WHITE	2 SITKA	3 SITKA/WHITE
L_1	1.16	1.43	1.23 : 1
L_2	0.99	1.04	1.05 : 1
L_3	0.44	0.85	1.93 : 1
W_1	0.92	0.76	0.83 : 1
W_2	0.82	0.52	0.63 : 1
L_1/L_2	1.17	1.38	1.18 : 1
L_1/L_3	2.70	1.71	0.63 : 1
L_1/W_1	1.27	1.91	1.50 : 1
L_1/W_2	1.42	2.77	1.95 : 1
$L_1/L_2 \times L_3$	0.52	1.16	2.2 : 1

Column 3 represents the number of times each of the 10 measurements for Sitka deviates positively or negatively from the corresponding measurement for white spruce.

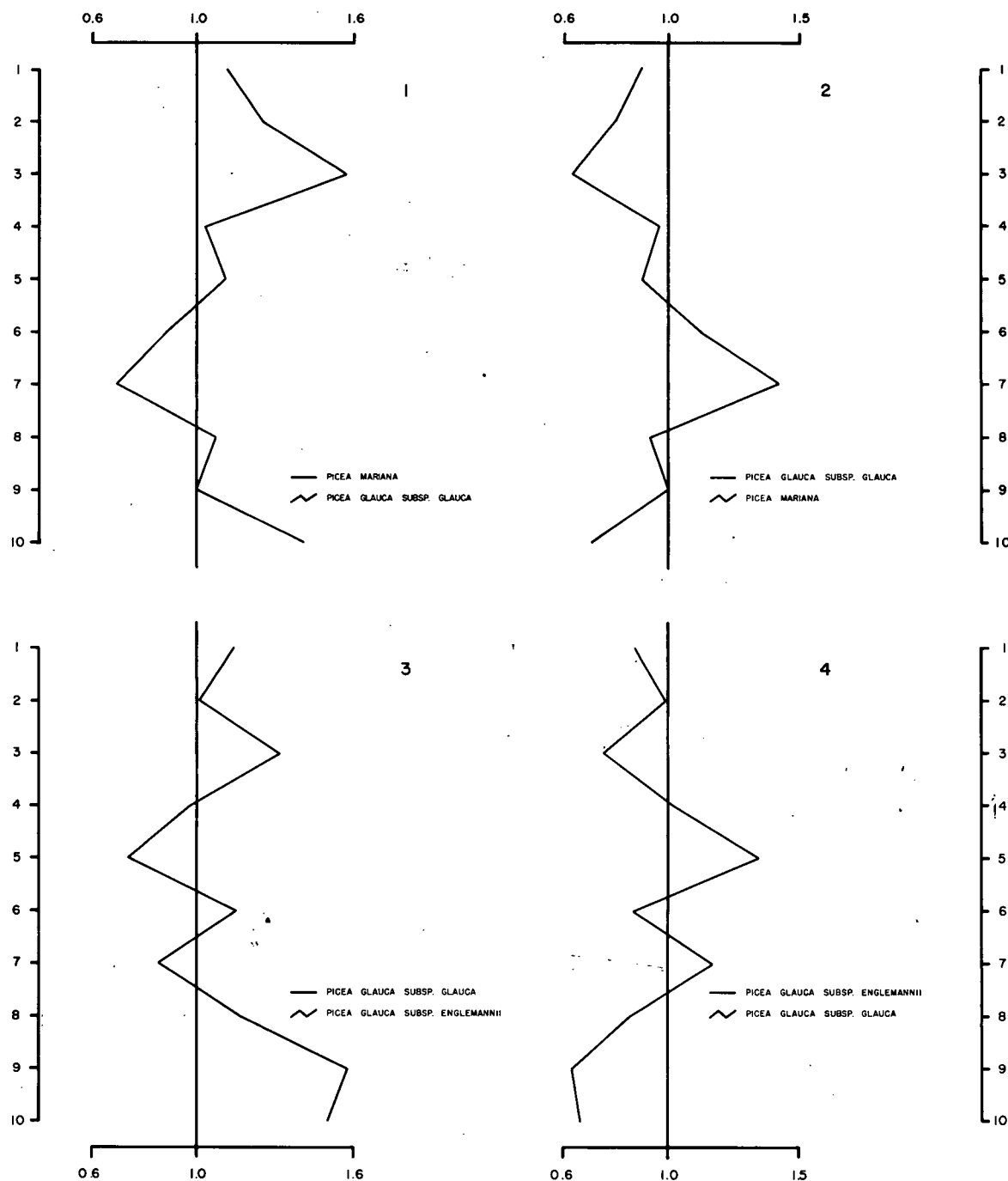
M - measurements illustrated in fig. 1.

Fig. 2 Characteristic curves obtained when cone scale morphology of populations from allopatric zones of white, Engelmann and Sitka spruce is compared by line of shape method (see page 41 for further explanation).



The numbers 1 to 10 on the vertical bars represent the 10 cone scale measurements illustrated in fig. 1. The numbers on the horizontal bars represent the number of times each measurement on one species deviates positively or negatively from the corresponding measurement on the species with which it is being compared.

Fig. 3 Characteristic curves obtained when cone scale morphology of population from allopatric zones of white and Engelmann spruce is compared by line of shape method. The black spruce sample is not from an allopatric zone. (See page 41 for further explanation).



The numbers 1 to 10 on the vertical bars represent the 10 cone scale measurements illustrated in fig. 1. The numbers on the horizontal bars represent the number of times each measurement on one species deviates positively or negatively from the corresponding measurement on the species with which it is being compared.

RESULTS

PART A

GEOGRAPHIC VARIATION IN IMMATURE POPULATIONS OF WHITE SPRUCE

GERMINATION AND GROWTH BEHAVIOUR OF 150 SPRUCE PROVENANCES SOWN IN THE SPRING OF 1965.

There is no significant correlation between germination behaviour at 15°C. and the indices of seed quality ED₄ and ED₃ + ED₄, but the index of seed quality ED₃ and germination behaviour are significantly correlated at this temperature (see Table 2 for definition of ED₃ and ED₄).

At 20°, 25° and 30°C. there is no significant correlation between the index of seed quality ED₃ and germination behaviour, but germination behaviour and the indices of seed quality ED₄ and ED₃ + ED₄ are highly correlated. The highest correlation between germination behaviour and seed quality occurs at 25°C, and is between AGP (actual germination percent) and ED₃ + ED₄ (Tables 14 to 17).

Germination behaviour is correlated positively with altitude and negatively with the index of the vegetative period. The correlation is strongest at extreme temperatures, that is, at 15° and 30°C, and weakest at intermediate temperatures, that is 20° and 25°C. The latter temperatures also result in maximum germinative values (Table 18).

Germination behaviour is also significantly correlated with latitude, but only at extreme temperatures. It is not significantly correlated with latitude at 20° and 25°C. However, when germination behaviour at 25°C. is corrected for embryo development, the correlation between germination behaviour at this temperature and factors of the environment is increased, and rate of germination (PV) at this temperature is then significantly correlated with latitude (Table 18).

All measures of total growth, except root collar diameter in the first year, are highly correlated with altitude and the index of the vegetative period both in the first and second year; negatively with altitude and positively with the index of the vegetative period. Of the first year's measurements, root collar diameter (RCD) and the ratio of shoot length (SL) and root collar diameter (SL/RCD) are significantly correlated with latitude; RCD negatively, and SL/RCD positively (Table 21).

The percent of seedlings flushed on April 6 in the second year, which is the first date on which flushing was assessed, is not correlated with any factor of the environment. However, percent flushed on April 14, and April 20 is correlated with all three factors of the environment, positively with latitude and the index of the vegetative period, and negatively with altitude. Percent flushed on April 27 is not correlated with latitude, but is positively correlated with the index of the vegetative period and negatively with altitude. Therefore, low elevation provenances flushed before high elevation provenances (see Table 19).

The correlation between flushing and factors of the environment is much weaker than the correlation between dormancy and factors of the environment (Fig. 19).

Of the other second year's measurements SL/RCD, percent dormant on June 30, July 7, 14, 21, are significantly correlated with latitude; SL/RCD positively, and percent dormant on all four dates negatively. Percent dormant on June 30, July 7, 14, 21, 28, and August 4 is very highly correlated with altitude and the index of the vegetative period, positively with altitude and negatively with the index of the vegetative period. The highest correlation between any one measurement of growth behaviour and factors of the environment is that between percent dormant on July 14 and altitude.

The correlation coefficient in this instance is 0.862 (Table 21 and Fig. 8).

There is a high correlation between date of entering dormancy and total growth of seedlings. Those seedlings which were the first to enter dormancy in midsummer had the lowest dry weight. The correlation coefficient for dry weight and percent dormant on July 28 is - 0.80 (Table 21).

There is a weak correlation between growth during the second growing season and latitude. However, growth is highly correlated with altitude and the index of the vegetative period. Growth to May 10, is positively correlated with altitude, and negatively with the index of the vegetative period (Table 20).

Growth between May 10 and May 24 is not correlated with any factor of the environment, but growth from May 24 to June 6 is again highly correlated with factors of the environment as expressed by altitude, and the index of the vegetative period. However, at this phase of the growing season the relationship is reversed, and growth from May 24 to July 6 is negatively correlated with altitude, and positively with the index of the vegetative period (Table 20).

The strongest correlation between growth and factors of the environment is that between the index of the vegetative period and growth on June 20 (Table 20).

Percent flushed on the dates assessed is correlated with other measurements of growth, but these correlations are considerably weaker than the correlations between dormancy and the same measurements (Table 22).

Seventeen of the variables assessed in the 150 provenances at Cowichan Lake were subjected to principal component analysis. These variables

are listed in Tables 22 and 23, and identified in Table 2. The results of the analysis are given in Tables 22 to 24 inclusive.

Table 22 shows the degree to which these 17 variables are correlated. It is obvious from this table that many of the 17 variables are highly correlated, and that a much smaller number of "fundamental dimensions" (Gardiner and Jeffers 1963) could account for a high percentage of the total variation measured.

Table 24 gives the percentage of variation accounted for by each of four new variates. These new variates or components, are based on the matrix of correlation coefficients given in Table 22. The first component alone accounts for 57.85 percent of the original variation, and all four components account for 87 percent of the variation.

Table 23 gives the weighting for the original variables in the computed components. From this table it is possible, to a considerable extent, to assign biological significance to at least the first two components, which between them account for 72.77 percent of the total variation.

Referring to Table 23 it is clear that measurements of dormancy, and associated measurements of growth (variables 3, 6, 14, 15, 16, 17 in Table 23) are strongly represented in the first component and that dormancy is one of the most significant measurements made in elucidating the variation pattern in immature spruce populations. A measurement of flushing is strongly represented in the second component (variable 4 in Table 23). The third component is not easily identified, but measurements of germination rate appear to be incorporated in the fourth component.

GROWTH BEHAVIOUR OF THE 12 PROVENANCES SOWN IN THE SPRING OF 1964.

Growth behaviour of the 12 provenances sown in the spring of 1964 in the Cowichan Lake nursery was significantly different in the first year at the 0.01 level of probability, and there was no interaction between the

differential growth response of the 12 provenances and soil type. On the prepared soil the 12 provenances, segregated according to growth response, formed two intergrading groups. Group one comprised high-elevation provenances from southern latitudes, and group two low elevation provenances from northern latitudes (Fig. 6).

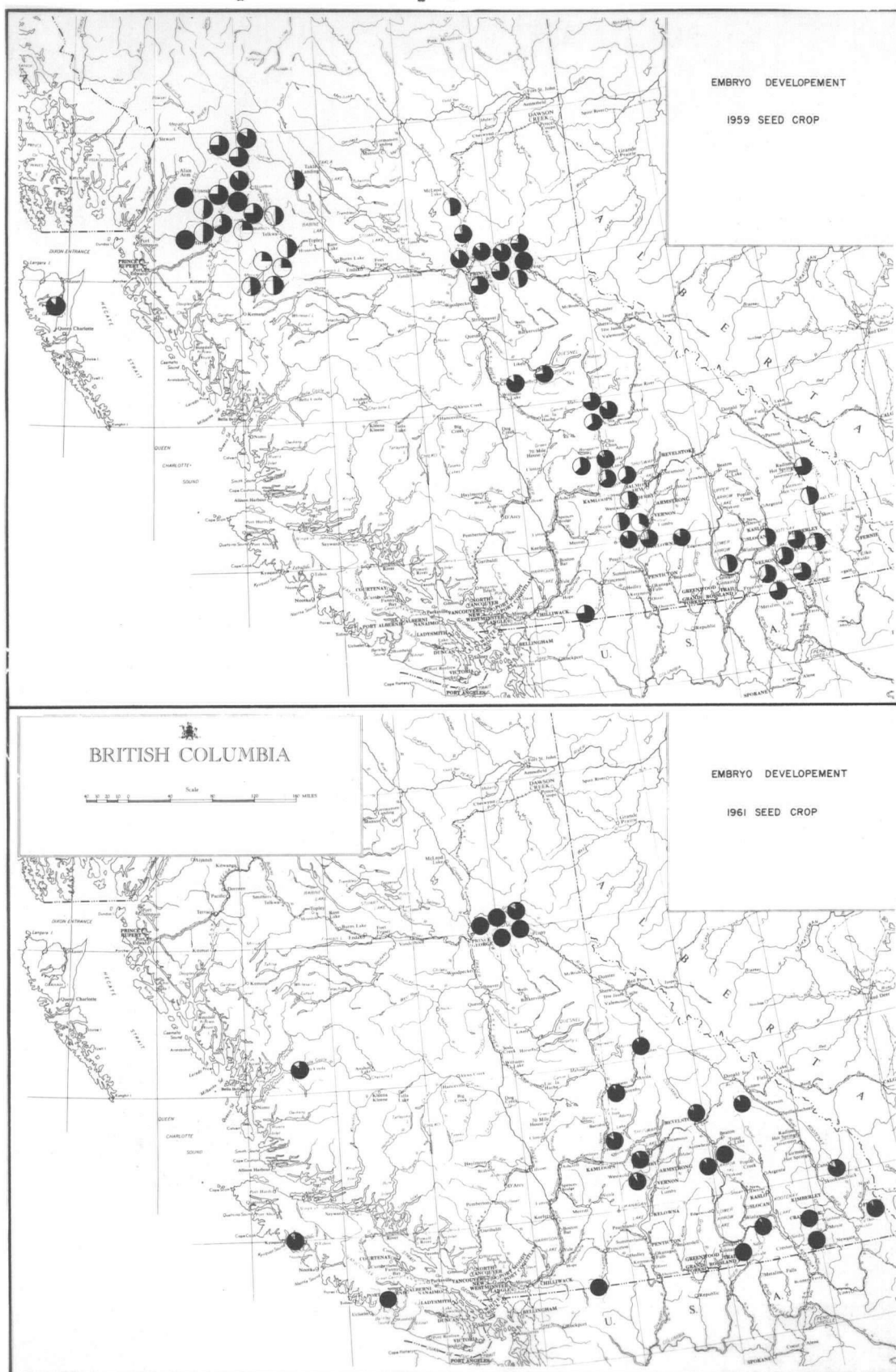
Maximum differences between provenances occurred in the greenhouse on the local soil during the second growing season. Growth rate during the second growing season is illustrated in Fig. 7, and differences in total growth between high and low elevation provenances in the greenhouse is shown in Illus. 4. Table 13 gives the means of flushing and dormancy measurements made in the second year.



Illus. 4. The differential growth behaviour of spruce populations from different elevations when grown in a plastic greenhouse on regular nursery soil.

- 2 - 30 miles northeast of Prince George, elev. 2200 ft.
- 8 - 40 miles north of Prince George, elev. 2300 ft.
- 1 - 30 miles southeast of Nelson, elev. 4000 ft.
- 5 - 25 miles northwest of Nelson, elev. 5700 ft.

Fig. 4 Variation in embryo development in a number of provenances from two spruce seed crops.



Note the uniform quality of the 1961 crop in relation to the heterogeneity of the 1959 crop. A completely occluded circle indicates that the seed has an embryo development of 100% class IV. (See Illus. 2)

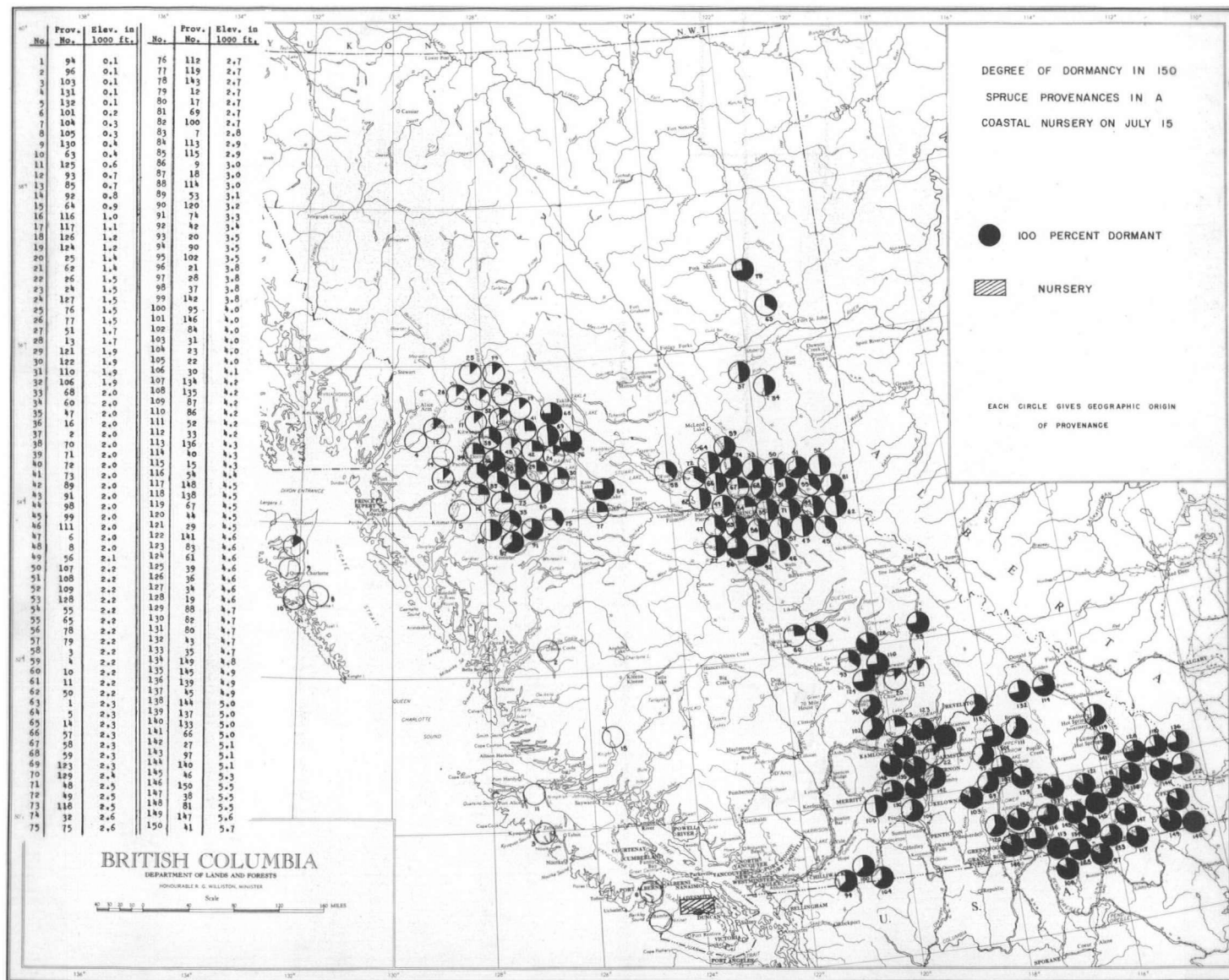


Fig. 5 Relationship between degree of dormancy at the Cowichan Nursery on July 15 and altitude at place of origin of each provenance. Note that high elevation provenances go dormant first, then low elevation provenances followed by those from areas of coastal influence, e.g. the Nass and Sheena river basins.

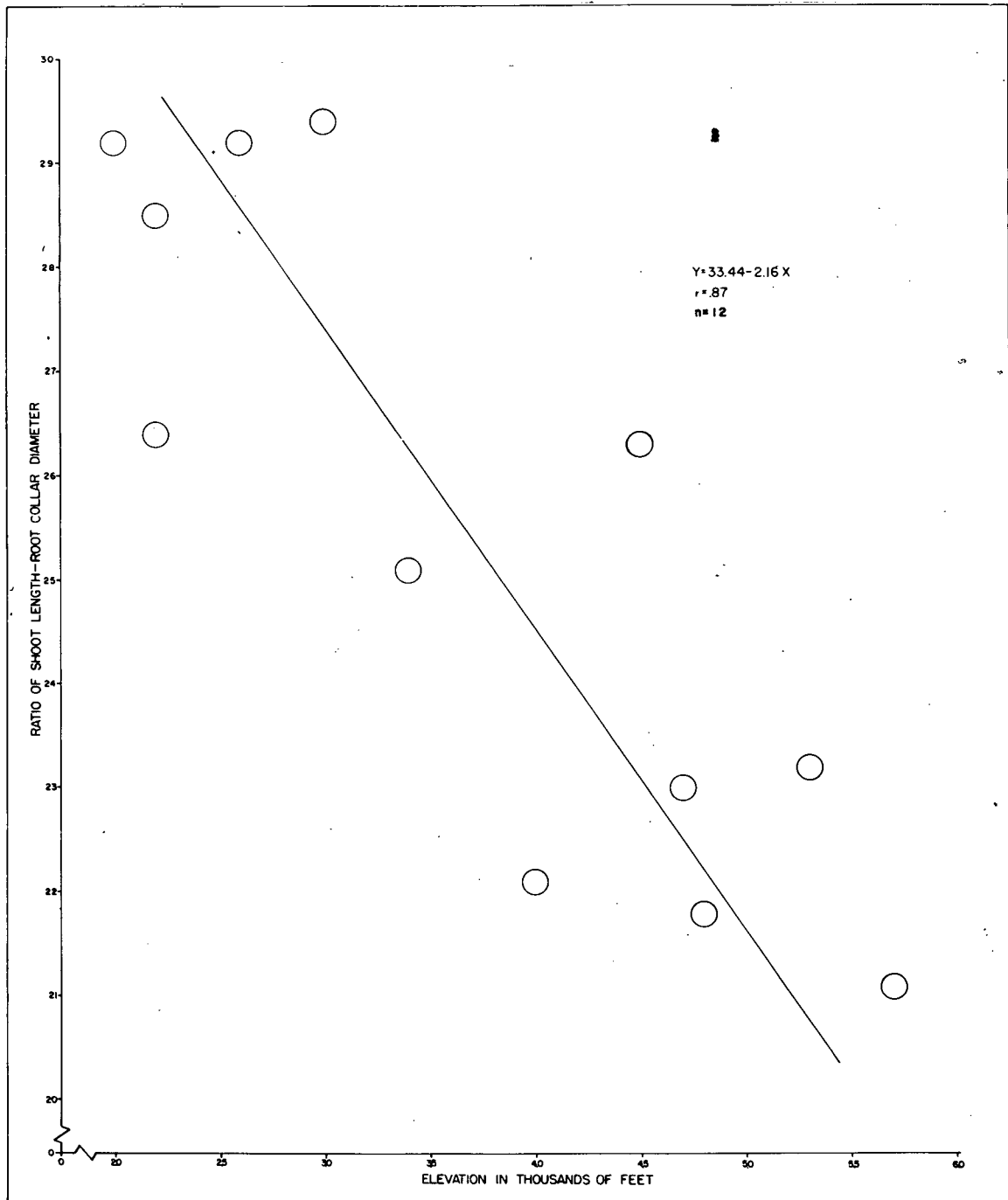


Fig. 6 Relationship between growth of 12 spruce provenances in a uniform environment and elevation at place of origin. Each point on the curve represents the mean of 20 1-year-old seedlings.

89



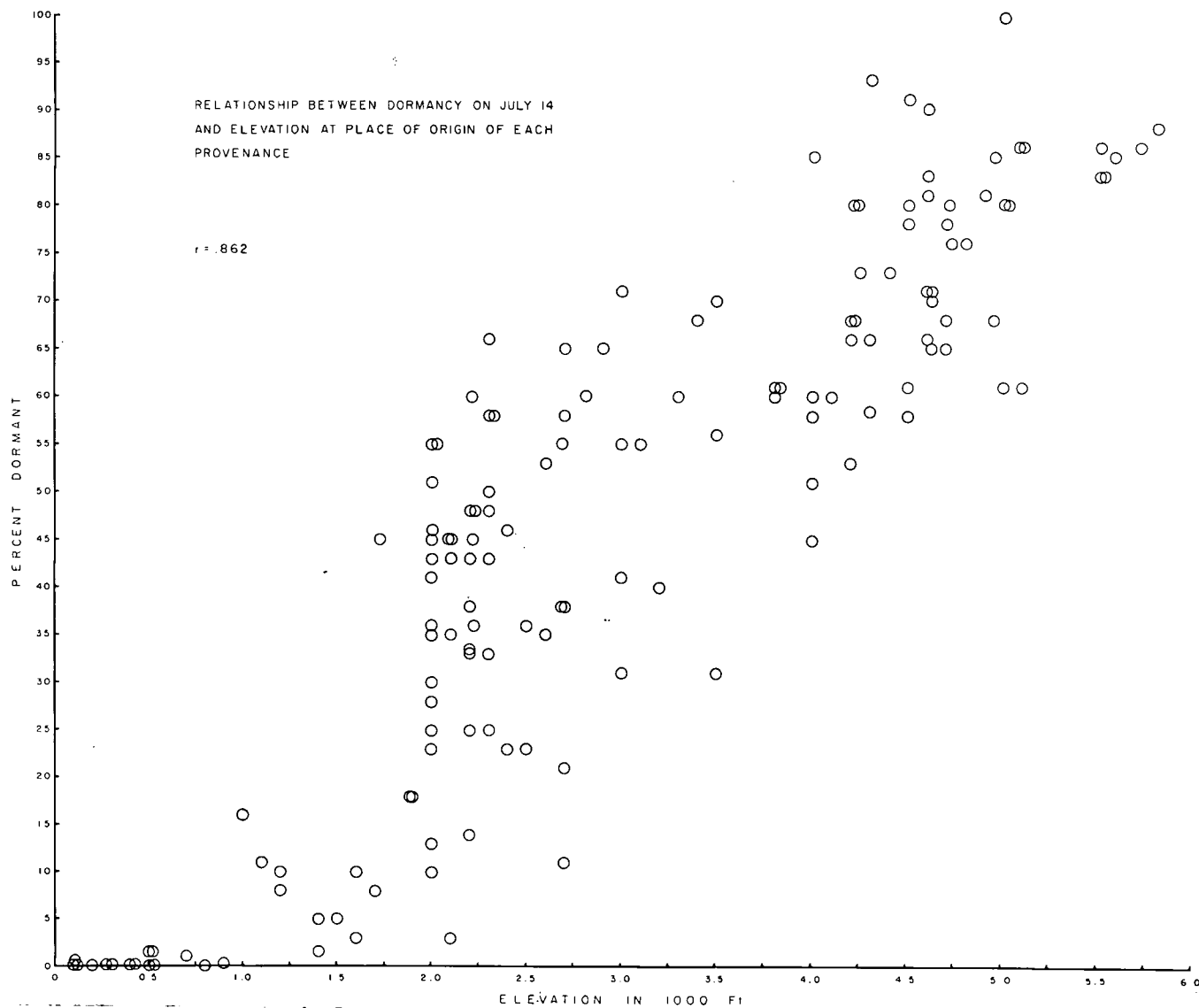


Fig. 8 Relationship between altitude at place of origin and degree of dormancy of each provenance on July 14 at the Cowichan nursery. Each point on the curve is the mean of 60 seedlings. A seedling was scored as dormant when the terminal needles of the epycotil were stiff and whorled, and a terminal bud visible. It is obvious that a more sophisticated method of assessing dormancy would reveal an even stronger relationship with altitude. Two provenances of uncertain origin have not been included in this graph.

TABLE 8
SEED CHARACTERISTICS OF 150 SPRUCE PROVENANCES ARRANGED IN ORDER OF
INCREASING EMBRYO DEVELOPMENT

No.	Prov. No.	Reg. No.	Elev. in 1000 ft.	FSP	ED		SW gms.	SA years
					C III	C IV		
1	133	545	5.0	84.5	14.3	0.3	0.169	2
2	68	325	2.0	70.5	5.0	14.0	0.128	7
3	75	373	2.6	23.0	3.3	14.3	0.137	7
4	114	790	3.0	75.3	4.5	16.3	0.155	4
5	125	801	0.6	20.3	0.3	20.0	0.136	4
6	129	808	2.4	28.3	1.5	25.3	0.150	4
7	145	641	4.9	69.0	32.8	27.8	0.149	2
8	137	888	5.0	59.5	19.8	29.5	0.155	2
9	140	541	5.1	86.3	36.8	30.0	0.196	2
10	72	366	2.0	43.3	5.0	33.0	0.139	7
11	81	394	5.5	86.5	33.5	33.0	0.174	7
12	127	806	1.5	41.0	3.5	33.8	0.129	4
13	128	807	2.2	38.5	2.8	35.3	0.140	4
14	66	336	5.0	91.0	7.8	38.0	0.177	7
15	134	576	4.2	48.0	5.8	38.0	0.198	2
16	73	369	2.0	49.0	2.3	40.0	0.117	7
17	85	426	0.7	47.8	0.5	40.0	0.162	7
18	43	898	4.7	86.3	25.3	41.0	0.174	2
19	42	773	3.4	55.5	3.8	41.3	0.186	4
20	23	147	4.0	81.5	8.3	41.5	0.211	9
21	135	858	4.2	44.0	0.5	41.8	0.194	2
22	124	800	1.2	47.0	2.5	42.3	0.140	4
23	41	337	5.7	90.0	18.0	43.0	0.184	7
24	18	356	3.0	56.8	9.5	43.0	0.160	7
25	4	493	2.2	53.0	3.0	44.0	0.167	7
26	14	370	2.3	57.0	9.5	44.0	0.204	7
27	150	857	5.5	68.8	9.0	44.3	0.187	2
28	74	371	3.3	85.8	17.3	44.3	0.150	7
29	121	797	1.9	50.5	1.0	45.5	0.111	4
30	71	365	2.0	55.3	1.5	45.5	0.176	7
31	144	635	5.0	85.5	22.0	47.8	0.193	2
32	61	66	4.6	85.3	28.5	48.0	0.216	9
33	82	395	4.7	59.5	7.5	48.3	0.165	7
34	64	284	0.9	53.3	2.5	49.0	0.135	8
35	139	540	4.9	87.0	25.3	50.5	0.190	2
36	17	374	2.7	57.5	1.5	50.5	0.134	7
37	147	654	5.6	94.5	32.8	51.5	0.202	2
38	148	655	4.5	55.8	1.8	51.5	0.175	2
39	45	338	4.9	76.3	8.5	52.5	0.105	7
40	87	430	4.2	94.8	28.0	52.8	0.172	7
41	119	795	2.7	62.0	7.5	53.0	0.169	4
42	138	539	4.5	88.0	30.3	54.0	0.185	2
43	120	796	3.2	99.0	17.8	55.0	0.172	4
44	37	344	3.8	64.0	2.0	56.3	0.169	7
45	79	390	2.2	92.3	2.5	56.3	0.202	7
46	149	657	4.8	92.3	28.5	57.5	0.218	2
47	88	447	4.7	89.8	23.0	57.5	0.172	7
48	104	766	0.3	62.8	1.3	59.0	0.158	4
49	22	150	4.0	69.8	4.5	59.0	0.197	9
50	70	364	2.0	85.3	12.8	60.8	0.139	7
51	141	542	4.6	91.0	22.5	61.8	0.188	2
52	20	427	3.5	75.0	1.3	62.3	0.127	7
53	39	345	4.6	80.8	9.3	63.0	0.206	7
54	83	416	4.6	94.0	18.5	63.3	0.164	7
55	84	417	4.0	66.5	2.0	63.3	0.131	7
56	38	341	5.5	88.5	14.8	64.0	0.186	7
57	122	798	1.9	78.5	6.3	64.5	0.168	4
58	67	340	4.5	85.0	10.5	65.8	0.168	7
59	118	794	2.5	81.3	3.3	66.5	0.200	4
60	136	868	4.3	75.0	5.5	67.0	0.186	2
61	111	780	2.0	80.3	1.8	67.3	0.117	4
62	9	388	3.0	84.3	9.8	67.3	0.183	7
63	69	359	2.7	86.0	10.0	68.3	0.146	7
64	32	387	2.6	86.3	12.8	68.5	0.196	7
65	62	905	1.4	77.0	2.3	68.5	0.183	2
66	8	353	2.0	74.0	2.0	68.8	0.166	7
67	108	771	2.2	82.8	4.0	69.0	0.156	4
68	28	334	3.8	88.8	9.0	69.5	0.180	7
69	80	392	4.7	96.5	16.0	70.0	0.164	7
70	146	644	4.0	74.5	1.5	70.8	0.195	2
71	115	791	2.9	97.8	8.0	71.8	0.191	4
72	29	343	4.5	83.8	4.3	72.3	0.173	7
73	12	380	2.7	80.0	5.0	72.3	0.173	7
74	109	772	2.2	81.0	2.8	72.5	0.130	4
75	46	335	5.3	83.5	4.5	73.0	0.185	7
76	78	389	2.2	93.0	2.8	73.3	0.166	7
77	126	805	1.2	81.5	5.5	73.8	0.202	4
78	19	429	4.6	98.5	17.8	74.0	0.184	7
79	113	789	2.9	96.0	12.5	75.5	0.194	4
80	3	42	2.2	78.0	1.8	75.8	0.209	10
81	77	382	1.5	85.3	5.5	76.3	0.171	7
82	130	809	0.4	81.8	2.3	76.5	0.211	4
83	57	43	2.3	86.3	3.8	77.3	0.212	10
84	44	732	4.5	96.3	1.3	77.5	0.200	5
85	16	367	2.0	92.3	8.0	77.5	0.142	7
86	59	47	2.3	80.5	1.5	78.0	0.206	10
87	60	49	2.0	85.3	2.8	78.8	0.190	10
88	11	523	2.2	82.8	2.0	79.0	0.142	7
89	110	777	1.9	94.0	4.0	79.8	0.186	4
90	76	379	1.5	86.3	4.5	79.8	0.168	7
91	112	784	2.7	97.8	11.0	80.5	0.177	4
92	90	488	3.5	87.3	4.5	80.8	0.216	7
93	107	770	2.2	89.8	2.8	80.8	0.139	4
94	142	575	3.8	86.8	3.8	80.8	0.212	2
95	132	464	0.1	91.8	5.3	81.3	0.134	2
96	106	769	1.9	89.3	2.0	82.0	0.162	4
97	143	623	2.7	94.8	6.5	82.3	0.200	2
98	47	779	2.0	96.3	1.8	82.5	0.182	4
99	86	428	4.2	96.3	7.8	83.5	0.170	7
100	58	46	2.3	87.8	3.3	83.5	0.269	8
101	48	385	2.5	89.0	2.0	84.0	0.164	7
102	94	529	0.1	98.8	2.3	84.0	0.195	7
103	15	737	4.3	87.8	1.0	84.8	0.233	5
104	96	692	0.1	93.0	3.3	84.8	0.224	5
105	10	522	2.2	91.8	2.3	84.8	0.147	7
106	5	494	2.3	93.0	3.5	85.0	0.168	7
107	13	358	1.7	89.5	2.8	85.0	0.159	7
108	24	741	4.2	92.0	2.3	85.3	0.236	5
109	1	50	2.3	90.3	3.0	85.3	0.204	10
110	123	779	2.3	96.8	6.3	85.8	0.182	4
111	30	393	4.1	93.3	3.5	86.5	0.181	7
112	31	346	4.0	98.5	4.8	86.5	0.193	7
113	50	431	2.2	93.3	1.8	86.5	0.176	7
114	89	454	2.0	97.0	6.3	87.0	0.194	7
115	51	41	1.7	90.8	1.5	87.0	0.224	10
116	21	418	3.8	97.3	6.0	87.5	0.140	7
117	6	746	2.0	90.5	1.8	87.5	0.192	5
118	36	701	4.6	94.8	1.5	87.8	0.197	5
119	55	37	2.2	91.3	2.3	88.3	0.206	10
120	116	792	1.0	98.5	4.5	88.5	0.189	4
121	54	715	4.4	95.5	2.5	88.8	0.212	5
122	117	793	1.1	94.8	3.8	89.3	0.201	4
123	92	525	0.8	93.3	1.8	89.5	0.185	7
124	34	710	4.6	95.3	3.3	90.0	0.204	5
125	2	48	2.0	93.8	2.5	90.0	0.215	8
126	56	39	2.1	95.3	2.8	90.3	0.205	10
127	91	499	2.0	97.8	3.8	90.3	0.173	7
128	26	738	4.2	98.3	1.5	91.3	0.232	5
129	25	740	1.4	96.0	1.8	91.3	0.233	5
130	105	767	0.3	99.3	3.3	91.8	0.242	4
131	40	709	4.3	96.5	1.0	92.0	0.189	5
132	103	748	0.1	94.3	0.8	92.5	0.203	5
133	27	720	5.1	98.0	2.0	92.8	0.193	5
134	53	240	3.1	97.8	2.5	93.5	0.252	8
135	97	703	5.1	98.8	3.3	93.5	0.220	5
136	35	699	4.7	99.3	1.8	93.8	0.218	5
137	102	745	3.5	98.3	2.8	93.8	0.203	5
138	49	51	2.5	96.8	1.8	93.8	0.175	10
139	52	725	4.2	99.3	3.5	94.0	0.235	5
140	33	747	4.2	98.8	1.8	94.0	0.217	5
141	7	722	2.8	97.8	1.8	94.0	0.193	5
142	63	281	0.4	100.0	3.0	94.0	0.283	8
143	131	840	0.1	98.8	3.8	94.0	0.172	4
144	98	718	2.0	98.8	2.0	94.0	0.187	5
145	101	742	0.2	97.8	1.8	94.3	0.256	5
146	95	691	4.0	97.8	1.8	94.5	0.276	5
147	65	296	2.2	99.3	3.0	94.8	0.264	9
148	99	719	2.0	97.3	1.3	95.0	0.171	5
149	100	723	2.7	99.3	2.0	95.8	0.204	5
150	93	526	0.7	99.0	2.3	95.8	0.195	7

FSP - full seed percent; ED - embryo development; C III - percent embryo class III (embryo measures between half and three quarters embryo cavity); C IV - percent embryo class IV (embryo completely occupies embryo cavity); SA - seed age; SW - seed weight is the average of 4 replications of 100 seeds.

TABLE 9
GROWTH BEHAVIOUR DURING THE FIRST YEAR IN THE NURSERY

Prov.	Reg.	Lat.	Long.	Elev.	Days	S.L.	R.C.D.	S.L./R.C.D.	Dry Wt.
No.	No.					(cm)	(cm)		(gm)
1	50	56.50	121.10	2.3	73	6.9	.133	52.90	1.77
2	48	55.67	122.20	2.0	85	7.4	.142	52.21	2.06
3	42	54.50	121.25	2.2	88	7.6	.141	54.86	1.99
4	493	54.50	122.67	2.2	88	7.7	.150	51.95	2.15
5	494	54.33	122.67	2.3	87	7.8	.154	51.12	2.22
6	746	54.10	122.05	2.0	95	9.0	.163	55.38	2.80
7	722	54.07	121.45	2.8	77	8.9	.160	55.99	2.59
8	353	54.93	127.42	2.0	90	8.1	.142	58.17	2.01
9	388	53.67	122.42	3.0	75	7.9	.158	49.81	2.29
10	522	52.33	121.67	2.2	102	7.9	.143	55.23	2.04
11	523	52.42	121.42	2.2	101	8.0	.149	54.12	2.03
12	380	55.60	127.83	2.7	70	7.1	.146	49.38	1.87
13	358	55.47	127.83	1.7	93	8.3	.152	54.69	2.14
14	370	55.33	126.63	2.3	80	7.8	.154	51.43	2.13
15	737	51.12	118.25	4.3	62	8.5	.174	48.79	2.64
16	367	54.93	127.42	2.0	90	6.5	.129	50.75	1.39
17	374	54.45	126.90	2.7	77	6.3	.125	50.24	1.42
18	356	54.13	127.15	3.0	76	6.6	.168	49.81	1.88
19	429	51.37	120.17	4.6	51	7.1	.159	44.00	2.02
20	427	51.70	120.17	3.5	76	7.3	.145	50.63	1.73
21	418	51.17	120.25	3.8	73	7.2	.152	47.18	1.86
22	150	49.92	120.58	4.0	76	8.7	.168	52.03	2.66
23	147	49.17	120.58	4.0	81	7.8	.174	44.91	2.43
24	741	50.87	119.83	4.2	66	10.8	.185	58.13	3.65
25	740	51.62	119.83	1.4	125	11.2	.178	63.74	3.27
26	738	50.70	119.50	4.2	67	10.8	.173	63.30	3.20
27	720	50.48	119.75	5.1	48	7.4	.159	46.45	2.09
28	334	49.00	116.75	3.8	87	6.8	.157	42.99	1.77
29	343	49.02	116.27	4.5	65	7.6	.163	46.79	2.07
30	393	49.92	119.77	4.1	74	9.9	.183	54.54	3.01
31	346	49.92	118.58	4.0	76	8.6	.168	54.45	2.84
32	387	49.37	122.50	2.6	80	8.1	.155	52.11	2.18
33	747	49.33	117.25	4.2	76	8.2	.158	52.88	2.27
34	710	49.37	114.58	4.6	66	7.1	.157	44.74	2.00
35	699	49.17	116.13	4.7	65	8.6	.173	49.77	2.56
36	701	50.13	115.43	4.6	61	9.0	.176	51.55	2.80
37	344	49.58	115.98	3.8	83	8.8	.176	50.26	2.58
38	341	49.30	116.00	5.5	46	6.9	.156	44.99	1.84
39	345	49.08	116.75	4.6	68	7.8	.178	43.61	2.41
40	709	51.13	117.08	4.3	62	8.0	.175	45.45	2.54
41	337	49.58	117.80	5.7	40	7.6	.170	44.11	2.15
42	773	53.33	122.17	3.4	68	8.5	.168	50.39	2.59
43	898	51.12	117.25	4.7	53	7.9	.170	46.46	2.27
44	732	49.42	118.03	4.5	68	8.5	.163	51.29	2.78
45	338	49.75	117.00	4.9	57	7.3	.172	42.40	2.17
46	335	49.33	116.13	5.3	51	6.9	.155	44.68	1.75
47	779	54.10	122.05	2.0	95	8.0	.156	51.74	2.13
48	385	54.25	122.25	2.5	83	8.4	.159	52.93	2.38
49	51	54.33	123.08	2.5	82	8.8	.168	52.74	2.76
50	431	54.12	122.83	2.2	90	8.1	.155	52.72	2.24
51	41	53.42	122.67	1.7	106	8.3	.157	53.71	2.46
52	725	50.65	117.53	4.2	67	7.1	.163	43.08	2.03
53	240	50.17	118.00	3.1	95	6.9	.156	43.50	2.15
54	715	49.48	117.23	4.4	70	8.1	.169	47.85	2.38
55	37	54.08	122.05	2.2	91	7.0	.129	54.36	1.79
56	39	54.08	122.05	2.1	93	8.8	.162	54.18	2.64
57	43	54.28	122.63	2.3	87	8.6	.162	53.29	2.62
58	46	54.08	122.08	2.3	88	8.0	.166	48.90	2.52
59	47	54.08	122.08	2.3	88	8.7	.172	51.41	2.21
60	49	55.50	121.58	2.0	86	6.9	.136	50.59	1.74
61	66	51.67	120.17	4.6	52	5.5	.120	44.69	1.22
62	905	51.58	119.85	1.4	125	11.0	.165	66.78	3.01
63	281	53.10	132.05	.4	138	12.2	.187	65.87	3.37
64	284	51.18	125.57	.9	139	10.8	.178	60.95	2.88
65	296	54.17	122.17	2.2	90	8.1	.151	53.79	2.38
66	336	50.25	115.75	5.0	52	7.7	.161	47.91	2.07
67	340	50.53	115.92	4.5	61	9.5	.177	45.54	2.68
68	355	54.23	127.37	2.0	94	6.0	.124	47.66	1.24
69	359	54.17	121.50	2.7	79	7.6	.147	51.74	2.00
70	364	54.93	127.42	2.0	90	8.1	.141	58.01	1.84
71	365	54.93	127.42	2.0	90	7.9	.141	55.66	2.01
72	366	54.93	127.42	2.0	90	6.8	.129	52.51	1.50
73	369	54.93	127.42	2.0	90	7.2	.129	56.29	1.71
74	371	54.10	127.20	3.3	66	6.9	.136	50.91	1.77
75	373	54.08	127.25	2.6	82	6.4	.130	49.81	1.60
76	379	55.60	127.83	1.5	97	8.8	.153	53.09	2.42
77	382	55.60	127.83	1.5	97	8.7	.149	59.08	2.35
78	389	54.08	122.08	2.2	91	8.1	.150	54.23	2.19
79	390	54.08	122.08	2.2	91	8.1	.151	50.67	2.13
80	392	50.07	119.68	4.7	60	7.6	.162	47.18	2.14
81	394	50.02	119.70	5.5	42	6.4	.156	40.76	1.64
82	395	50.12	119.70	4.7	59	7.6	.163	47.09	2.05
83	416	50.85	119.87	4.6	57	7.7	.165	46.35	2.20
84	417	51.23	120.25	4.0	68	7.9	.150	52.34	2.10
85	426	54.67	128.75	.7	121	10.0	.168	60.74	2.65
86	428	51.73	120.08	4.2	60	6.8	.151	45.16	1.81
87	430	50.67	119.58	4.2	67	7.1	.157	45.44	1.85
88	447	51.00	119.87	4.7	54	7.2	.159	44.82	2.01
89	454	54.93	127.42	2.0	90	8.6	.155	55.78	2.45
90	488	49.07	120.88	3.5	93	8.0	.161	47.82	2.24
91	499	54.08	122.33	2.0	95	8.2	.162	50.61	2.53
92	525	54.75	128.75	.8	118	8.3	.149	56.58	2.04
93	526	55.08	128.33	.7	118	9.6	.164	59.10	2.45
94	529	53.67	132.33	.1	141	10.5	.172	60.44	2.93
95	681	49.12	120.88	4.0	82	8.4	.190	44.51	2.68
96	692	52.37	126.75	.1	149	10.1	.159	64.13	2.48
97	703	49.43	116.13	5.1	55	7.5	.177	41.93	2.44
98	718	54.18	122.12	2.0	95	8.8	.161	54.84	2.56
99	719	54.18	122.12	2.0	95	8.2	.164	50.68	2.58
100	723	54.25	121.92	2.7	78	8.3	.162	51.41	2.63
101	742	49.13	125.42	.2	168	13.9	.202	70.58	3.77
102	745	52.20	119.25	3.5	73	8.0	.178	44.43	2.59
103	748	50.05	127.05	.1	164	11.9	.178	61.31	3.07
104	766	48.83	124.75	.3	167	12.1	.184	66.45	3.41
105	767	53.08	132.08	.3	140	11.4	.178	63.88	3.09
106	769	54.17	122.17	1.9	97	7.9	.149	52.80	2.12
107	770	54.25	122.33	2.2	90	7.8	.152	51.69	2.21
108	771	54.25	122.33	2.2	90	8.2	.157	52.74	2.26
109	772	54.17	122.25	2.2	90	7.4	.147	51.07	2.06
110	777	54.17	122.17	1.9	97	8.2	.155	53.18	2.23
111	780	54.08	121.88	2.0	95	7.0	.134	52.21	1.72
112	784	54.88	126.73	2.7	74	7.6	.147	51.89	1.93
113	789	54.35	125.43	2.9	73	7.6	.144	53.07	1.97
114	790	54.07	127.22	3.0	73	7.6	.156	48.15	2.24
115	791	55.08	127.33	2.9	68	8.4	.154	54.77	2.09
116	792	55.13	127.40	1.0	111	9.6	.153	62.90	2.75
117	793	55.30	127.70	1.1	108	8.5	.127	61.33	1.81
118	794	54.63	127.20	2.5	80	8.4	.160	56.90	2.53
119	795	54.12	125.42	2.7	79	8.7	.152	57.26	2.32
120	796	55.00	127.00	3.2	62	7.6	.145	52.80	1.98
121	797	54.80	129.03	1.9	93	8.8	.154	57.10	2.26
122	798	54.75	127.00	1.9	93	9.1	.158	57.77	2.44
123	799	55.03	126.50	2.3	82	7.6	.144	53.20	1.85
124	800	55.28	127.40	1.2	106	9.3	.153	61.15	2.36
125	801	50.53	127.25	.6	150	12.5	.191	65.87	3.61
126	805	55.47	127.70	1.2	105	10.1	.151	67.12	2.60
127	806	54.90	127.25	1.5	101	7.9	.138	57.64	1.92
128	807	55.30	127.15	2.2	83	9.0	.151	59.89	2.25
129	808	54.67	127.25	2.4	82	8.9	.155	57.45	2.55
130	809	53.50	132.25	.4	135	10.0	.165	60.24	2.62
131	840	55.08	129.42	.1	132	10.0	.163	61.62	2.50
132	464	54.05	128.65	.1	139	11.3	.167	67.90	2.79
133	545	49.05	114.67	5.0	59	4.6	.125	36.21	1.11

TABLE 10
GROWTH BEHAVIOUR DURING THE SECOND YEAR IN THE NURSERY

Prov. No.	Reg. No.	Lat.	Long.	Elev.	Days	S.L. (cm)	R.C.D. (cm)	Dry Wt. (gm)	Prov. No.	Reg. No.	Lat.	Long.	Elev.	Days	S.L. (cm)	R.C.D. (cm)	Dry Wt. (gm)		
1	50	56.50	121.10	2.3	73	15.0	.230	64.72	9.07	76	379	55.60	127.83	1.5	97	18.5	.293	65.60	13.23
2	48	55.67	122.20	2.0	95	15.5	.249	62.18	10.77	77	382	55.60	127.83	1.5	97	17.3	.263	55.65	11.63
3	42	54.50	124.25	2.2	88	14.4	.234	61.79	10.81	78	389	54.08	122.08	2.2	91	15.9	.249	63.91	9.42
4	493	54.50	122.67	2.2	88	15.0	.249	59.99	10.05	79	390	54.08	122.08	2.2	91	17.0	.283	60.80	12.58
5	494	54.33	122.67	2.3	87	15.4	.255	60.79	10.29	80	392	50.07	119.58	4.7	60	15.5	.265	58.61	10.19
6	746	54.10	122.05	2.0	95	16.9	.267	63.58	12.24	81	394	50.02	119.70	5.5	42	13.4	.238	56.03	7.35
7	722	54.07	121.45	2.3	77	17.2	.274	62.94	11.84	82	395	50.12	119.70	4.7	59	15.2	.263	57.69	9.51
8	353	54.93	127.42	2.0	90	16.0	.249	64.52	10.07	83	416	50.85	119.87	4.6	57	15.8	.265	59.79	9.86
9	388	53.67	122.42	3.0	75	15.8	.265	60.16	10.13	84	417	51.23	120.25	4.0	68	15.1	.246	60.55	9.19
10	522	52.33	121.67	2.2	102	16.1	.238	68.22	9.60	85	426	54.67	128.75	.7	121	19.1	.311	62.95	16.92
11	523	52.42	121.42	2.2	101	17.0	.257	66.17	10.57	86	428	51.73	120.08	4.2	60	12.4	.214	58.39	6.79
12	380	55.60	127.83	2.7	70	15.6	.277	56.73	11.19	87	430	50.67	119.58	4.2	67	15.3	.264	57.96	10.06
13	358	55.47	127.83	1.7	93	16.7	.261	64.49	11.53	88	447	51.00	119.87	4.7	54	15.1	.256	58.59	8.99
14	370	55.33	126.63	2.3	80	14.4	.238	60.22	8.70	89	454	54.93	127.42	2.0	90	17.0	.277	63.01	11.12
15	737	51.12	118.25	4.3	62	15.8	.270	58.89	11.53	90	488	49.07	120.88	3.5	93	15.5	.274	56.56	11.70
16	367	54.93	127.42	2.0	90	13.5	.231	58.59	7.36	91	499	54.08	122.33	2.0	95	16.9	.269	63.00	11.49
17	374	54.45	126.90	2.7	77	14.1	.235	59.98	8.45	92	525	54.75	128.75	.8	118	17.4	.293	59.46	14.12
18	356	54.13	127.15	3.0	72	15.8	.259	60.97	11.15	93	526	55.08	129.33	.7	118	17.3	.274	63.61	12.23
19	429	51.77	120.17	4.6	51	13.2	.240	54.02	8.09	94	529	53.67	132.33	.1	141	21.8	.362	60.10	25.19
20	427	51.70	120.17	3.5	76	16.5	.258	61.35	10.35	95	691	49.12	120.85	4.0	82	15.2	.278	54.24	11.92
21	418	51.17	120.25	3.8	73	14.7	.253	58.07	9.01	96	692	52.37	126.75	.1	149	19.4	.309	62.94	17.12
22	150	49.92	120.58	4.0	76	17.1	.278	61.71	12.72	97	703	49.43	116.13	5.1	55	14.5	.269	55.33	10.19
23	147	49.17	119.83	4.2	81	17.0	.298	57.08	13.95	98	718	54.18	122.12	2.0	95	16.2	.259	63.60	11.34
24	741	50.87	119.83	4.2	66	20.0	.287	70.10	15.20	99	719	54.18	122.12	2.0	95	16.8	.269	62.07	12.98
25	740	51.62	119.83	1.4	125	15.8	.288	72.36	15.71	100	723	54.25	121.92	2.7	78	17.5	.285	61.89	14.15
26	738	50.70	119.58	4.2	67	11.3	.297	72.08	16.73	101	742	49.13	125.42	.2	168	22.7	.346	66.10	23.05
27	720	50.38	119.75	5.1	48	16.1	.270	59.00	11.12	102	745	52.20	119.25	3.5	73	15.2	.281	54.19	12.52
28	334	49.00	116.75	3.8	87	13.8	.249	55.43	8.21	103	748	50.05	127.05	.1	164	21.4	.319	67.21	19.16
29	343	49.82	116.27	4.5	66	15.0	.258	59.56	9.30	104	766	48.83	124.75	.3	167	21.7	.336	64.39	19.02
30	393	49.92	119.77	4.1	74	17.8	.287	62.26	13.91	105	767	53.08	132.08	.3	140	20.8	.331	62.72	19.23
31	346	49.92	118.58	4.0	76	16.3	.263	61.56	10.13	106	769	54.17	122.17	1.9	97	15.4	.259	60.15	10.55
32	387	54.37	122.50	2.6	80	15.8	.250	63.44	9.55	107	770	54.25	122.33	2.2	90	15.8	.261	61.25	10.79
33	747	49.33	117.25	4.2	76	16.4	.256	64.17	10.96	108	771	54.25	122.33	2.2	90	16.2	.257	63.22	9.62
34	710	49.37	114.58	4.6	66	13.8	.281	54.33	9.21	109	772	54.17	122.25	2.2	90	14.7	.248	59.42	10.04
35	699	49.17	116.13	4.7	65	16.1	.251	57.77	12.36	110	777	54.17	122.17	1.9	97	15.9	.250	63.73	9.46
36	701	50.13	115.43	4.6	61	17.6	.281	63.59	13.33	111	780	54.08	121.88	2.0	95	15.3	.259	61.92	9.54
37	344	49.55	115.98	3.8	83	17.9	.280	64.15	12.71	112	784	54.88	126.73	2.7	74	15.0	.236	63.44	8.24
38	341	49.30	116.00	5.5	46	14.5	.244	59.36	8.02	113	789	54.35	125.43	2.9	73	14.6	.234	62.94	7.89
39	345	49.08	116.75	4.6	68	15.8	.284	55.89	12.19	114	790	54.07	127.22	3.0	73	15.5	.257	60.51	10.07
40	709	51.13	117.08	4.3	62	16.1	.275	58.53	11.81	115	791	55.08	127.33	2.9	68	17.5	.276	63.49	10.70
41	337	49.58	117.30	5.7	40	15.2	.266	57.46	9.78	116	792	55.13	127.40	1.0	111	19.4	.284	68.60	13.45
42	773	53.33	122.17	3.4	68	15.8	.263	60.47	10.60	117	793	55.30	127.70	1.1	108	15.7	.229	68.64	8.21
43	898	51.12	117.25	4.7	53	16.9	.285	59.55	12.90	118	794	54.63	127.20	2.5	80	16.2	.263	61.56	12.19
44	732	49.42	118.03	4.5	68	16.5	.275	59.84	12.76	119	795	54.12	125.42	2.7	79	17.8	.257	68.97	11.28
45	338	49.75	117.00	4.9	57	14.9	.272	54.60	10.38	120	796	55.00	127.00	3.2	62	17.3	.267	66.02	12.21
46	335	49.33	116.13	5.3	51	14.2	.252	56.23	7.83	121	797	54.80	129.03	1.9	93	17.9	.271	66.49	12.12
47	779	54.10	122.05	2.0	95	15.8	.256	63.69	10.81	122	798	54.75	127.00	1.9	93	17.4	.273	63.70	11.30
48	385	54.25	122.25	2.5	83	18.0	.276	65.63	13.10	123	799	55.03	126.50	2.3	82	17.6	.267	66.32	11.15
49	51	54.33	123.08	2.5	82	18.1	.283	63.89	13.72	124	800	55.28	127.40	1.2	106	18.0	.264	67.80	11.00
50	431	54.12	122.83	2.2	90	16.7	.262	63.97	11.01	125	801	50.53	127.25	.6	150	24.1	.367	66.13	25.49
51	41	53.42	122.67	1.7	106	16.8	.260	64.30	11.07	126	805	55.47	127.70	1.2	105	18.9	.272	69.08	11.40
52	725	50.65	117.73	4.2	67	14.5	.251	57.12	9.21	127	806	54.90	127.25	1.5	101	15.4	.239	64.42	9.34
53	240	50.17	118.00	3.1	95	14.2	.264	53.41	12.12	128	807	55.30	127.15	2.2	83	17.5	.262	66.75	11.10
54	715	49.48	117.23	4.4	70	16.0	.283	57.09	11.77	129	808	54.67	127.25	2.4	82	18.0	.277	64.12	12.87
55	37	54.08	122.05	2.2	91	14.8	.246	59.94	11.28	130	809	53.50	132.25	.4	135	20.2	.340	60.10	21.00
56	39	54.08	122.05	2.1	93	15.9	.260	61.38	11.19	131	840	55.08	129.42	.1	132	19.4	.309	62.62	15.91
57	43	54.28	122.62	2.3	87	17.1	.264	65.44	11.65	132	844	54.05	128.65	.1	139	22.1	.342	65.27	19.48
58	46	54.08	122.08	2.3	88	16.6	.278	59.91	13.08	133	845	49.05	114.67	5.0	59	10.2	.209	48.13	5.55
59	47	54.08	122.08	2.3	88	16.8	.273	62.09	12.39	134	876	50.25	117.83	4.2	70	16.2	.272	59.46	11.40
60	49	55.50	121.58	2.0	86	14.8	.241	60.25	9.84	135	859	49.00	116.67	4.2	78	18.3	.289	63.86	13.93
61	66	51.67	120.17	4.6	52	12.2	.222	53.25	7.80	136	865	49.05	116.97	4.3	75	16.2	.269	60.11	10.79
62	905	51.58	119.85	1.4	125	20.6	.284	73.05	15.37	137	888	50.08	117.75	5.0	53	13.8	.262	52.96	9.27
63	281	50.13	132.05	.4	138	24.2	.359	68.35	23.08	138	539	49.92	114.77	4.5	65	16.5	.260	63.19	9.62
64	284	51.18	125.57	.9	139	20.2	.323	63.02	18.17	139	540	49.92	114.92	4.9	56	12.7	.230	54.35	7.76
65	296	54.17	122.17	2.2	90	16.0	.262	61.04	11.86	140	541	49.92	114.73	5.1	51	12.5	.239	51.93	8.46
66	335	50.25	115.75	5.0	52	14.0	.240	58.04	8.08	141	542	49.92	114.75	4.6	63	16.0	.251	63.65	9.30
67	340	50.53	115.92	4.5	61	18.1	.271	67.39	12.33	142	575	50.25</							

TABLE 11
PERCENT FLUSHED ON 4 DIFFERENT DATES DURING THE SECOND YEAR IN THE NURSERY

Prov. No.	Reg. No.	Lat.	Long.	Elev.	Days	Apr. 6	Apr. 14	Apr. 20	Apr. 27
1	50	56.50	121.10	2.3	73	10.0	63.3	95.0	100.0
2	48	55.67	122.20	2.0	85	3.3	55.0	91.7	100.0
3	42	54.50	124.25	2.2	88	11.7	71.7	93.3	100.0
4	493	54.50	122.67	2.2	88	3.3	48.3	81.7	95.0
5	494	54.33	122.67	2.3	87	3.3	38.3	81.7	96.7
6	746	54.10	122.05	2.0	95	1.7	36.7	76.7	95.0
7	722	54.07	121.45	2.8	77	0.0	31.7	80.0	100.0
8	353	54.93	127.42	2.0	90	3.3	41.7	85.0	100.0
9	388	53.67	122.42	3.0	75	0.0	18.3	63.3	95.0
10	522	52.33	121.67	2.2	102	3.3	51.7	96.7	98.3
11	523	52.42	121.42	2.2	101	10.0	55.0	96.7	100.0
12	350	55.60	127.53	2.7	70	0.0	23.3	75.0	66.7
13	358	55.37	127.53	1.7	93	0.0	35.0	81.7	98.3
14	370	55.33	126.53	2.3	80	3.3	48.3	96.7	98.3
15	737	51.12	118.25	4.3	62	5.0	26.7	76.7	96.7
16	367	54.93	127.42	2.0	90	1.7	58.3	96.7	98.3
17	374	54.45	126.90	2.7	77	10.0	55.0	90.0	98.3
18	356	54.13	127.15	3.0	72	0.0	33.3	86.7	100.0
19	429	51.77	120.17	4.6	51	3.3	18.3	76.7	95.0
20	427	51.70	120.17	3.5	76	3.3	45.0	93.3	95.0
21	418	51.17	120.25	3.8	73	1.7	33.3	68.3	95.0
22	150	44.92	120.58	4.0	76	1.7	38.3	88.3	96.7
23	147	46.17	120.58	4.0	91	0.0	20.0	73.3	96.7
24	741	50.87	119.83	4.2	66	6.7	50.0	95.0	100.0
25	740	51.62	119.83	1.4	125	3.3	45.0	90.0	98.3
26	738	50.70	119.53	4.2	67	13.3	61.7	95.0	100.0
27	720	50.48	119.75	5.1	48	0.0	13.3	63.3	95.0
28	334	49.00	116.75	3.8	87	1.7	35.0	80.0	95.0
29	343	49.82	116.27	4.5	66	0.0	23.3	81.7	95.0
30	393	49.92	119.77	4.1	74	0.0	30.0	73.3	91.7
31	346	49.92	118.58	4.0	76	0.0	18.3	81.6	96.7
32	387	54.37	122.50	2.6	80	1.7	38.3	90.0	98.3
33	747	49.33	117.25	4.2	76	5.0	35.0	78.3	98.3
34	710	46.37	114.58	4.5	66	3.3	30.0	76.7	95.7
35	699	49.17	116.13	4.7	65	0.0	30.0	75.0	95.0
36	701	50.13	115.43	4.6	61	5.0	45.0	85.0	100.0
37	344	49.58	115.98	3.8	83	6.7	48.3	88.3	96.6
38	341	49.30	116.00	5.5	46	0.0	13.3	73.3	95.7
39	345	49.78	116.75	4.5	69	5.0	21.7	68.3	91.7
40	799	51.13	117.08	4.3	62	3.3	31.7	73.3	95.0
41	337	49.58	117.80	5.7	40	3.3	16.7	76.7	96.7
42	773	53.33	122.17	3.4	68	1.6	11.7	71.7	93.3
43	898	51.12	117.25	4.7	53	6.7	41.7	75.0	96.7
44	732	49.42	118.03	4.5	68	1.7	21.7	83.3	100.0
45	338	49.75	117.00	4.9	57	6.7	41.7	85.0	93.3
46	335	49.33	116.13	5.3	51	0.0	16.7	78.3	98.3
47	779	54.10	122.05	2.0	95	13.3	56.7	88.3	95.0
48	385	54.25	122.25	2.5	83	1.7	38.3	78.3	98.3
49	51	54.33	123.08	2.5	82	0.0	46.7	88.3	96.7
50	431	54.12	122.83	2.2	90	3.3	56.7	91.7	98.3
51	41	53.42	122.57	1.7	106	10.0	65.0	90.0	98.3
52	725	50.55	117.53	4.2	67	5.0	46.7	88.3	95.0
53	240	50.17	118.00	3.1	95	15.0	48.3	85.0	96.7
54	715	49.48	117.23	4.4	70	3.3	30.0	75.0	96.7
55	37	54.08	122.05	2.2	91	6.7	56.7	91.7	98.3
56	39	54.08	122.05	2.1	93	3.3	51.7	88.3	93.3
57	43	54.28	122.62	2.3	87	1.7	50.0	86.7	100.0
58	46	54.08	122.08	2.3	88	3.3	51.7	93.3	98.3
59	47	54.08	122.08	2.3	88	18.3	46.7	90.0	98.3
60	49	55.50	121.58	2.0	84	3.3	28.3	91.7	100.0
61	66	51.67	120.17	4.6	52	3.3	25.0	86.7	93.3
62	905	51.58	119.85	1.4	125	3.3	51.7	86.7	98.3
63	281	53.10	132.05	4	138	1.7	46.7	90.0	100.0
64	284	51.18	125.57	9	139	3.3	56.7	95.0	100.0
65	296	54.17	122.17	2.2	90	6.7	43.3	83.3	100.0
66	336	50.25	115.75	5.0	52	1.7	26.7	73.3	96.7
67	340	50.53	115.92	4.5	61	3.3	60.0	90.0	98.3
68	355	54.23	127.37	2.0	94	1.7	43.3	81.7	98.3
69	359	54.17	121.50	2.7	79	0.0	16.7	65.0	98.3
70	364	54.93	127.42	2.0	90	13.3	75.0	98.3	100.0
71	365	54.93	127.42	2.0	90	0.0	36.7	85.0	98.3
72	366	54.93	127.42	2.0	90	3.3	45.0	98.3	98.3
73	369	54.93	127.42	2.0	90	0.0	11.7	74.3	98.3
74	371	54.10	127.29	3.3	65	0.0	28.3	80.0	96.6
75	373	54.08	127.25	2.6	82	3.3	45.0	90.0	100.0
76	379	55.60	127.33	1.5	97	0.00	33.3	85.0	98.3
77	382	55.60	127.33	1.5	97	1.7	45.0	91.7	96.7
78	389	54.08	122.08	2.2	91	3.3	46.7	90.0	100.0
79	390	54.08	122.08	2.2	91	6.7	35.0	85.0	100.0
80	392	50.07	119.68	4.7	60	0.0	16.7	65.0	93.3
81	394	50.02	119.70	5.5	42	0.0	10.0	60.0	93.3
82	395	50.12	119.70	4.7	59	1.7	8.3	66.6	95.0
83	416	50.85	119.87	4.6	57	1.7	15.0	70.0	95.0
84	417	51.23	120.25	4.0	63	0.0	16.7	56.7	91.7
85	426	54.67	128.75	1.7	121	1.7	31.7	80.0	98.3
86	428	51.73	120.08	4.2	60	0.0	10.0	66.7	96.7
87	430	50.67	119.58	4.2	67	0.0	21.7	63.3	91.7
88	447	51.00	119.67	4.7	54	0.0	20.0	86.7	100.0
89	454	54.93	127.42	2.0	90	1.7	36.7	86.7	100.0
90	488	49.07	120.88	1.5	93	3.3	25.0	71.7	95.0
91	499	54.08	122.33	2.0	95	0.0	35.0	90.0	95.0
92	525	54.75	128.75	.8	118	0.0	28.3	73.3	95.0
93	526	55.08	129.33	.7	118	0.0	40.0	86.6	100.0
94	529	53.67	132.33	.1	141	3.3	18.3	83.3	100.0
95	691	49.12	120.88	4.0	82	0.0	8.3	66.7	95.0
96	692	52.37	126.75	.1	149	0.0	26.7	75.0	100.0
97	703	49.43	116.13	5.1	55	1.7	40.0	73.3	96.7
98	718	54.18	122.12	2.0	95	3.3	53.0	90.0	98.3
99	719	54.18	122.12	2.0	95	6.7	38.3	86.7	98.3
100	723	54.25	121.92	2.7	78	3.3	41.7	86.7	96.7
101	742	49.13	125.42	.2	168	1.7	50.0	91.7	100.0
102	745	52.20	119.25	3.5	73	3.3	23.3	70.0	95.0
103	748	50.05	127.05	.1	164	5.0	41.7	91.7	100.0
104	766	48.83	124.75	.3	167	0.0	23.3	81.7	100.0
105	767	53.08	132.08	.3	140	1.7	36.7	96.7	100.0
106	769	54.17	122.17	1.9	97	3.3	41.7	85.0	95.0
107	770	54.25	122.33	2.2	90	1.7	58.3	83.3	98.3
108	771	54.25	122.33	2.2	90	8.3	60.0	85.0	96.7
109	772	54.17	122.25	2.2	90	5.7	50.0	88.3	96.7
110	777	54.17	122.17	1.9	97	3.3	40.0	83.3	96.7
111	780	54.08	121.88	2.0	95	16.7	50.0	95.0	96.7
112	784	54.88	126.73	2.7	74	1.7	40.0	86.7	100.0
113	789	54.35	125.43	2.0	73	1.7	56.7	86.7	100.0
114	790	54.37	127.22	3.0	73	0.0	25.0	78.3	96.7
115	791	55.08	127.33	2.9	68	0.0	28.3	73.3	95.0
116	792	55.13	127.40	1.0	111	0.0	46.7	93.3	98.3
117	793	55.30	127.70	1.1	108	0.0	68.3	61.7	90.0
118	794	54.63	127.20	2.5	80	5.0	18.3	98.3	95.0
119	795	54.12	125.42	2.7	79	5.0	65.0	96.7	98.3
120	796	55.00	127.00	3.2	62	5.0	51.7	98.3	96.7
121	797	54.80	129.03	1.9	93	16.7	55.0	96.7	100.0
122	798	54.75	127.00	1.9	93	0.0	18.3	78.3	100.0
123	799	55.03	126.50	2.3	82	1.6	49.3	85.0	98.3
124	800	55.28	127.40	1.2	104	0.0	28.3	75.0	96.7
125	801	50.53	127.25	.6	150	5.0	41.7	95.0	98.3
126	805	55.47	127.70	1.2	105	5.0	36.7	81.7	96.7
127	806	54.90	127.25	1.5	101	3.3	33.3	68.3	93.3
128	807	55.30	127.15	2.2	83	0.0	35.0	75.0	96.7
129	808	54.67	127.25	2.4	82	5.0	33.3	83.3	100.0
130	809	53.50	132.25	.4	135	3.3	35.0	93.3	100.0
131	840	55.08	129.42	.1	132	3.3	38.3	80.0	98.3
132	464	54.05	128.65	.1	139	3.3	43.3	93.3	98.3
133	545	49.05	114.67	5.0	59	3.3	21.7	78.3	98.3

TABLE 12
PERCENT DORMANT ON 6 DIFFERENT DATES DURING THE SECOND YEAR IN THE NURSERY

Prov. Reg. No.	No.	Lat.	Long.	Elev.	Days	Jun.30	Jul.7	Jul.14	Jul.21	Jul.28	Aug.4
1	50	56.50	121.10	2.3	73	18.3	21.7	33.3	43.3	90.0	93.3
2	48	55.67	122.20	2.0	85	13.3	20.0	41.7	63.3	91.7	93.3
3	42	54.50	124.25	2.2	88	11.7	16.7	33.3	41.7	80.0	85.0
4	493	54.50	122.67	2.2	88	18.3	33.3	58.3	70.0	88.3	93.3
5	494	54.33	122.67	2.3	87	8.3	11.7	43.3	61.7	85.0	85.0
6	746	54.10	122.05	2.0	95	11.7	15.0	35.0	55.0	86.7	90.0
7	722	54.07	121.45	2.8	77	28.3	36.7	60.0	78.3	93.3	95.0
8	353	54.93	127.42	2.0	90	3.3	5.0	10.0	25.0	73.3	81.7
9	388	53.67	122.42	3.0	75	21.7	33.3	71.7	90.0	96.7	96.7
10	522	52.33	121.67	2.2	102	3.3	5.0	13.3	35.0	76.7	85.0
11	523	52.42	121.42	2.2	101	6.7	16.7	33.3	53.3	91.7	93.3
12	380	55.60	127.83	2.7	70	0.0	1.7	11.7	33.3	66.7	73.3
13	358	55.47	127.83	1.7	93	0.0	1.7	8.3	25.0	73.3	86.7
14	370	55.33	126.63	2.3	80	26.7	31.7	66.7	91.7	98.3	100.0
15	737	51.12	118.25	4.3	62	31.7	36.7	58.3	75.0	91.7	95.0
16	367	54.93	127.42	2.0	90	16.7	31.7	51.7	76.7	95.0	95.0
17	374	54.45	126.90	2.7	77	13.3	16.7	38.3	70.0	95.0	95.0
18	356	54.13	127.15	3.0	72	15.0	23.3	55.0	73.3	91.7	95.0
19	429	51.77	120.17	4.6	51	36.7	50.0	76.7	83.3	91.7	91.7
20	427	51.70	120.17	3.5	76	11.7	15.0	31.7	56.7	98.3	98.3
21	418	51.17	120.25	3.8	73	38.3	41.7	61.7	80.0	95.0	95.0
22	150	49.92	120.58	4.0	76	15.0	21.7	45.0	61.7	90.0	91.7
23	147	49.17	120.58	4.0	81	31.7	36.7	58.3	80.0	91.7	93.3
24	741	50.87	119.83	4.2	66	1.7	3.3	15.0	30.0	73.3	91.7
25	740	51.62	119.83	4.4	125	0.0	0.0	5.0	6.7	40.0	90.0
26	738	50.70	119.50	4.2	67	3.3	3.3	10.0	25.0	61.7	85.0
27	720	50.48	119.75	5.1	48	30.0	40.0	61.7	83.3	93.3	96.7
28	334	49.40	116.75	3.8	87	36.7	75.0	86.7	95.0	96.7	96.7
29	343	49.82	116.27	4.5	66	40.0	48.3	78.3	81.7	90.0	91.7
30	393	49.92	119.77	4.1	74	18.3	25.0	60.0	80.0	86.7	93.3
31	346	49.92	118.58	4.0	76	45.0	53.3	80.0	91.7	93.3	93.3
32	387	54.37	122.50	2.6	80	23.3	28.3	53.3	78.3	98.3	98.3
33	747	49.33	117.25	4.2	76	26.7	30.0	68.3	83.3	98.3	98.3
34	710	49.37	114.58	4.6	66	51.7	60.0	83.3	98.3	100.0	100.0
35	699	49.17	116.13	4.7	65	43.3	46.7	65.0	71.7	93.3	93.3
36	701	50.13	115.43	4.6	61	26.7	38.3	65.0	78.3	95.0	95.0
37	344	49.58	115.98	3.8	83	25.0	31.7	60.0	78.3	96.7	98.3
38	341	49.30	116.00	5.5	46	53.3	71.7	86.7	93.3	95.0	95.0
39	345	49.08	116.75	4.6	68	43.3	56.7	85.0	88.3	98.3	98.3
40	709	51.13	117.08	4.3	62	38.3	50.0	66.7	88.3	91.7	91.7
41	337	49.58	117.80	5.7	40	45.0	50.0	86.7	98.3	100.0	100.0
42	773	53.33	122.17	3.4	68	28.3	43.3	73.3	81.7	95.0	96.7
43	898	51.12	117.25	4.7	53	31.0	40.0	73.3	86.7	96.7	100.0
44	732	49.42	118.03	4.5	68	33.3	41.7	61.7	80.0	88.3	88.3
45	338	49.75	117.00	4.9	57	40.0	50.0	81.7	91.7	93.3	98.3
46	335	49.33	116.13	5.3	51	56.7	70.0	83.3	91.7	100.0	100.0
47	779	54.10	122.05	2.0	95	16.7	23.3	45.0	70.0	93.3	95.0
48	385	54.25	122.25	2.5	83	13.3	15.0	46.7	70.0	96.7	100.0
49	51	54.33	123.08	2.5	82	11.7	13.3	36.7	68.3	91.7	91.7
50	431	54.12	122.83	2.2	90	15.0	18.3	38.3	55.0	90.0	91.7
51	41	53.42	122.67	1.7	106	16.7	23.3	45.0	68.3	98.3	100.0
52	725	50.65	117.53	4.2	67	31.7	43.3	53.3	71.7	85.0	88.3
53	240	50.17	118.00	3.1	95	23.3	31.7	55.0	75.0	90.0	93.3
54	715	49.48	117.23	4.4	70	40.0	46.7	73.3	85.0	95.0	95.0
55	37	54.08	122.05	2.2	91	8.3	13.3	25.0	41.7	83.3	88.3
56	39	54.08	122.05	2.1	93	13.3	28.3	43.3	61.7	88.3	93.3
57	43	54.28	122.62	2.3	87	8.3	20.0	50.0	60.0	90.0	95.0
58	46	54.08	122.08	2.3	88	8.3	10.0	25.0	68.3	88.3	93.3
59	47	54.08	122.08	2.3	88	23.3	36.7	58.3	76.7	93.3	96.7
60	49	55.50	121.58	2.0	86	16.7	20.0	43.3	63.3	93.3	95.0
61	66	51.67	120.17	4.6	52	35.0	40.0	66.7	73.3	85.0	95.0
62	905	51.58	119.85	4.4	125	1.7	1.7	1.7	10.0	50.0	73.3
63	281	53.10	132.05	4.4	138	0.0	0.0	0.0	0.0	5.0	63.3
64	284	51.18	125.57	4.9	139	0.0	0.0	0.0	0.0	1.7	36.7
65	298	54.17	122.17	2.2	90	21.7	25.0	36.7	60.0	91.7	96.7
66	336	50.25	115.75	5.0	52	35.7	40.0	61.7	78.3	93.3	93.3
67	340	50.53	115.92	4.5	61	28.3	41.7	58.3	80.0	96.7	96.7
68	355	54.23	127.37	2.0	94	13.3	15.0	28.3	65.0	93.3	96.7
69	359	54.17	121.50	2.7	79	20.0	23.3	55.0	70.0	85.0	86.7
70	364	54.93	127.42	2.0	90	6.7	8.3	30.0	56.7	95.0	95.0
71	365	54.93	127.42	2.0	90	6.7	6.7	13.3	35.0	73.3	85.0
72	366	54.93	127.42	2.0	90	1.7	10.0	36.7	68.3	90.0	91.7
73	369	54.93	127.42	2.0	90	5.0	6.7	23.3	53.3	78.3	80.0
74	371	54.10	127.20	3.3	66	18.3	31.7	60.0	75.0	90.0	93.3
75	373	54.08	127.25	2.6	82	5.0	13.3	35.0	56.7	93.3	91.7

Prov. Reg. No.	No.	Lat.	Long.	Elev.	Days	Jun.30	Jul.7	Jul.14	Jul.21	Jul.28	Aug.4
76	379	55.60	127.83	1.5	97	1.7	1.7	3.3	13.3	65.0	76.7
77	382	55.60	127.83	1.5	97	0.0	1.7	10.0	15.0	63.3	76.7
78	389	54.08	122.08	2.2	91	16.7	26.7	48.3	60.0	95.0	95.0
79	390	54.08	122.08	2.2	91	18.3	23.3	48.3	68.3	95.0	98.3
80	392	50.07	119.68	4.7	60	43.3	55.0	80.0	90.0	91.7	93.3
81	394	50.02	119.70	5.5	42	43.3	65.0	83.3	95.0	96.7	96.7
82	395	50.12	119.70	4.7	59	35.0	40.0	76.7	85.0	90.0	90.0
83	416	50.85	119.87	4.6	57	48.3	56.7	81.7	90.0	93.3	95.0
84	417	51.23	120.25	4.0	68	25.0	33.3	51.7	70.0	91.7	86.7
85	426	54.67	128.75	7	121	0.0	0.0	1.7	1.7	23.3	76.7
86	428	51.73	120.08	4.2	60	41.7	48.3	68.3	88.3	90.0	91.7
87	430	50.67	119.58	4.2	67	28.3	43.3	80.0	86.7	91.7	98.3
88	447	51.00	119.87	4.7	54	36.7	56.7	78.3	83.3	88.3	90.0
89	454	54.93	127.42	2.0	90	5.0	8.3	25.0	51.7	81.7	93.3
90	488	49.07	120.88	3.5	93	26.7	30.0	56.7	73.3	91.7	95.0
91	499	54.08	122.33	2.0	95	11.7	23.3	46.7	76.7	90.0	93.3
92	525	54.75	128.75	8	118	0.0	0.0	0.0	0.0	26.7	80.0
93	526	55.08	129.33	7	118	0.0	0.0	1.7	1.7	20.0	61.7
94	529	53.67	132.33	1	141	0.0	0.0	1.7	1.7	16.7	55.0
95	691	49.12	120.88	4.0	82	35.0	36.7	60.0	80.0	93.3	96.7
96	692	52.37	126.75	1	149	0.0	0.0	0.0	0.0	3.3	50.0
97	703	49.43	116.13	5.1	55	51.7	73.3	86.7	90.0	93.3	96.7
98	718	54.13	122.12	2.0	95	16.7	23.3	45.0	70.0	90.0	91.7
99	719	54.18	122.12	2.0	95	11.7	18.3	35.0	55.0	85.0	85.0
100	723	54.25	121.92	2.7	78	15.0	20.0	38.3	68.3	86.7	90.0
101	742	49.13	125.42	2	158	0.0	0.0	0.0	0.0	0.0	21.7
102	745	52.20	119.25	3.5	73	33.3	38.3	70.0	78.3	93.3	93.3
103	748	50.05	127.05	1	164	0.0	0.0	0.0	0.0	1.7	45.0
104	766	48.83	124.75	3	167	0.0	0.0	0.0	0.0	1.7	35.0
105	767	53.08	132.08	3	140	0.0	0.0	0.0	0.0	5.0	61.7
106	769	54.17	122.17	1.9	97	21.7	25.0	55.0	71.7	91.7	91.7
107	770	54.25	122.33	2.2	90	20.0	28.3	43.3	61.7	86.7	93.3
108	771	54.25	122.33	2.2	90	18.3	28.3	60.0	76.7	98.3	98.3
109	772	54.17	122.25	2.2	90	18.3	26.7	45.0	80.0	91.7	91.7
110	777	54.17	122.17	1.9	97	28.3	35.0	55.0	81.7	86.7	91.7
111	780	54.12	121.88	2.0	95	10.0	25.0	45.0	65.0	85.0	93.3
112	784	54.88	126.73	2.7	74	31.7	41.7	63.3	70.0	91.7	96.7
113	789	54.35	125.43	2.9	73	25.0	31.7	65.0	83.3	96.7	98.3
114	790	54.07	127.22	3.0	73	11.7	23.3	41.7	63.3	91.7	91.7
115	791	55.08	127.33	2.9	68	6.7	8.3	31.7	55.0	86.7	88.3
116	792	55.13	127.40	1.0	111	3.3	6.7	16.7	26.7	71.7	86.7
117	793	55.30	127.70	1.1	108	1.7	1.7	11.7	18.3	71.7	80.0
118	794	54.63	127.20	2.5	80	5.0	8.3	23.3	43.3	80.0	85.0
119	795	54.12	125.42	2.7	79	8.3	8.3	21.7	48.3	91.7	98.3
120	796	55.12	127.00	3.2	62	21.7	26.7	10.0	55.0	86.7	93.3
121	797	54.80	126.03	1.9	63	3.3	1.7	17.3	23.3	50.0	80.0
122	798	54.75	127.00	1.9	93	1.7	3.3	18.3	33.3	58.3	78.3
123	799	55.01	126.50	2.3	82	10.0	20.0	48.3	61.7	93.3	93.3
124	800	55.28	127.40	1.2	106	3.3	3.3	10.0	16.7	53.0	80.0
125	801	50.53	127.25	1.6	150	0.0	0.0	0.0	0.0	10.0	68.3
126	805	55.47	127.70	1.2	105	3.3	3.3	8.3	15.0	63.3	80.0
127	806	54.90	127.25	1.5	101	1.7	3.3	5.0	18.3	68.3	76.7
128	807	55.30	127.15	2.2	83	1.7	1.7	3.3	25.0	55.0	76.7
129	808	54.67	127.25	2.4	82	5.0	6.7	23.3	46.7	86.7	95.0
130	809	53.50	132.25	4	135	0.0	0.0	0.0	0.0	3.3	66.7
131	840	55.08	129.42	1	132	0.0	0.0	0.0	0.0	16.7	75.0
132	464	54.05	128.65	1	139	0.0	0.0	0.0	0.0	20.0	73.3
133	545	49.05	118.67	5.0	59	63.3	83.3	100.0	100.0	100.0	100.0
134	576	50.25	117.83	4.2	70	48.3	56.7	71.7	83.3	91.7	93.3
135	858	49.00	116.67	4.2	78	33.3	43.3	80.0	86.7	91.7	98.3
136	868	49.05	116.97	4.3	75	46.7	55.0	93.3	95.0	98.3	98.3
137	888	50.08	117.75	5.0	53	48.3	65.0	80.0	90.0	96.7	96.7
138	539	49.92	117.73	5.5	63	31.7	43.3	70.0	83.3	95.0	98.3
139	540	49.92	117.73	4	56	41.7	45.0	68.3	88.3	98.3	98.3
140	541	49.92	118.91	5.1	51	55.0	63.3	80.0	95.0	100.0	100.0
141	542	49.92	118.75	4.6	63	26.7	38.3	71.7	88.3	98.3	98.3
142	575	50.25	118.00	3.8	79	20.0	33.3	61.7	75.0	88.3	90.0
143	623	57.17	121.83	2.7	60	35.0	38.3	65.0	86.7	98.3	100.0
144	636	49.47	115.40	5.0	55	41.7	51.7	80.0	90.0	91.7	93.3
145	641	50.67	119.48	4.9	52	45.0	58.3	85.0	88.3	90.0	93.3
146	644	50.63	118.00	4.0	72	45.0	53.3	73.3	85.0	90.0	95.0
147	654	49.10	114.67	5.6	45	61.7	70.0	85.0	100.0	100.0	100.0
148	655	49.08	115.78	4.5	70	40.0	46.7	80.0	91.7	95.0	95.0
149	657	49.25	116.23	4.8	63	46.7	56.7	76.7	91.7	96.7	96.7
150	857	49.25	117.75	5.5	47	48.3	63.3	83.3	91.7	96.7	96.7

TABLE 13

DATES OF FLUSHING AND DORMANCY OF 12 SPRUCE PROVENANCES ON TWO SOIL TYPES BOTH INSIDE AND OUTSIDE PLASTIC GREENHOUSE

		CM inside greenhouse			RVS inside greenhouse			CM outside greenhouse			RVS outside greenhouse			Average no. of days between D & F in all four environments
		Block 1		No. of days between F & D	Block 2		No. of days between F & D	Block 3		No. of days between F & D	Block 4		No. of days between F & D	
P	E	F	D		F	D		F	D		F	D		
12	2. 1	Mar. 16	Jun. 2	78	Mar. 16	Jun. 2	78	Apr. 12	Jun. 24	73	Apr. 9	Jun. 17	69	74.50
2	2. 2	Mar. 16	Jun. 30	106	Mar. 16	Jul. 30	136	Apr. 12	Jun. 30	79	Apr. 6	Jun. 17	72	98.25
8	2. 3	Mar. 16	May 25	70	Mar. 16	Aug. 13	150	Apr. 12	Jun. 24	73	Apr. 6	Jun. 24	79	93.00
4	2. 6	Mar. 16	Jun. 2	78	Mar. 16	Aug. 5	142	Apr. 12	Jun. 24	73	Apr. 15	Jun. 17	63	89.00
6	3. 0	Jun. 16	Jun. 10	86	Mar. 16	Jun. 2	78	Apr. 15	Jun. 17	63	Apr. 9	Jun. 10	62	72.25
7	3. 7	Mar. 16	Jun. 2	78	Mar. 16	May 25	70	Apr. 21	Jun. 30	70	Apr. 9	Jun. 10	62	70.00
1	3. 9	Mar. 16	May 25	70	Mar. 16	May 25	70	Apr. 12	Jun. 24	73	Apr. 2	Jun. 10	69	70.50
3	4. 5	Mar. 16	May 25	70	Mar. 16	May 25	70	Apr. 12	Jun. 17	66	Apr. 9	Jun. 10	62	67.00
9	4. 7	Mar. 16	May 25	70	Mar. 16	May 25	70	Apr. 12	Jun. 10	59	Apr. 9	Jun. 17	69	67.00
10	4. 9	Mar. 16	May 25	70	Mar. 16	May 25	70	Apr. 21	Jun. 17	57	Apr. 6	Jun. 10	65	65.50
11	5. 3	Mar. 16	May 25	70	Mar. 16	May 25	70	Apr. 12	Jun. 10	59	Apr. 12	Jun. 10	59	64.50
5	5. 7	Mar. 19	May 25	67	Mar. 16	May 25	70	Apr. 15	Jun. 24	70	Apr. 12	Jun. 10	59	66.50

RVS - Robertson Valley soil, CM - California mix, E - Elevation, P - Provenance, F - Flushing, D - Dormancy, A provenance was considered flushed when more than 50% of seedlings scored were flushed. Dormancy was similarly assessed. Since flushing and dormancy in each environment was assessed on the basis of only 10 seedlings, it is likely that assessments based on a larger sample would exhibit a period of growth (last column in above table) more strongly correlated with altitude than that indicated in table.

TABLE 14

RELATIONSHIP BETWEEN GERMINATION BEHAVIOUR AND SEED QUALITY AT 15°C.

		ED3	ED4	RD3+ED4	MDG	PV	GV	AGP
Seed quality	ED3	1.00000						
	ED4	-0.41835	1.00000					
	ED3 + ED4	-0.05863	0.93125	1.00000				
	MDG	0.28526	0.04948	0.16883	1.00000			
	PV	0.28527	0.04808	0.16729	0.99992	1.00000		
	GV	0.25423	0.03729	0.14297	0.94381	0.94457	1.00000	
	AGP	0.28524	0.04958	0.16893	0.99999	0.99991	0.94379	1.00000
		Coefficients of correlation between pairs of variables.						
Germination behaviour								

See Table 2 for explanation of symbols.

r > .159 is significant at .05 level of probability.

r > .208 is significant at .05 level of probability.

n = 150

TABLE 15

RELATIONSHIP BETWEEN GERMINATION BEHAVIOUR AND SEED QUALITY AT 20°C.

		ED3	ED4	ED3+ED4	MDG	PV	GV	AGP
Germination behaviour	Seed quality	ED3	1.00000					
		ED4	-0.41835	1.00000				
		ED3 +	-0.05863	0.93125	1.00000			
		ED4						
		MDG	0.00028	0.62638	0.68856	1.00000		
		PV	-0.00148	0.55422	0.60854	0.96208	1.00000	
		GV	-0.01925	0.54915	0.59584	0.95685	0.97851	1.00000
		AGP	0.00022	0.62643	0.68859	1.00000	0.96210	0.95692

Coefficients of correlation between pairs of variables.

See Table 2 for explanation of symbols.

r > .159 is significant at .05 level of probability.

r > .208 is significant at .05 level of probability.

n = 150

TABLE 16

RELATIONSHIP BETWEEN GERMINATION BEHAVIOUR AND SEED QUALITY AT 25°C.

		ED3	ED4	ED3+ED4	MDG	PV	GV	AGP
Germination behaviour	Seed quality	ED3	1.00000					
		ED4	-0.41835	1.00000				
		ED3 + ED4	-0.05863	0.93125	1.00000			
		MDG	0.04401	0.63975	0.72080	1.00000		
		PV	0.06279	0.52722	0.60465	0.95355	1.00000	
		GV	0.01395	0.53961	0.59868	0.94642	0.97814	1.00000
		AGP	0.04400	0.63977	0.72081	1.00000	0.94634	1.00000

Coefficients of correlation between pairs of variables.

See Table 2 for explanation of symbols.

r > .159 is significant at .05 level of probability.

r > .208 is significant at .01 level of probability.

n = 150

TABLE 17

RELATIONSHIP BETWEEN GERMINATION BEHAVIOUR AND SEED QUALITY AT 30°C.

		ED3	ED4	ED3+ED4	MDG	PV	GV	AGP
Seed quality	ED3	1.00000						
	ED4	-0.41835	1.00000					
	ED3 + ED4	-0.05863	0.93125	1.00000				
					Coefficients of correlation between pairs of variables.			
Germination behaviour	MDG	-0.03705	0.46839	0.49994	1.00000			
	PV	-0.01525	0.44094	0.47851	0.99561	1.00000		
	GV	-0.06880	0.40867	0.42157	0.93589	0.94692	1.00000	
	AGP	-0.03714	0.46835	0.49986	1.00000	0.99560	0.93587	1.00000

See Table 2 for explanation of symbols.

r > .159 is significant at .05 level of probability.

r > .208 is significant at .01 level of probability.

n = 150

TABLE 18

RELATIONSHIP BETWEEN GERMINATION BEHAVIOUR AND FACTORS OF THE ENVIRONMENT

Factors of the Environment			L	A	D	PV15	PV10	PV25	PV30	GV15	GV20	GV25	GV30	PVJ	GVJ
			1	2	3	4	5	6	7	8	9	10	11	12	13
			L	A	D	PV15	PV10	PV25	PV30	GV15	GV20	GV25	GV30	PVJ	GVJ
GERMINATION BEHAVIOUR	L	1	1.000												
	A	2	-.680	1.000											
	D	3	.306	-.906	.999										
	PV15	4	-.363	.540	-.490	1.000									
	PV20	5	-.121	.255	-.263	.591	1.000								
	PV25	6	-.223	.346	-.322	.449	.852	1.000							
	PV30	7	-.336	.463	-.408	.485	.714	.823	1.000						
	GV15	8	-.383	.452	-.365	.928	.468	.308	.350	1.000					
	GV20	9	-.087	.210	-.221	.536	.949	.762	.621	.464	1.000				
	GV25	10	-.165	.288	-.280	.384	.878	.977	.791	.259	.776	1.000			
	GV30	11	-.298	.377	-.318	.377	.645	.750	.954	.277	.593	.756	1.000		
	PVA25	12	-.281	.456	-.431	.462	.727	.911	.764	.347	.702	.931	.712	1.000	
	GVA25	13	-.181	.337	-.334	.348	.708	.890	.760	.239	.705	.943	.752	.966	1.000

Coefficients of correlation between pairs of variables

See Table 2 for explanation of symbols

r > .159 is significant at .05 level of probability

r > .208 is significant at .01 level of probability

n = 150

TABLE 19

RELATIONSHIP BETWEEN FLUSHING AND FACTORS OF THE ENVIRONMENT

Factors of
the
Environment

Flushing
Second
Year

		L	A	D	FL6	FL14	FL20	FL27
		1	2	3	4	5	6	7
L	1	1.000						
A	2	-.680	1.000					
D	3	.306	-.906	.999				
FL6	4	.1148	-.1140	.096	1.000			
FL16	5	.400	-.395	.281	.604	1.000		
FL20	6	.329	-.424	.361	.496	.793	1.000	
FL 27	7	.099	-.261	.280	.205	.331	.493	1.000

Coefficients of correlation between
pairs of variables

See Table 2 for explanation of symbols

r > .159 is significant at .05 level of probability

r > .208 is significant at .01 level of probability

n = 150

TABLE 20

RELATIONSHIP BETWEEN GROWTH DURING SECOND YEAR AND FACTORS OF THE ENVIRONMENT

			L	A	D	SM10	SM24	SJ6	SJ20	SJY4	SJY18	FM10	FM24	PJ6	PJ20	PJY4	PJY18	
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
FACTORS OF THE ENVIRONMENT	L	1	1.000															
	A	2	-.680	1.000														
	D	3	.307	-.906	.999													
	SM10	4	.030	.067	-.105	1.000												
	SM24	5	.029	-.083	.091	.865	1.000											
	SJ6	6	.135	-.336	.358	.686	.928	1.000										
	SJ20	7	.142	-.450	.503	.559	.844	.975	1.000									
	SJY4	8	.141	-.481	.543	.516	.812	.960	.995	1.000								
	SJY18	9	.130	-.484	.553	.506	.803	.954	.994	.996	1.000							
SHOOT EXTENSION	FM10	10	-.121	.566	-.666	.446	-.002	-.329	-.486	-.528	-.540	1.000						
	FM24	11	-.121	.045	.011	-.478	-.032	.065	.104	.118	-.113	-.617	.999					
	PJ6	12	.331	-.700	.720	-.269	-.037	.402	.529	.561	.567	-.853	.245	1.000				
	PJ20	13	.115	-.653	.782	-.217	.076	.359	.554	.589	.604	-.816	.701	0.722	1.000			
	PJY4	14	.027	-.372	.468	-.330	-.173	.003	.105	.202	.176	-.483	.164	0.389	.410	1.000		
	PJY18	15	-.097	-.096	.181	-.036	.007	.068	.117	.089	.171	-.206	.048	0.147	.228	-.300	1.000	
			Coefficients of correlation between pairs of variables.															
			See Table 2 for explanation of symbols															
			r > .159 is significant at .05 level of probability															
			r > .208 is significant at .01 level of probability															
			n = 150															
GROWTH RATE																		

Coefficients of correlation between pairs of variables.

See Table 2 for explanation of symbols

r > .159 is significant at .05 level of probability

r > .208 is significant at .01 level of probability

n = 150

TABLE 21

RELATIONSHIP BETWEEN GROWTH AND DORMANCY DURING FIRST AND SECOND YEAR AND FACTORS OF THE ENVIRONMENT

			L	A	D	SL1	RC1	SL1/RC1	DW1	SL2	RC2	SL2/RC2	DW2	DJ30	DJY7	DJY14	DJY21	DJY28	DA4
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
DORMANCY	SECOND YEAR	ENVIRONMENT	L	1	1.000														
		A	2	-.682	1.000														
		D	3	.308	-.906	1.000													
	GROWTH SECOND YEAR	SL1	4	-.020	-.548	.724	1.000												
		RC1	5	-.555	.128	.154	.645	1.000											
		SL1/RC1	6	.427	-.814	.813	.806	.078	1.000										
		DW1	7	-.190	-.286	.483	.892	.842	.521	1.000									
	GROWTH FIRST YEAR	SL2	8	.085	-.594	.724	.936	.530	.810	.805	.999								
		RC2	9	-.163	-.405	.622	.835	.706	.534	.798	.878	1.000							
		SL2/RC2	10	.446	-.596	.517	.625	.020	.824	.428	.696	.276	1.000						
		DW2	11	-.038	-.538	.722	.868	.598	.653	.793	.909	.954	.395	1.000					
	FACTORS OF THE ENVIRONMENT	DJ30	12	-.661	.857	-.733	-.538	.140	-.821	-.308	-.623	-.367	-.717	-.510	1.000				
		DJY7	13	-.635	.856	-.745	-.566	.117	-.839	-.328	-.645	-.400	-.711	-.543	0.981	1.000			
		DJY14	14	-.562	.862	-.796	-.616	.065	-.857	-.361	-.678	-.461	-.671	-.603	0.928	.951	1.000		
		DJY21	15	-.430	.827	-.828	-.698	-.050	-.871	-.428	-.733	-.560	-.623	-.682	0.843	.869	.953	1.000	
		DJY28	16	-.131	.699	-.834	-.768	-.293	-.752	-.523	-.752	-.735	-.687	-.800	0.607	.638	.760	.875	1.000
		DA4	17	-.089	.656	-.803	-.727	-.274	-.713	-.497	-.672	-.644	-.364	-.720	0.583	.610	.720	.813	.923

Coefficients of correlation between pairs of variables

See Table 2 for explanation of symbols

r > .159 is significant at .05 level of probability

r > .208 is significant at .01 level of probability

n = 150

Coefficients of correlation between pairs of variables

See Table 2 for explanation of symbols

r > .159 is significant at .05 level of probability

r > .208 is significant at .01 level of probability

n = 150

TABLE 22

CORRELATIONS BETWEEN MEASURED VARIABLES INCLUDED IN THE PRINCIPAL COMPONENT ANALYSIS

		PVA25	SL1	SL1/RC1	FL14	FL20	SL2	RC2	SL2/RC2	DW2	PM10	PJ6	PJ20	PJY4	DJ30	DJY7	DJY14	DJY21
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
PVA25	1	1.000																
SL1	2	-.227	1.000															
SL1/RC1	3	-.371	.807	1.000														
FL14	4	-.224	.154	.320	1.000													
FL20	5	-.367	.232	.365	.793	1.000												
SL2	6	-.264	.936	.811	.204	.310	1.000											
RC2	7	-.216	.836	.538	-.025	.111	.880	1.000										
SL2/RC2	8	-.211	.627	.824	.463	.453	.697	.282	1.000									
DW2	9	-.257	.868	.654	.117	.239	.910	.955	.397	1.000								
PM10	10	.333	-.623	-.621	.270	.123	-.649	-.670	-.291	-.679	1.000							
PJ6	11	-.271	.630	.722	-.022	.035	.679	.606	.457	.660	-.852	1.000						
PJ20	12	-.394	.751	.714	.031	.178	.760	.750	.380	.796	-.809	0.723	1.000					
PJY4	13	-.251	.337	.328	-.001	.142	.352	.414	.070	.449	-.516	.386	.409	1.000				
DJ30	14	.400	.542	-.822	-.403	-.402	-.627	-.377	-.714	-.516	.504	-.675	-.570	-.214	1.000			
DJY7	15	.367	-.570	-.841	-.380	-.387	-.649	-.408	-.709	-.548	.543	-.708	-.599	-.237	.980	1.000		
DJY14	16	.367	-.621	-.859	-.357	-.385	-.682	-.472	-.668	-.610	.613	-.760	-.698	-.314	.927	.950	1.000	
DJY21	17	.369	-.703	-.872	-.253	-.311	-.736	-.569	-.620	-.687	.718	-.803	-.802	-.392	.841	.867	.953	1.000

Note the high correlation between dormancy and measurements of growth and the relatively low correlation between flushing and the same measurements.

See Table 2 for explanation of symbols

r > .159 is significant at .05 level of probability

r > .208 is significant at .01 level of probability

n = 150

TABLE 23
WEIGHTING FOR ORIGINAL VARIABLES
IN COMPUTED COMPONENTS

Variable		Components			
		1	2	3	4
1	PVA25	-.424	-.179	-.002	.676
2	SIL	.854	-.175	.310	.250
3	SIL/RC1	.922	.160	-.094	.116
4	FI14	.275	.825	.321	-.056
5	FI20	.367	.415	.426	-.023
6	SL2	.903	-.120	.299	.223
7	RC2	.745	-.444	.424	.080
8	SL2/RC2	.701	.441	-.036	.348
9	DW2	.839	-.299	.377	.057
10	FM10	-.760	.521	.226	.160
11	PJ6	.827	-.256	-.300	-.001
12	PJ20	.847	-.286	.046	-.114
13	PJY4	.441	-.287	.171	-.551
14	DJ30	-.839	-.344	.321	-.012
15	DJY7	-.861	-.303	.321	-.029
16	DJY14	-.902	-.219	.279	.018
17	DJY21	-.930	-.051	.212	.041

See Table 2 for explanation of symbols, and pages 32, 33 and 54 for a discussion of the significance of this table.

TABLE 24

PERCENTAGE OF VARIATION ACCOUNTED FOR BY FOUR PRINCIPAL COMPONENTS.

Component	Percentage of variation accounted for	Cumulative percentage
1	57.85	57.85
2	14.92	72.77
3	9.67	80.44
4	6.56	87.00

DISCUSSION

From Tables 14 to 22, which show the correlation coefficients between pairs of variables, it is clear that environmental pressures associated with altitude have been the principal selective pressures resulting in the adaptation of spruce populations to a wide range of environments. Furthermore, it appears that these factors of the environment associated with altitude vary progressively, resulting in a clinal pattern of variation (Fig. 8).

Because of the inadequacies of available climatic data for British Columbia (Chapman 1952, Chapman and Brown 1966) it is not possible to obtain climatic data for the place of origin of each of the 150 spruce provenances grown at Cowichan Lake, or even for a small proportion of these provenances. Nevertheless, despite the inadequacies of the climatic data an attempt is made to explain the pattern of variation in the immature spruce populations grown at Cowichan Lake in terms of the environment as determined by altitude at their place of origin. In regard to provenances from the area of the Nass and Skeena rivers the variation pattern is explained in terms of the environment as determined by continentality.

There is sufficient evidence from Langlet's work (Langlet 1963a) to warrant the conclusion that, in the interpretation of the growth behaviour of diverse provenances grown in a uniform environment, the day length on the first day of the year which shows an average temperatures of plus 6°C. (43°F) is an extremely valuable index of the environment at the place of origin of these provenances. Consequently this index is used in the present study, and will henceforth be referred to as day length at 43°F or DL43.

Cowichan Lake is situated on Vancouver Island at ca.lat. $49^{\circ}00'$, and has an average frost free period of 147 days (Connor 1949). The annual climatic pattern at this station is given in Figs. 9 and 10 and compared with the climatic pattern at meteorological stations at increasing altitudes (Fig. 10) and decreasing continentality (Fig. 9). Figs. 11 to 18 show the relationship between temperature and photoperiod at different ecological zones in the interior of British Columbia, and at the Cowichan nursery, and compare each of these zones with the photoperiod and temperature regime at Cowichan Lake during growing season of 1966¹.

It will be seen from Figs. 11 to 18 that DL43 at Cowichan Lake is generally shorter than that of high elevation provenances from the interior. The lower the elevation of the interior provenances the closer the line AB and CD, which respectively indicate the DL43 at Cowichan Lake and at a representative weather station. For example at Vavenby, which is a DOT² station of the same elevation, and is very close to the Birch Island provenances (25 and 62, elev. 1400 ft., lat. $51^{\circ}35'$, long. $119^{\circ}50'$) the DL43 is almost identical with that of Cowichan Lake (Fig. 11).

The percent dormant on six different dates is given in Table 12 for all provenances, and in Figs. 11 to 13 for a number of representative high and low elevation provenances. From Figs. 11 to 13 it is clear that high elevation provenances entered dormancy during the 1966 growing season at Cowichan Lake when temperatures were increasing, but the photoperiod had begun to decrease. Low elevation provenances also entered dormancy when temperature was increasing, but at a much later date than the high elevation provenances. For example, the Clearwater provenance (61, lat. $54^{\circ}40'$,

¹ In determining photoperiod for a given latitude it was not considered necessary to adjust for altitude.

² Department of Transport weather station.

elev. 4600 ft.) showed 35 percent dormancy on June 30, when the Birch Island provenance from approximately the same latitude, but lower elevation, showed no sign of dormancy, and showed only 5 percent dormancy on July 14 when the Clearwater provenance was 65 percent dormant (Fig. 11).

Similarly provenance 42 from a region south of Prince George, but at 3400 ft. showed 28 percent dormancy on June 30 when temperatures were increasing. Provenance 10 from Soda Creek, elev. 2200 ft., showed only 3 percent dormancy on this date. As in the previous example, temperature was increasing and photoperiod decreasing at the outset of dormancy (Fig. 13).

These examples are typical of the general pattern of the outset of dormancy in all populations from the white-Engelmann complex growing at Cowichan Lake. The pattern varies, however, in populations from the general region of the Nass and Skeena rivers. It seems clear that the intrusion of Sitka spruce genes, as a result of decreasing continentality, influences the pattern of variation in these populations.

For example it will be seen from Fig. 12 that provenance 128 from the region of Hazelton (lat. $55^{\circ}18'$, long. $127^{\circ}19'$, elev. 2200 ft.) and provenance 14 from Babine Lake (lat. $55^{\circ}20'$, long. $126^{\circ}38'$, elev. 2300 ft.) differ significantly only in regard to longitude. Yet there is a striking difference in time of entering dormancy. On June 30, the Hazelton provenance showed only 1 percent dormancy while the Babine Lake provenance showed 25 percent dormancy.

In regard to time of entering dormancy the Hazelton provenance is typical of all the provenances from the Nass and Skeena river drainages. All of these provenances entered dormancy much later than provenances from east of this general region. As in the previous two examples the Babine Lake and Hazelton provenances entered dormancy when temperature was in-

creasing at Cowichan Lake, but photoperiod decreasing.

Because of the clinal pattern of variation in the time of entering dormancy (Fig. 8) the relationship between temperature, photoperiod and degree of dormancy illustrated in Figs. 11 to 13 will vary similarly for all other provenances. It seems, therefore, that, as in the case of the many other tree species referred to in a previous section, the onset of dormancy in white spruce and its related forms is photoperiodically determined.

THE ECOLOGICAL SIGNIFICANCE OF PHOTOPERIODIC
ADAPTATION IN WHITE SPRUCE.

In the last section evidence was provided in regard to the photoperiodic control of dormancy in the spruce populations grown at Cowichan Lake. In this section an attempt is made to clarify the ecological significance of photoperiodic control of dormancy in these populations, and to indicate the manner in which the photoperiodic stimulus may be received by the spruce seedling, and translated into metabolic activity leading to dormancy.

It is well known that organs which are growing are much more susceptible to injury by freezing temperatures than organs which are dormant. It is also generally known that the decrease of growth activity in the buds of perennial plants "manifests itself in a lowered capacity to react immediately by continued growth to certain conditions which are growth-promoting during the active phase" (Vegis 1963). The capacity to enter dormancy well in advance of the average occurrence of early fall frosts confers a survival advantage on that proportion of a population of trees which possesses it. For such trees have the capacity to survive temperatures damaging to those which continue growth.

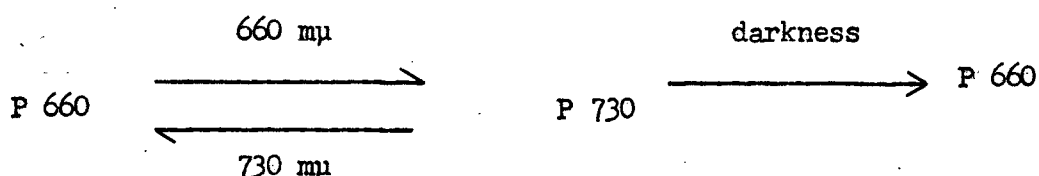
The selective action of fall frosts operates both on seedlings and mature trees. But it is clear that a temperature which is lethal for seedlings may only injure, or have very little effect on mature trees (Parker 1963). Most coniferous trees including white spruce are predominantly cross pollinators. Consequently, the individuals tend to be heterozygous and the population heterogenous. There is, therefore, a wide range of genetic

variability within any one population even though that population in nature occupies a relatively uniform environment. There is little doubt that this intra-population variability is itself an adaptive characteristic for it buffers the population against yearly fluctuations of the environment, as well as long term gradual changes in climate. It is this pool of genetic variability which is acted upon by the selective pressures of the environment.

The date of the occurrence of the first killing frost in any one environment will vary from year to year, and each year will exercise its maximum effect at the seedling and sapling stage. Now, that proportion of the population which enters dormancy at an early date, as a result of a capacity to receive and transmit a stimulus from a factor of the environment, other than temperature, will avoid the lethal effects of freezing temperatures which eliminate, i.e. select, those seedlings not possessing this capacity. These seedlings will survive, therefore, and pass on the capacity to their progenies. The factor of the environment must be continuous and increasing in intensity so that if temperatures should rise again above the critical point growth will not consequently be induced.

As indicated in Figs. 11 to 18, the one single factor of the environment which shows a progressive, unfluctuating increase with the passing of time from summer to fall, and which does not fluctuate from year to year, is the length of the dark period, or nyctoperiod - and it is the nyctoperiod and not the photoperiod which is the critical factor (Nitch 1963 p. 176). If a portion of a population of spruce seedlings possessed a leaf pigment which, as a result of decreasing day length (increasing nyctoperiod), receives and transmits a stimulus resulting in dormancy, such seedlings would have a survival advantage over those not possessing the pigment, for day length - and this is the important point - decreases before temperatures decrease (see Figs. 11 to 18).

Hendricks and Borthwick (1963) have shown that a bright blue protein termed phytochrome regulates many aspects of plant growth and development, including dormancy. Phytochrome has two interconvertible forms with absorption maxima at 660 mμ. and 730 mμ. Hendricks and Borthwick represented the conversion reaction as follows:



and gave four ways in which phytochrome may link the plant to its environment. These are given below in full:

- (1) It changes with light quality independently of the intensity above low values.
- (2) It reverts in darkness from P 730 to P 660 and thereby determines photoperiodism.
- (3) The substrates upon which it acts and the products that it forms depend upon photosynthetic and reserve metabolic activity.
- (4) The rates of the crucial reactions in which P 730 is involved, including its own dark transformation, are temperature dependent.

The investigations of the manner and extent of the control of plant growth by phytochrome referred to above were not conducted on tree species. However, there is evidence that dormancy in trees is initiated as a result of the accumulation of growth inhibitors under short photoperiods (Giertych 1964 page 298, Nitsch 1963 page 184, Steward 1963 page 206, Wareing 1956 page 205). Steward (1963) has reported that in conifer leaves and in buds, glutamine and arginine levels fell with the onset of shorter days, lower temperature, and lower light intensities, and that as the glutamine and arginine levels decrease, asparagine and proline increase. When plants

enter into long days this trend is reversed. Metabolic changes such as these can have phenotypic expression. For example the onset of dormancy of the spruce populations at Cowichan Lake, particularly in the first year, was always accompanied by a vivid purple coloration of the leaves.

From the work of Hendricks and Borthwick (1963) it appears likely that the metabolic processes leading to increased levels of inhibitors and eventual dormancy in white spruce seedlings are mediated by phytochrome, or a phytochrome-like substance, following reception of the stimulus of decreasing day length. It is possible, however, that the photoperiodic reaction is determined, not only by the dark conversion of P 730 to P 660, but is the result of an interaction between an endogenous circadian rhythm and phytochrome (Bunning 1961, Hamner 1963). For example, there is some indication that provenances from areas of short growing season, i.e., provenances from northern latitudes and/or high elevations, are more closely adapted to photoperiod than provenances from areas of long growing season, i.e., provenances from low elevations and/or low latitudes (Irgens-Moller 1957, Olsen et al. 1959). In the latter instance circadian rhythms may be of greater importance than photoperiod, though it must be pointed out that the theories of Bunning in regard to circadian rhythms and photoperiod have not been universally accepted (Romberger 1963 p. 120).

It is not, of course, possible to provide evidence concerning the effect of photoperiod on flowering in spruce from a study of geographic variation in immature spruce populations. There is, however, evidence from other studies that photoperiod may have little or no effect in regard to flowering in conifers.

In a paper, which is of considerable significance in this connection, Mirov (1956) showed that there is no definite relationship between photoperiod and flowering in the genus Pinus. Most of the pine species of the world are

represented at the Institute of Forest Genetics at Placerville, California, lat. $38^{\circ}44'$, and at the University of California at Berkeley, lat. $37^{\circ}52'$. In these two localities the longest day in summer is approximately 15 hours. Pine from north of these latitudes were not inhibited in the production of both male and female flowers. For example, Pinus sylvestris var. lapponica, which has a northern distribution between lat. $60^{\circ}00'$ and $70^{\circ}00'$, produced abundant male and female flowers at 29 years of age, despite the fact that the longest day in summer at latitudes spanning its natural range is approximately 19 hours.

It is customary in Swedish forestry practice to take cuttings from trees of high elevations and high latitudes for grafting on stock near the coast where the climate is much less severe. The species concerned are Pinus sylvestris (Scots pine) and Picea excelsa (Norway spruce). Seed production is enhanced by this transfer, and if flowering were under strong photoperiodic control it is unlikely that such a result could be obtained.

Kramer and Kozlowski (1960) Matthews (1963) and Anderson (1965) have reviewed the literature pertaining to the flowering and seed setting in forest trees. From these reviews it is clear that climate, other than photoperiod, edaphic conditions and the age of the tree are the principal factors affecting flowering and seed setting in conifers. Little evidence was provided indicating that photoperiod exercised as important an influence in flowering in conifers as it obviously does in regard to dormancy. It is likely, therefore, that the ecological significance of photoperiodism in white spruce in British Columbia is confined to flushing and dormancy - particularly the latter - and is of little significance in regard to flowering.

Wareing (1956 p. 209) has pointed out that in regard to herbaceous species it is generally assumed that the biological significance of photoperiodism lies in the control of flowering, and that vegetative responses

are secondary. He goes on to state: "it does not follow that this is true also for woody species, however, in which the primary significance of photoperiodism may concern dormancy phenomena". This is an important hypothesis. It relates dormancy rather than flushing to photoperiod, and also gives dormancy greater significance than flowering as a photoperiodic response in woody species.

The evidence presented above is in agreement with Wareing's remarks concerning flowering and photoperiodism in woody species. Evidence will be presented in the following section which indicates that Wareing's special emphasis on dormancy in relation to photoperiodism in woody species is also essentially correct, at least in regard to the growth of immature spruce populations in British Columbia.

THE RELATIVE IMPORTANCE OF FLUSHING AND DORMANCY
AS ADAPTIVE FACTORS IN THE MICROEVOLUTION OF WHITE SPRUCE

In the last two sections evidence was provided in regard to the photoperiodic control of dormancy in spruce, and the ecological significance of photoperiodic adaptation discussed. The manner in which the photoperiodic stimulus may be received by the spruce seedling and translated into metabolic activity leading to dormancy was also indicated.

The question remains, however, as to the extent and importance of photoperiodic control of flushing as well as dormancy. A second and related question refers to the strong correlation between factors of the environment and dormancy, and the relatively weak correlation between the same factors and flushing (Fig. 19).

The writer has not found a satisfactory answer to these questions in the literature (reviewed by Vegis 1963), and because of this, and because of its obvious importance in relation to the latitudinal and altitudinal displacement of forest tree seed, the subject is treated here separately, and an explanation attempted.

Surprisingly few studies of variation within tree species are designed to assess variation in times of flushing and dormancy. Indeed, much of our present knowledge concerning both of these vital phases in the growth cycle of forest trees comes, not from provenance trials, but from physiological studies in controlled environments e.g. Wareing (1950 a, b, c; 1951, 1956), who has also stressed the silvicultural aspects of this work (1966).

Wareing (1951 p. 51) has stated that there is no evidence that the breaking of dormancy in Scots pine in the spring under natural conditions is

photoperiodically controlled. He pointed out that dormancy is readily broken at any time from early January onwards simply by transferring the plants to warm conditions regardless of the length of the natural photoperiod.

Pauley and Perry (1954) have shown that neither light nor its periodicity appears to be directly concerned in the breaking of dormancy in Populus. The onset of flushing occurred even in darkness. On the other hand, these authors conclude that the role of photoperiod in the annual growth cycle of Populus appears primarily to influence the timing of physiological processes concerned in the onset of dormancy.

Morris et al. (1957) have shown that the date of flushing in the same provenances of Pseudotsuga menziesii (Douglas fir) may vary as much as a month between years. They also reported that the time of flushing had no apparent relation to annual height growth. The results of Ching and Bever (1960) support the conclusion that flushing and height growth in Douglas fir are not correlated.

Burley (1966) has shown that flushing in Sitka spruce is controlled largely by temperature, and that bud formation in the same species is a response to photoperiod.

In a study of the seasonal height growth of 5 conifers, including white spruce, Kozlowski (1957) found that all trees started growth in the spring before danger of frost was over, and stopped growth in the summer usually long before fall frosts began. Hanover (1963), in a study of geographic variation in Pinus ponderosa Laws. (ponderosa pine), found an identical situation in regard to flushing and dormancy, and has reported that all trees began growth in the spring before danger from frost has passed, and ceased growing before the beginning of fall frosts.

Mitchell (1965) studied leader growth in 42 different conifers growing at a single site in southern England. Two of his conclusions are

relevant to the present discussion. These are: (1) adverse climatic conditions in the spring had no appreciable effect on the time of flushing (2) in the year of planting, trees usually began their height growth several weeks later than when they are established, but end at about the same time. These conclusions have particular significance when it is considered that they are based on observations made during several growing seasons on 42 different species of conifers growing in a uniform garden. From the point of view of survival in white spruce - which was one of the species studied - during the first year of outplanting, and its obvious significance in regard to the relative importance of flushing and dormancy as adaptive factors in the same species, special interest is attached to the conclusion that the after effects of planting can delay flushing for several weeks whereas it has no appreciable effect on the time of growth cessation.

Fig. 19 shows the relationship between factors of the environment at the place of origin and flushing and dormancy in the white spruce populations at Cowichan Lake. It will be seen that the correlation between dormancy and factors of the environment is high, and much higher than the correlation between flushing and factors of the environment. The correlation coefficient for dormancy on July 14 and altitude is .862. This is the highest correlation coefficient obtained between any one factor of the environment, and a measure of growth behaviour. Furthermore, as will be seen from Table 21, the date of entering dormancy and dry weight are highly correlated. The correlation coefficient between dormancy on July 28 of the 2nd year, and dry weight of two year old seedlings is -.800.

The curves for dormancy and flushing of high and low elevation provenances, and for continental and maritime species are compared in Figs. 20 to 27. It will be seen that there is very little difference between high and low elevation provenances, and continental and maritime species in

the curves for flushing. On the other hand, there are striking differences between high and low elevation provenances, and between continental and maritime species in the curves for dormancy. Indeed the dormancy curve characterizes a provenance with considerable precision (see Fig. 22).

From the data concerning the growth behaviour of 12 spruce provenances sown in the spring of 1964 in the Cowichan Lake nursery (Table 13) it will be seen that all 12 provenances inside the greenhouse flushed approximately 3 weeks before those outside the greenhouse, and all provenances from elevations above 3000 ft. inside the greenhouse entered dormancy by May 25 when temperatures were increasing, and moisture regime kept at optimum. All provenances from below 3000 ft. inside the greenhouse showed considerable variation in time of entering dormancy. The average number of days between flushing and dormancy for provenances below 3000 ft. is approximately 90 days, and 70 days for provenances above 3000 ft.

The apparent discrepancy between Fig. 7 and Table 13 is attributable to the fact that a provenance was considered dormant when 50 per cent of the seedlings measured were dormant, even though one or two seedlings had not entered dormancy and continued shoot extension.

There appears to be sufficient evidence both from controlled environment studies, and from studies of periodicity both in the nursery and in natural stands of coniferous species, as well as from the results of the present study, to warrant the conclusion that flushing in white spruce is predominantly influenced by temperature, and that dormancy is predominantly under the control of photoperiod. This does not imply, of course, that temperature has no effect on dormancy, and that photoperiod has no effect on flushing. On the contrary it is possible that both of these factors of the environment have some influence on each of these phases in the growth

cycle of coniferous species. Similarly winter chilling exercises an important influence on the plant's reaction to photoperiod (Nienstaedt 1967). Nevertheless, the weight of evidence indicates that in regard to white spruce photoperiod exercises its predominant influence on growth cessation and dormancy, and temperature exercises its predominant influence on flushing.

The following hypothesis is presented in regard to the apparent photoperiodic control of dormancy in white spruce and the lesser importance of photoperiod and greater importance of temperature in the control of flushing. It is possible that this hypothesis can be extended to other tree species of the Pacific Northwest, e.g. the inland form of Douglas fir.

There are two major differences, which the writer has not seen previously stated, between the environmental pressures operating on the plant in the spring, and those operating in the fall. In the spring the probability of occurrence of killing frost is decreasing with the passing of time. In the fall the probability of the occurrence of killing frost increases with the passing of time. Secondly in the spring temperatures and photoperiod are increasing simultaneously, whereas in the fall photoperiod decreases before temperatures decrease (see Figs. 11 to 18).

Because the probability of the occurrence of lethal frost increases with the passing of time in the fall, it is clear that in respect to dormancy a plant adapted to photoperiod has a greater survival advantage than one adapted to temperature alone. For the plant adapted to photoperiod will enter dormancy in advance of the plant adapted to temperature alone, and consequently has a greater chance of avoiding the effects of freezing temperatures. In the spring a plant remains dormant until temperatures reach a certain threshold (approximately 43°F). Each day after the occurrence of temperatures say above 43°F the probability of the occurrence of lethal frosts decreases rapidly. This decrease is particularly rapid in areas of continentality.

Therefore, no overwhelming survival advantage is conferred on the plant in the spring by the photoperiodic control of flushing. These considerations also, to some extent, explain why dormancy is more closely adapted to the environment than is flushing.

There is one other observation which may appropriately be made in this section. Fig. 8 shows the relationship between time of entering dormancy and elevation at place of origin of 150 spruce provenances. Though the pure forms of white, Engelmann and Sitka spruce and their intermediate forms are represented by these 150 provenances, there is no disjunct pattern of variation in time of entering dormancy, and a clinal pattern is obvious. It may be concluded, in regard to spruce species at least, that this is evidence justifying the assumption that environmental pressures which result in microevolution, i.e. genecological differentiation, differ only in degree rather than in kind from the environmental pressures which result in macroevolution, i.e. speciation.

Langlet (1963a) has concluded that the faculty for normal development and survival in Picea excelsa (Norway spruce) is not conditioned by the time of flushing, but that on the contrary it is the time of cessation of growth, and initiation of dormancy which determines its fitness for use in practical silviculture. From the evidence presented in the last three sections it seems clear that this conclusion is equally valid in regard to the growth of white spruce in British Columbia.

GERMINATION BEHAVIOUR IN THE LABORATORY

Germination behaviour can be affected by a large number of factors other than those which are purely genetic, e.g. time of harvesting and methods of extraction and storage (Allen 1958, Roche 1965). For these reasons it is obviously advantageous if the experimental material is completely uniform, that is, if each provenance has been similarly treated, and if the quality of the seed of each provenances is identical. This is rarely possible, particularly when large numbers of provenances are involved; for almost certainly collections will have been made in different years, and the handling of cones and seed will also vary to some extent from year to year.

There is one other major factor which will considerably increase the complexity of the problem. When forest tree seed is collected in natural stands, the processes of natural selection which would operate on that seed are bypassed. Consequently, seed thus collected contains a much greater range of genetic variability than is likely to be found in nature in the seedling progenies resulting from that seed had it been allowed to propagate in its natural environment. These considerations also apply, of course, to the nursery propagation of collected seed. However, in this instance some selection will occur in the nursery bed, which in the optimum conditions of an incubator will not occur.

The seed used in the present study is highly heterogenous in quality. Only one non-genetic factor influencing germination behaviour is, to some extent, accounted for, that is, embryo development. The influence of other factors are unknown. Nevertheless, despite this heterogeneity in quality some general trends are apparent in germination behaviour which can be

attributed to selection and adaptation at the place of origin of the seed, rather than to the non-genetic factors discussed above.

It is clear from the results of this study that in assessing provenance difference in the germination behaviour of spruce, extreme temperatures are more effective than optimum temperatures (Table 18). Allen (1961), who obtained similar results with Douglas fir, demonstrated that coastal and interior provenances of this species can be distinguished best on the basis of germination behaviour at 10 or 15°C.

The effect of differences in embryo development on germination behaviour is most pronounced at optimum temperatures, that is those temperatures at which seed is usually tested. At extreme temperatures, particularly at low temperatures, the effect of differences in embryo development appears to be overwhelmed by the effect of provenance differences (Tables 14 to 17). For example, certain provenances from the general region of the Nass and Skeena rivers behaved similarly to strictly coastal provenances, e.g. provenance 85, lat. 54°40', long. 128°45' (near Kitsum Kalum lake), provenance 116, lat. 55°08', long. 127°24' (near Beaumont North of Smithers), in that they did not germinate at all, or had extremely low germination values at 15°C. The general relationship between germination values at 15°C and altitude is shown in Table 25.

Germination behaviour is positively correlated with altitude at all four temperatures. This would indicate that in regard to germination behaviour high elevation provenances are less narrowly adapted to temperature conditions than are low elevation provenances. In other words, high elevation provenances are capable of germinating over a wider range of temperatures than are low elevation provenances. This is also true in regard to species, for the Sitka spruce provenances did not germinate at all

at 15°C. The relatively high germination vigor of the high elevation Engelmann spruce provenances is further illustrated by the data given in Table 26, which is compiled from the Woody-Plant Seed Manual (see Alexander 1958 p. 9).

It is well known that interior provenances of Douglas fir and lodgepole pine germinate more rapidly than coastal provenances when incubated at the same temperatures (Allen 1958, Critchfield 1957, Roche 1962). This difference in germination behaviour is the result of adaptation to continental and maritime climates. Similarly the differences in germination behaviour between high and low elevation provenances of white spruce can be attributed to the differential selection pressures prevailing in the subalpine and montane forest regions.

The similarity in germination behaviour between the coastal provenances of Sitka spruce, and provenances from areas of coastal influence, but within the range of white spruce, suggest that there is an intrusion of Sitka spruce genes into the white spruce populations in this region.

Since germination behaviour is habitat-correlated it may be used in conjunction with measures of growth behaviour to discriminate clusters of similarity in the provenances studied.

TABLE 25

PERCENT OF PROVENANCES IN EACH OF FIVE ELEVATION GROUPS
WITH A GERMINATION VALUE¹ OF LESS THAN ONE AT 15°C.

	Elev. (ft.)	Percent
1	0 - 1000	100
2	1100 - 2000	45
3	2100 - 3000	53
4	3100 - 4000	19
5	4100 - 5700	0

¹ Germination value estimated in the manner proposed by Czabator (1962)

TABLE 26

AVERAGE GERMINATION CAPACITY OF ENGELMANN SPRUCE IN
COMPARISON WITH OTHER SPECIES

Species	Germination capacity	Species	Germination capacity
Engelmann spruce	69	Western white pine	54
Lodgepole pine	64	White spruce	49
Black spruce	61	Subalpine fir	38
Sitka spruce	60	Grand fir	28
Red spruce	60	Western larch	27
Western hemlock	56	Pacific silver fir	24

RESULTS

PART B

GEOGRAPHIC VARIATION IN MATURE POPULATIONS OF WHITE SPRUCE

Regression analysis of data resulting from sampling in the white-Engelmann spruce complex both in 1963 and 1964 showed that the index of cone scale morphology $L1/L2$ is highly correlated with altitude (Figs. 28 and 29). Fig. 34 shows the variability in cone scale morphology along an altitudinal transect at Stone Creek, 25 miles south of Prince George (lat. $53^{\circ}40'$, long. $122^{\circ}25'$). This transect passes from montane white spruce forest to subalpine Engelmann spruce forest.

Of the 10 measurements of cone scale morphology made the single measurement $L1/L2 \times L3$ was most effective in distinguishing species and intermediate forms. Figs. 30 to 32 show the pattern of variation in this measurement for the 1963 and 1964 collections, and also for the miscellaneous collections.

Sympatric populations of white and black spruce occur between latitudes $54^{\circ}00'$ and $60^{\circ}00'$ (Figs. 35 to 44), and sympatric populations of white and Sitka spruce occur between latitudes $54^{\circ}30'$ and $55^{\circ}30'$, and longitudes $127^{\circ}30'$ and $128^{\circ}40'$. Fig. 33 shows the pattern of variation in cone scale morphology in a longitudinal transect which passes from coastal Sitka spruce forest to montane white spruce forest. The actual samples used in constructing the line of shape for this transect are shown in Illus. 7.

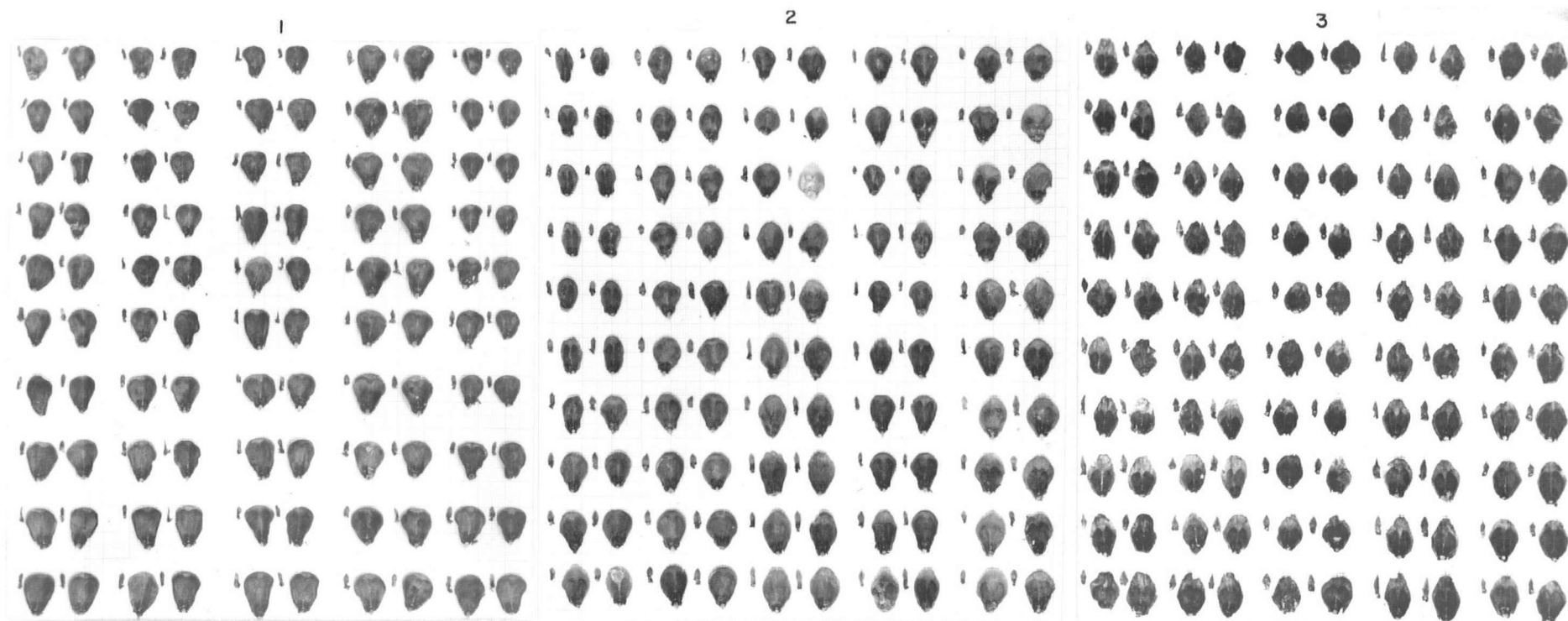
In all areas where white spruce is sympatric with any one of the other three spruce species which occur in British Columbia the line of shape of cone scales from these sympatric populations exhibited characteristics of

both species (Figs. 33, 34, 35 - 44).

The means and geographic origin of foliage samples are given in Table 27, and the results of the discriminant function analysis of all cone scale data for 1963 and 1964 collections are illustrated in Figs. 45 and 46.

In the black-white spruce complex along the Alaska highway every gradation in bark type was observed from that of pure white spruce to that of pure black (Illus. 14). A spruce population exhibiting a bark type identical with that which characterizes Picea glauca var. Porsildii was observed at Telegraph Creek, lat. $57^{\circ}52'$, long. $131^{\circ}12'$, elev. 1325 ft. (Illus. 14).

Individual trees and populations exhibiting atypical branching habit were located in numerous areas throughout the province (Illus. 13).



Mile 64 Alaska highway

Birch Island

Manning Park

No. 149

117

62

Lat. 5625

5135

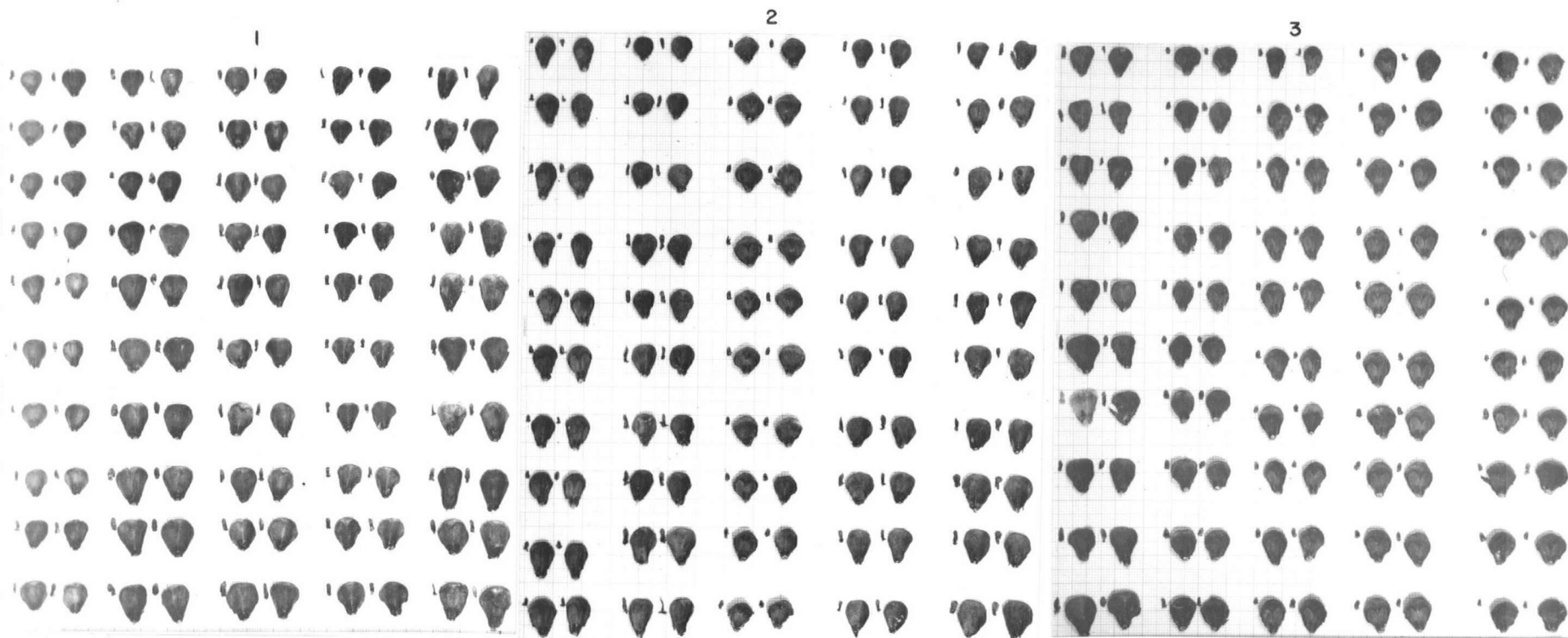
4905

Elev. 3000 ft.

1400 ft.

4800 ft.

Illus. 5 Cone scale morphology of pure white and Engelmann spruce samples (149 and 62) and intermediate form (117). Each column of scales and bracts represents a single tree.



Nr. Telegraph Creek

Alaska highway

Fort Nelson

No. 140

143

145

Lat. 5814

5939

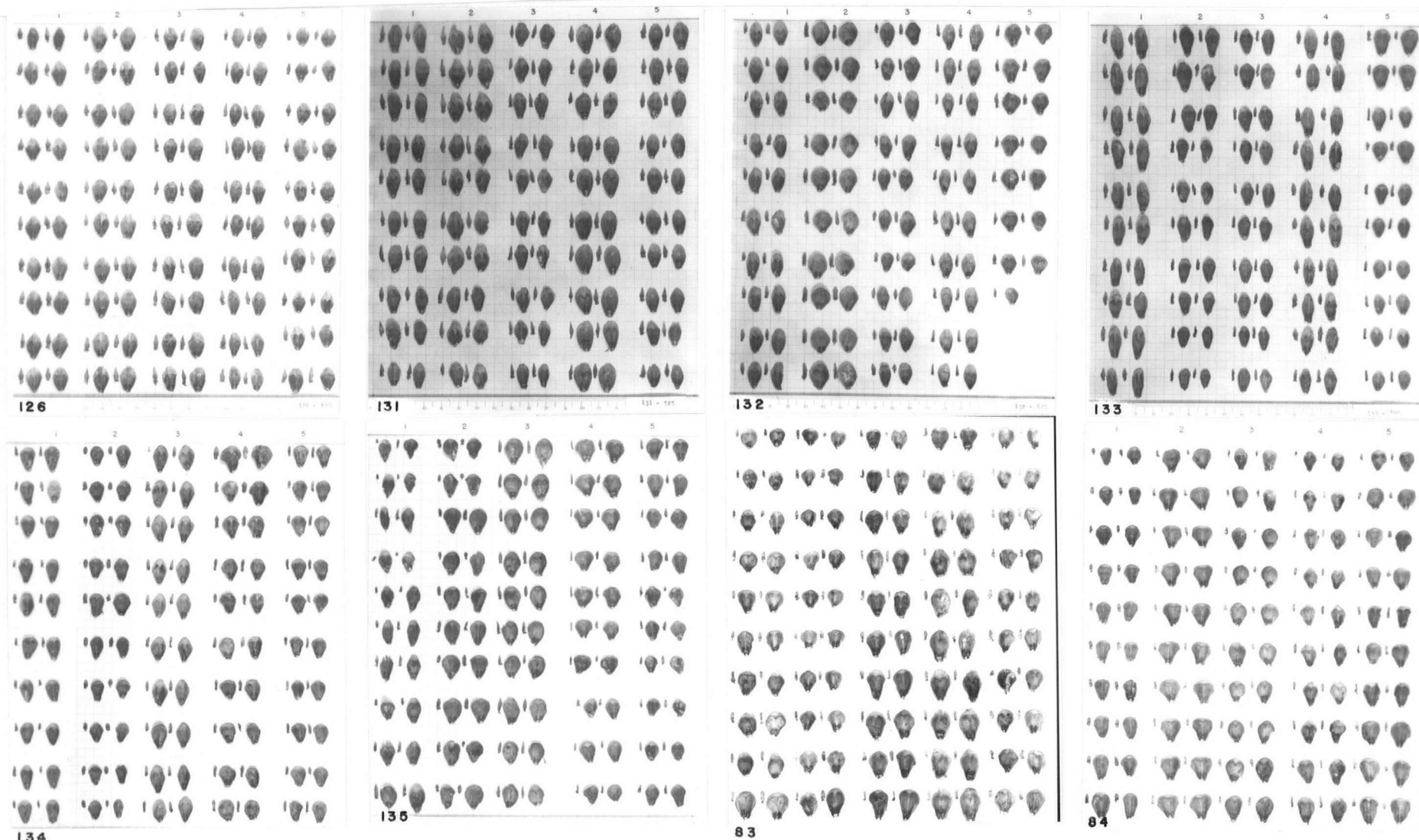
5837

Elev. 2300 ft.

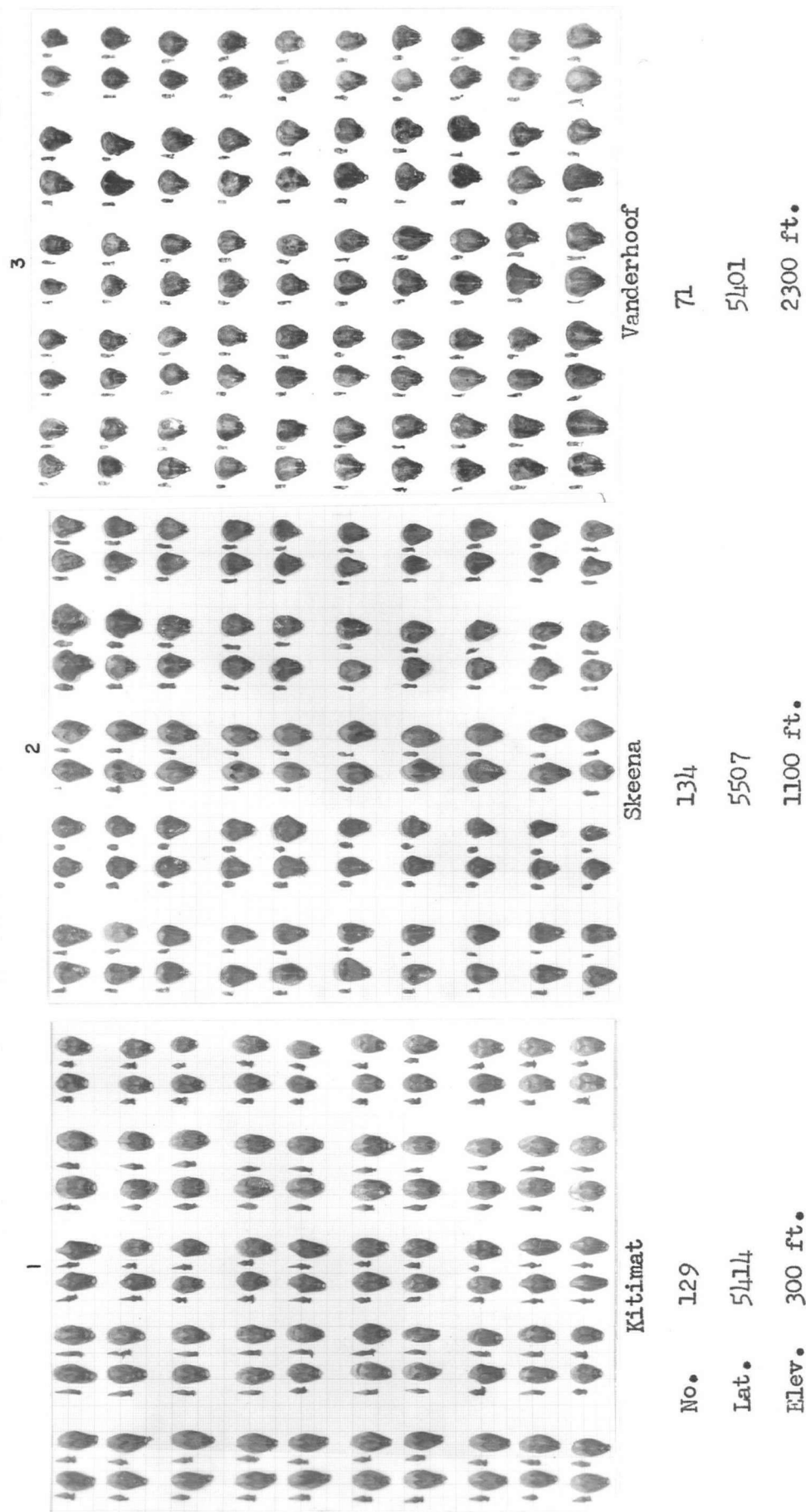
1700 ft.

1600 ft.

Illus. 6 Cone scale morphology of sympatric populations of white and black spruce in the boreal forests of Northern British Columbia.



Illus. 7 The variation pattern in cone scale morphology along a longitudinal transect from coastal Sitka spruce to montane white spruce forest. See fig. 33 for line of shape of samples 131 to 135 and 83 to 84 inclusive.



Illus. 8 Cone scale morphology of pure Sitka and white spruce (129 and 71) and intermediate form (134). Each column of scales and bracts represents a single tree.

TABLE 27
MEANS AND GEOGRAPHIC ORIGIN OF FOLIAGE SAMPLES FROM SIXTY TREES

Sample No	Tree No	Lat.	Long.	Elev. in 1000 ft.	L(mm)	T(mm)	L/T	S ₁	S ₂	S ₁ /S ₂	V	R
127	1 ^c	54.13	130.15	0.4	17.0	0.82	20.6	18.4	1.0	18.40	G	1
	2				14.3	0.72	19.8	13.7	1.0	13.70	G	1
	3				15.3	0.57	26.4	12.7	1.0	12.70	G	1
	4				13.7	0.75	18.3	14.3	1.0	14.30	G	0
	5				12.9	0.69	18.7	12.0	1.7	7.05	G	0
120	1 ^c	55.3	129.30	0.5	19.5	0.82	23.8	12.0	1.3	9.23	G	0
	2 ^c				11.2	0.73	16.3	14.8	2.5	5.92	G	0
	3 ^c				19.8	0.91	21.8	15.2	4.8	3.79	G	0
	4 ^c				14.7	0.79	18.6	14.6	1.4	10.43	G	0
	5 ^c				10.4	0.77	13.4	16.1	3.1	5.19	G	0
139	1	57.55	131.11	1.3	21.3	1.04	20.5	5.0	5.0	1.00	G	1
	2				17.7	1.10	16.0	6.4	4.7	1.36	G	0
	3				17.4	1.01	17.4	6.2	4.8	1.29	G	1
	4 ^c				17.8	1.31	13.6	7.3	5.8	1.26	P	1
	5				18.9	1.12	16.9	6.6	5.1	1.29	G	1
122	1 ^c	55.28	128.47	1.4	14.2	0.91	15.6	12.9	5.2	2.48	G	0
	2 ^c				15.4	0.99	15.5	10.4	3.7	2.81	G	0
	3 ^c				14.7	1.00	14.7	13.6	5.7	2.38	G	0
	4 ^c				17.0	1.00	17.0	12.1	4.4	2.75	G	0
	5 ^c				13.1	1.05	12.5	14.9	6.0	2.48	G	0
154	1	54.15	122.36	2.3	17.0	1.26	13.5	5.7	5.3	1.07	P	0
	2				12.3	0.86	14.2	5.7	3.3	1.70	G	0
	3				18.1	1.09	16.6	5.6	4.0	1.40	P	1
	4				15.2	0.97	15.5	6.7	4.7	1.42	P	1
	5				9.9	1.06	9.3	9.8	6.1	1.61	P	2
157	1 ^c	54.45	122.52	2.4	12.1	1.00	12.1	5.1	5.2	0.98	G	0
	2 ^c				15.8	1.05	15.2	7.2	5.1	1.41	G	0
	3 ^c				12.5	0.98	12.7	4.2	4.6	0.91	P	0
	4 ^c				16.8	0.92	18.3	4.4	4.2	1.05	P	0
	5 ^c				16.9	1.02	16.7	5.3	4.0	1.32	P	0
138	1 ^c	59.48	129.08	2.9	12.0	1.21	10.0	8.7	6.7	1.30	G	1
	2				16.5	1.14	14.5	6.1	6.4	0.95	P	0
	3 ^c				7.2	0.97	7.4	8.8	6.5	1.35	P	2
	4				16.2	1.31	12.3	7.8	7.6	1.02	G	0
	5 ^c				17.8	1.09	16.3	6.9	7.0	0.98	G	0
144	1 ^c	56.44	124.55	3.3	7.2	0.90	8.0	7.7	5.2	1.48	P	2
	2				8.8	1.11	8.0	6.9	6.4	1.08	G	0
	3				9.0	1.07	8.5	8.5	6.4	1.33	G	1
	4				8.7	0.98	8.9	7.0	5.1	1.37	G	0
	5				10.8	0.99	11.0	7.7	5.1	1.51	G	1
147	1 ^c	57.17	122.45	3.9	10.9	0.91	11.9	7.2	4.9	1.47	P	2
	2 ^c				13.6	1.08	12.5	6.8	5.2	1.30	G	0
	3 ^c				13.9	1.18	11.8	9.1	6.5	1.40	P	2
	4 ^c				11.4	1.20	9.5	10.0	5.5	1.81	P	2
	5 ^c				13.9	0.95	14.7	7.0	4.9	1.75	G	0
155	1 ^c	53.04	121.31	4.2	21.9	1.27	17.2	7.9	4.7	1.68	P	1
	2 ^c				15.8	1.14	13.8	7.3	5.3	1.38	P	0
	3 ^c				17.3	1.18	14.8	7.4	5.2	1.42	P	0
	4 ^c				19.2	1.15	16.7	7.0	5.6	1.25	P	0
	5 ^c				13.2	0.90	13.7	7.8	5.3	1.47	P	1
106	1	51.02	115.58	4.3	14.2	1.09	13.0	7.6	8.5	0.89	P	0
	2				17.9	1.16	15.2	7.5	6.4	1.17	P	0
	3				14.7	1.19	12.3	6.5	6.0	1.08	P	0
	4				13.3	1.24	10.7	8.4	6.9	1.21	P	0
	5				17.1	1.31	13.0	7.5	5.4	1.36	P	0
110	1	50.59	119.33	4.7	17.1	1.30	13.1	7.8	5.5	1.41	P	0
	2				20.1	1.34	15.0	8.7	6.2	1.40	P	0
	3				17.4	1.22	14.3	6.2	6.2	1.00	P	0
	4				20.5	1.24	18.3	7.9	5.0	1.58	P	0
	5				22.2	1.26	17.6	7.4	5.0	1.48	P	1

L - needle length, T - needle thickness, S₁ - stomatic lines on dorsal surface, S₂ - stomatic lines on ventral surface, R - no. of resin canals in needles; V - vestiture, P - pubescent, G - glabrous, c - cone samples taken from the same tree.

DISCUSSION

It is clear from the results that geographic variation in cone scale morphology is habitat-correlated. The assumption is warranted, therefore, that this variation is genetically based (Heslop-Harrison 1964 p. 217), and that variation in cone scale morphology is the phenotypic expression of a pattern of physiological variation resulting from (1) adaptation to the varying environments occupied by the species (2) hybridization and the production of hybrid swarms which are also subjected to the environmental pressures similar in kind to those acting on the parental forms.

It is not possible to determine the extent to which variation in cone scale morphology per se confers a survival advantage on spruce populations. The characteristic shape of the scale of high and low elevation populations in the white-Engelmann spruce complex, for example, may have a direct effect in facilitating pollination at varying elevations; for the characteristic shape of the scale is already present in young female strobili at the time of pollination, both in high and low elevation populations. More likely, however, this variation in cone scale morphology is a "neutral" character, and therefore a selective value must be ascribed not to the character as such, "but to the influence of the genes responsible for it upon the relative viability of a specific gene combination in a specific local environment" (Timofeeff-Ressovsky 1940 p. 123).

The results show that white spruce is sympatric in British Columbia, not only with Engelmann spruce, but also with black and Sitka spruce. Therefore in the interest of coherence and clarity the pattern of variation in cone scale morphology will be discussed in three separate sections under

the following headings:

- (1) The pattern of variation in the white-Engelmann spruce complex.
- (2) The pattern of variation in the white-black spruce complex.
- (3) The pattern of variation in the white-Sitka spruce complex.

THE PATTERN OF VARIATION IN THE WHITE-ENGELMANN SPRUCE COMPLEX

The results obtained in this study support Taylor's conclusion that the phylogenetic relationship between P. glauca and P. engelmanni in British Columbia "is best indicated by regarding them as subspecies of a single species..." (Taylor 1959).

It seems clear that both forms hybridize freely, and that the hybrid is occupying an ecological niche intermediate between that of the parental forms.

It is unlikely that the hybrid can successfully compete in the ecological niche occupied by either parent, for the parental forms will almost certainly be better adapted to their respective environments than the hybrid form. Therefore, for a hybrid to be successful an ecological niche must be available for colonization. If the ecological niche is intermediate between that of the parental forms, and is in the vicinity of the zone of hybridization then the hybrid will colonize it.

In British Columbia such an ecological niche appears to be available to the hybrid between white and Engelmann spruce. For between the low elevation, allopatric white spruce populations of the montane forest, and the high elevation, allopatric Engelmann spruce populations of the subalpine forest there lies a broad transition zone which is available to the hybrid.

Such a hypothesis will explain the clinal pattern of variation in cone scale morphology obvious in the white-Engelmann spruce complex. The selection pressures associated with altitude will, as a rule, vary progressively, and consequently it is to be expected that the transition from pure white spruce, through the hybrid swarms to pure Engelmann will be

progressive. This situation is clearly shown by the pattern of variation along a single altitudinal transect at Stone Creek, south of Prince George, illustrated in Fig. 34.

In the section dealing with the distribution and phylogenetic relationship of spruce in British Columbia, evidence was presented which indicated that white spruce during late-Wisconsin time was much more widely distributed than in historic time. Brink and Farstad (1949) have observed that in northern and central British Columbia it is apparent that aspen forest is advancing into grassland, and have suggested that one of the conifers which often succeeds aspen is P. glauca. These authors also point out that there is evidence that Douglas fir has been replaced by spruce in north central British Columbia.

White spruce is normally associated with the northern montane and boreal forest region in British Columbia. The present study, however, indicates that white spruce and its related forms occur in a wide variety of environments outside the northern montane forest, not of course as large forests, but as small, fragmented, though not isolated, populations. From the evidence of post-glacial forest succession presented in a previous section, and from the observations of Brink and Farstad (1949), it can be assumed that these populations are colonizing populations, and not remnants of past distributions.

For these reasons special interest is attached to those small, fragmented populations, such as the Birch Island population which is discussed below.

Sample 117, lat. $51^{\circ}35'$, elev. 1450 ft. was made at Birch Island, which is approximately 90 miles north of Kamloops. The sample area is situated in the valley of the North Thompson River, and therefore is in the southern section of the columbia forest region (Rowe 1959). This same

area is also represented in the immature spruce populations grown at Cowichan Lake, and the Birch Island provenance was the last provenance of the white-Engelmann complex to enter dormancy in the fall of 1966. Illus. 5:2 shows the pattern of variation in this population, which the discriminant function analysis showed to be a sympatric population of white and Engelmann spruce (Fig. 46), and it will be seen that in cone scale morphology the population has elements of both species.

It is clear, however, for the following reasons that the Birch Island population (and populations with similar cone scale morphology) is not simply a first generation hybrid between white and Engelmann spruce. Firstly there are no large allopatric populations of white and Engelmann spruce at this elevation (1400 ft.) in the immediate area. Secondly, if the Birch Island population were a first generation hybrid then it is to be expected that the seed collected from this population would be extremely variable. On the contrary, the population at Cowichan Lake showed very little variation. Furthermore, the delayed dormancy, and related growth behaviour of this provenance at Cowichan Lake can be explained in terms of the environment at its place of origin rather than in terms of heterosis resulting from hybridization.

The conclusion is that the low elevation, Birch Island population, and similar populations in the interior of British Columbia are the product of introgressive hybridization followed by selection and adaptation of fractions of the resulting hybrid swarms.

Introgressive hybridization results in the production of great variability, and consequently the colonizing potential of white spruce is greatly increased. For example, sample 63 (elev. 3300 ft., lat. $50^{\circ}00'$, long. $120^{\circ}36'$), which the discriminant function analysis classifies as a sympatric population of white and Engelmann spruce, was taken from trees

growing in association with ponderosa pine 13 miles south of Merritt and well outside the normally accepted ecological zone of white spruce in British Columbia.

For these reasons it is suggested that introgressive hybridization is one other factor which may account for the expansion of spruce in north central British Columbia referred to by Brink and Farstad (1949).

From the point of view of practical silvicultural and tree improvement, these low elevation scattered populations of spruce in southern latitudes have considerable interest, and will be referred to in another section (page 134).

The white spruce populations in the Rocky Mountain Trench do not fit into the general pattern of variation outlined above. In the first instance they occur at much higher elevations than white spruce in all other areas of the province east of long. $127^{\circ}00'$. West of long. $127^{\circ}00'$ white spruce also occurs at high elevations. However, this region is more appropriately discussed in relation to the pattern of variation in the white-Sitka complex.

The discriminant function analysis indicates that The Rocky Mountain samples 104 to 106 inclusive and sample 108 are from sympatric populations of white and Engelmann spruce. Samples 104 to 107 are all from above 4000 ft. Sample 108 is from 3850 ft. The flora is generally sparse, and distinct from that common to typical Engelmann spruce stands at 4000-5000 ft. elsewhere in the Province (Illus. 10). One of the most common shrub in many of these areas is Shepherdia canadensis. It is possible that these white spruce populations at relatively high elevations in the Rocky Mountain Trench, e.g. sample 108, are a modern analogue of the late-Wisconsin forest described by Watts and Wright (1966), and referred to in the section dealing with distribution and phylogeny (Illus. 10).

The results of this study indicate that in regard to cone scale morphology in the white-Engelmann spruce complex the change from pure white spruce to pure Engelmann spruce is a progressive one. Furthermore, it seems clear that the hybrid swarms, representing every degree of backcrossing, and intercrossing between hybrid forms, are extending the range of spruce beyond the boundaries of the ecological zone generally associated with white spruce.

THE PATTERN OF VARIATION IN THE WHITE-BLACK SPRUCE COMPLEX

Fifteen areas were sampled in the boreal forest lying approximately between latitudes $56^{\circ}00'$ and $60^{\circ}00'$. The cone scale morphology of individual trees in 10 of these areas is illustrated in Figs. 35 to 44. It will be seen that black spruce is a component of each sample except sample 140 (forest section Stikine plateau, lat. $57^{\circ}55'$, elev. 1300 ft.) and 139 (forest section upper Liard, lat. $59^{\circ}48'$, elev. 1300 ft.). Sample 140 is identified as pure white spruce. Two trees of sample 139 are identified as white spruce, but the cone scale morphology of the remaining three trees of the sample corresponds neither to white or black spruce, or the intermediate form of these species (Fig. 36). In this regard special interest is attached to the fact that this population (139) at Telegraph Creek exhibited a bark type unlike the bark either of white or black spruce. (Illus. 14).

Another characteristic which distinguished the Telegraph Creek population was the fact that male and female stroboli were present at the base of the crown, whereas the common position for reproductive organs in white spruce is in the uppermost part of the crown. However, there is no striking difference in needle morphology of this population and other populations of white spruce (Table 27).

Sample 141, which is also from the Stikine plateau section of the boreal forest appears to have a black spruce component (Fig. 38). Samples 138, 142, 143 and 145 are from the upper Liard section of the boreal forest. The population represented by sample 138 was examined in some detail in the field. Trees numbered 1 and 3 were felled, and foliage was collected from

trees numbered 1, 3 and 5. It was not possible to distinguish clearly black and white spruce by field observations in these areas. Tree number 1, for example, had foliage which in general appearance looked like black spruce though its cones had the appearance of white spruce. The needles of this tree were 12 mm. long, which is closer to black than white spruce (Table 27).

The cone scale morphology of tree number 3 is apparently intermediate between black and white spruce (Fig. 35). Its needles are strikingly short, 7.2 mm in relation to the length of the needles of the other 4 trees sampled, and its twigs are pubescent. Both of these are black spruce characteristics, yet the line of shape clearly shows characteristics of both white and black spruce (Fig. 35, tree no. 3).

Taylor (1959) has shown that foliage characteristics are not correlated with cone type in intermediate populations of white and Engelmann spruce, and suggests in explanation that both characteristics are probably due to the independent segregation of several genes. The lack of strong correlation between cone scale morphology and needle morphology illustrated by trees number 1 and 3 of sample 138 (Fig. 35) suggests that Taylor's explanation may also be extended to intermediate forms of black and white spruce in the boreal forests of northern British Columbia.

Sample 142 (Fig. 39) was made 30 miles south of Watson Lake near the Hyland River elev. 2075. Trees number 4 and 5 of this sample are intermediate between white and black spruce in cone scale morphology. Trees number 1, 2 and 3 are clearly white spruce.

Sample 143 (Fig. 40), elev. 1725 ft. was made 143 miles south of Watson Lake. Trees numbered 1 and 3 are classified as black spruce, and 2, 4 and 5 as white.

Sample 145 was made at mile 281 on the Alaska highway, elev. 1650

ft. Tree number 1 is classified as white spruce, and trees 2, 3, 4 and 5 as black (Fig. 42).

Samples 144, 146, and 147 were made in the northern foothills section of the boreal forest (Illus. 11). Foliage samples were taken in sample area 144, but except for tree number 1, the foliage was taken from trees other than those which provided the cones. It will be seen that, in general, needle morphology for the entire sample is more characteristic of black spruce than white. Tree number 1 is identified as black spruce, number 3 as intermediate, and numbers 2, 4 and 5 as white (Fig. 41). See also Illus. 14 which shows variation in bark type in this area.

The line of shape for each of the five trees in sample 146, mile 244 of the Alaska highway, elev. 1760 ft., is relatively clear cut. Tree number 1 is classified as an intermediate, numbers 2, 4 and 5 as black, and number 3 as white (Fig. 43).

Foliage and cones were all taken from the same trees in sample 147, mile 168 of the Alaska highway, elev. 3900 ft. Again it will be seen that there is no apparent correlation between foliage characteristics, and cone scale morphology (Table 27, Fig. 44). Trees 1 and 3 are classified, according to line of shape, as black spruce, mean needle length is respectively 10.9 mm. and 13.9 mm. Trees number 2 and 5 are classified according to line of shape as white, mean needle length is respectively 13.6 and 13.9 mm. Tree number 4 is classified as intermediate, mean needle length is 11.4 mm. Trees number 1, 3 and 4 are pubescent, whereas 2 and 5 are glabrous. (Table 27, Fig. 44).

Sample 148 is not graphed for line of shape but from Fig. 46 it will be seen that it is classified as an allopatric zone of white spruce. This sample was made at mile 103 of the Alaska highway, elev. 3200 ft., and field observations indicated that the ecology of the population sampled

was quite different from all other areas to the north, and that the area is located in the mixedwood section of the boreal forest region. The deep moss covering (see Illus. 11) typical of all sampled areas to the north, except sample area 139, is absent.

Sample area 149, elev. 3000 ft., is also in the mixedwood section of the boreal forest, and the discriminant function analysis, as in the case of sample 148, indicates that it is from an allopatric population of white spruce. This area lies approximately 18 miles north of Fort St. John. The ground flora in this area is similar to that of sampled area 148, and is quite distinct from all other northern samples, in that the deep covering of moss and Ledum is absent.

The ecology of samples to the south of sampled area 149, except sample 154, which will be discussed separately, are in general typical of the spruce forests of the montane forest region at 2000 ft. in the general region of Prince George, lat. ca. $54^{\circ}00'$.

It is clear from the results of this study that black spruce is a much more important component of the spruce forests along the Alaska highway than has been hitherto acknowledged (Garman 1957). Of the 10 areas sampled north of latitude $57^{\circ}00'$, only one, sample area 139, at Telegraph Creek in the Stikine canyon, did not exhibit a black spruce influence.

North of lat. $57^{\circ}00'$ on the Alaska highway, black and white spruce appear to occupy the same ecological niche. South of this latitude (it is emphasized that lat. $57^{\circ}00'$ is an arbitrary line for the change is transitional), there is a gradual change in the composition of the spruce populations, and black spruce moves to bog areas, and is not generally found in association with white spruce (e.g. samples 148 and 149). Occasionally, however, white spruce will be found in association with black in poorly

drained areas south of lat. $57^{\circ}00'$, e.g. sampled area 154.

It will be observed both from the results of the discriminant function analysis, and the results obtained by line of shape method, that Engelmann spruce is absent throughout the sampled areas north of latitude $56^{\circ}00'$.

As will be seen from the results of the discriminant function analysis (Fig. 46) all three spruce species, white, black and Engelmann are represented in sample 154. Sample 154 was made on the periphery of a bog near Summit Lake, 35 miles north of Prince George. Foliage samples were taken in this area, and it will be observed that the foliage samples of 4 of the 5 trees sampled exhibited dense pubescence (Table 27).

This bog, and its associated flora, represent a fairly typical ecological niche where black and white spruce may be found in association south of lat. $57^{\circ}00'$. However, in contrast to the situation north of latitude $57^{\circ}00'$, such an association is atypical for white spruce in the montane forest region, where it is usually found in pure stands, and where black spruce is relegated to areas of poor drainage. On the other hand, in the boreal forest region along the Alaska highway north of lat. $57^{\circ}00'$, white spruce is typically associated with black spruce on muskeg over a very large area as indicated by samples 138 and 140 to 146. Consequently it is not exceptional that intermediate forms of black and white spruce are represented in these samples.

THE PATTERN OF VARIATION IN THE WHITE-SITKA SPRUCE COMPLEX

In the study of variation in immature spruce population at the Cowichan Lake nursery on Vancouver Island it was observed that provenances from the general region of the Nass, Skeena and Bulkley river basins entered dormancy later than provenances from further east but at similar elevations. For example, all provenances from Doughty (lat. ca. $55^{\circ}00'$, long. ca. $127^{\circ}30'$, elev. 2000 ft.) north of Smithers, and from the region of Hazelton, entered dormancy much later than provenances from further east, e.g. Fort Babine (lat. ca. $55^{\circ}20'$, long. ca. $126^{\circ}28'$, elev. 2300 ft.). Furthermore, certain provenances from this same region, in regard to germination behaviour at 15°C. , behaved like Sitka spruce in that they did not germinate at all at this temperature, or showed very low germination values.

The pattern of variation in mature populations in the same general region of the Nass, Skeena and Bulkley river basins, as determined by cone scale morphology, presents strong evidence as to why the progenies of spruce populations in this area behave as indicated above when germinated or grown in a uniform environment (Fig. 33 and Illus. 7). It seems clear that there is a broad sympatric zone of white and Sitka spruce in northwestern British Columbia, and that Sitka spruce genes appear to have penetrated along the valley bottoms as far east as Hazelton and Smithers, and south east into the valley of the Morice River.

As will be seen from Fig. 33 and Illus. 7 there is every gradation in cone scale morphology from that of pure Sitka (sample 131) to that of pure white (sample 84); though sample 84 still shows the influence of Sitka spruce. There is, therefore, considerable evidence that introgressive hybridization

is occurring in this area. The variation pattern is quite striking, and obvious even in the field. For example, sample 132 was made in the Skeena valley 43 miles east of Terrace. The associated species in the sampled area are western red cedar and western hemlock. Field notes indicate that from west to east this was the first sample which showed a strong influence of white spruce. The cone scale morphology of tree number 5 of this sample is clearly intermediate between that of white and Sitka spruce (Illus. 7). It is, perhaps, significant that it was not possible to obtain more than 15 cones from this tree.

Sample 133 was made 58 miles east of Terrace. The strong influence of Sitka spruce in this area is still quite obvious, and even by a visual examination of the photograph of the sample from this area it is possible to identify intermediate forms of white and Sitka spruce.

Fig. 33 and Illus. 7 show the pattern of variation in cone scale morphology in the Skeena and Bulkley river valleys only. It is important to note, however, that the pattern is similar in the Nass river valley.

A major complicating factor in the interpretation of the variation pattern in this general region is that intermediate forms of white and Sitka spruce are almost identical with pure Engelmann spruce in cone scale morphology. This fact has emerged from the present study, and is, perhaps, an explanation for the reported occurrence of Engelmann spruce at very low elevations, in areas of the Nass and Skeena rivers (Garman 1957). Almost certainly it is the reason why samples in this area have been classified as a sympatric population of Sitka, Engelmann and white spruce by the discriminant function analysis.

The best way to discriminate between spruce species and their intermediate forms is by a combination of measurements. No single measurement by itself is sufficiently accurate. Nevertheless, it is possible to distinguish between white, Engelmann and Sitka spruce, though not intermediate forms, by

the measurement $L1/L2 \times L3$. The means of this measurement are graphed in Figs. 30 to 32 for both standard and miscellaneous samples. It will be seen that to the north and east of the general region of the Nass, Skeena and Bulkley valleys the cone scale morphology is that of pure white spruce. The samples to the immediate south are pure Sitka spruce. There are, then, in the vicinity of the sympatric zone extensive allopatric populations of white and Sitka spruce.

From the results reported here, and from field notes, there is no indication that extensive allopatric populations of Engelmann spruce occur in the region under discussion. In fact at high elevations (above 4000 ft.) to the north of the Skeena and Nass rivers the miscellaneous samples clearly indicate the presence of pure white spruce. To the writer's knowledge, therefore, the nearest extensive allopatric population of Engelmann spruce is several hundred miles to the east at 3500 ft. in the region south of the McGregor river and north of Sinclair Mills (lat. ca. $54^{\circ}00'$, long. ca. $121^{\circ}44'$).

The conclusion is, therefore, that the variability in cone scale morphology in northwestern British Columbia is the result of introgressive hybridization between white and Sitka spruce in this region. Subsequent selection and adaptation gives a pattern of variation (Fig. 33, Illus. 7) which varies parallel with the progressive change in environment illustrated in Fig. 9.

THE RELATIONSHIP BETWEEN THE VARIATION PATTERN IN
MATURE AND IMMATURE SPRUCE POPULATIONS IN BRITISH COLUMBIA

As already stated the clinal pattern of variation in cone scale morphology in the white-Engelmann spruce complex is the phenotypic expression of physiological adaptation to the varying environments occupied by these species and their intermediate forms.

The variation pattern of cone scale morphology in the Nass and Skeena river basins indicates that there is a broad sympatric zone of white and Sitka spruce in this area, and that there is a clinal pattern of variation in cone scale morphology along a longitudinal transect from coastal Sitka spruce forests to the interior montane white spruce forests.

These results, therefore, and the results obtained in regard to the growth behaviour of the immature spruce populations at Cowichan Lake, are mutually corroborative. The results of both studies testify to the overwhelming influence of environmental pressures associated with altitude with respect to variation in the white-Engelmann complex. In regard to the pattern of variation in the white-Sitka complex both studies indicate the extent and effect of the penetration of Sitka spruce populations into populations of white spruce in the montane forest region.

Sampling in mature populations was more extensive than the sampling in immature populations; consequently, there is no corroborative evidence from the variation pattern in immature populations to support the results obtained in regard to the pattern of variation in cone scale morphology in the boreal forests of northern British Columbia.

Obviously, it would have been considerably better to have conducted

the study of variation in cone scale morphology on cones which also supplied the seed for the study of variation in immature populations at Cowichan Lake. Had this been done it is clear that a high correlation could be established between the cone scale morphology of the parents and the performance of the progeny in the nursery. However, even though cones and seed were obtained from different samples it is obvious that seedlings from a seed sample obtained from cones with a morphology similar to that for high elevation spruce in Table 6 and Illus. 3 are likely to enter dormancy at a relatively early date in a coastal nursery. On the other hand seedlings from a sample with a cone scale morphology similar to that for low elevation spruce in Table 6 and Illus. 3 are likely to enter dormancy at a later date than the high elevation sample. These considerations do not, of course, apply to spruce populations from the boreal forest.

One of the most recent, and most detailed taxonomic studies of natural populations of a coniferous tree species is Ruby's (1967) study of Scots pine. Six hundred and eighty-nine, cone seed and leaf specimens of Scots pine were collected from 39 stands in Europe and Asia. Nineteen variable characters of cone and seed morphology were measured. Compilation of the components of variance for eight of these characters showed that more than 95 percent of the variance was attributable to between-region differences, and less than 3 percent to stands within regions.

The particular significance of these results is that they could be compared with the results of an associated 122-origin provenance study of juvenile characters of Scots pine from the same regions but grown in a uniform environment in East Lansing, Michigan (Wright and Bull 1963).

The regional groupings obtained by both studies were nearly identical, and it was concluded that it is possible to delimit a race or variety of Scots pine nearly as well by studying morphological variation

in parental specimens collected in natural stands in Europe as by growing their progenies in a uniform environment (Ruby 1967).

Correlation between morphological and physiological characteristics are not unusual, and are the rule rather than the exception if the morphological characteristics are associated with the reproductive organs. For example the seed of the coastal and interior forms of Douglas fir (Pseudotsuga menziesii (Mirb) Franco) is distinct morphologically, and this difference is closely paralleled by a striking difference in germination behaviour at certain temperatures (Allen 1961). As Diver (1940) has stated "morphological variation may only be a part of the whole field of variability, but there is little variation in the rest of the field which is not correlated with some morphological change, however slight".

The study of variation in spruce cone scale morphology referred to above is not a special case, and a number of similar investigations have yielded information which is of immediate value to the forester engaged in provenance research, e.g. Prichäusser 1958; Parker 1963; Myers and Bormann 1963; Hall and Carr 1964.

The principal value of studies of this nature is that they provide information concerning the broad pattern of variation in the wild, mature populations of tree species which have undergone selection and adaptation, and possibly (as in the case under discussion) hybridization in their natural habitat. A relatively large sample can be made and rapidly assessed, and in this way the scope of subsequent experimental work with immature populations in controlled and partially controlled environments is narrowed. These tests in turn narrow the scope of the field tests which ultimately follow all preliminary assessments of variation.

The correlation between physiological variation in immature populations and morphological variation in mature populations obtained in this

study supports the view that biometrial^c_^ studies on field specimens of
cones and foliage can provide valuable evidence concerning broad patterns
of variation in the mature populations.

THE TAXONOMIC SIGNIFICANCE OF GEOGRAPHIC
VARIATION IN WHITE SPRUCE IN BRITISH COLUMBIA

The pure forms of white and Engelmann spruce in British Columbia are distinct taxonomically and occupy quite distinct ecological niches. As a result of introgressive hybridization, however, the intervening ecological zone is also occupied by hybrid swarms, with the result that white and Engelmann spruce in British Columbia, as the present study indicates, are the extreme forms of a clinal pattern of variation which ranges from low elevation montane forest to high elevation subalpine forest. Therefore, though the taxonomic relationship between white and Engelmann spruce in British Columbia is, somewhat analogous to that of Abies balsamea var balsamea and A. balsamea var phanerolepis described by Myers and Bormann (1963), there is little doubt about the taxonomic validity of the subspecific status (Taylor 1959) of the extreme forms of the white-Engelmann cline. The question remains however, as to how the great array of variability along the cline can be classified taxonomically.

Langlet (1962, 1963) has discussed in some detail the whole question of nomenclature in regard to infraspecific variability in tree species. Langlet's main thesis is that a species distributed over a region with a continuously changing environment will exhibit a clinal pattern of variation, and that it is futile and unnecessary "to attempt to construct special terminology in order to summarize, and at the same time discriminate between, the various patterns which may occur" (Langlet 1963). Langlet goes on to say that when dealing with facts and problems of ecological infraspecific adaptation and variability, as few terms as possible ought to be used.

The writer is in full agreement with this view, and believes that the best way to identify a spruce population in British Columbia is to assign to the sample, whether it is seed for future propagation, or foliage and cone specimens for an herbarium, the exact elevation, latitude and longitude at its place of origin. At a later date if a name must be assigned to the sample then it may be classified by referring to Table 6 and determining the line of shape of the cone scale morphology of the sample in the manner presented here.

If a small portion of cones of all seed lots, collected for reforestation purposes in sympatric zones of white and Engelmann spruce were retained it would be possible to identify all such seedlots by the line of shape method, and classify them accordingly. In this way each provenance may be named simply as Picea glauca (Moench) Voss subsp. glauca; P. glauca (Moench) Voss subsp. engelmannii (Parry) Taylor; or P. glauca X P. engelmannii, depending on its classification (see Taylor 1959).

The results of the present study strongly indicate that the simplified nomenclature proposed by Taylor (1959) more accurately reflects the taxonomic relationships of white and Engelmann spruce in British Columbia than that which existed prior to his recommendations. It is suggested, therefore, that this nomenclature be used in the registering of spruce seed in this province.

Natural hybrids of white and Sitka spruce, and white and black spruce have already been identified and described. The white-Sitka hybrid was described from material collected on the Kenai Peninsula in Alaska. The white-black hybrid was described from material collected in Minnesota (Little 1953, Little and Pauley 1958). It appears, however, that the evidence presented in this study is the first indication of the possible occurrence of both hybrids in British Columbia, though, clearly, much more detailed taxonomic

work in the sympatric zones demarcated for these species is required before it will be possible to select such hybrids in British Columbia for tree improvement work.

The varietal epithet albertiana should be discarded, for as Taylor (1959) has pointed out, and as indicated by the present study, it refers to the white-Engelmann hybrid which is more accurately designated in the manner indicated above.

There is no evidence from the present study which indicates that the Porsild variety of white spruce occurs extensively in northern British Columbia. It is possible that the small population at Telegraph Creek (sample area 139) is of this variety. If so, it is obviously worthy of further investigation to determine its correct taxonomic status, and the value of the population in regard to tree improvement work. This observation could be equally applicable to all the hybrid components of the spruce complex of British Columbia.



Illus. 9 Subalpine Engelmann spruce forest. The upper photo gives a general view of sample area 103, 64 miles NE of Cranbrook, Lat. $49^{\circ}47'$, long. $115^{\circ}27'$, elev. 4625 ft. The lower photo illustrates the dense shrub understory common in subalpine Engelmann spruce forests. Sample area 112, 48 miles NE of Kamloops, Lat. $50^{\circ}48'$, long. $119^{\circ}52'$, elev. 4800 ft.



Illus. 10 The white-Engelmann complex in the Rocky Mountain Trench. The upper photo shows structures of stand at sample area 105. Lat. $50^{\circ}48'$, long. $116^{\circ}00'$, elev. 4000 ft. and the lower photo sample area 108. Lat. $51^{\circ}21'$, long. $116^{\circ}34'$, elev. 3850 ft. Note the xeric appearance of the stands and the lack of dense ground vegetation. Contrast with illus. 9.



Illus. 11 The white-black spruce complex of the Alaska highway. Mile 402 Alaska highway, sample area 144. Lat. $58^{\circ}44'$, Long. $124^{\circ}55'$, Elev. 3300 ft. Note the deep Moss layer.

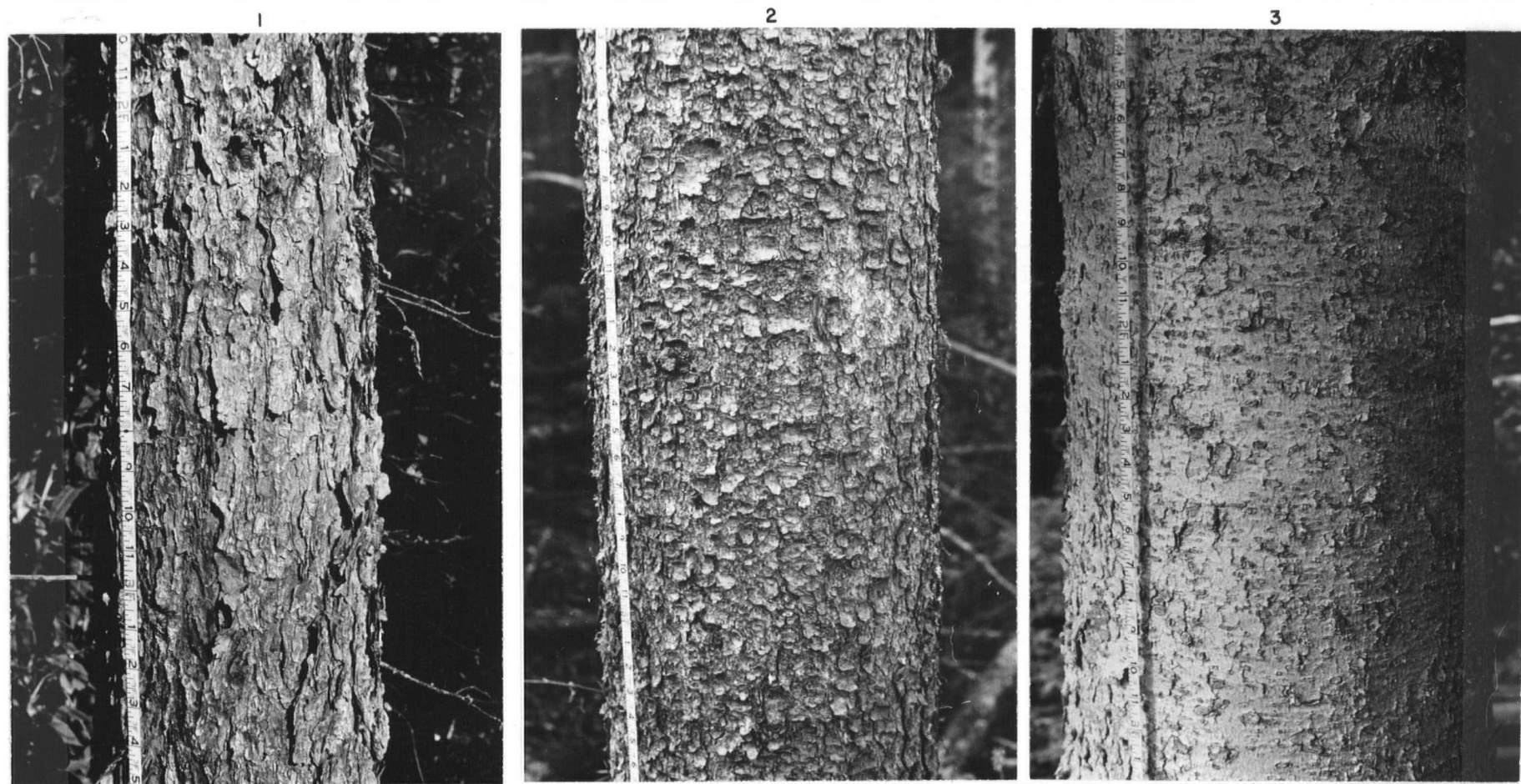


Illus. 12 Characteristic branching habit in high (1) and low (2) elevation spruce in B.C.
 1 - 38 miles West of Needles, elevation 4100 ft.
 2 - 40 miles East of Prince George, elevation 2000 ft.



Illus. 13 Variation in branching habit in spruce in B.C.
 1 - 18 miles Northeast of Nelson; elevation 4425 ft.
 2 - 48 miles Northwest of Smithers; elevation 1200 ft.
 3 - 30 miles North of Kamloops; elevation 3500 ft.
 4 - 104 miles North of Terrace; elevation 1375 ft.

Fig. Variation in spruce bark type in B.C.



Illus. 14 Fig. 14:1 and 14:2 illustrate variation in bark type in a sympatric zone of white and black spruce on the Alaska highway in Northern B.C. in the general region of sampled area 144, elev. 3300 ft., lat. $58^{\circ}44'$. Along the Alaska highway there is every gradation between these two extremes of bark type. Fig. 14:3 illustrates the unusual bark type of the Telegraph Creek population (see fig. 36). 14:1 black spruce, 14:2 white spruce.

THE SILVICULTURAL SIGNIFICANCE OF GEOGRAPHIC
VARIATION IN WHITE SPRUCE IN BRITISH COLUMBIA

Turesson (1925), who proved the existence of maritime and inland, northern and southern, low and high altitude strains within species, was the first investigator to demonstrate that the greater the range of climates the species is able to occupy the greater the variability within the species. Furthermore, Turesson also demonstrated that climatic races of widely different species showed parallel variation in regard to both morphological and physiological properties (Hiesey et al. 1942).

The present study indicates that, in common with the numerous plant species investigated by Turesson, white spruce is adapted to a wide variety of environments, ranging from areas of coastal influence, e.g. the Nass, Skeena and Bulkley river basins, through the montane and Columbia forest to subalpine forests. The study also shows that the colonizing potential of white spruce has been increased by hybridization, and that this species and its related forms have penetrated a variety of ecological niches well outside the ecological zone normally associated with spruce.

The general significance of photoperiodicity for the practice of forestry has already been discussed by Wiersma (1958) and will not be repeated here. It is, perhaps, sufficient to note that all recommendations in regard to the silviculture and breeding of white spruce in British Columbia must take this factor into consideration.

The ecotype concept of variation (Wright and Baldwin 1957) tends to oversimplify the complex pattern of variation normally found within a tree species. It is not intended to repeat here the lengthy debate as to

what is an ecotype, and what is a cline (Langlet 1959). The writer believes that the overwhelming evidence, including the evidence of the present study, indicates that the variation pattern in most widely distributed coniferous species is clinal and not ecotypic. Ecotypes in coniferous tree species are more frequently the artifacts of inadequate sampling or statistical procedures than a true expression of the variation pattern.

However, it is obvious that from the point of view of practical silviculture the ecotype concept is a useful one, and it will be resorted to here in making recommendation, in regard to the silviculture of white spruce in British Columbia. It is emphasized, however, that when latitudinal and altitudinal boundaries are referred to, it is not implied that these boundaries circumscribe an ecotype which, in its pattern of variation, is discrete from that of the populations immediately to the north or south in the case of latitude, or higher and lower in the case of elevation.

White and Engelmann spruce in British Columbia are the extreme forms of a clinal pattern of variation associated with altitude. Therefore, there are no sharp zonal boundaries marking the region outside which a given population cannot be moved. Nevertheless, if a population is displaced by 1000 ft. upwards it is obvious that in general its growth rhythm will be out of phase with the more severe environment at its new position. If it is displaced downwards, but retained at the same latitude its growth rhythm will also be out of phase with the environment at the lower elevation. But since in most instances this environment will be less harsh than at 1000 ft. higher no profound detrimental effect will follow as a result of a displacement downward. However, no silvicultural gain can be expected either.

For example, the high elevation populations from approximately the same latitude as Cowichan Lake were unable to avail of the mild condition pre-

vailing in the coastal environment, and very low elevation of the Cowichan Lake nursery. All these populations entered dormancy when temperatures were increasing.

If, however, the displacement is downwards, and to the north, then it is likely that a silvicultural gain will result from this transfer. There is no silvicultural gain obtained by propagating high elevation spruce provenances in a coastal nursery at southern latitudes in British Columbia as is the practice at present. On the contrary, such a practice will almost certainly increase the cost of planting stock because of the necessity of repeated transplanting to obtain seedlings of suitable size for outplanting.

For these reasons it is suggested that the propagation of high elevation spruce provenances in coastal nurseries at southern latitudes, either on Vancouver Island, or on the mainland of British Columbia should be discontinued. Such populations growing in coastal nurseries at southern latitudes enter dormancy early, and have a stunted "rosette" appearance resulting from decreased internode length. On the other hand, these same populations are likely to produce seedlings with desirable silvicultural characteristics much more rapidly in a northern nursery, such as Telkwa (lat. ca. $55^{\circ}00'$) in west central British Columbia, which is approximately six degrees north of the coastal nurseries. Consequently, as will be seen from Fig. 14, there is an appreciable gain in photoperiod during the growing season.

Corroborative evidence for the conclusions stated in the above paragraph is available from a study initiated by the writer in 1963 at the Telkwa nursery, and at the Duncan nursery on Vancouver Island, which is approximately the same latitude as the Cowichan Lake nursery, and six degrees south of the Telkwa nursery. Thirteen provenances of white and Engelmann

spruce were sown at both nurseries in the spring of 1963. Table 28 shows the percentage of seedlings at both nurseries which had entered dormancy by August 22, 1964 (Roche 1964a). It will be seen that a much greater percentage of seedlings of all provenances at the Duncan nursery had entered dormancy by the date given.

TABLE 28

PERCENTAGE OF 2-YEAR-OLD SEEDLINGS OF 13 SPRUCE PROVENANCES DORMANT BY AUGUST 22 AT A SOUTHERN AND A NORTHERN NURSERY IN BRITISH COLUMBIA.

Provenance	Lat.	Elev. (ft.)	Percent Dormant	
			Duncan (ca.lat. 49°00')	Telkwa (ca.lat. 55°00')
1	56°00'	2300	69	23
2	55°40'	2000	52	15
3	54°20'	2000	54	16
4	54°10'	2000	37	17
5	54°07'	2300	42	18
6	53°25'	1800	22	11
7	52°30'	2200	34	12
8	51°40'	1400	1	0
9	51°15'	3800	69	36
10	50°40'	4000	55	18
11	50°15'	3200	39	9
12	49°30'	4700	33	18
13	49°15'	4700	63	23

High elevation southern populations cannot avail of a long growing season, but they can avail of increased day length. This is a major conclusion deduced from the performance of these populations of Cowichan Lake, and it should be taken into consideration in all plans relating to the displacement and propagation of these populations, whether in nurseries or plantations.

All spruce provenances south of latitude $53^{\circ}00'$, and from below 2500 ft. may be expected to grow rapidly in coastal nurseries in southern latitudes. Indeed, some of these populations, i.e. the Birch Island population, will grow as rapidly as Sitka spruce in a coastal nursery.

Most of these low elevations, southern latitude provenances are fragmented in their distribution, and lie outside the main body of the species. Nevertheless, it is clear that they have considerable silvicultural potential, and that they will represent an important component in any tree improvement program which may develop for white spruce in British Columbia. For these reasons, a special effort should be made to collect seed from these populations. This has already been done for the Birch Island population, and there is now ample seed of this population available for further experimentation.

Spruce populations from below 2500 ft. between latitudes $53^{\circ}00'$ and $55^{\circ}00'$ produce seedlings with desirable silvicultural characteristics more rapidly in coastal southern nurseries than high elevation populations from southern latitudes. Nevertheless, even these populations will do less well, silviculturally speaking, in a coastal nursery at low latitudes than in a northern nursery. Indeed, the evidence of this study suggests that a nursery in the vicinity of Telkwa is likely to produce desirable spruce stock in a shorter period of time than coastal nurseries at southern latitudes. Assuming that the microenvironment at the nursery site is

optimum, it is possible that a nursery situated further east, but at the same latitude as Telkwa, is equally preferable for the propagation of high elevation provenances from southern latitudes. This remark, however, does not apply to the populations from low elevation and low latitudes already referred to.

These conclusions appear to contradict the recommendations of Eis (1966) in regard to the propagation of white spruce seedlings in coastal nurseries. However, the contradiction is more apparent than real for the provenance effect was not investigated by Eis.

However, it is also clear from the results of this study that provenances from below 2500 ft., and south of latitude $55^{\circ}00'$ will respond extremely well to increased temperature irrespective of the day length (within limits). Therefore, these provenances can be grown on the coast with optimum silvicultural advantage if temperatures are increased artificially, e.g. by the use of plastic greenhouse. Furthermore, these populations do not require the stimulus of an artificial soil mix, and will respond vigorously to increased temperatures while growing on ordinary nursery soil (Illus. 4).

High elevation provenances on the other hand do not respond to increased temperatures to the same extent as low elevation provenances, and appear to require a long day length, such as that obtaining in a northern nursery. For this reason if a nursery area is selected at a low elevation in southern latitudes in the interior of British Columbia it is likely that high elevation spruce provenances will not thrive in such a nursery.

Very few populations from north of latitude $55^{\circ}00'$ and east of longitude $124^{\circ}00'$ are represented in the study of variation in immature spruce population at Cowichan Lake. Consequently it is not possible to

indicate, with any accuracy, the effect expected as a result of a displacement to south of low elevation northern populations. Nevertheless, it is to be expected that they will behave similarly to high elevation populations from southern latitudes. The results of the study of variation in mature populations show, however, that a black spruce component can be expected to occur in any extensive seed collections made to the north, and indicates the need for further genecological investigation in spruce populations north of latitude $55^{\circ}00'$.

Frequently reforestation projects are scheduled for areas for which no seed of local origin is available, and consequently seed from other regions is used instead. The results of this study indicate that a displacement of 1000 ft. upwards will almost certainly result in a pronounced detrimental silvicultural effect in most instances. A displacement of 500 ft. is also likely to result in a measurable effect. In this regard, survival during the first 1 - 3 years is not a good measure of the ill-effects of the environment on a displaced population. A displaced population, which shows 100% survival during the first few years, could, nevertheless be quite ill-adapted to its new environment. There are a number of reasons for this. In the first place the climatic pattern during a short number of years may be atypical, and not representative of the average environment. Secondly, the outplanting technique in relation to size of stock can have a drastic effect on survival. Survival is an important parameter three to four years after the establishment of the plantation.

Though initial survival may not be drastically affected by a displacement of seed upwards, growth will be affected. Consequently, it is obviously unwise silviculturally to displace seed upwards more than 500 ft. anywhere in British Columbia. No serious detrimental effect may be expected

to result from a downwards displacement of seed, while a downwards and northwards displacement will probably result in silvicultural gain.

The question as to how far north high elevation southern populations and low elevation southern populations can be displaced without detrimental silvicultural effects can be determined in the long run only from the field test. In this regard it is worth noting that certain populations of Norway spruce can be transferred 10 degrees northwards without any detrimental effect (Langlet 1963b). This is not meant to imply that spruce populations from southern latitudes in British Columbia can be moved similar distances. It is very likely however, that (other things being equal e.g. site index and moisture regime) a displacement of 4-5 degrees north may be silviculturally feasible for high elevation provenances from southern latitudes. On the other hand, it is likely that a transfer north of 4 degrees will result in a detrimental silvicultural effect in southern populations from low elevations (Roche and Revel 1966).

Not infrequently the question is asked by the practical forester concerning the extent to which the variation pattern in juvenile populations assessed in controlled environments (growth chambers) and semi-controlled environments (greenhouse and nurseries) adumbrates the variation pattern in the same populations at a later date.

There is little doubt that the optimum climatic requirements for growth and development in forest trees, as in other plant species (Cooper 1963 p. 392) vary at all stages of the life cycle. Consequently the optimum climatic conditions for germination in a given species under natural conditions are not likely to be the same as those which are optimum for seedling growth. Similarly, the conditions best suited for seedling growth are not likely to be the same as those which result in maximum growth in a 50-year-old tree.

However, natural selection in forest trees operates primarily at the seedling stage, and the growth rhythm of a population adapted to its particular climatic environment is determined at this stage. Therefore, if 2-year-old seedlings of provenance A enter dormancy eight weeks before provenance B when both are grown in environment C, and if they are both left in environment C, there is no reason to believe that this relationship between the two provenances, assuming that they both survive, will be reversed when the trees are 50 years old. Furthermore, if this difference in time of entering dormancy shows a clear cut relationship with the environment at place of origin of each provenance, then, to a considerable extent, it is possible to predict the relative adaptability of both provenances A and B when outplanted in climatic zone D in the field test (Roche and Revel 1966). It is important to note, however, that the characteristics measured in juvenile populations must be those which are of adaptive significance, and are habitat-correlated.

For example, the low elevation, Birch Island provenance, and similar provenances, did best, silviculturally speaking, at the Cowichan Lake nursery. This does not mean that, in another environment, the Birch Island provenance will always exhibit silvicultural characteristics superior to those of the other populations with which it was grown at Cowichan Lake. On the contrary, if the same provenances were transplanted to a nursery at 4000 ft. in the interior of British Columbia, then it is certain that the Birch Island provenance, and similar provenances, would do least well silviculturally, and that other provenances would do better.

To say that this is a reversal of growth at a later date in the life cycle of the Birch Island population is to misunderstand the principles of genecology. The vitally important point is that if studies of variation in immature populations in controlled and partially-controlled environments

are carried out on a sufficient large sample, and in sufficient detail, then the relative adaptability of any population in a different environment is to a considerable extent, predictable.

In this regard it is perhaps worth mentioning that the above statement is not based on supposition, but has considerable experimental evidence to support it (Went 1957, Hudson 1957, Evans 1963). To give but one example, Went (1957), by controlled environment studies, established the climatic requirements of the plant species Veratrum viride. This plant had never been grown in cultivation, and field tests completely failed to give any indication of the factors controlling its growth. On the basis of growth chamber work it was possible to suggest locations where it might be grown, and when tried out in these places it grew as predicted (see Fogg 1963, p. 243).

Had 150 to 200 populations from all sections of the boreal forest of northern British Columbia been represented in the study of variation in immature populations carried out at Cowichan Lake, it is certain that some criteria would be provided in regard to the silvicultural consequences of a displacement from south to north. For the variation pattern of these boreal populations in a southern nursery would reflect the environmental pressures operating in the diverse sections of the Northern Boreal Forest.

Apart then from the study of variation in cone scale morphology reported here, there is no information concerning the genecology of the great spruce forests of northern British Columbia. The need for such information may not be pressing at the present time, but with the increase in the pulpwood industry in British Columbia it is certain that such information will be required in the near future.

For these reasons, it would be wise to anticipate increased logging and reforestation activities in these northern forests by initiating geneco-

logical studies as soon as possible. As Haddock (1961) has pointed out in regard to Canadian spruce forests in general, and western Canada in particular "if planting is to be advocated as a widespread solution, even if for only the best quality sites, much more must be learned about how to grow high quality (physiologically) and inexpensive nursery stock of the best possible genetic constitution".

It is clear that the coastal influence penetrates well into the interior of British Columbia, and that in the Nass, Skeena and Bulkley river basins there are sympatric populations of white and Sitka spruce, and evidence of hybridization between these species in the sympatric zone.

Assuming that there is hybridization between white and Sitka spruce in the areas stipulated, it is not certain that the hybrid is of silvicultural value. For example, Thaarup (1945) reported that the hybrid Sitka-white spruce has poor stem form, and warned against collecting seed in the zone of hybridization, and Mergen (1959) has pointed out that hybrid seedlings do not possess any advantages over their parents in their native habitat.

In any event, it is likely that no silvicultural advantages can be gained by moving seed out of this zone into other parts of British Columbia. It is possible, however, that high elevation southern provenances, or low elevation northern provenances (to lat. $55^{\circ}00'$) can be transferred into this area without serious detrimental effect.

It is stressed that the general recommendations given above concerning the transfer of seed, and the propagation of seedlings in the nursery, are tentative. These are recommendations which will be modified as further knowledge accumulates concerning the genecology of white spruce in British Columbia. A major source of new information in this respect will be the field trials following the study of variation in immature and mature spruce

populations reported here.

It is suggested that plantations of representative provenances should be established in six forest regions (Rowe 1959) according to the following general plan:

Area	Forest Region	Approximate elev.(ft.)
1	Interior subalpine	4500
2	Central Douglas fir	3000
3	Southern Columbia	1500
4	Interior subalpine (North)	2000
5	Montane transition	2000
6	Southern Pacific Coast	Sea level to 500

All provenances below 1500 ft., except numbers 25 and 62, should be planted only at areas 5 and 6 (see Table 3). Areas 1, 2 and 3 should be in the same general region between latitudes $51^{\circ}00'$ and $52^{\circ}00'$ if suitable sites can be found. In this general region these three plantations, especially if placed along a single mountain transect, will yield information concerning the effects of a gross altitudinal displacement which will allow the modification of the general recommendations already stated.

Area 4 should be in the region of Germansen Landing at approximately latitude $56^{\circ}00'$. This plantation will yield information concerning the effects of a gross latitudinal displacement.

Area 5 should be situated in the region of Telkwa, latitude ca. $55^{\circ}00'$ longitude ca. $127^{\circ}30'$. Consequently, as indicated by the study in mature populations, this plantation will be in a transition zone between the northern pacific coast section and the montane transition section, and will yield information in regard to the effect of a gross displacement to the north

west, an area for which there is a chronic shortage of spruce seed.

It has already been stated that all provenances below 1500 ft. except provenances 25 and 62, should be planted only at areas 5 and 6. These provenances represent Sitka spruce populations, both strictly coastal and inland forms, from a series of latitudes between latitude $49^{\circ}00'$ and $56^{\circ}00'$. Therefore if area 6 is selected on the south western tip of Vancouver Island much information will eventually be obtained concerning the effects of a latitudinal displacement, while the same populations at Telkwa will yield information concerning the effects of continentality on coastal populations. These same populations at Telkwa will therefore further clarify the pattern of variation in the sympatric zone of white and Sitka spruce.

It will be seen from Table 3 that any one altitude (to the nearest 100 ft.) is represented by a number of provenances. The results of the study reported here indicate that 5 provenances from each 100 ft. of altitude will adequately sample the population at that altitude. It is suggested, therefore, that this criterion be applied in selecting provenances for outplanting.

For some altitudes there are less than 5 provenances available, but for many altitudes there are more than 5. Where there is a choice it is obvious that the five provenances selected at a given altitude should be selected to represent the widest area at that altitude. For example at 2000 ft. there are 16 provenances from which to select 5. Clearly it is better to select only one from the region of Doughty near Smithers rather than select all 5 from this area which is well represented at this elevation (Table 3). If this procedure is followed, there will be a considerable reduction in the number of provenances selected for outplanting with a consequent reduction in costs.

The above remarks do not apply to provenances below 1500 ft. all of which should be outplanted as indicated above.

Each of the outplanting areas, except area 6, will be well represented by the provenances selected for outplanting. Consequently there will be a control available for comparison with alien populations.

In regard to a tree improvement program, it is suggested that the main task in the immediate future is to find and exploit by selection and breeding the great array of genetic variation in white spruce populations identified and demarcated by the present study.

The X-ray method of assessing seed quality has considerable merit, and is obviously superior to methods in use at the present time. It is also clear that the environmental requirements for optimum germination vary for spruce seed from different elevations, and that an accurate assessment of germinability in the laboratory cannot be obtained by germinating high and low elevation provenances all at the same temperatures.

The X-ray method of assessing germination capacity described here is accurate only when applied to seed undamaged physiologically as a result of handling prior to extraction, extraction methods, and conditions of storage. The low germination capacity of many provenances used in the present study cannot be fully explained in terms of embryo development or provenance effect, and it seems clear that this seed has suffered damage during one or all of the processes referred to above. However, a comparison of figures for germination capacity obtained in this study with figures obtained as a result of routine germination tests following extraction, indicate that the condition of the seed prior to storage rather than storage conditions per se, is probably the principal cause of low germination capacity of seed which has fully developed embryos, and shows no structural damage.

There is, nevertheless, a relationship between embryo development and germination behaviour even in seed which has a percentage of physiologi-

cally unsound seed. Consequently seed lots used in research, particularly research related to direct seeding, should be assessed by radiography.

Seed which has deteriorated physiologically can also be assessed by the X-ray method, but only if the seed has been treated by suitable contrast agents which vary with species and which are absorbed differentially by live and dead tissue, and consequently, present varying patterns of density in the radiograph.

The results of the study of germination behaviour reported here indicate a considerable need for more detailed studies of all factors affecting germination behaviour in white spruce in the manner of Allen's (1958) and Sziklai's (1965, 1966) comprehensive and detailed work on Douglas fir.

GENERAL CONCLUSIONS

1. White and Engelmann spruce in British Columbia are the extreme forms of a clinal pattern of variation.
2. Throughout the Province south of lat. $55^{\circ}00'$ and east of long. $123^{\circ}00'$ intermediate forms of both species occupy the broad transitional zone between the montane and subalpine forest regions.
3. The intermediate forms are found, not as large forests, but as small, fragmented, though not isolated populations.
4. These populations are colonizing populations and not remnants of past distributions. They may be identified on the basis of cone scale morphology.
5. The environmental factors, which exercise selection pressure on the white-Engelmann spruce complex, vary progressively from the montane to the subalpine forest region.
6. The clinal pattern of variation in the white-Engelmann complex referred to in 1 above is the result of introgressive hybridization, followed by selection and adaptation of fractions of the hybrid swarm.
7. No populations of Engelmann spruce occur along the Hart and Alaska highways north of lat. $55^{\circ}00'$.
8. White spruce occurs throughout the Province from lat. $49^{\circ}00'$ to the Yukon border, and west to long. $129^{\circ}00'$ in the vicinity of the Nass and Skeena rivers, and long. $131^{\circ}00'$ in the vicinity of the Stickine river.

9. The pattern of variation in spruce populations in the transitional zone between coastal Sitka spruce forest and montane white spruce forest in the Skeena valley is clinal.
10. Intermediate forms of both species occur in the Skeena valley and may be recognized on the basis of cone scale morphology.
11. The intermediate forms of white and Sitka spruce are very similar to pure Engelmann spruce in regard to cone scale morphology. It is possible, therefore, that in the past these forms have been mistakenly identified as Engelmann spruce.
12. The environmental factors exercising selection pressure on the white-Sitka complex in northwest British Columbia vary progressively from coastal to montane forest.
13. The clinal pattern of variation referred to in 9 above is probably the result of introgressive hybridization between white and Sitka spruce followed by selection and adaptation of fractions of the hybrid swarm.
14. It is probable that sympatric populations of Sitka and white spruce occur in other regions of the Province where coastal influences penetrate the valleys of the major rivers.
15. Sympatric populations of black and white spruce occur along the Alaska highway throughout northern British Columbia.
16. North of lat. $57^{\circ}00'$ on the Alaska highway, black and white spruce occupy the same ecological niche. South of this latitude there is a gradual change in the composition of the spruce populations, and black spruce moves to areas of poor drainage.

17. Individuals exhibiting characteristics of both black and white spruce occur in the sympatric zones referred to in 15 above. It is possible therefore that hybridization is occurring between these species.

18. These individuals occur at random, and there is no evidence that intermediate forms of black and white spruce are successfully colonizing areas in the vicinity of the sympatric zones.

19. In regard to the white-Engelmann spruce complex in British Columbia there is sufficient evidence from this study to warrant the assumption that the environmental pressures which result in microevolution, i.e. geographic differentiation within the species, differ only in degree rather than in kind from the environmental pressures which result in macroevolution, i.e. speciation.

20. The faculty for normal development and survival of white spruce, and its related forms is conditional by the cessation of growth and initiation of dormancy.

21. Time of cessation of dormancy in a population in any one region where the species occurs naturally is conditioned by its genetic constitution.

22. The genetic constitution of a natural population is predominantly determined by the photothermal regime prevailing in that region.

23. In so far as there is a difference in the photothermal regime between any two regions the genetic constitution of the populations occupying those regions will differ.

24. One of the most important external manifestations of this difference is the time of cessation of growth, and initiation of dormancy.

25. Time of cessation of growth and initiation of dormancy is a population parameter. Therefore, the dormancy curve will accurately characterize a spruce provenance only if assessed on the basis of a relatively large number of seedlings.

26. Between the time of the initiation of dormancy and its completion in any one spruce provenance there is a period when the correlation between dormancy and factors of the environment at the place of origin is maximum for this provenance. Therefore, in order to determine this period a dormancy curve must be constructed.

27. On the basis of conclusions 19 to 23 inclusive recommendations may be made in regard to the silviculture of spruce populations from the interior of British Columbia.

28. High elevation spruce provenances should not be grown in coastal nurseries at southern latitudes on Vancouver Island or on the Mainland. Such provenances cannot avail of the long growing season at these nurseries, as they enter dormancy even when temperatures are increasing. The breaking of dormancy during the same growing season is the exception rather than the rule in these high elevation provenances. Consequently they have a stunted "rosette" appearance resulting from decreased internode length, and are inferior planting stock even after transplanting.

29. High elevation provenances cannot avail of a long growing season, but there is evidence that these provenances will respond to increased day length. Therefore, high elevation spruce provenances other things being

equal e.g. conditions of soil, general supervision, etc., are likely to produce seedlings with desirable silvicultural characteristics much more rapidly in a northern nursery, such as Telkwa, which is approximately 6 degrees north of the coastal nurseries.

30. Assuming that the microenvironment at the nursery site is optimum, it is possible that a nursery situated further east, but at the same latitude as Telkwa, is equally feasible for the propagation of high elevation provenances from southern latitudes.

31. All spruce provenances south of latitude $53^{\circ}00'$ and from below 2500 ft. may be expected to grow with relative rapidity in coastal nurseries in southern latitudes, and some will grow as rapidly as Sitka spruce in these nurseries.

32. These small, fragmented, populations, e.g. the Birch Island population, have considerable silvicultural value, and are of importance in tree improvement work. For these reasons, efforts should be made to collect seed from these populations.

33. Spruce provenances from below 2500 ft., between latitudes $53^{\circ}00'$ and $55^{\circ}00'$ will produce seedlings with desirable silvicultural characteristics more rapidly in southern coastal nurseries than high elevation provenances from southern latitudes. These same low elevation provenances, however, are likely to do much better silviculturally speaking, in the Telkwa nursery also, where spring and summer temperatures are not much lower than those of the southern coastal nurseries, but where day length during the same season is considerably longer.

34. Provenances from below 2500 ft., and south of latitude $55^{\circ}00'$ will respond extremely well to artificially increased temperature irrespective of day length (within limits). Therefore, these provenances can be grown on the coast with optimum silvicultural advantage if temperatures are increased artificially, e.g. by the use of plastic greenhouses. Furthermore, these populations do not require the stimulus of a prepared soil, and will respond vigorously to increased temperatures while growing on regular nursery soil. High elevation provenances, on the other hand, do not so respond.

35. White and Engelmann spruce in British Columbia are the extreme forms of a clinal pattern of variation associated with altitude. Therefore, when latitudinal and altitudinal boundaries are referred to above, it is not implied that these boundaries circumscribe an ecotype which, in its pattern of variation, is discrete from that of the populations immediately to the north or south in the case of latitude, or immediately above or below in the case of altitude. Therefore, there are no sharp zonal boundaries marking the region outside which a given provenance cannot be moved.

36. Spruce provenances north of latitude $55^{\circ}00'$ may contain a black spruce component. Such provenances from north of latitude $55^{\circ}00'$, whether from allopatric zones of white spruce or sympatric zones of white and black spruce, are likely to behave similarly to high elevation southern provenances in regard to time of entering dormancy in southern coastal nurseries.

37. Embryo development in spruce will vary with the seed crop year, date of harvesting, and place of origin within any one year. Germination behaviour is strongly influenced by embryo development. Consequently, care must be taken to ensure that seed lots used for experimental purposes,

e.g. direct seeding tests, are standardized in regard to embryo development.

38. An accurate, and quick method of assessing embryo development and seed quality in general is by radiography using the methods described in this study.

39. In assessing population differences in germination behaviour, extreme temperatures are more effective than moderate temperatures. Maximum differences are observable at 15°C . 30°C . is also effective, but less so than 15°C . Least effective temperatures are 20 and 25°C .

40. The temperature requirements for optimum germination are different for high and low elevation populations.

41. Spruce provenances from sympatric zones of white and Sitka spruce in the Skeena, Bulkley and Nass river basins may be identified as to species if germinated at 15°C . At this temperature Sitka spruce will not germinate at all within 14 days, or will show very low germination values. White spruce will germinate at this temperature. In making the test the germination percent must be corrected on the basis of embryo development.

42. Reduced germination capacity of spruce seed during storage appears to result not from storage conditions per se but from the condition of the seed prior to storage.

43. In regard to a program of tree improvement for white spruce it is concluded that the main task in the immediate future is to find and exploit by selection and breeding the great array of genetic variation in white spruce identified and demarcated by the present study.

44. Both the assessment of physiological differences in immature

populations in controlled and partially controlled environments and the assessment of patterns of variation in mature populations in the wild are essential preliminary investigations to the field test, that is, the provenance trial.

45. When the problem of infraspecific variation in a tree species is considered as a problem in microevolution, rather than a purely silvicultural problem, the emphasis in research is shifted to the genecological investigations referred to in 42 above.

46. Much greater emphasis, therefore, should be given both to the assessment of physiological investigations in immature populations in controlled and partially controlled environments, and the assessment of morphological variation in mature populations.

47. The field test, that is the provenance trial, is rightly considered the last stage in the assessment of variation. Such trials then fall within the scope of the silviculturist, and can become part of an overall planting program. The data concerning the performance of these plantations, which will accumulate over the years, may be used to modify the silvicultural recommendations drawn up by the genecologist on the basis of the investigations referred to in 44 above.

LITERATURE CITED

- Alexander, R.R., 1958. Silvical characteristics of Engelmann spruce.
Station paper 31, Rocky Mountain For. and Range, Exp. Sta. 20 pp.
- Allen, G.S., 1958. Factors affecting the viability and germination behaviour of coniferous seed. Parts I, II and III. Forestry Chronical, 34: 266-298.
- Allen, G.S., 1961. Testing Douglas fir seed for provenance. Proceedings of the International Seed Testing Association, 26: 388-403.
- Anderson, E., 1949. Introgressive hybridization. Wiley, New-York. 109 pp.
- Anderson, E., 1965. Cone and seed studies in Norway spruce (Picea abies (L.) Krast.) Nr. 23, Studia Forestalia Suecica. Stockholm. 214 pp.
- Barber, J.C., and B.J. Zobel, 1959. Comments on genetic variation within geographic ecotypes of forest trees and its role in tree improvement. Journal of Forestry, 57: 439-441.
- Brink, V.C., and L. Farstad, 1949. Forest advance in north and central British Columbia. The Canadian Field - Naturalist, Jan.-Feb. 1949. p. 37.
- Bunning, E., 1961. Endogenous rhythms and morphogenesis. Can. J. Botany, 39: 461-467.
- Burley, J., 1966. Genetic variation in seedling development of Sitka spruce Picea sitchensis (Bong). Carr. Forestry, 39: 68-92.
- Callahan, R.Z., 1959. Experimental Taxonomy - more than seed source studies. Proc. IX Internate Bot. Cong. Vol. 11, Abs. p. 57.
- Chapman, J.D., 1952. The climate of British Columbia. Fifth British Columbia Natural Resources Conference. University of B.C. 1952. 47 pp.

- Chapman, L.J., and D.M. Brown, 1966. The climates of Canada for agriculture. The Canada Land Inventory report no. 3. Canada Dept. of Forestry and Rural Development. 24 pp.
- Ching, K.K., and D. Bever, 1960. Provenance study of Douglas fir in the Pacific northwest region. *Silvae Genetica* 9: 11-17.
- Clausen, J., Keck, D.D., and W.M. Hiesey, 1940. Experimental studies on the nature of the species. I. Effect of varied environments on Western North American Plants. Carn. Inst. Wash. Publ., 520. 452 pp.
- Clausen, J., Keck, D.D., and W.M. Hiesey, 1945. Experimental studies on the nature of the species. II. Plant evolution through amphiploidy and autopolloidy, with examples from the Madiinae. Carn. Inst. Wash. Publ. 564. 174 pp.
- Clausen, J., Keck, D.D., and W.M. Hiesey, 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of Achillea. Carn. Inst. Wash. Publ. 581. 129 pp.
- Clausen, J., and Hiesey, W.M., 1958. Experimental studies on the nature of the species. IV. Genetic structure of ecologic races. Carn. Inst. Wash. Publ. 615. 312 pp.
- Connor, A.J., 1949. The frost-free season in British Columbia. Meteorological Division, Dept. of Transport, Toronto. 20 pp.
- Constance, L., 1957. Plant taxonomy in an age of experiment. *American Jour. Bot.* 44: 88-92.
- Cooper, J.P., 1963. Species and population differences in climatic response. In. L.T. Evans, ed., *Environmental control of plant growth*. Academic Press, New-York. 449 pp.
- Critchfield, W.B., 1957. Geographic variation in Pinus contorta. Publication no. 3. Harvard University, Cambridge, Mass. 117 pp.

- Czabator, F.J., 1962. Germination value: an index combining speed and completeness of pine seed germination. *Forest Science* 8: 386-396.
- De Beer, G., 1963. Bearing of modern research on evolution. *Nature* 200: 200-201.
- Diver, C., 1940. The problem of closely related species living in the same area. In: J.S. Huxley, ed., *The new systematics*. Oxford University Press, London. 582 pp.
- Dugle, J.R., 1966. A taxonomic study of Western Canadian species in the genus Betula. *Canadian Journal of Botany* 44: 929-1007.
- Eastham, J.W., 1949. Observations on the flora of the southern Rocky Mountain Trench in British Columbia. *Trans. Royal Soc. of Canada*, 43: 1-9.
- Edwards, M.V., 1956. The design, layout and control of provenance experiments. *Zeitschrift Für Forstgenetik*. 5: 169-180.
- Ehrlich, P.R., and Holm, R.W., 1962. Patterns and populations. *Science* 137: 652-657.
- Eis, E., 1966. Survival and growth of white spruce wildlings, and coastal nursery seedlings in the interior of British Columbia. *For. Chron.* 42: 346-349.
- Evans, L.T., 1963. *Environmental control of plant growth*. Academic Press, New York. 449 pp.
- Fernald, M.L., 1945. Notes on Betula in eastern North America. *Rhodora* 47: 303-329.
- Fogg, G.E., 1963. *The growth of plants*. Penguin Books. London, 288 pp.
- Fowler, D.P., 1965. A new spruce hybrid - Picea schrenkiana x P. glauca. Second genetics workshop of the Society of American Foresters. Research paper NC-6, North Central For. Exp. Sta. U.S. Forest Service: 44-47.

- Gardiner, A.S., and Jeffers, J.N.R., 1963. Analysis of the collective species Betula alba on the basis of leaf measurements. *Silvae Genetica*, 11: 156-161.
- Garman, E.H., 1957. The occurrence of spruce in the interior of British Columbia. Technical publication T. 49. Dept. of Lands and Forests, British Columbia Forest Service. 31 pp.
- Garner, W.W., and Allard, H.A., 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Jour. Agric. Res.* 18: 553-606.
- Giertych, M.M., 1964. Endogenous growth regulators in Trees. *The Botanical Review*, 30: 292-311.
- Good, R., 1964. The geography of flowering plants. Longmans, Green and Co. Ltd., London, 518 pp.
- Griffith, B.G., 1940. In a symposium on spruce regeneration in Canada. *For. Chron.* 16: 83-84.
- Greig-Smith, P., 1964. Quantitative plant ecology. Butterworth, London; and Academic Press New-York. 198 pp.
- Haddock, P.G., 1961. Silvicultural views on the Canadian spruce forests. *The Forestry Chronicle*, 37: 376-388.
- Hall, M.T., and Carr, C.J., 1964. Differential selection in juniper populations from the Baum Limestone and Trinity Sand of southern Oklahoma. *Butler University Botanical Studies*, 14: 21-40.
- Hamner, K., 1963. Endogenous rhythms in controlled environments. In L.T. Evans, ed. *Environmental control of plant growth*. Academic Press. New-York. 449 pp.
- Hanover, J.W., 1963. Geographic variation in ponderosa pine leader growth. *Forest Science*, 9: 86-95.

- Hansen, H.P., 1947. Postglacial forest succession, climate and chronology in the Pacific Northwest. *Trans. Am. Philos. Soc.* 37: 1-130.
- Hansen, H.P., 1955. Postglacial forests in South Central and central British Columbia. *American Journal of Sciences*, 253: 640-658.
- Hardy, A., 1965. The living stream: a restatement of evolution theory in relation to the spirit of man: Collins, London, 292 pp.
- Heikinheimo, O., 1954. Taimitarkan Maantieteellinen sijainti, siemenen alkuperä ja istutuskautet. *Geographische lage der Baumschule, Herkunft des Samens und Zeit der Pflanzung. Acta Forest Fenn.* 61: 9.
- Hendricks, S.B., and Borthwick, H.A., 1963. Control of plant growth by light. In L.T. Evans, ed. *Environmental control of plant growth.* Academic Press, New-York. 449 pp.
- Heslop-Harrison, J., 1964. Forty years of genecology. In J.B. Cragg, ed. *Advances in Ecological Research*, 2: 159-247.
- Heusser, C.J., 1960. Late-pleistocene environments of North Pacific America. Special publication no. 35, American Geographical Society. 308 pp.
- Heywood, V.H., and McNeill, J., 1964. Phenetic and phylogenetic classification. Publication no. 6. The systematics association. c/o British Museum, London. 164 pp.
- Hiesey, M., J. Clausen, and Keck, D.D., 1942. Relations between climate and intra-specific variation in plants. *The American Naturalist* 76: 5-22.
- Horton, K.W., 1959. Characteristics of subalpine spruce in Alberta. Tech. Note no. 76. Forest Research Division, Canada Dept. of Northern Affairs and National Resources. 20 pp.
- Hudson, J.P., 1957. Control of the plant environment. Butterworths scientific publications. 240 pp.

- Huxley, J., 1940. The New Systematics. Oxford University Press, London, 583 pp.
- Huxley, J., 1963. Evolution: the modern synthesis. Second edition. George Allan and Darwin Stat. 652 pp.
- Irgens-Moller, H., 1957. Ecotypic response to temperature and photoperiod in Douglas fir. Forest Science, 3: 79-83.
- Irgens-Moller, H., 1958. Genotypic variation in the time of cessation of height growth in Douglas fir. Forest Science, 4: 325-330.
- Irgens-Moller, H., 1962. Genotypic variation in photoperiod response of Douglas fir seedlings. Forest Science, 8: 360-362.
- Jeffers, J.W.R., 1965. The study of variation in taxonomic research. Statistics section paper No. 90. Brit. For. Comm. 11 pp.
- Jeffers, J.W.R., and Black, T.M., 1963. An analysis of variability in Pinus contorta. Forestry, 36: 199-218.
- Jentys-Szaferowa, J., 1959. A graphical method of comparing the shapes of plants. The Review of the Polish Academy of Sciences, 4: 9-37.
- Karschon, R., 1949. Untersuchungen Über Die Physiologische Variabilität Von Föhrenkeimlingen Autochter Populationen. Schweiz. Anstalt Forstl. Versuchsw. Mitt. 26: 205-244.
- Kozlowski, T.T., 1957. Seasonal height growth of conifers. Forest Science 3: 61-66.
- Krajina, V.J., 1965. Ecology of Western North America vol. I. Dept. of Botany, University of British Columbia. 94 pp.
- Kramer, P.J., and Kozlowski, T.T., 1960. Physiology of trees. McGraw-Hill, New-York. 642 pp.
- Langlet, O., 1959. A cline or not a cline - a question of Scots pine. Silvae Genetica. 8: 13-22.

- Langlet, O., 1962. Ecological variability and taxonomy of forest trees.
In T.T. Kozlowski, ed., Tree Growth. Ronald Press Co. New-York.
442 pp.
- Langlet, O., 1963a. Patterns and terms of intra-specific ecological variability. Nature, 200: 347-348.
- Langlet, O., 1963b. Practical results and current problems in provenance research in Sweden. Section 3. Report of world consultation on forest genetics and tree improvement. Stockholm, Aug. 1963.
F.A.O. Rome. 12 pp.
- Little, E.L., 1953a. Check list of the native and naturalized trees of the United States (including Alaska). Agricultural handbook No. 41.
Superintendent of documents, Washington, D.C. 472 pp.
- Little, E.L., 1953b. A natural hybrid in Alaska. Journal of Forestry, 51: 745-747.
- Little, E.L., and Pauley, S.S., 1958. A natural hybrid between black and white spruce in Minnesota. The American Midland Naturalist, 60: 202-211.
- Macdonald, J.A.B., 1958. Review of geographic variation in Pinus contorta by W.B. Critchfield. Empire Forestry Review, 37: 346.
- Matthews, J.D., 1963. Factors affecting the production of seed by forest trees. Forestry Abstracts, 24: 1-13.
- Mayr, E., 1963. Animal species and evolution Oxford University Press, London, 797 pp.
- McAllister, D.E., 1966. Numerical taxonomy and the smelt family, Osmeridae. The Canadian Field Naturalist, 80: 227-238.
- McKinnon, F.S., 1938. The relative importance of white spruce in the forests of the upper Fraser valley. Research note No. 5, British Columbia Forest Service. 2 pp.

- Melville, R., 1940. Intergrading among plants in relation to the provenance of forest trees. *Nature*, 145: 130-132.
- Mergen, F., 1959. Forest tree breeding research. *Unasylva*, 13: 129-137.
- Mirov, H.T., 1956. Photoperiod and flowering of pines. *Forest Science*, 2: 328-332.
- Mitchell, A.F., 1965. The growth in early life of the leading shoot of some conifers, *Forestry*, 38: 121-136.
- Morris, W.G., et al. 1957. Consistency of bud bursting in Douglas fir. *Journal of Forestry*, 55: 208-210.
- Morgenstern, E.K., and Farrar, J.L., 1964. Introgressive hybridization in red spruce and black spruce. Forest Research Branch publication no. 608. Canada Dept. of Forestry and Rural Development. 46 pp.
- Müller-Olsen, C., M. Simak, and Gustafsson, A., 1956. Germination analyses by the X-ray method: Picea abies (L.) Karst. Medd. fr. Stat. skogsforshn - inst. 46: 1-12.
- Myers, O., and Bormann, F.H., 1963. Phenotypic variation in Abies balsamea in response to altitudinal and geographic gradients. *Ecology*, 44: 429-436.
- Nienstaedt, H., 1960. The ecotype concept and forest tree genetics. Proceedings of the fourth Lake States forest tree improvement conference.
- Nienstaedt, H., 1967. Chilling requirements in seven Picea species. *Silvae Genetica*, 16: 65-68.
- Mitsch, J.P., 1963. The mediation of climatic effects through endogenous regulating substances. In L.T. Evans, ed. *Environmental control of plant growth*. Academic Press, New-York. 449 pp.
- Olson, J.S., F.W. Sterns, and Nienstaedt, H., 1959. Eastern hemlock seeds and seedlings: response to photoperiod and temperature.

- Bulletin 620 Connecticut Agricultural Experiment Station, New Haven, U.S.A. 70 pp.
- Orr-Erwing, A.L., 1966. Inter-and intraspecific crossing in Douglas fir (Pseudotsuga menziesii (mirb.) Franco). *Silvae Genetica*, 15: 121-126.
- Parker, E.L., 1963. The geographic overlap of noble fir and red fir. *Forest Science*, 2: 207-216.
- Parker, J., 1963. Cold resistance in woody plants. *The Botanical Review*, 29: 123-201.
- Pauley, S.S., and Perry, T.O., 1954. Ecotypic variation of the photoperiodic response in Populus. *Journal of the Arnold Arboretum*, 25: 167-188.
- Prichaüsser, G., 1958. Die Fichten-Variationen und kominatiomen des Bayr. Waldes nach phanotypischen Merkmalen mit Bestimmunesschlüssel. *Forst. Wiss. Clb.* 77: 151-172.
- Raup, H.M., 1945. Forests and gardens along the Alaska highway. *Geographical Rev.* 35: 22-48.
- Recknagel, A.B., 1939. Some notes on the upper Fraser River spruce of British Columbia. *Journal of Forestry*, 37: 656-657.
- Roche, L., 1962. Geographic variation in lodgepole pine and its role in the genetic improvement of coastal forms. MF thesis University of British Columbia. 95 pp.
- Roche, L., 1964. Geographic variation spruce cone scale morphology. British Columbia Forest Service Research Review for year ended March 1964: 37-39.
- Roche, L. 1964a. Genetic variation and its assessment in an indigenous coniferous species. Unpublished report available on loan from the British Columbia Forest Service Library, Victoria, B.C.

- Roche, L., 1965. The use of X-ray photography in assessing the maturity of Engelmann spruce seed. British Columbia Forest Service Research Review for year ended March 1965: 42-44.
- Roche, L., and Revel, J., 1966. Effects of altitudinal and latitudinal displacement of white and Engelmann spruce provenances. British Columbia Forest Service Research Review for year ended March 1966: 43-44.
- Romberger, J.A., 1963. Meristems, growth, and development in woody plants. Technical Bulletin no. 1293. U.S.D.A. Forest Service. 214 pp.
- Rowe, J.S., 1959. Forest regions of Canada. Bulletin 123, Canada Dept. of Northern Affairs and National Resources Forestry Branch. 71 pp.
- Ruby, J.L., 1967. The correspondence between genetic, morphological, and climatic variation in Scots pine. *Silvae Genetica*, 16: 50-56.
- Seal, H.L., 1964. Multivariate statistical analysis for biologists. Spottiswoode, Ballantyne, and Co. Ltd., London. 207 pp.
- Sokal, R.R., and Sneath, P.H.A., 1963. Principles of numerical taxonomy. V.H. Freeman and Co., San Francisco. 359 pp.
- Sprague, T.A., 1940. Taxonomic botany, with special reference to the Angiosperms. In J. Huxley ed., *The New Systematics*. Oxford University Press, London. 582 pp.
- Stanek, W., 1966. Occurrence, growth, and relative value of lodgepole pine and Engelmann spruce in the interior of British Columbia. Ph. D. thesis, University of British Columbia. 252 pp.
- Stebbins, G.L., 1950. Variation and evolution in plants. Columbia University Press, New-York. 643 pp.
- Stebbins, G.L., 1963. Perspectives - I. *American Scientist*, 51: 362-370.
- Stern, K., 1964. Herkunftsversuche für Zwecke der Forstpflanzenzüchtung erläutert am Beispiel Zweier Modellversuche. *Der Züchter*, 34: 181-219.

- Steward, F.C., 1963. Effects of environment on metabolic patterns. In L.T. Evans, ed. Environmental control of plant growth. Academic Press, New-York. 449 pp.
- Sziklai, O., 1965. Intra-tree variations of cone and seed characteristics of Douglas fir. Proceedings Western Forest Genetics Association, Olympia. Washington. p. 54.
- Sziklai, O., 1966. Work on forest genetics and tree improvement at the Faculty of Forestry, University of British Columbia. Progress report 10th Meeting Committee on Forest Tree breeding in Canada: 151-153.
- Taylor, T.M.C., 1959. The taxonomic relationship between Picea glauca (Moench) Voss and P. engelmannii Parry. Madrono, 15: 112-115.
- Thaarup, P., 1945. Bastarden sitkagran x hvidgran. Dansk skovforen. Tidsskr. No. 9: 381-384.
- Timofeeff-Ressovsky, 1940. Mutations and Geographical Variations. In J. Huxley, ed., The New Systematics. Oxford University Press, London. 583 pp.
- Turesson, C., 1923. The scope and impact of genecology. Hereditas, 4: 171-176.
- Turesson, C., 1925. The plant species in relation to habitat and climate. Hereditas. 6: 147-236.
- University of California, 1957. System of Producing healthy container plants. Manual 23, California Agr. Exp. Sta., Berkeley, California. 331 pp.
- Vaartaja, O., 1959. Evidence of photoperiodic ecotypes in Trees. Ecological Monographs, 29: 91-111.
- Van Der Veen, R., 1951. Influence of day length on the dormancy of some species of the genus Populus. Physiologia-Plantarum, 4: 35-40.

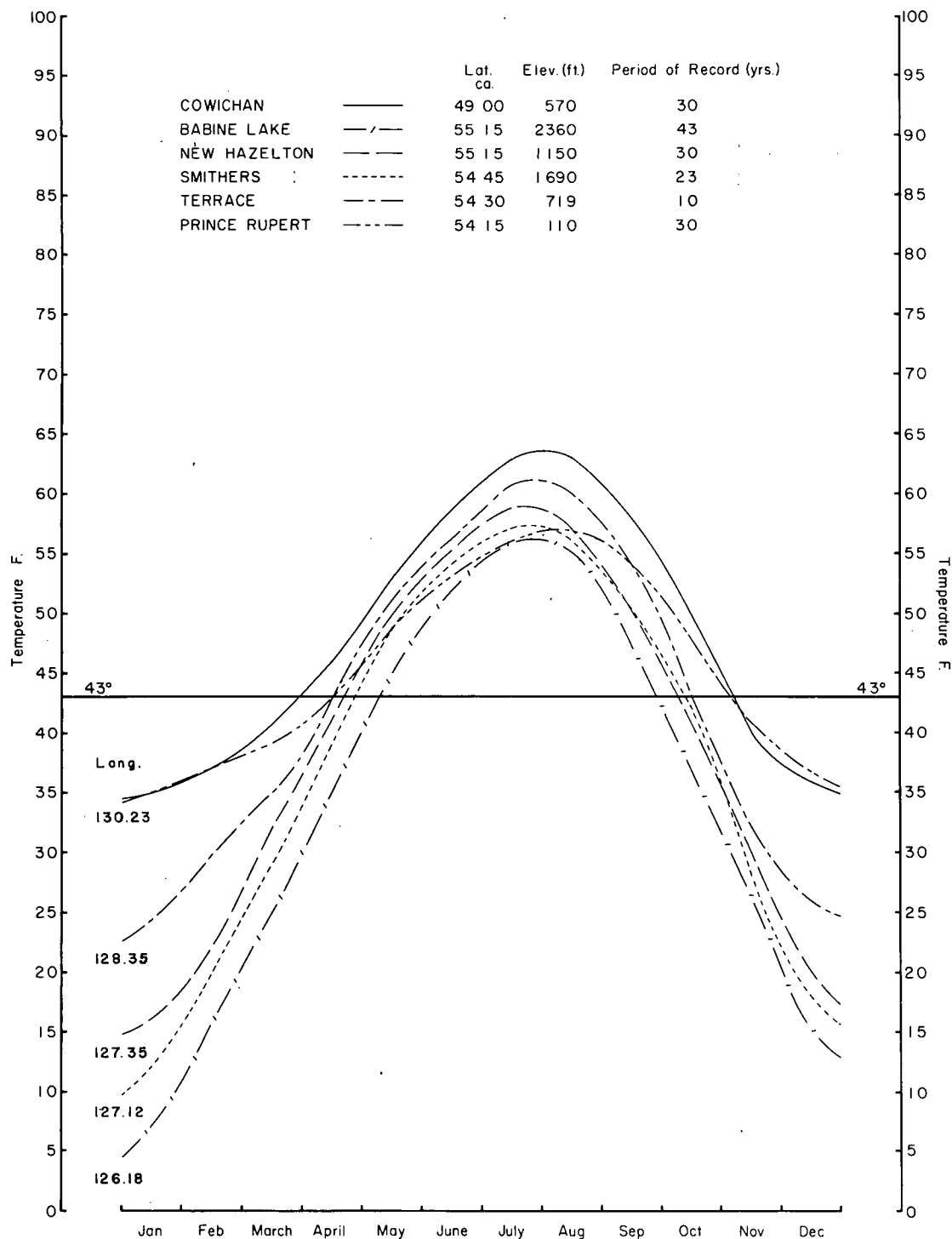
- Vegis, A., 1963. Climatic control of germination, bud break, and dormancy. In L.T. Evans, ed., Environmental control of plant growth. Academic Press, New-York, 449 pp.
- Wareing, P.F., 1950a. Growth studies in woody species I: Photoperiodism in first-year seedlings of Pinus silvestris. Phys. Plant. 3: 258-276.
- Wareing, P.F., 1950b. Growth studies in woody species II: Effect of day length on shoot-growth in Pinus silvestris after the first year: Phys. Plant. 3: 300-314.
- Wareing, P.F., 1950c. Extension and radial growth in trees. Nature, 166: 278.
- Wareing, P.F., 1951. Growth studies in woody species III. Further photoperiodic effects in Pinus silvestris. Phys. Plant. 4: 41-56.
- Wareing, P.F., 1956. Photoperiodism in woody plants. Annual review of plant physiology, 7: 191-214.
- Wareing, P.F., 1966. The physiologists approach to tree growth. In R.W.V. Palmer, Ed. Physiology in forestry. Supplement to Forestry. 39: 7-18.
- Watts, W.A., and Wright, H.E., 1966. Late-Wisconsin pollen and seed analysis from the Nebraska sandbills. Ecology, 47: 202-210.
- Webb, D.A., 1954. Is the classification of plant communities either possible or desirable? Botanisk Tidsskrift, 51: 362-370.
- Went, F.W., 1957. The experimental control of plant growth. Chronica Botanica Co. 343 pp.
- White, F., 1962. Geographic variation and speciation in Africa with particular reference to Diospyros. The Systematic Association London. Publication no. 4: 71-103.

- Whitford, H.N., and Craig, R.D., 1918. Forests of British Columbia. Commission of Conservation, Ottawa, 1918. 409 pp.
- Wiersma, J.H., 1958. De Betekenis van de Fotoperiodiciteit voor de praktijk van de Bosbouw. *Nederlandsch Boschbouw-tijdschrift*. Loo. 30: 139-144.
- Wiersma, J.H. 1963. A new method of dealing with the results of provenance tests. *Silvae Genetica*, 12: 200-205.
- Williams, W.T., and Dale, M.C., 1965. Fundamental problems in Numerical Taxonomy. In R.D. Preston ed., *Advances in Botanical Research* 2: 36-67.
- Wright, J.W., and Baldwin, H.I., 1957. The 1938 international union Scotch pine provenance test in New Hampshire. *Silvae Genetica*, 6: 2-14.
- Wright, J.W., Bingham, R.T., Dorman, K.W., 1958. Genetic variation within geographic ecotypes of forest trees and its role in tree improvement. *Journal of Forestry*, 56: 804-808.
- Wright, J.W., and Bull, I.W., 1963. Geographic variation in Scotch pine. *Silvae Genetica*, 12: 1-25.
- Wright, J.W., 1955. Species crossability in spruce in relation to distribution and taxonomy. *Forest Science*, 1: 319-349.
- Wright, J.W., 1962. Genetics of forest tree improvement. *FAO Forestry and Forest Products studies* No. 16. 399 pp.

A P P E N D I X

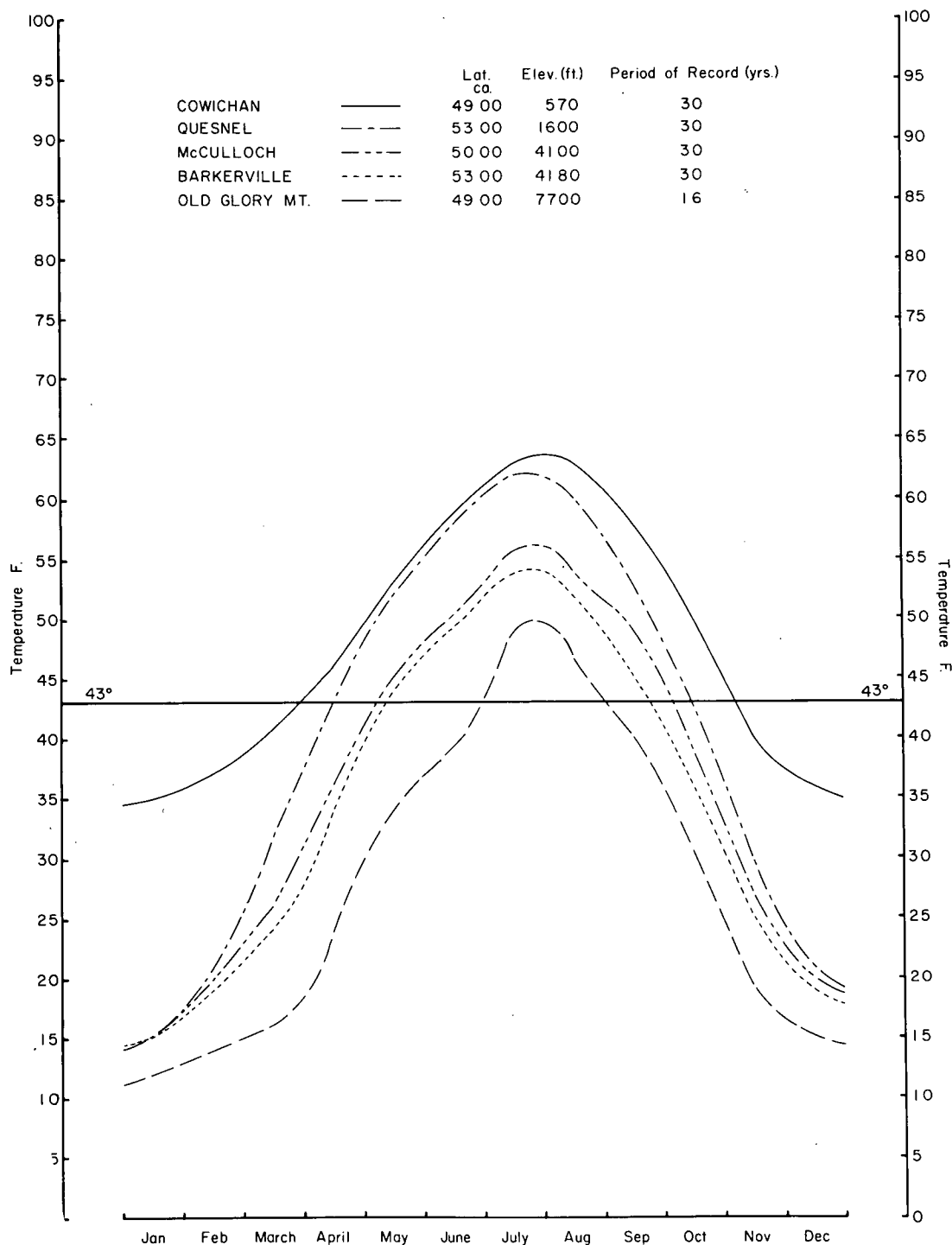
Figs. 9 to 46

Fig. 9 The relationship between continentality and temperature regime for representative climatic stations in British Columbia.



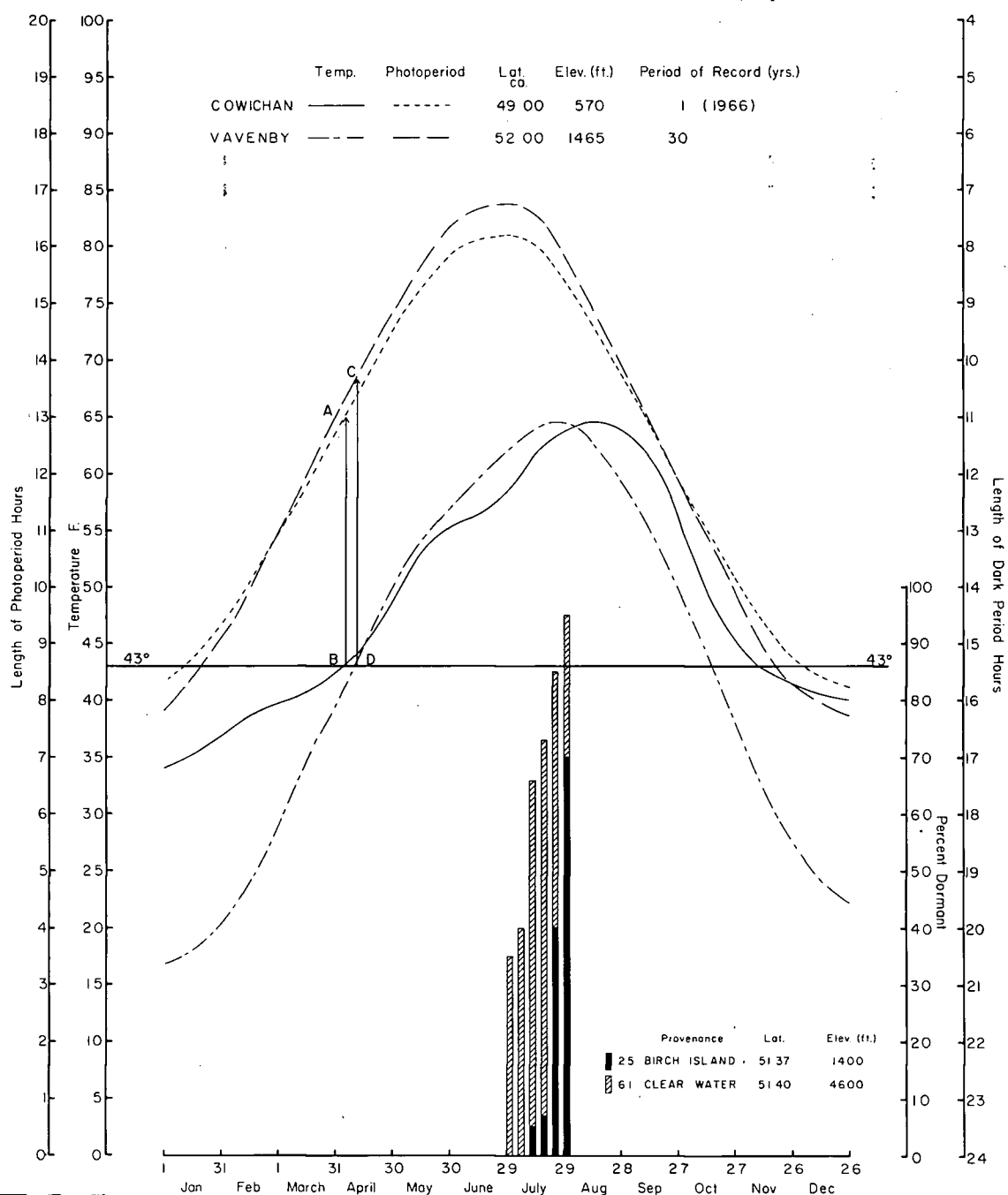
Note the general decrease in temperature within increasing continentality.

Fig. 10 The relationship between altitude and temperature regime for representative climatic stations in British Columbia.



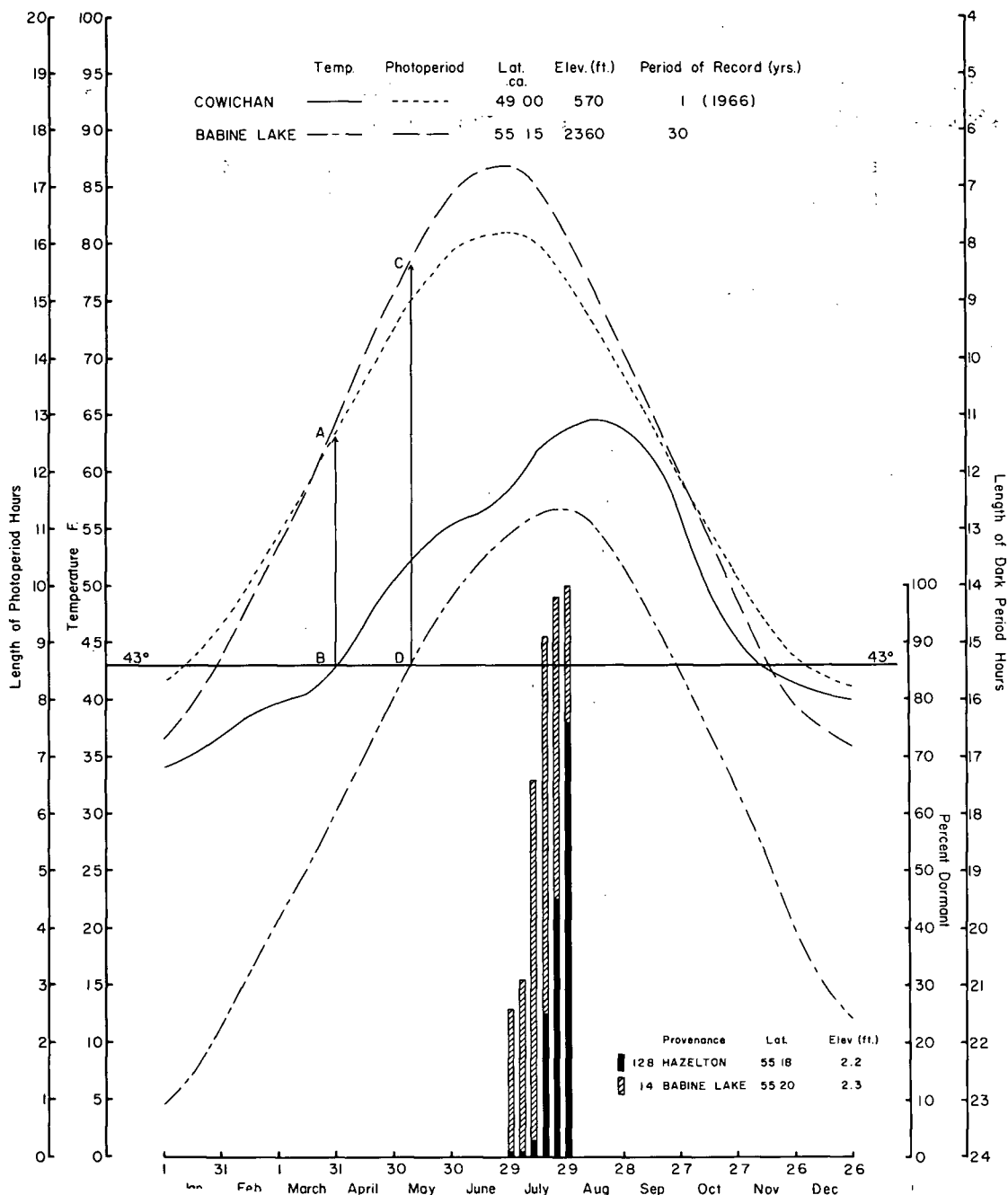
Note the general decrease in temperature with increasing altitude.

Fig. 11 The relationship between photoperiod and temperature at the Cowichan nursery and at Vavenby in south central British Columbia.



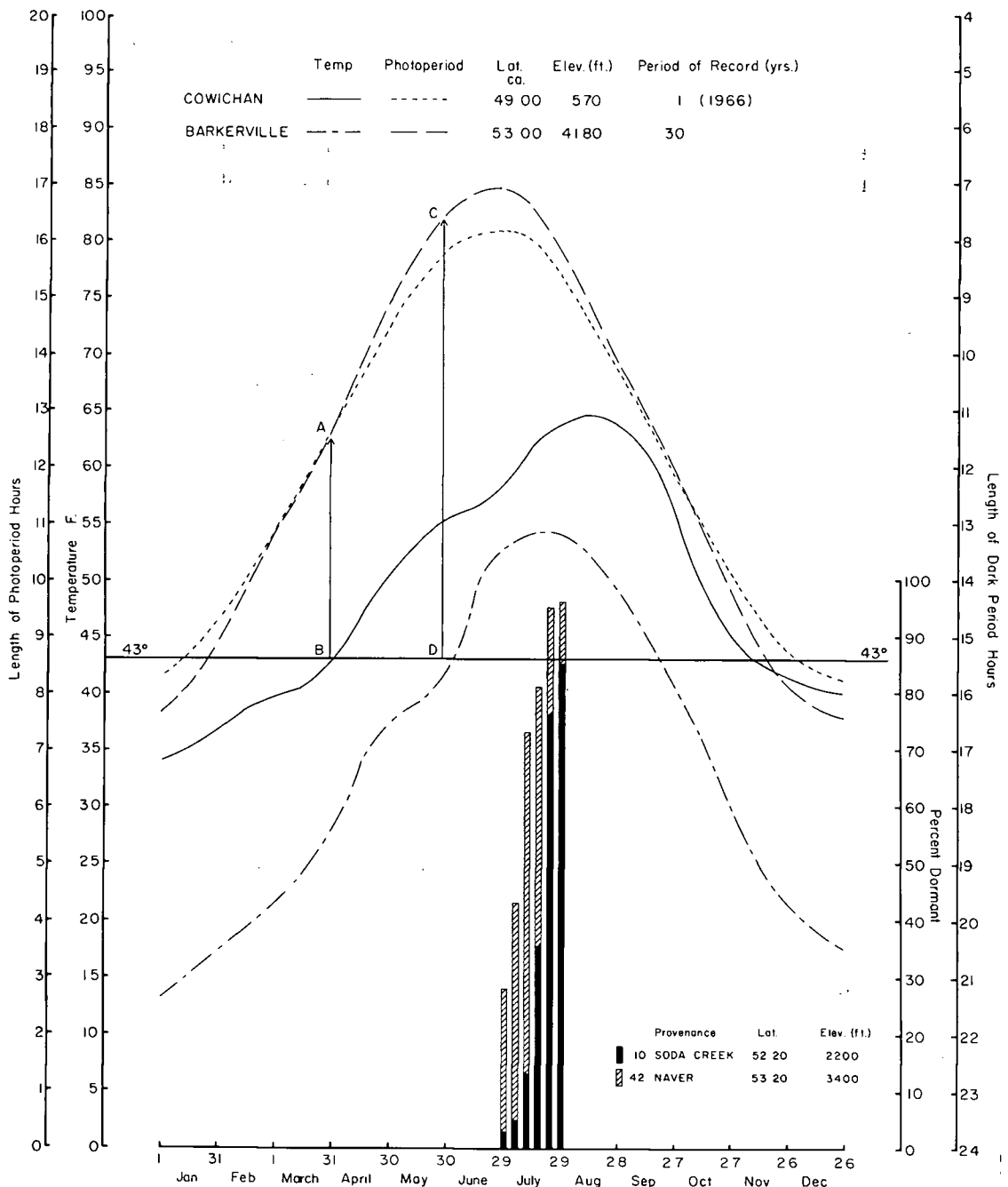
Note the striking similarity of the environments as represented by the Vavenby station and the environment at Cowichan in respect to the day length on the first day of the year showing a temp. of 43°C. The Birch Island provenance is represented by the Vavenby station. Note that it is much slower to enter dormancy at Cowichan than a provenance from approximately the same lat. and long. but higher elevation, and that it produced maximum shoot extension in the Cowichan nursery. Points A and C on the curves represent the daylength at each station when temperatures reach 43°C.

Fig. 12 The relationship between temperature and photoperiod at the Cowichan Nursery and at Babine Lake in Central British Columbia.



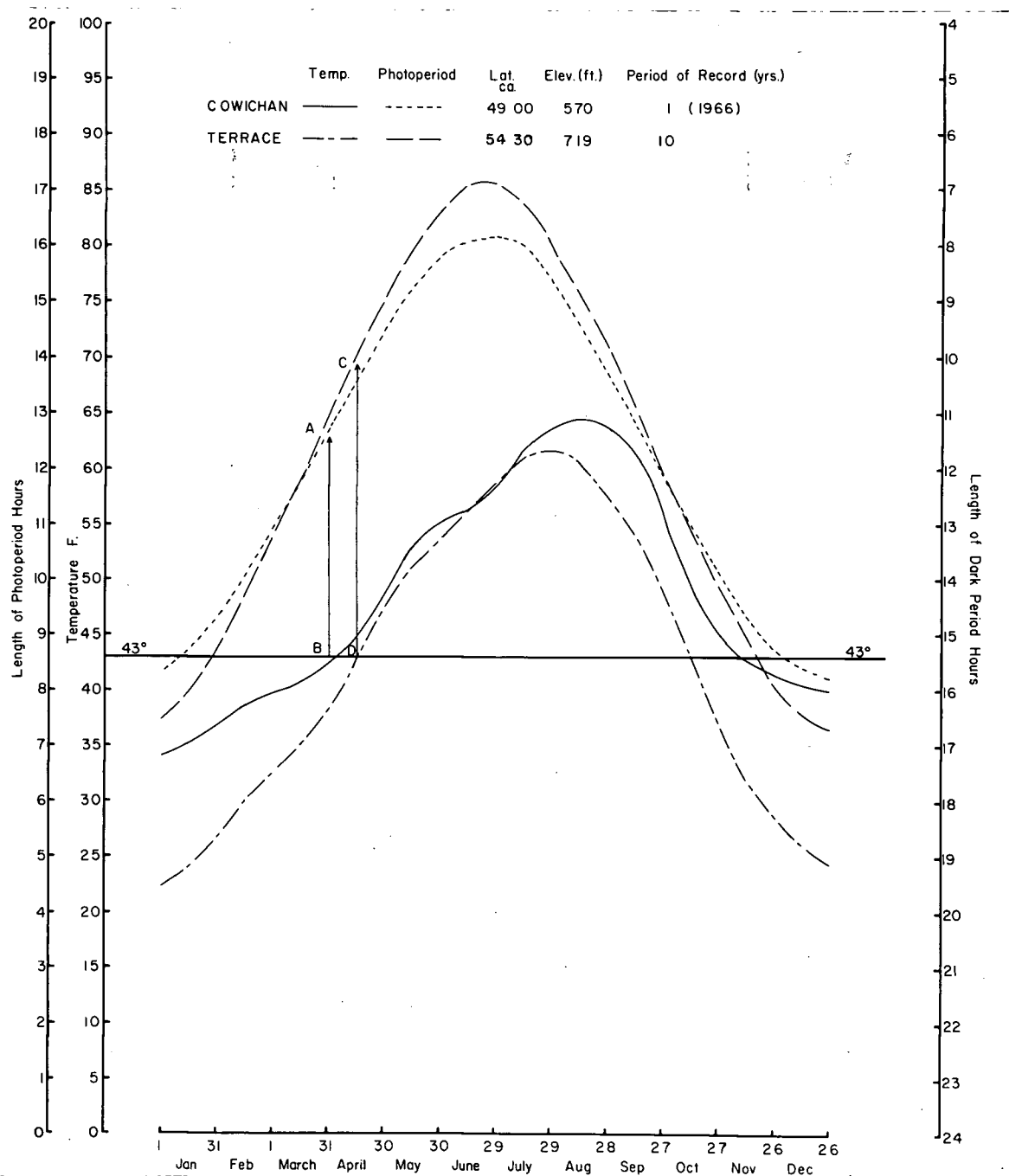
Note the disparity between the two regions in this index of the environment and compare with the Terrace station. Note that the Hazelton provenance, which is from the general region of Terrace, was much slower to enter dormancy than the Babine Lake provenance which is further to the east, and in a region of greater continentality. (See fig. 14 for Terrace data).

Fig. 13 The relationship between temperature and photoperiod at the Cowichan nursery and at Barberville in east central British Columbia.



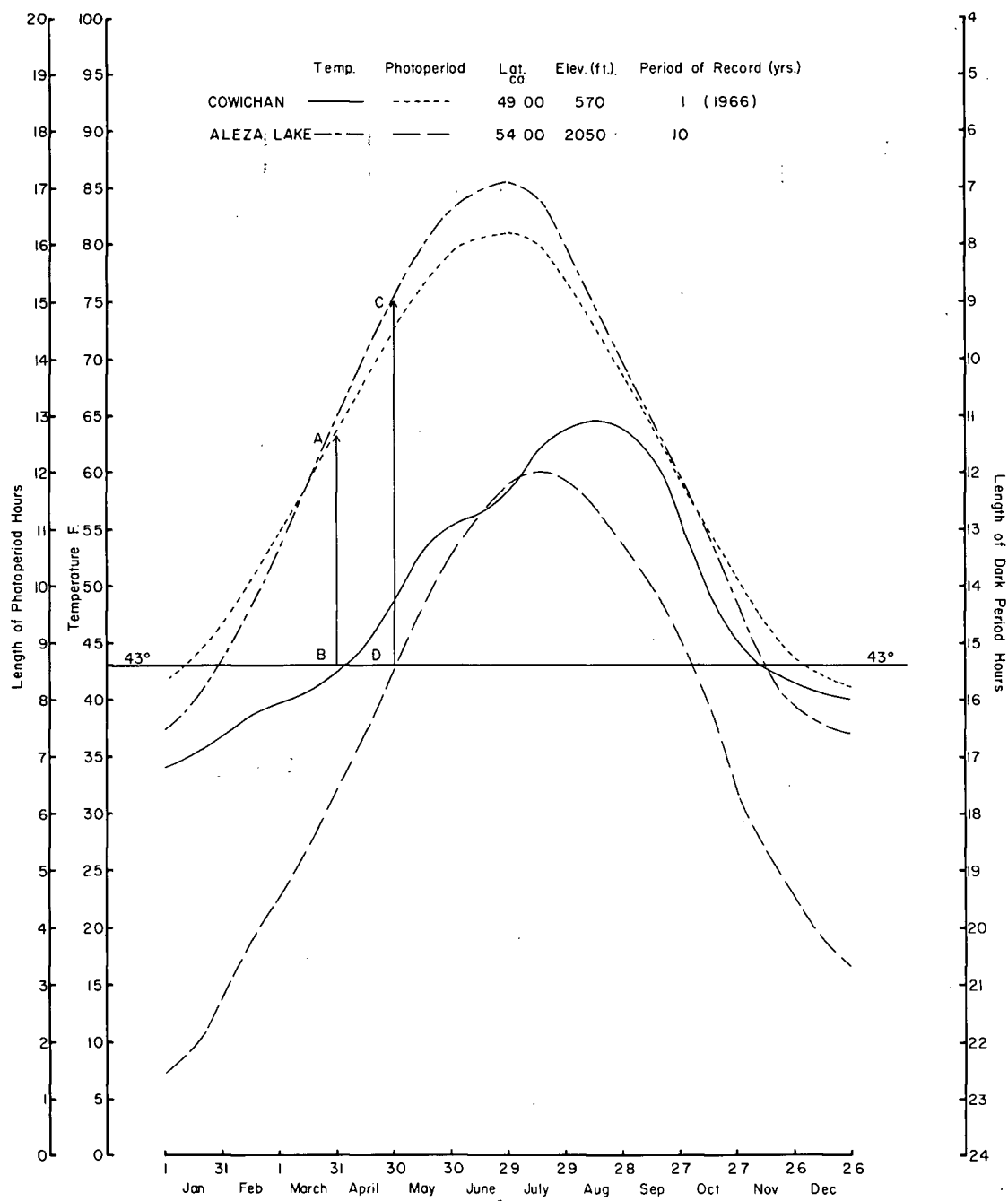
Note the disparity between the two environments and compare with the curves for Prince George and Aleza Lake. Note also that the Soda Creek provenance, which is from a relatively low lat. and elev., was much slower to enter dormancy than the Naver provenance. In regard to dormancy behaviour the Soda Creek provenances is comparable to the Birch Island provenance and other provenances from low elevations and low latitudes.

Fig. 14 The relationship between temperature and photoperiod at the Cowichan Nursery and at Terrace in Northwestern British Columbia.



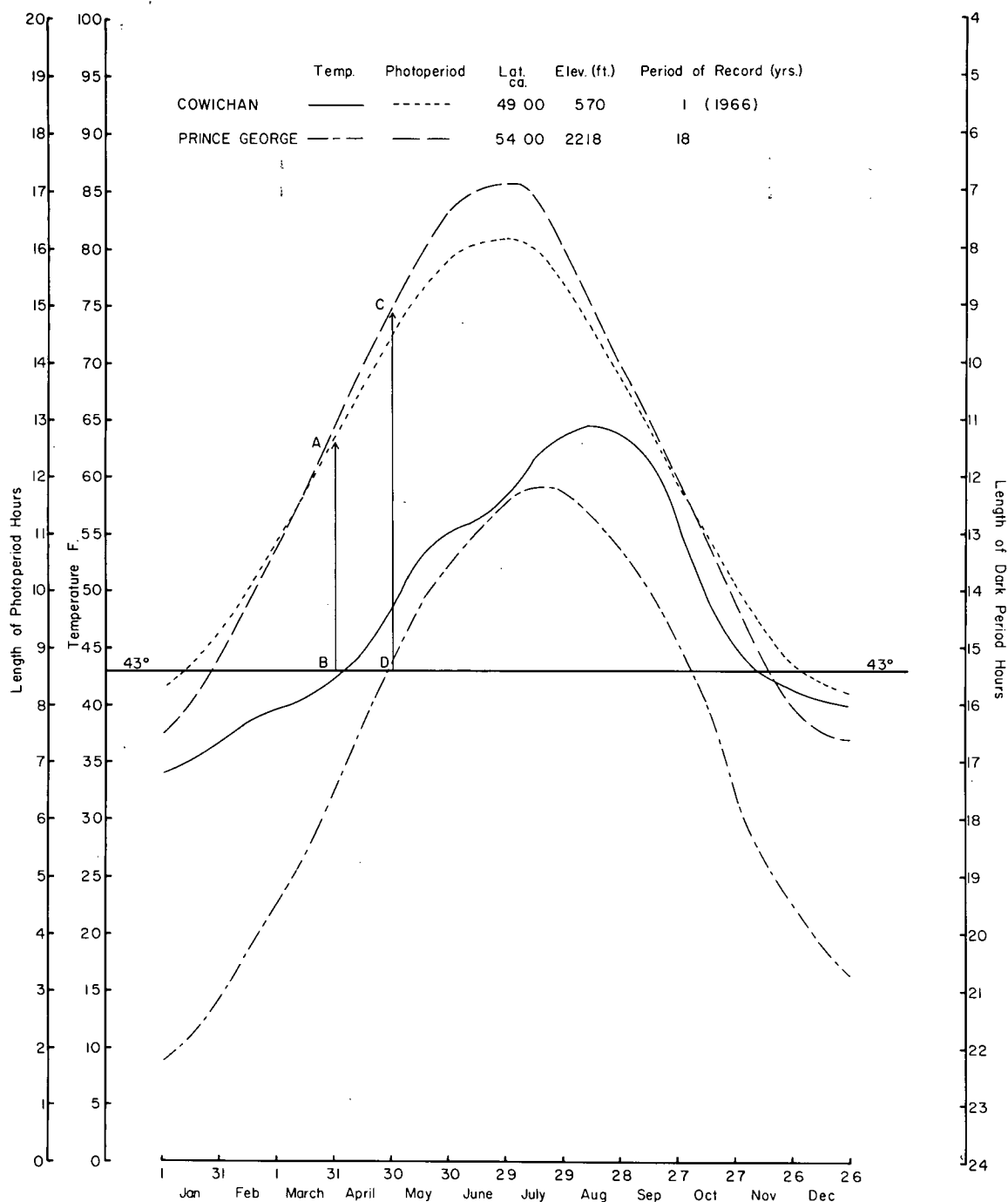
Note that on the basis of this index of the environment there is not a great disparity during the growing season between the environment at Cowichan and the environments represented by the Terrace station. The significant difference is not in temperatures during the growing season, but in winter temperatures.

Fig. 15 The relationship between temperature and photoperiod at the Cowichan nursery and at Aleza Lake in east central British Columbia.



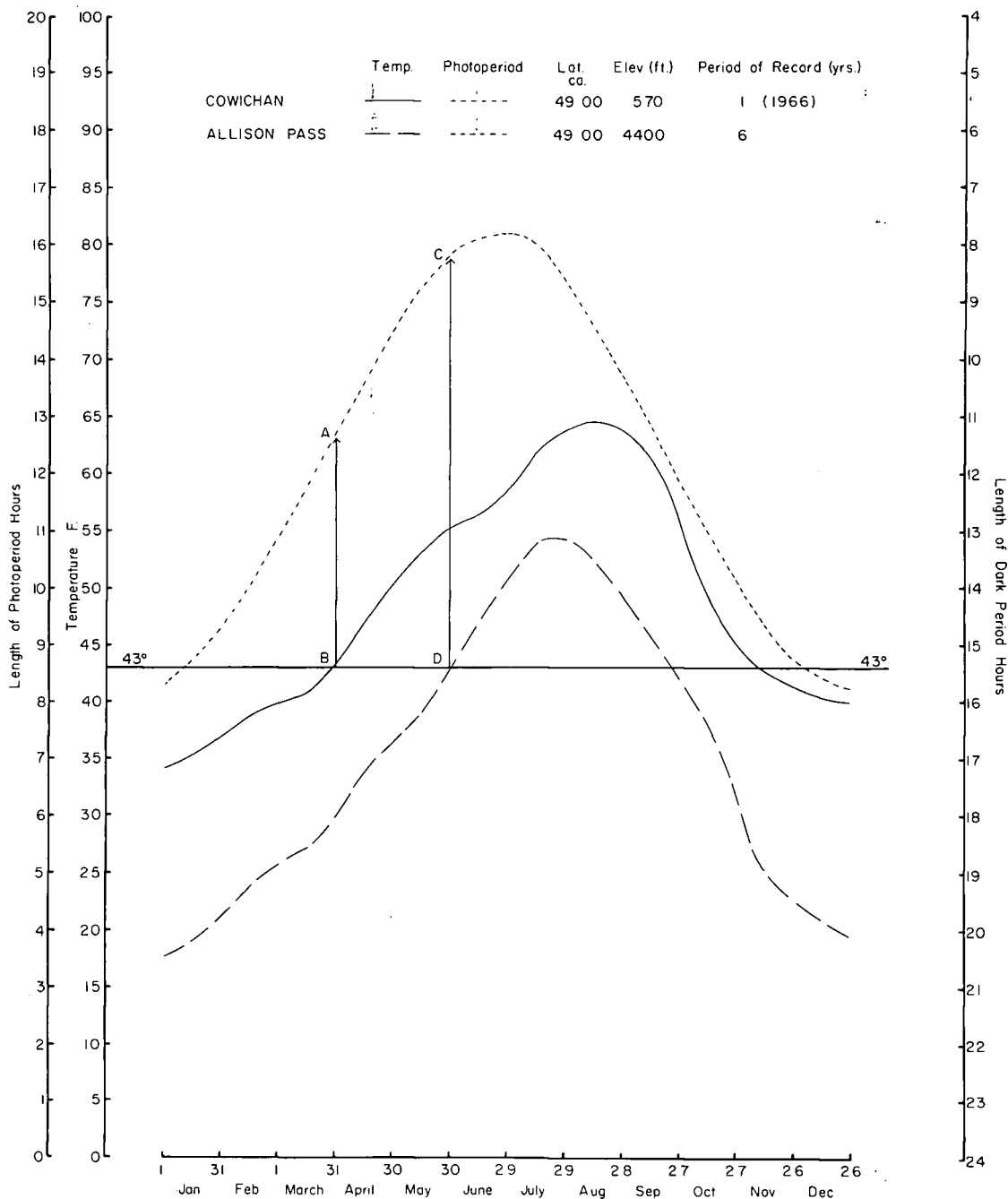
Note the similarity of the Aleza Lake curves with those of Prince George, and contrast with those of Babine Lake and Barkerville.

Fig. 16 The relationship between temperature and photoperiod at the Cowichan nursery and at Prince George in central British Columbia.



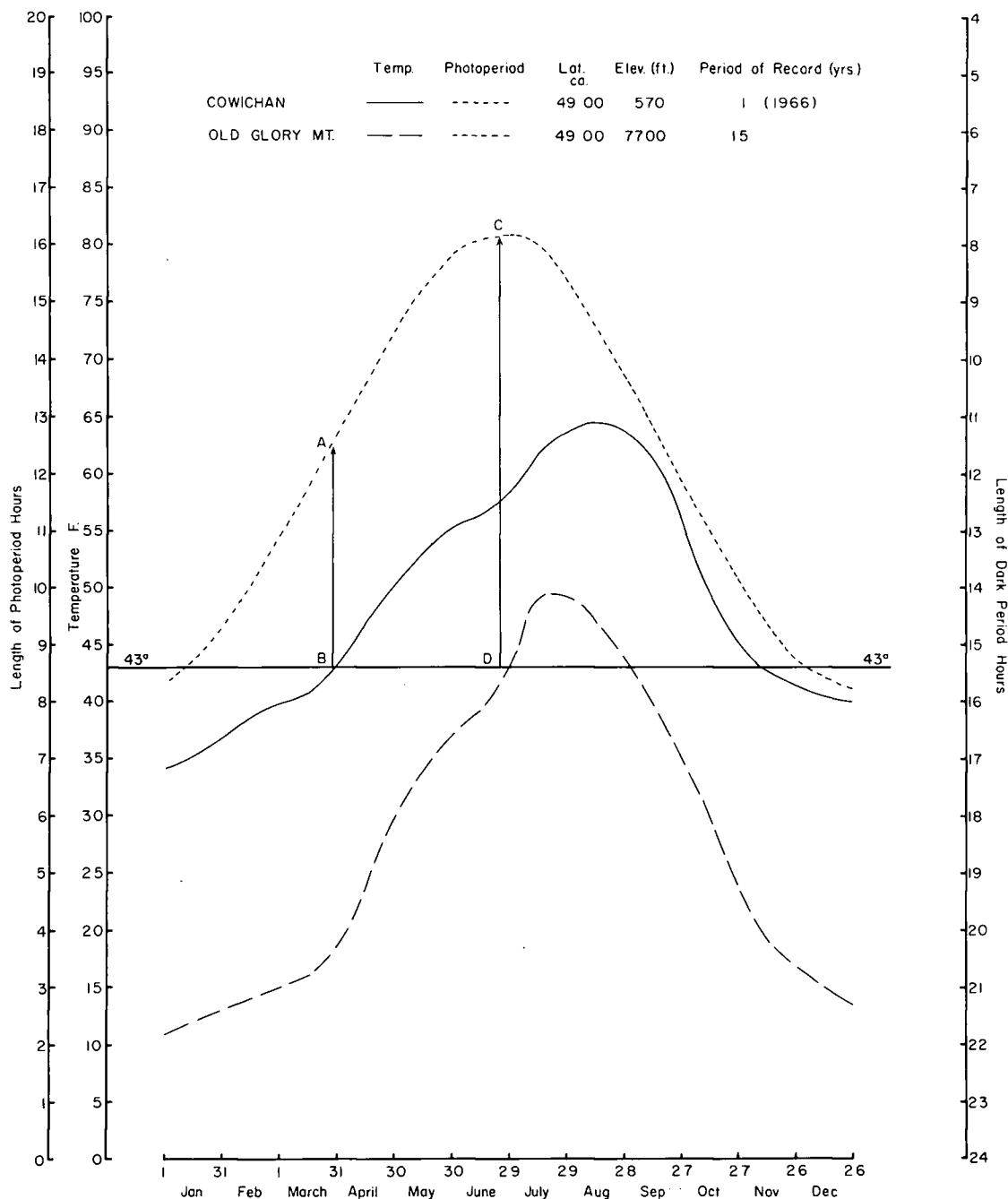
Note the similarity of the curves with those of Aleza Lake, and contrast with those of Babine Lake, Barkerville, Allison Pass, and Vavenby.

Fig. 17 The relationship between temperature and photoperiod at the Cowichan nursery and at Allison Pass in southern British Columbia.



Note that on the basis of this index of the environment there is a considerable disparity between the environment at Cowichan and the environments represented by the weather station at Allison Pass. Compare with the curves for Old Glory mountain and contrast with Vavenby.

Fig. 18 The relationship between temperature and photoperiod at the Cowichan nursery and on Old Glory Mountain in southern British Columbia.



Note the great disparity between the environment at this elevation, which is at approximately the same latitude as the Cowichan nursery, and the environment at Cowichan as measured by day length on the first day of the year with a temperature of 43°C. Approximately 33 percent of the provenances grown at Cowichan are from above 4000 ft.

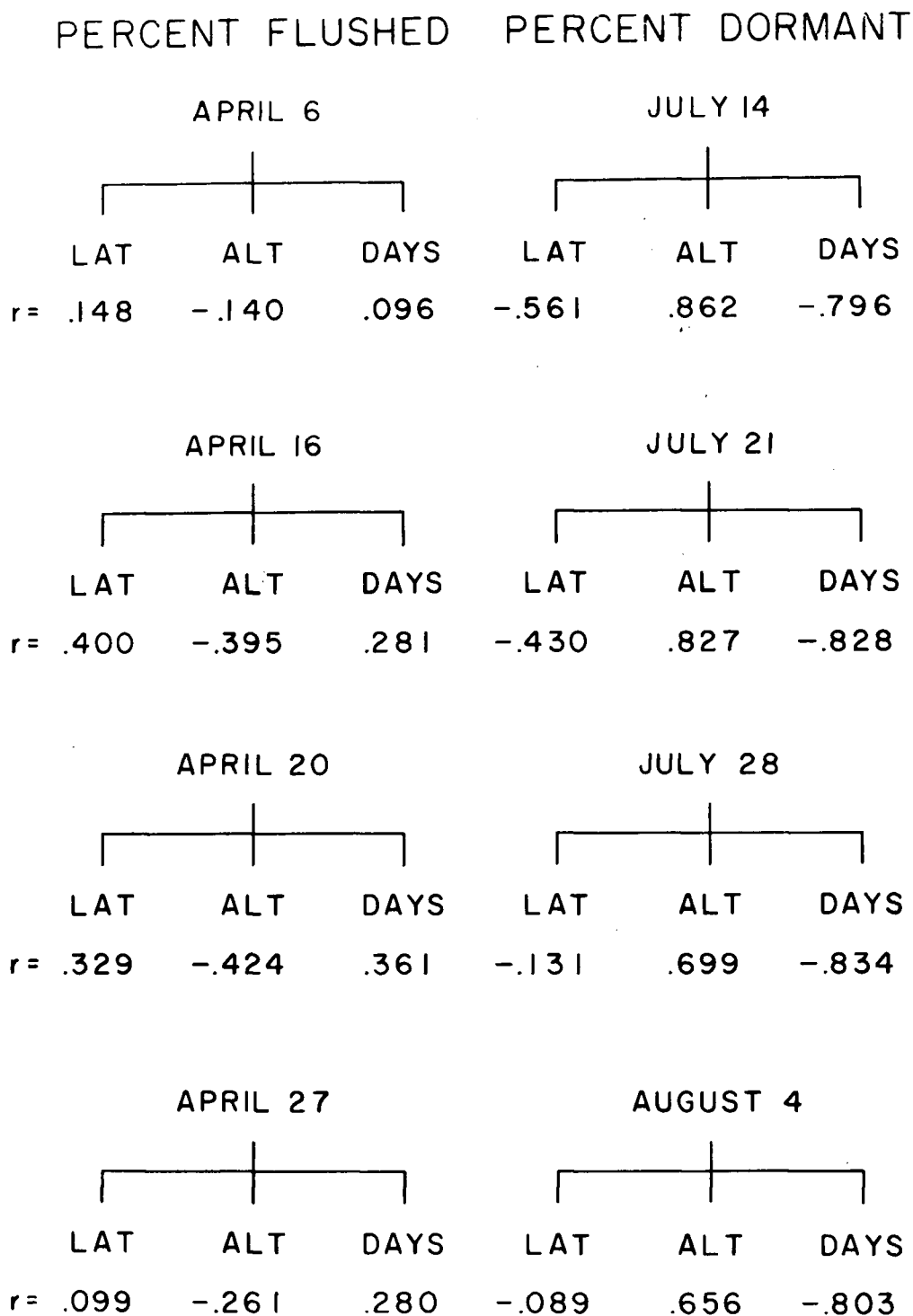
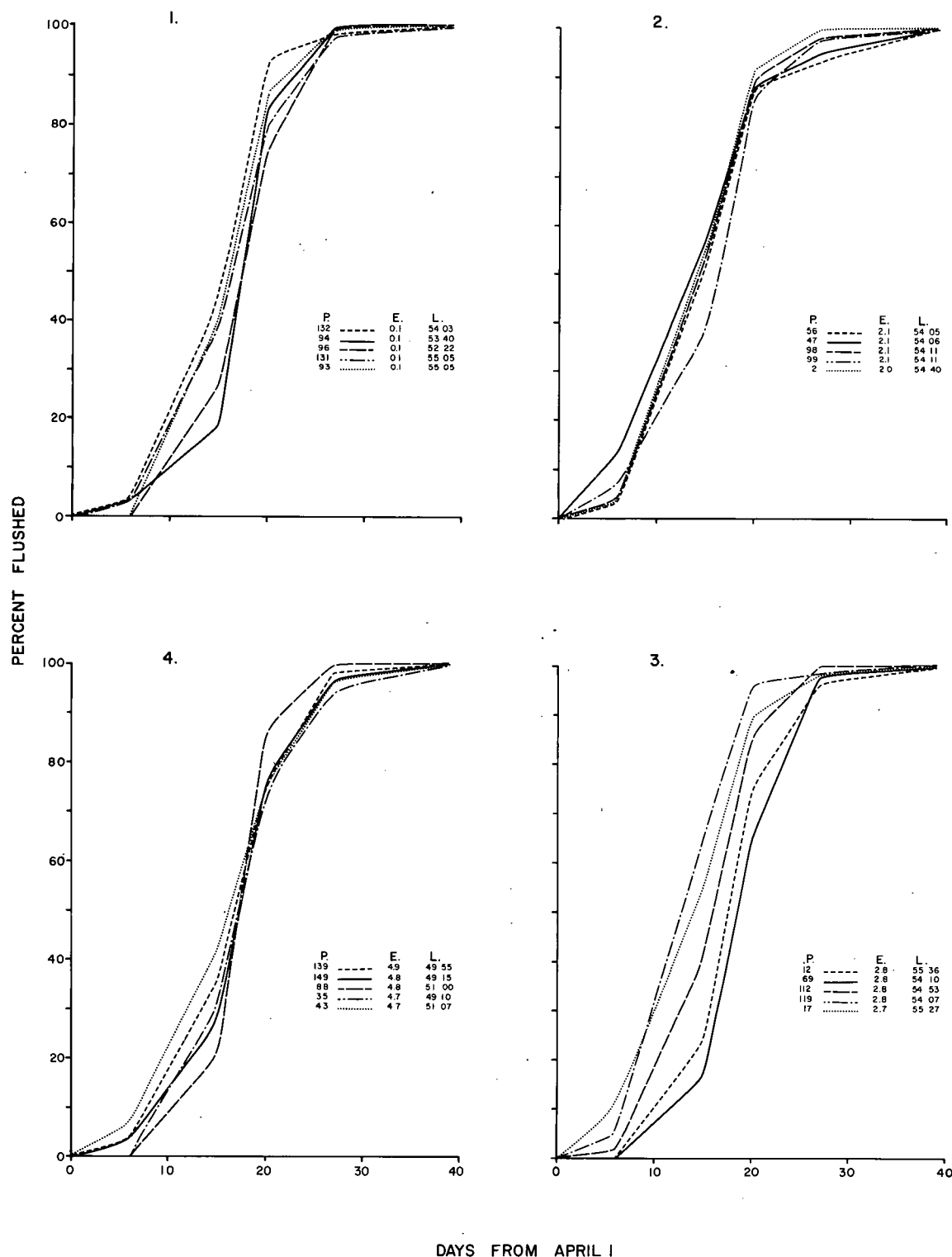


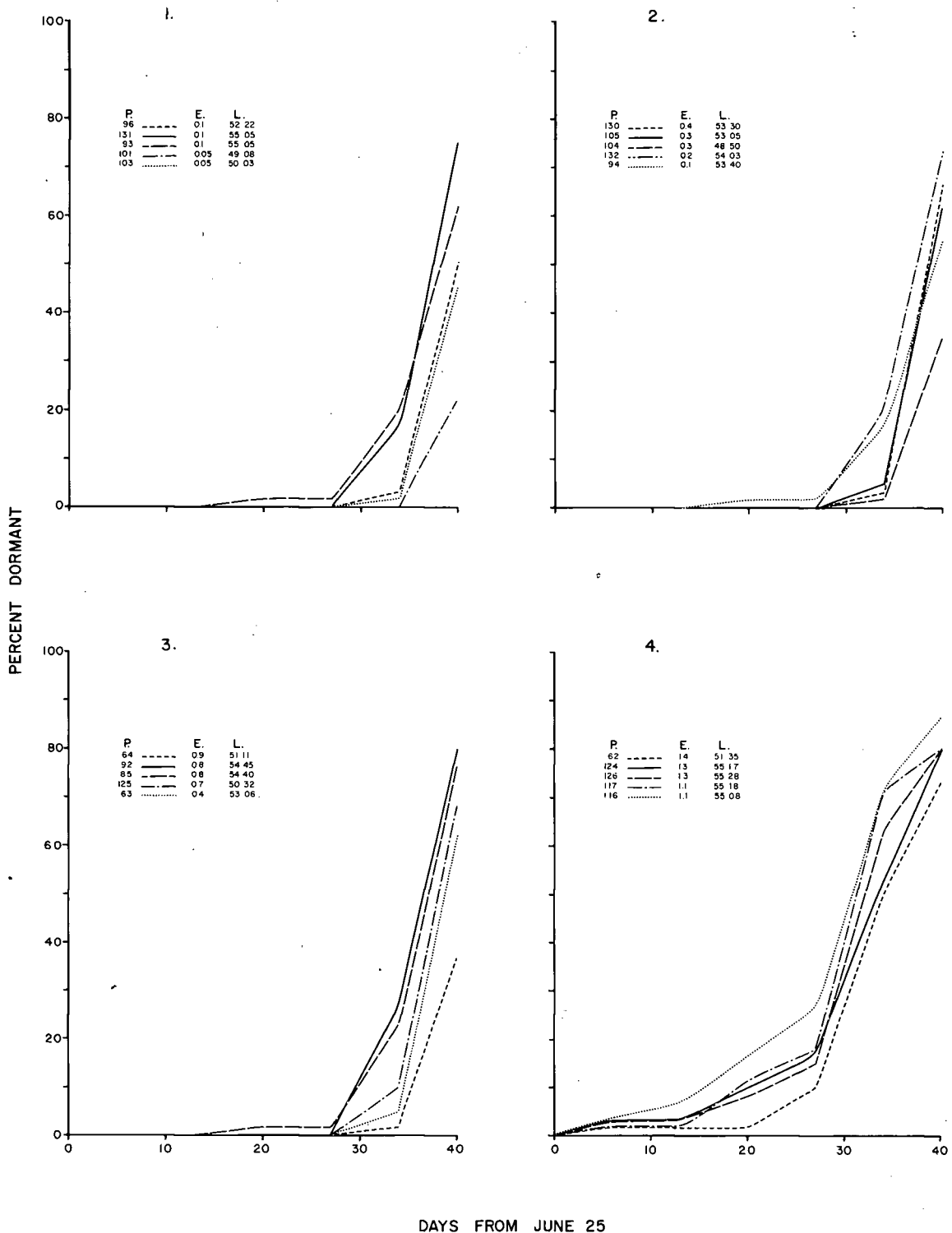
Fig. 19 Degree of correlation between factors of the environment and flushing and dormancy. r -correlation coefficient, LAT.-latitude, ALT.-altitude, DAYS-index of the vegetative period. (See tables 2, 19, 21).

Fig. 20 Curves of flushing for Sitka (1), white (2), sympatric populations of white-Sitka, and white-Engelmann (3), and Engelmann spruce (4).



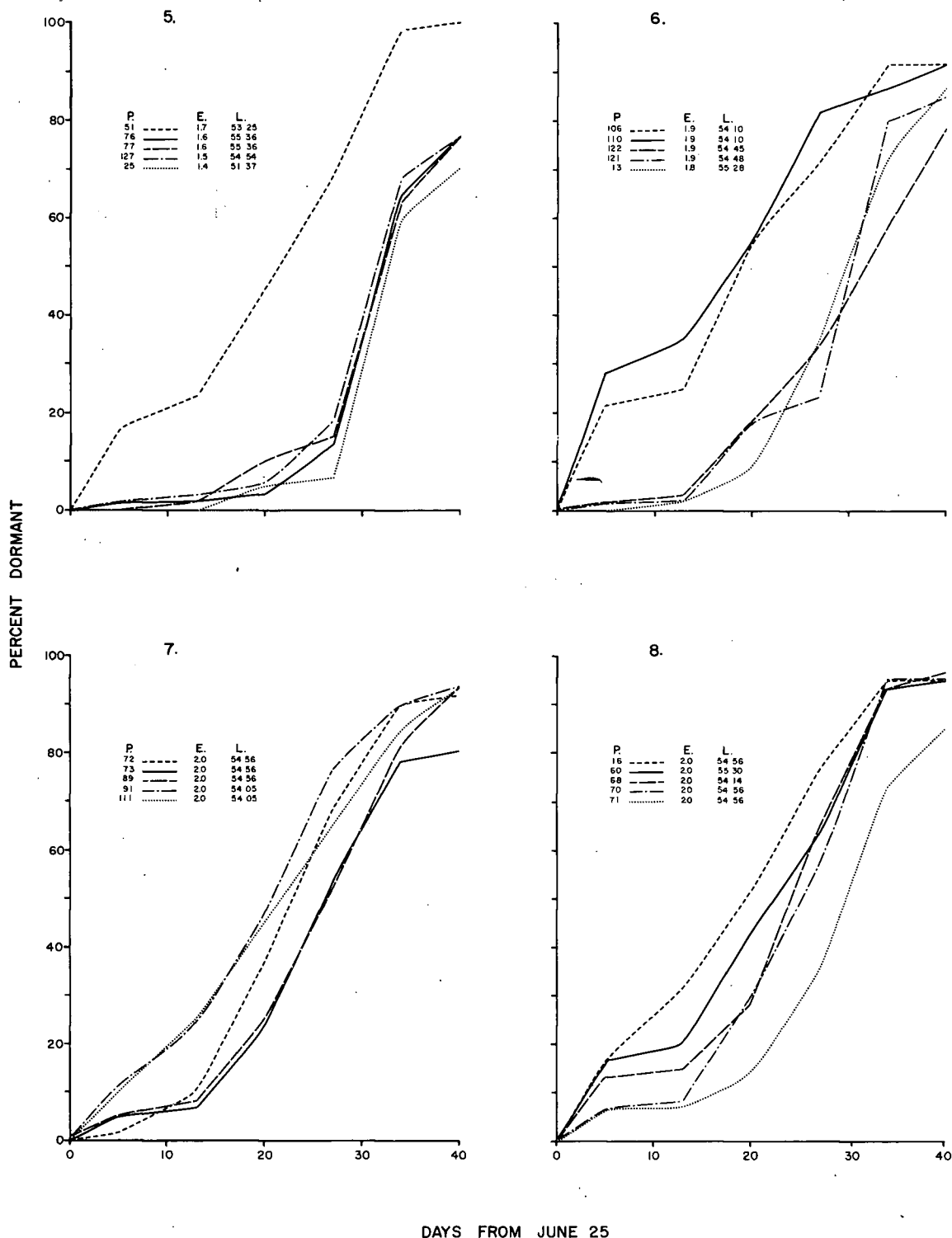
Note the striking similarity of the curves for diverse provenances which vary in altitude from sea level to 4700 ft. P-provenance; E-elevation; L-latitude.

Fig. 21 Curves of dormancy for Sitka spruce (1 and 2) and provenances from sympatric zones of white and Sitka spruce (3 and 4).



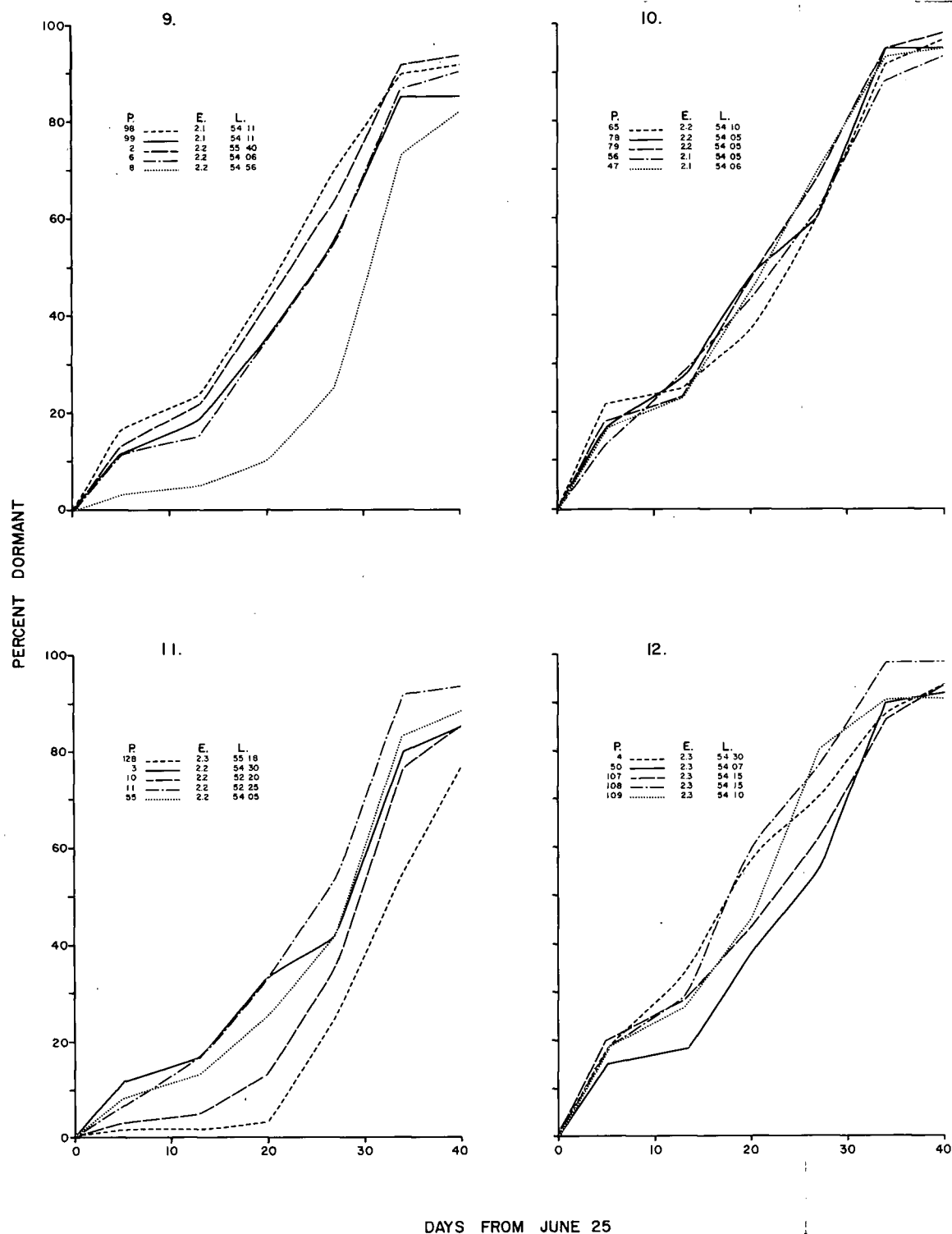
Note that all provenances in 4 except 62 are from the region of Hazelton in N.W. British Columbia. 62 is the Birch Island provenance and is from a sympatric zone of white and Engelmann spruce (see part B re sympatric spruce populations). Note also the similarity of the curves in 4 to the pure Sitka spruce populations, and compare with curves 5 and 6 in fig. 22.

Fig. 22 Curves of dormancy for provenances from sympatric populations of white and Sitka spruce, and low elevation allopatric spruce provenances. Note the great sensitivity of the dormancy curve in distinguishing provenances.



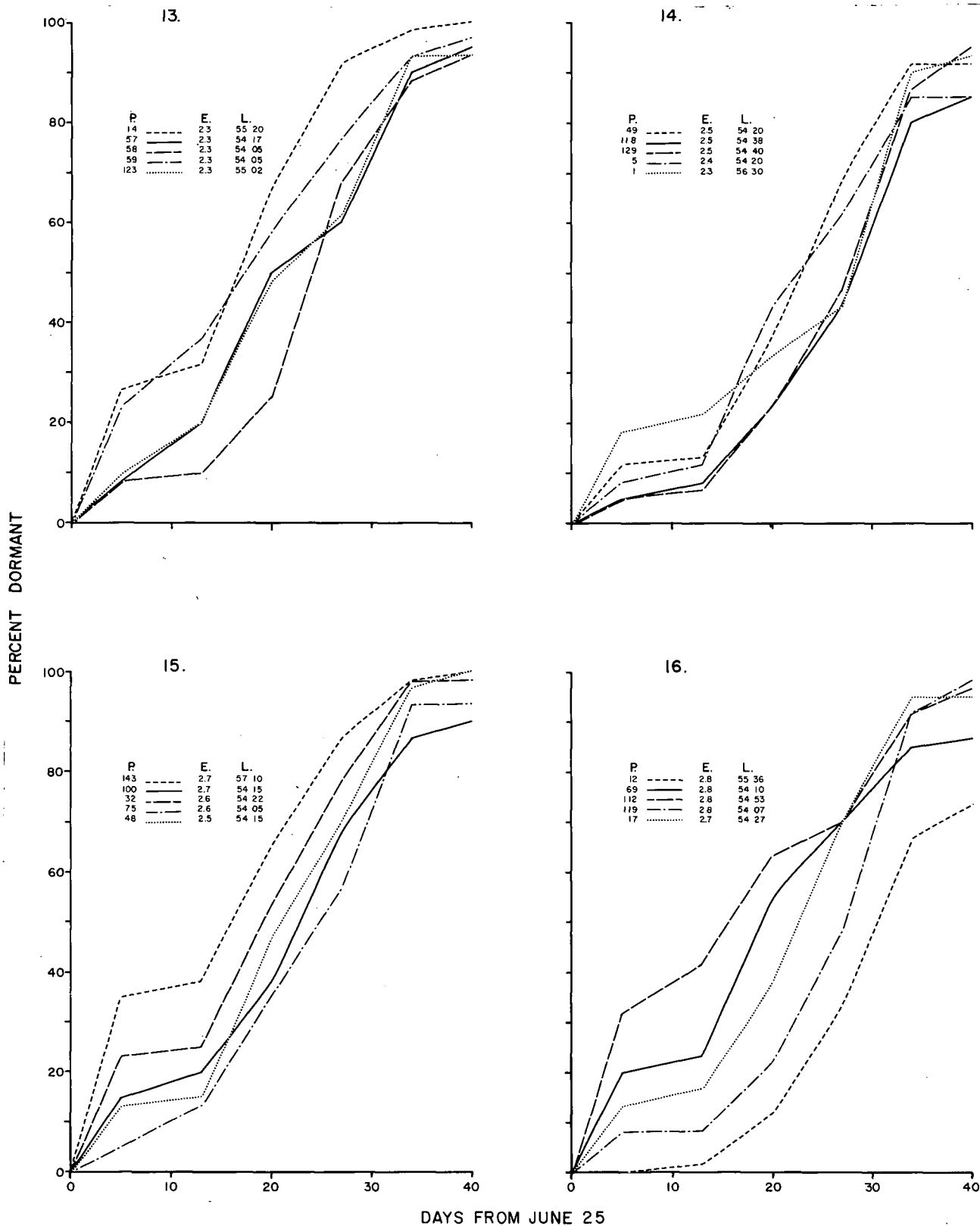
Provenance 51 in 5 is from Hixon south of Prince George in central British Columbia. 76, 77 and 127 are from N.W. British Columbia in the region of the Kispiox river. 25 is from the Birch Island region. In 6, 106 and 110 are from N.E. British Columbia: 13, 121 and 122 are from the Hazelton-Smithers region in N.W. British Columbia.

Fig. 23 Curves of dormancy for spruce provenances from elevations between 2000 and 2300 ft.



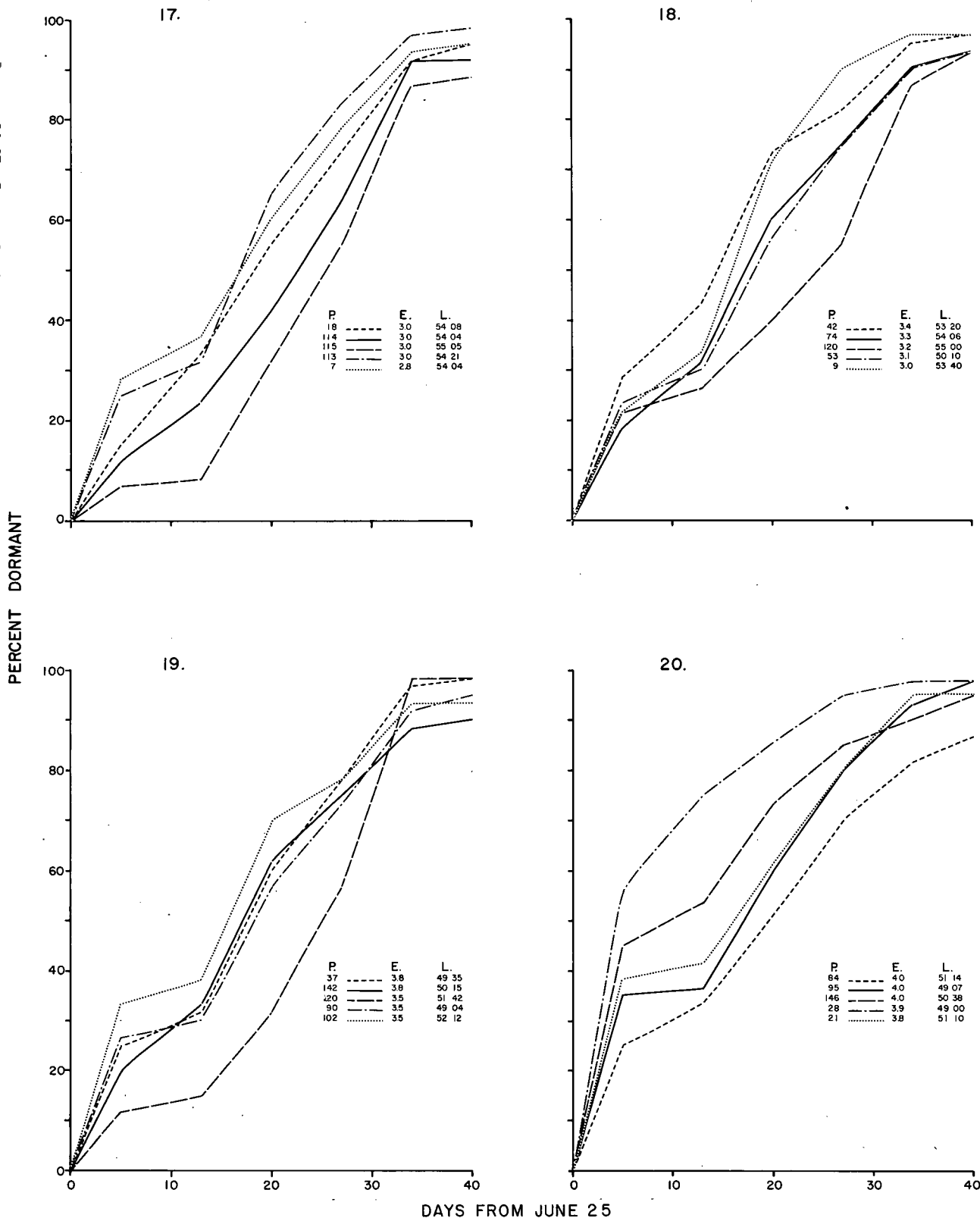
Note that all these provenances except 8 in 9 and 128 in 11 have similar curves. Both of these provenances are from the region of Hazelton. Even at relatively high elevations, therefore, provenances from N.W. British Columbia have a characteristic dormancy curve which distinguishes them from provenances of the same elevation but further east.

Fig. 24 Curves of dormancy for spruce provenances from elevations between 2300 and 2700 ft.



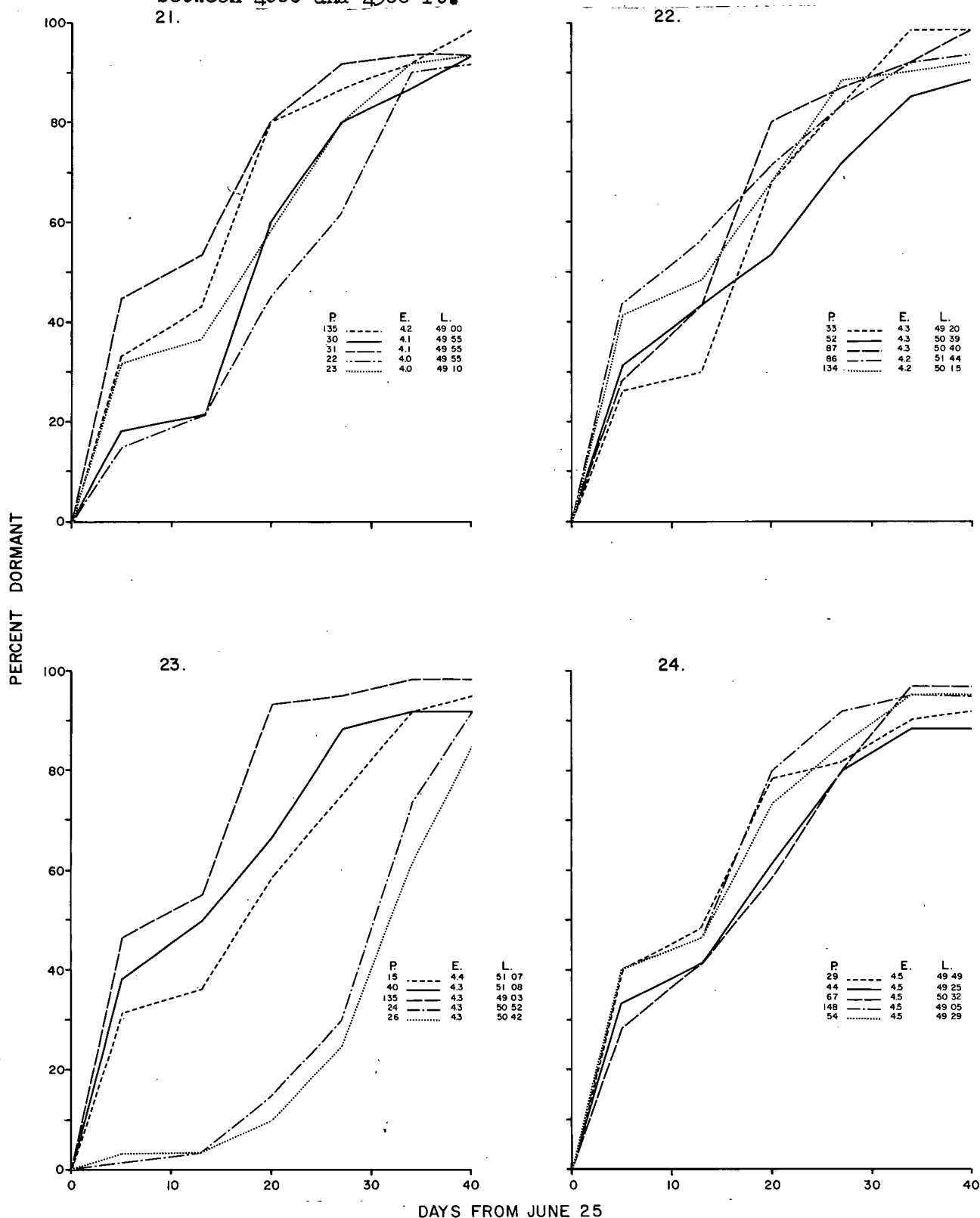
Note that the 5 provenances in 16 represent areas both in N.W. and N.E. British Columbia, hence the strikingly different curves for provenances from the same elevation.

Fig. 25 Curves of dormancy for spruce provenances from elevations between 3000 and 4000 ft.



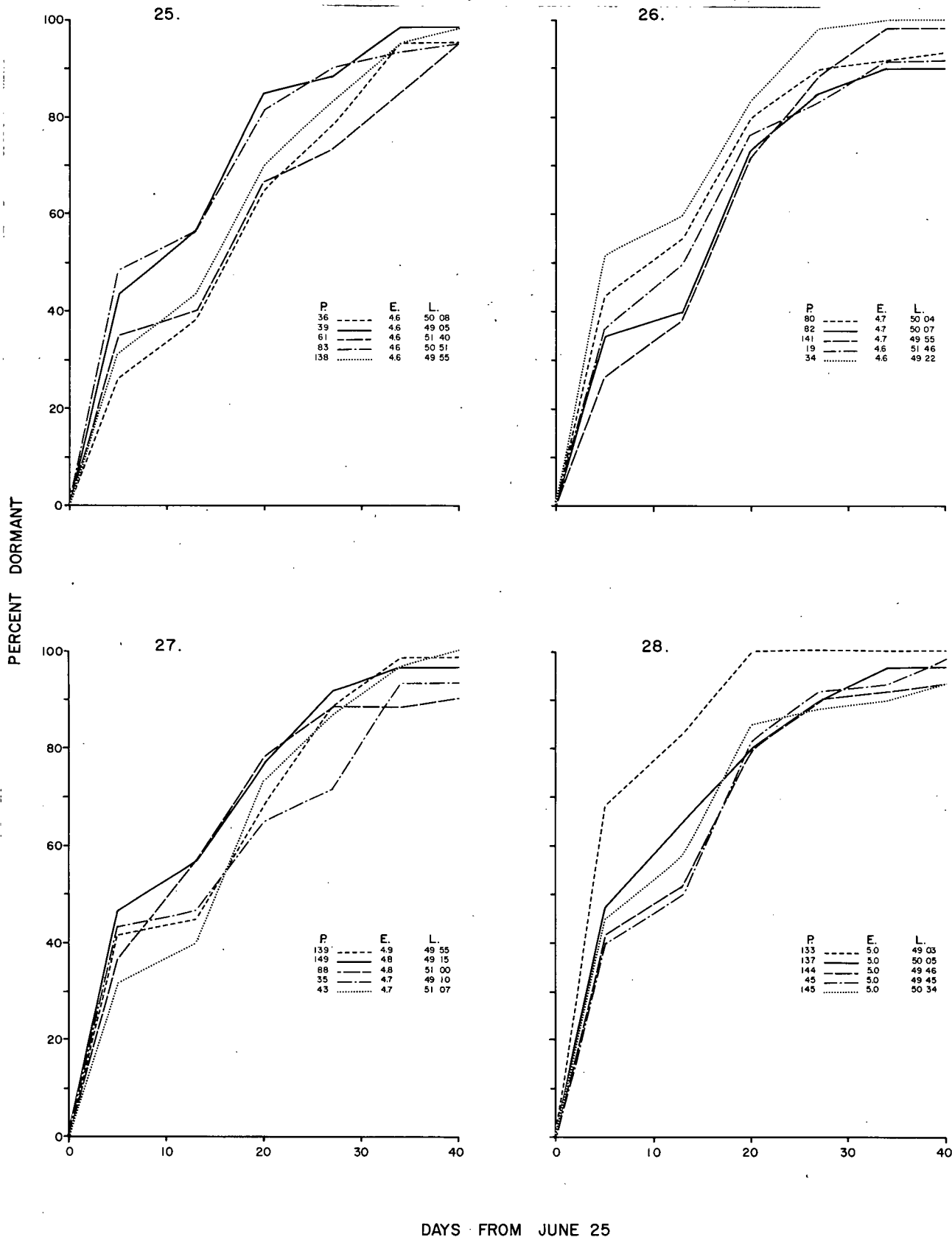
Note the gradual change in the shape of the dormancy curves, which at 4000 ft., show the rapidity with which provenances from high elevations enter dormancy in comparison with low elevation provenances from central British Columbia, and provenances from N.W. British Columbia.

Fig. 26 Curves of dormancy for spruce provenances from elevations between 4000 and 4500 ft.



Note that in regard to elevation provenances 24 and 26 in 23 are of doubtful origin. Following observations in the nursery it was confirmed by correspondence that both provenances were incorrectly registered. It is clear from the dormancy curves that these provenances are from low elevations, and are identical in growth rhythm to the Birch Island provenance.

Fig. 27 Characteristic dormancy curves for spruce provenances from elevations between 4600 and 5000 ft.



Note the change in form of the curves in comparison to those for provenances from elevations between 1500 and 2500 ft.

RELATIONSHIP BETWEEN ELEVATION AND SPRUCE

CONE SCALE—SEED WING RATIO

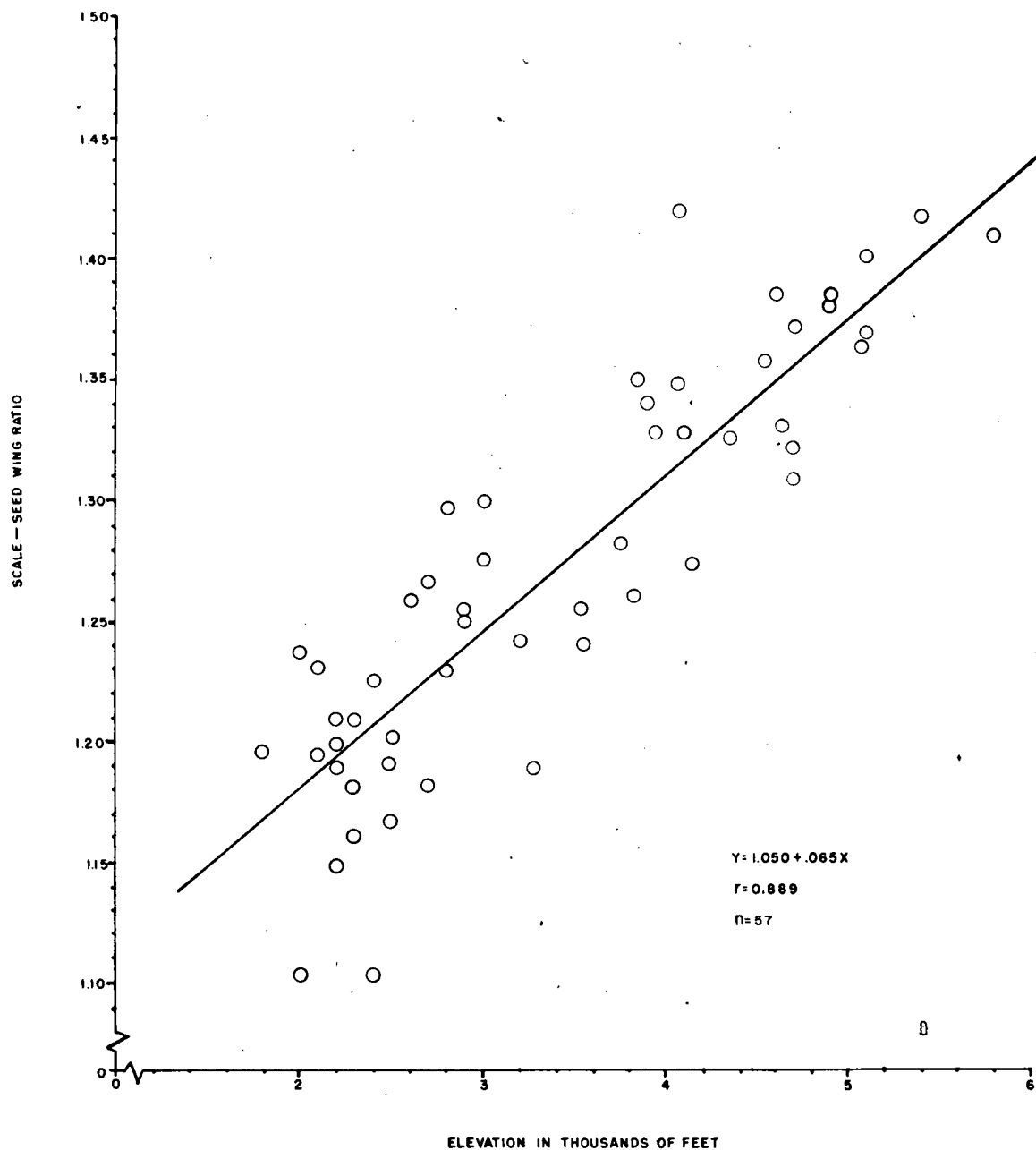


Fig. 28

Each point on the curve represents the mean of 100 cones.
1963 collection in the white-Engelmann spruce complex.

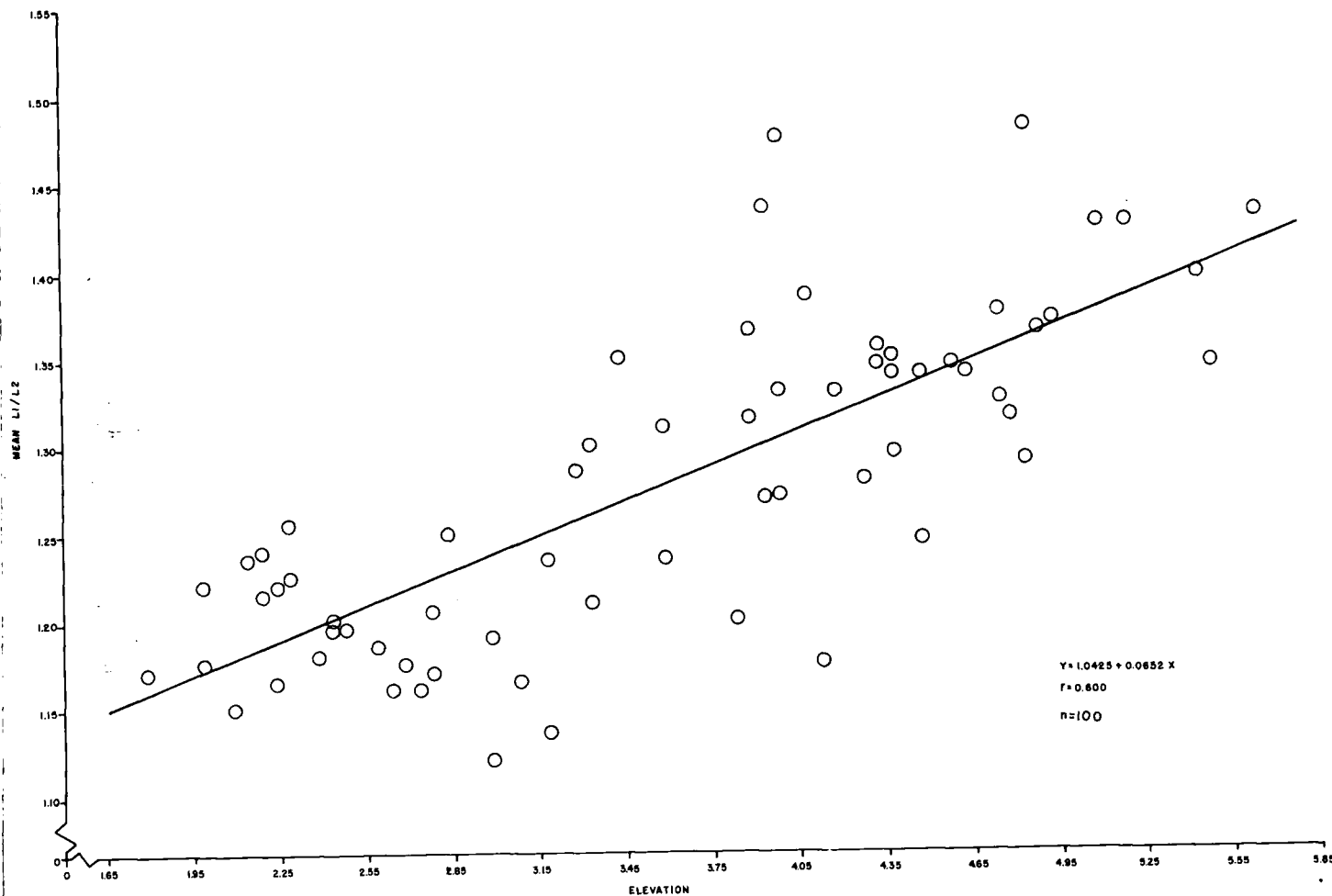


Fig. 29 Relationship between elevation and spruce cone scale - seed wing ratio. Each point on the curve represents the mean of 100 cones. 1964 collection in the white-Engelman spruce complex. L1/L2 - cone scale seed wing ratio.

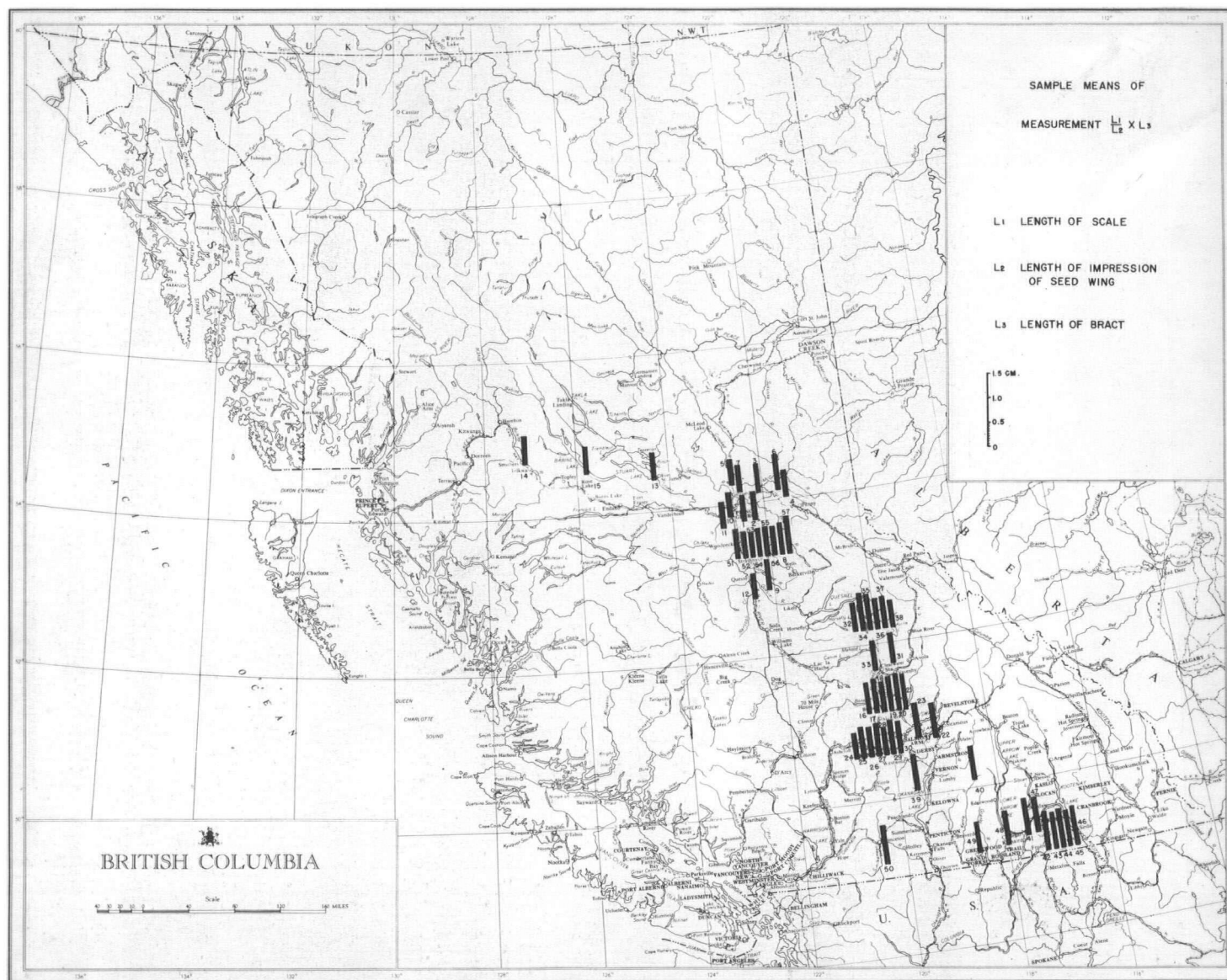


Fig. 30 Pattern of variation in a single measurement of cone scale morphology. Each bar represents the mean of 100 cones. 1963 collection.

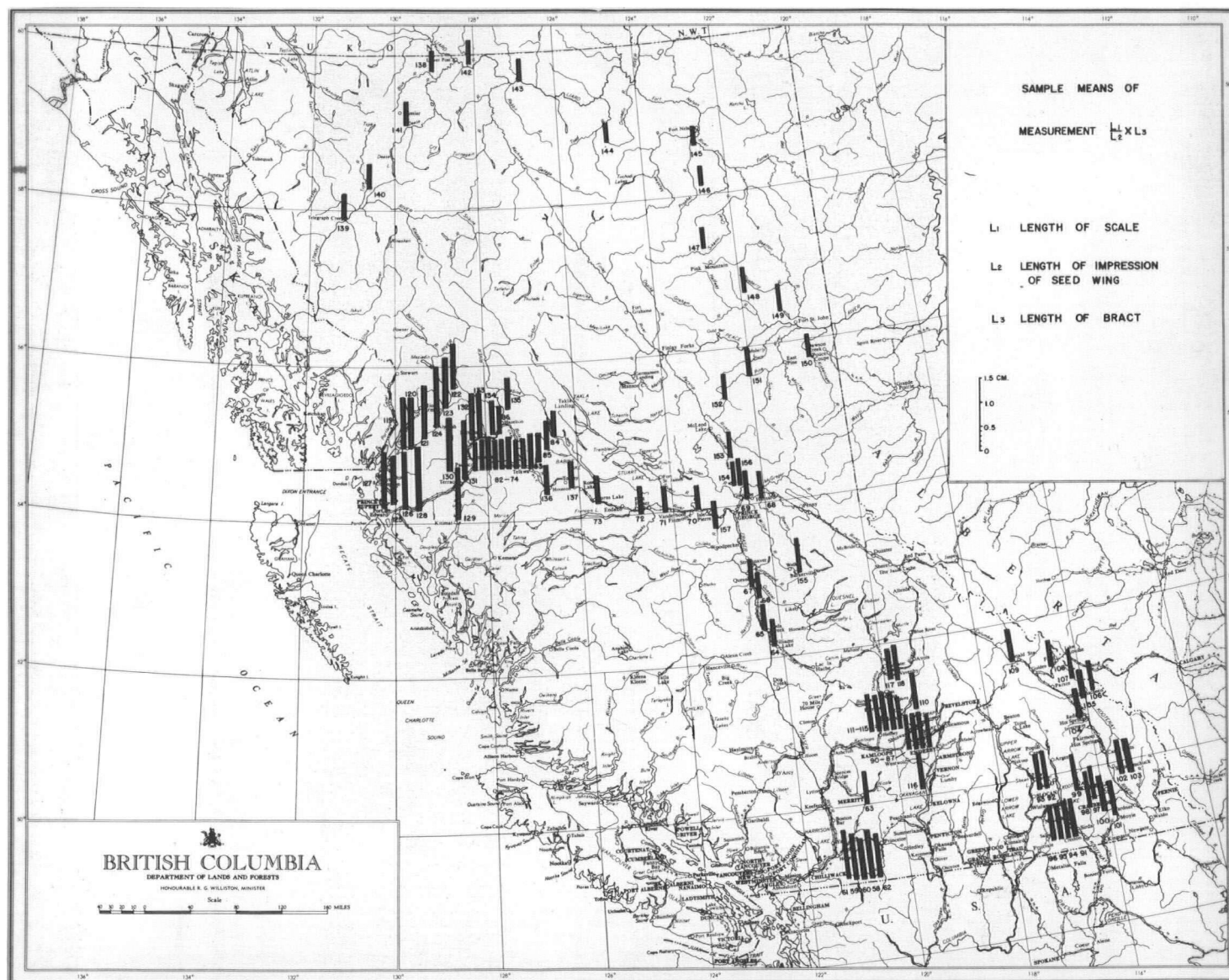


Fig. 31 Pattern of variation in a single measurement of spruce cone scale morphology. Each bar represents the mean of 100 cones. 1964 collection.

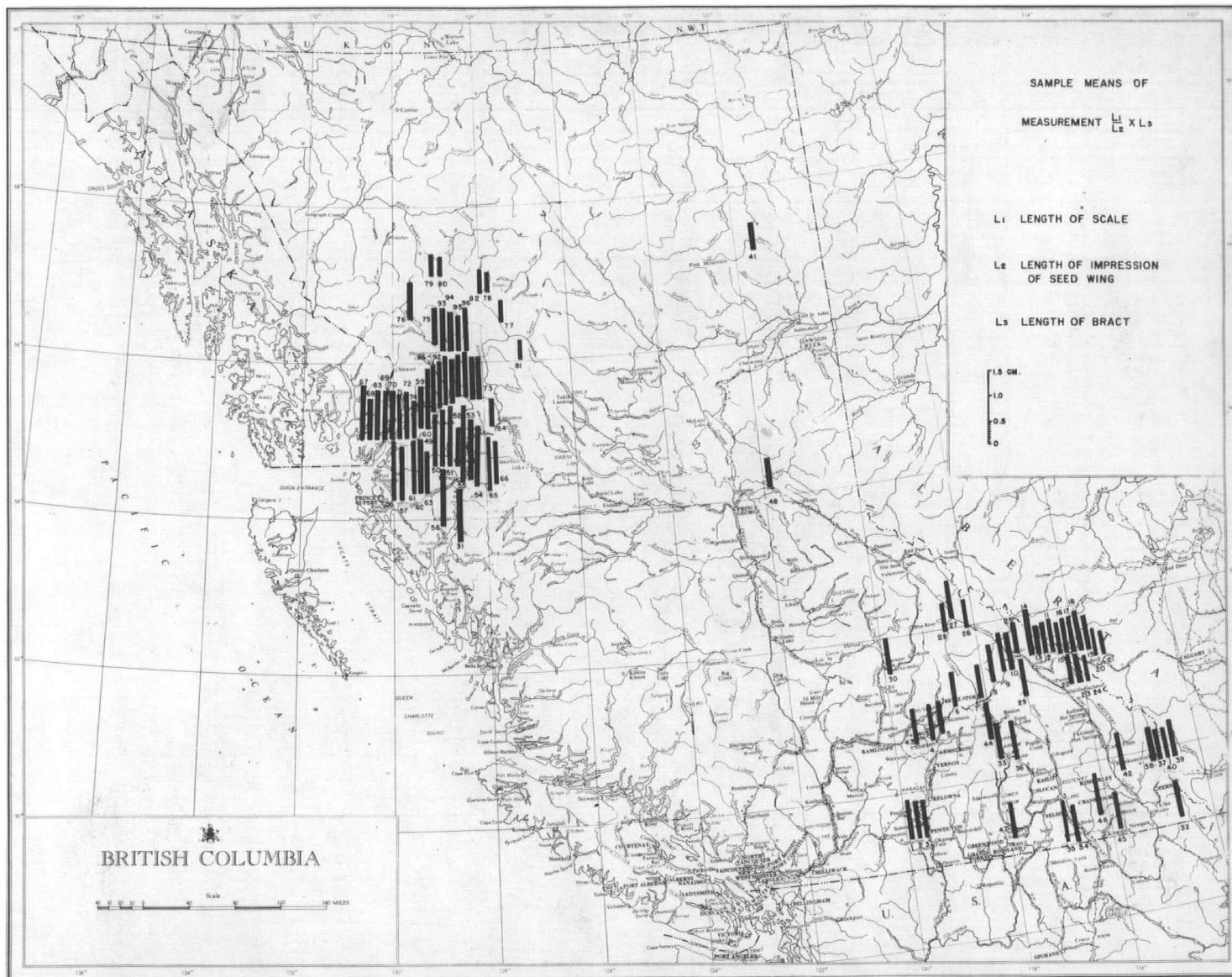
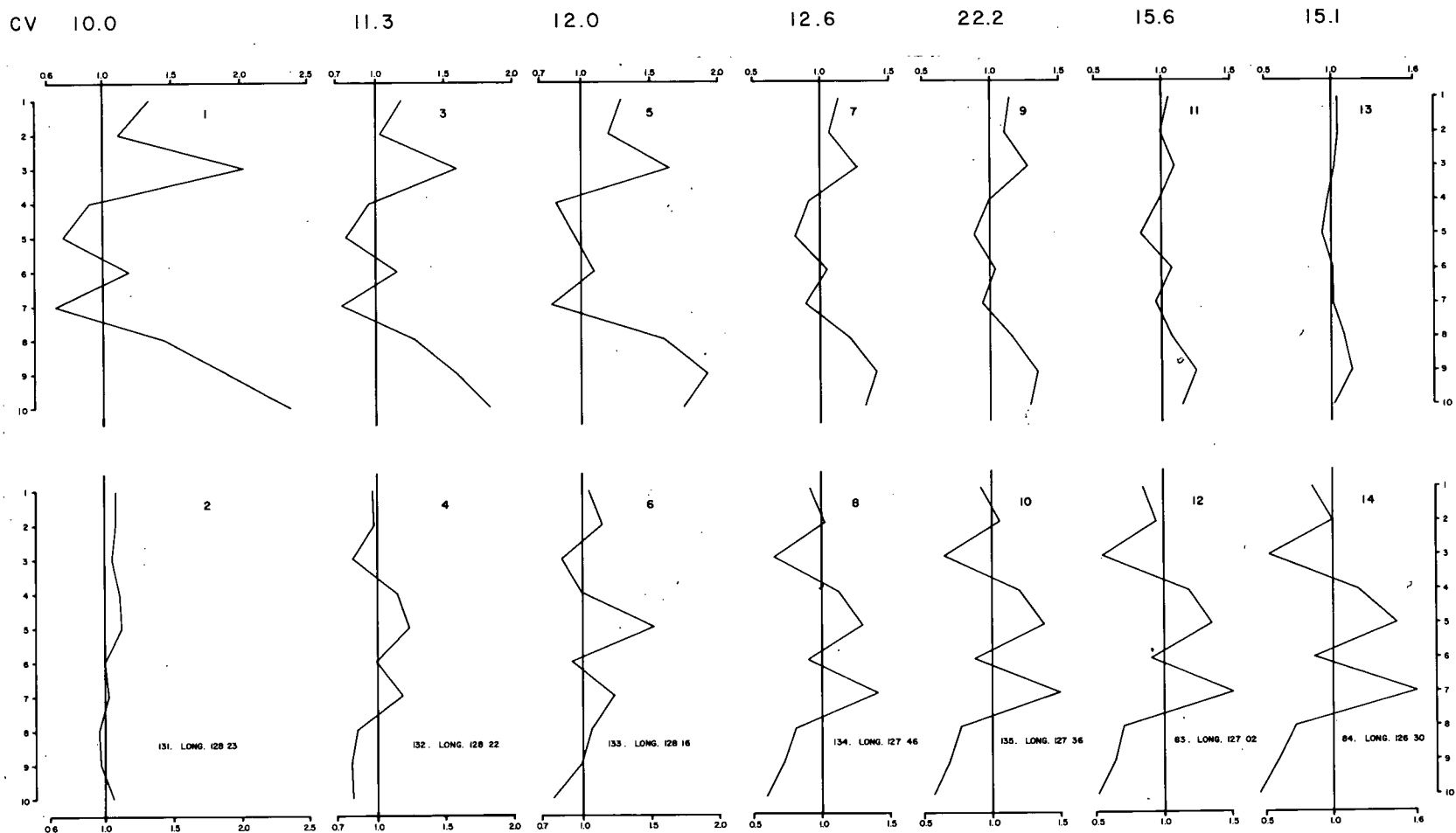


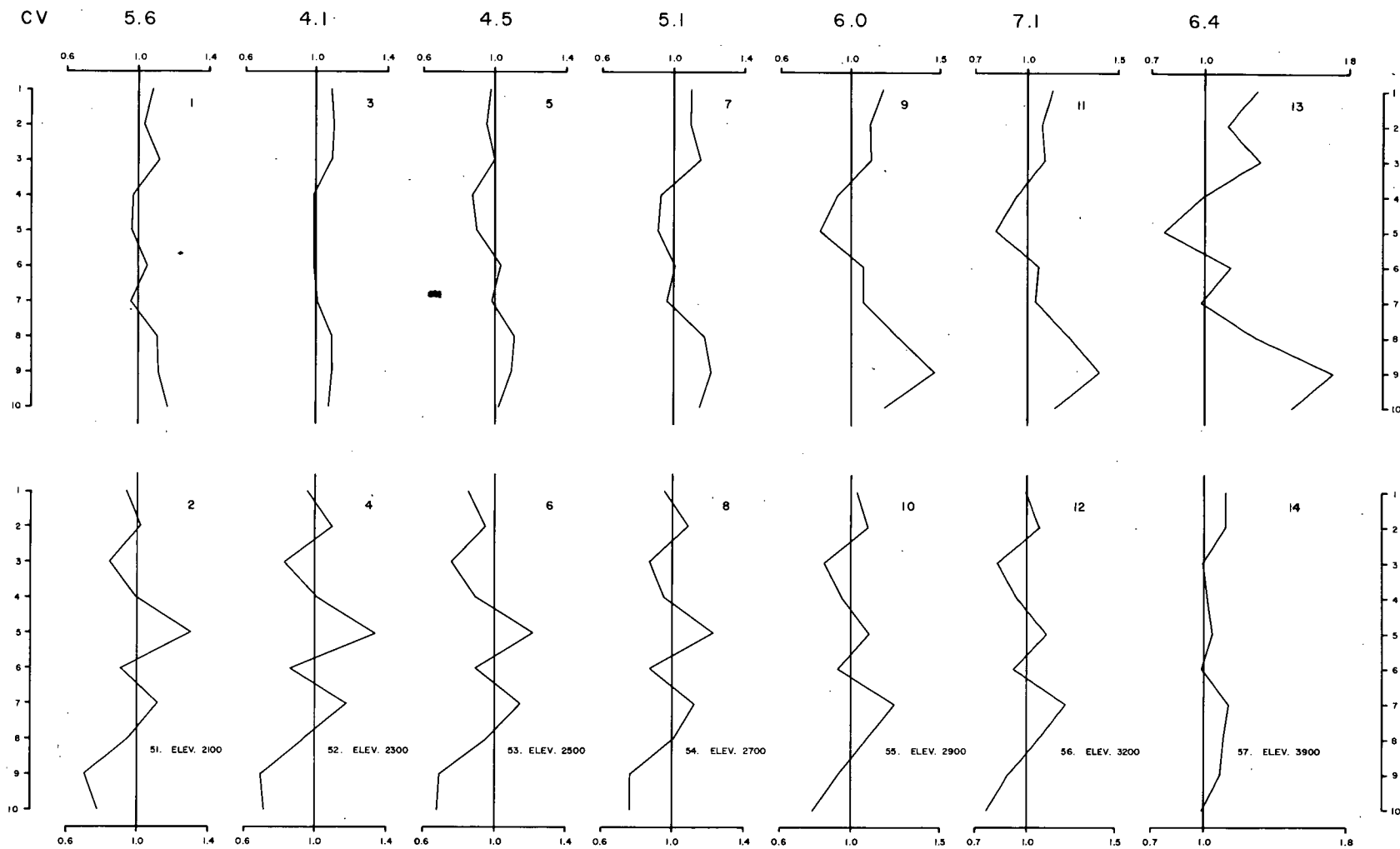
Fig. 32 Pattern of variation in a single measurement of cone scale morphology. Each bar represents the mean of a varying number of cones. Miscellaneous collections.

Fig. 33 The pattern of variation in spruce cone scale morphology along a longitudinal transect from coastal Sitka spruce forest to montane white spruce forest. Note the increase and decrease in CV (Coefficient of variation) as the transect crosses the sympatric zone.



The numbers 1 to 10 on the vertical bars at the extreme left and right represent the 10 cone scale measurements illustrated in fig. 1. In the top series of curves the mean for each longitude is plotted against pure white spruce; in the bottom series against pure Sitka. The figures on the horizontal bars represent the number of times each mean of the sample deviates positively or negatively from the corresponding measurement of pure white spruce (top series) and pure Sitka (bottom series). See page 41 for further explanation. CV refers to measurement 10, $11/12 \times 13$.

Fig. 34 The pattern of variation in spruce cone scale morphology along an altitudinal transect at Stone Creek, South of Prince George (lat. ca. 54°00').



In the top series of curves the mean for each altitude is plotted against pure white spruce, in the bottom series against pure Engelmann. The figures on the horizontal bars represent the number of times each mean of the sample deviates positively or negatively from the corresponding measurement for pure white spruce (top series) and pure Engelmann spruce (bottom series). Means are calculated from a 100-cone sample at each altitude (see page 41 for further explanation). CV refers to measurement 7, 11/12.

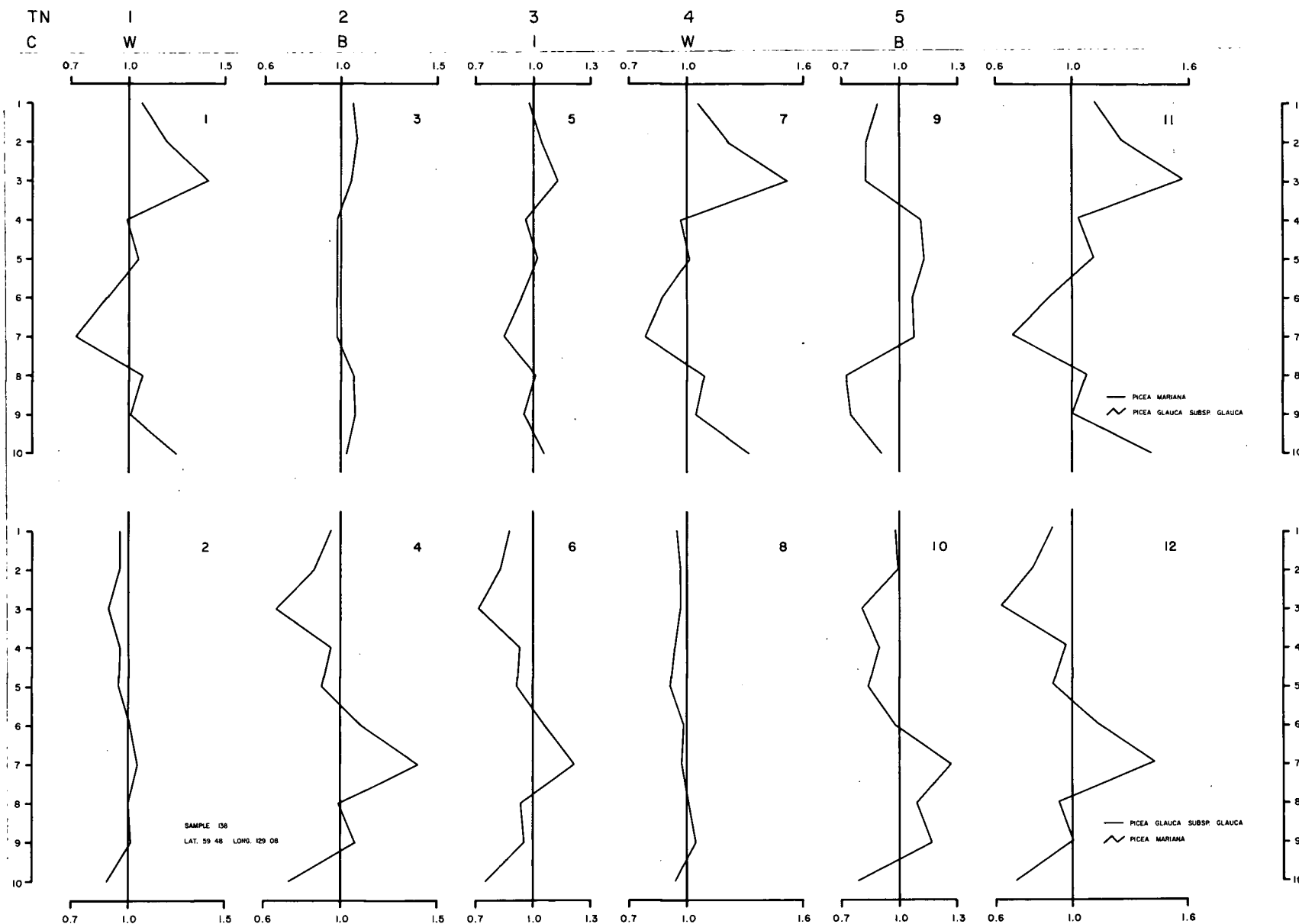


Fig. 35— Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

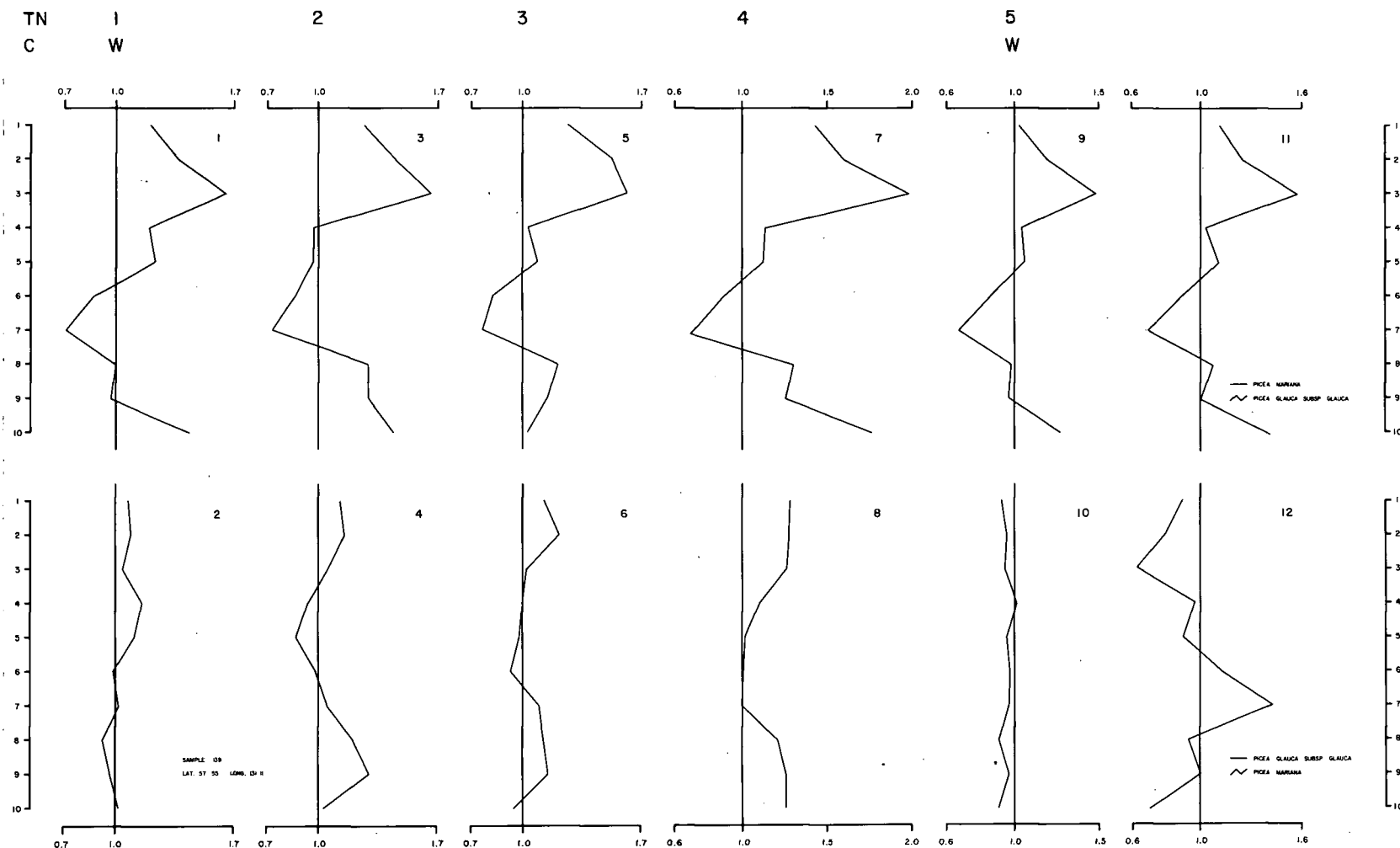


Fig. 36 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form. (it was not possible to classify trees 2-4).

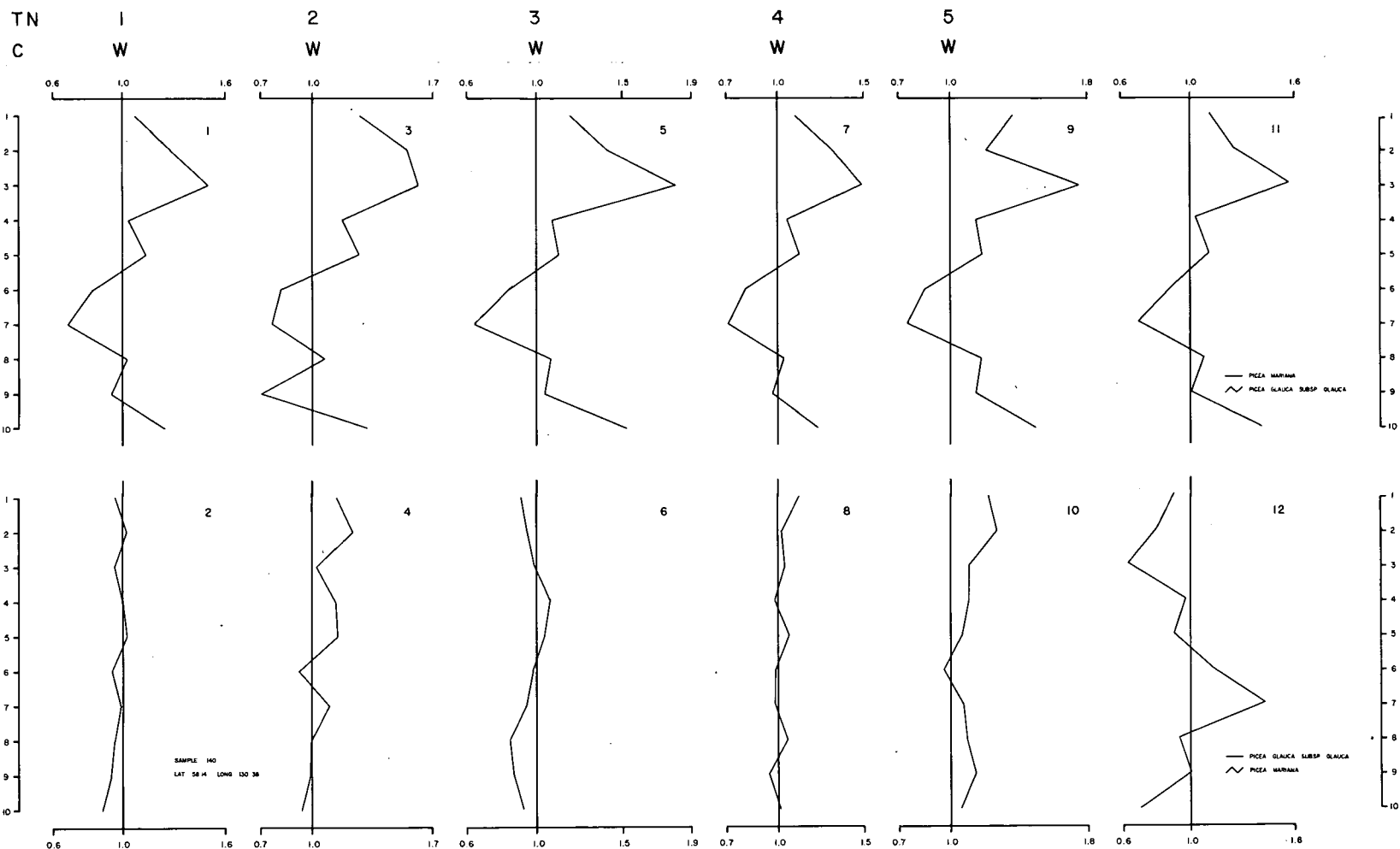


Fig. 37 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

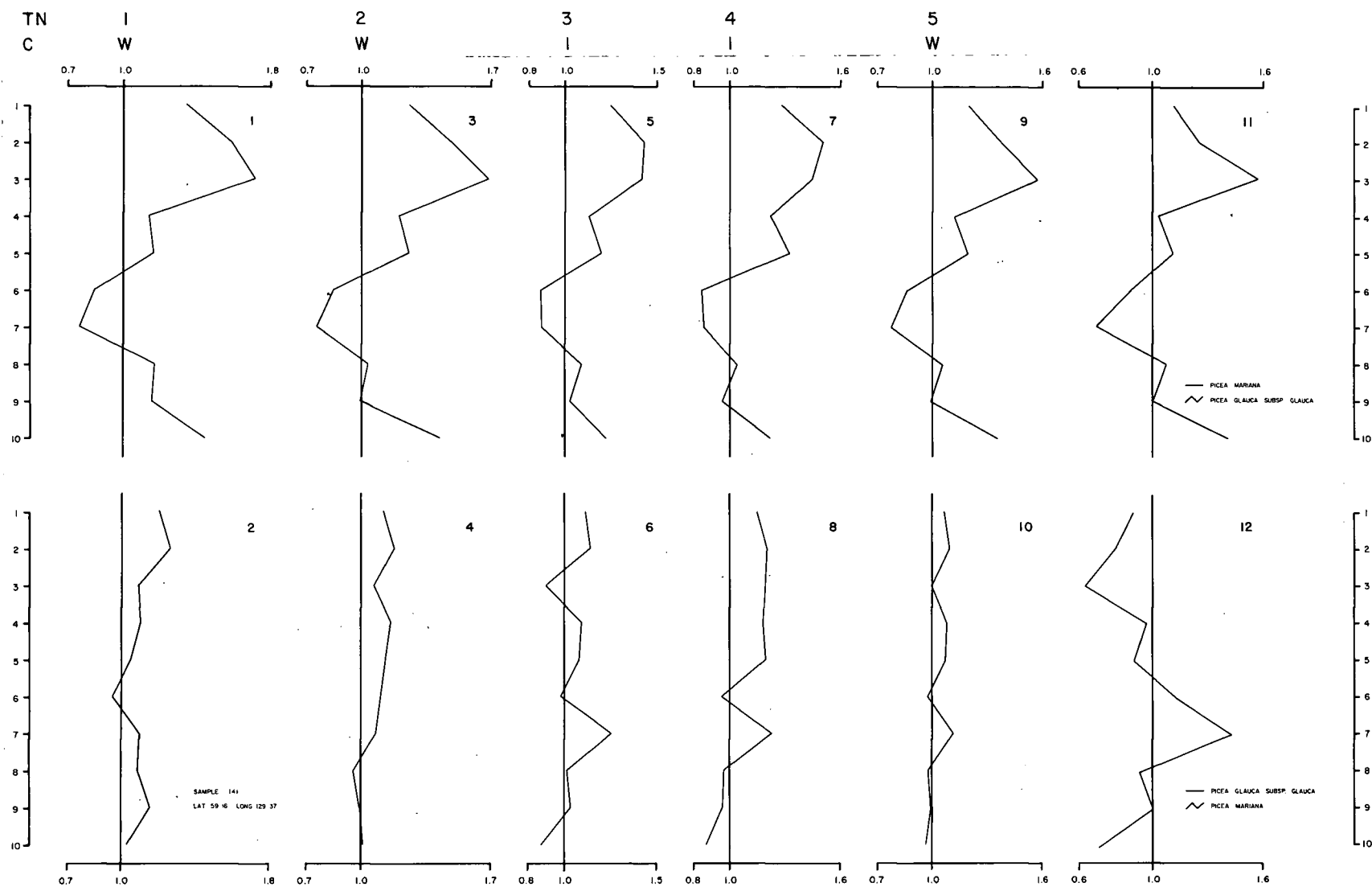


Fig. 38 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

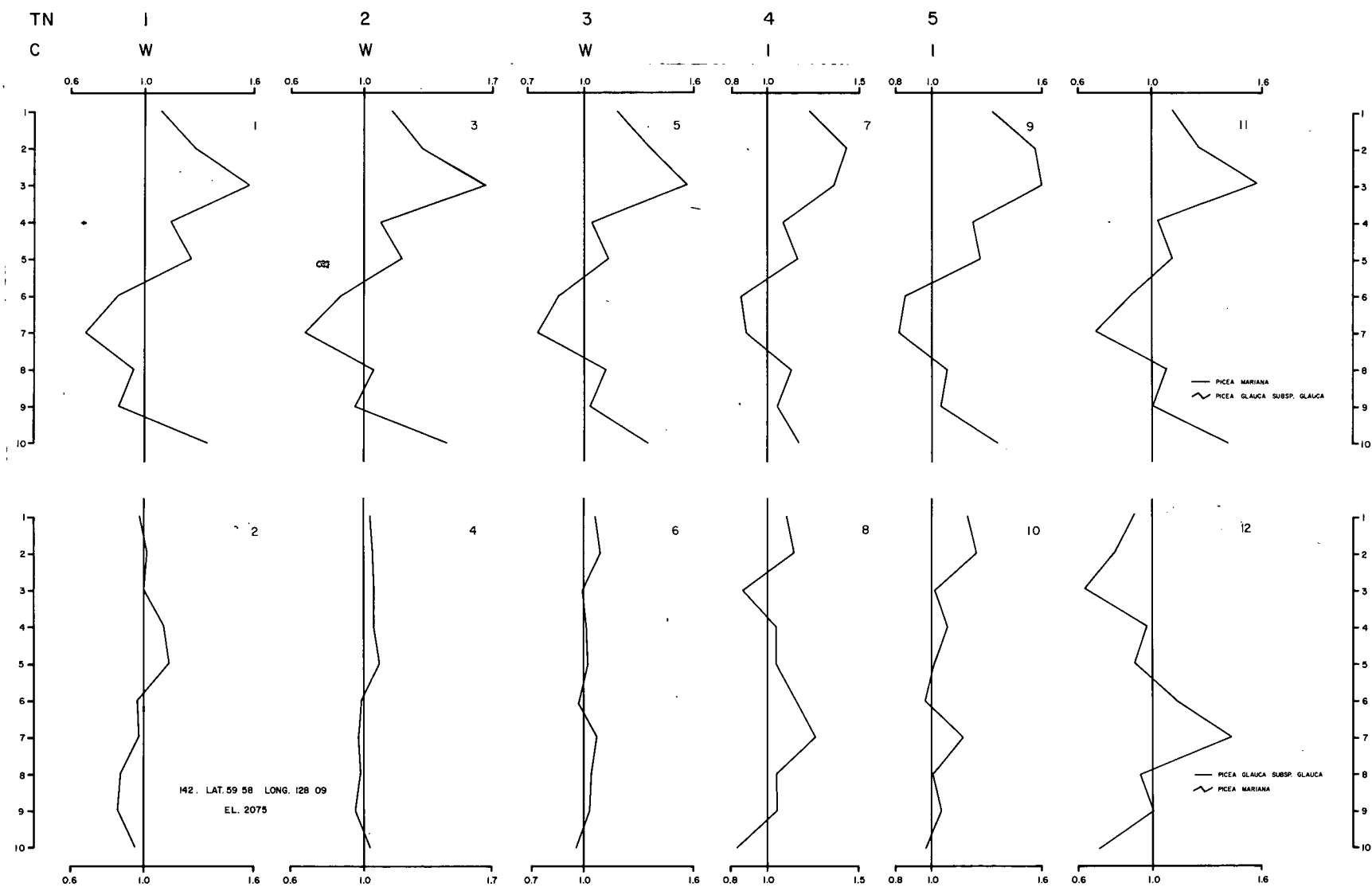


Fig. 39 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

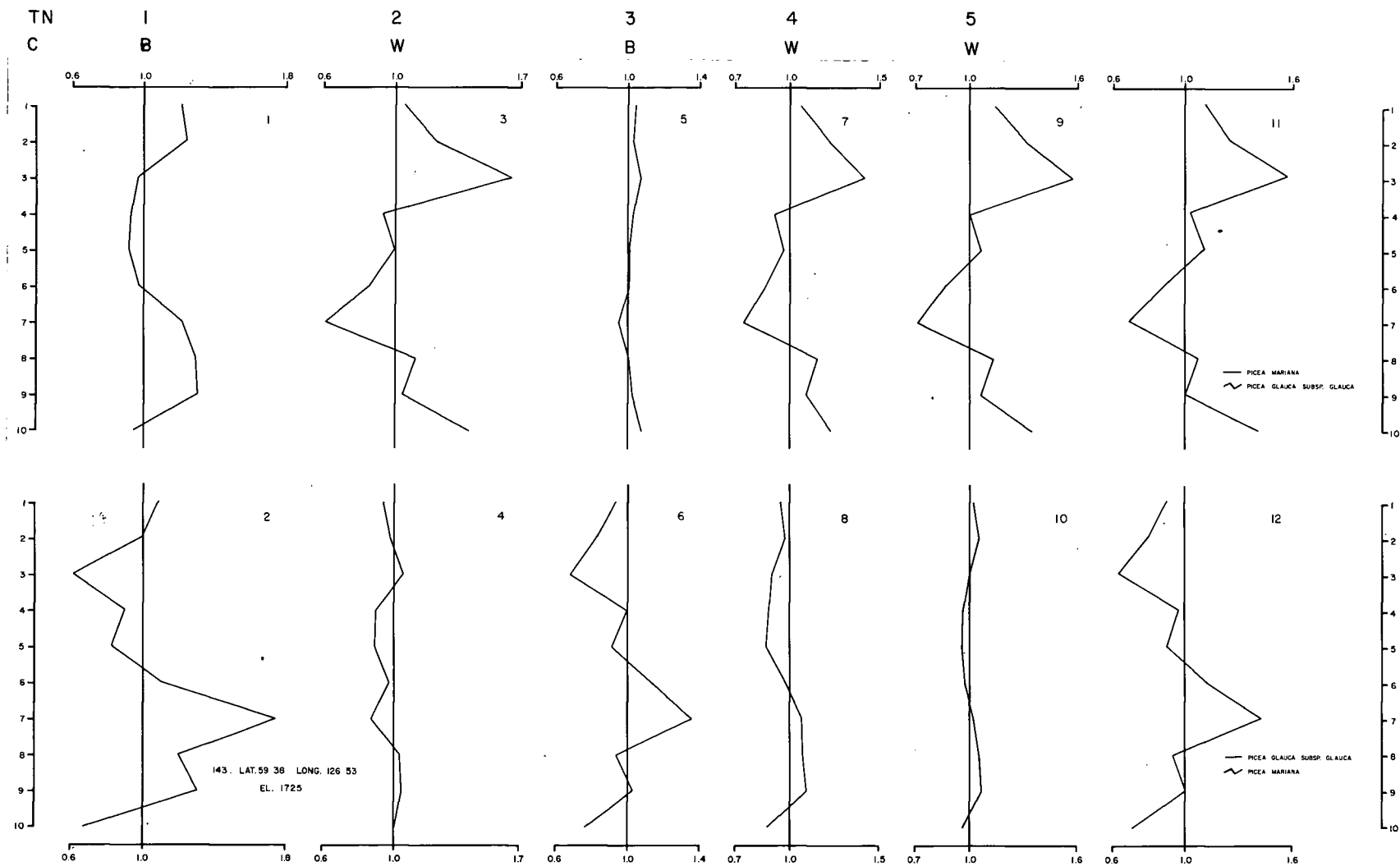


Fig. 40 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

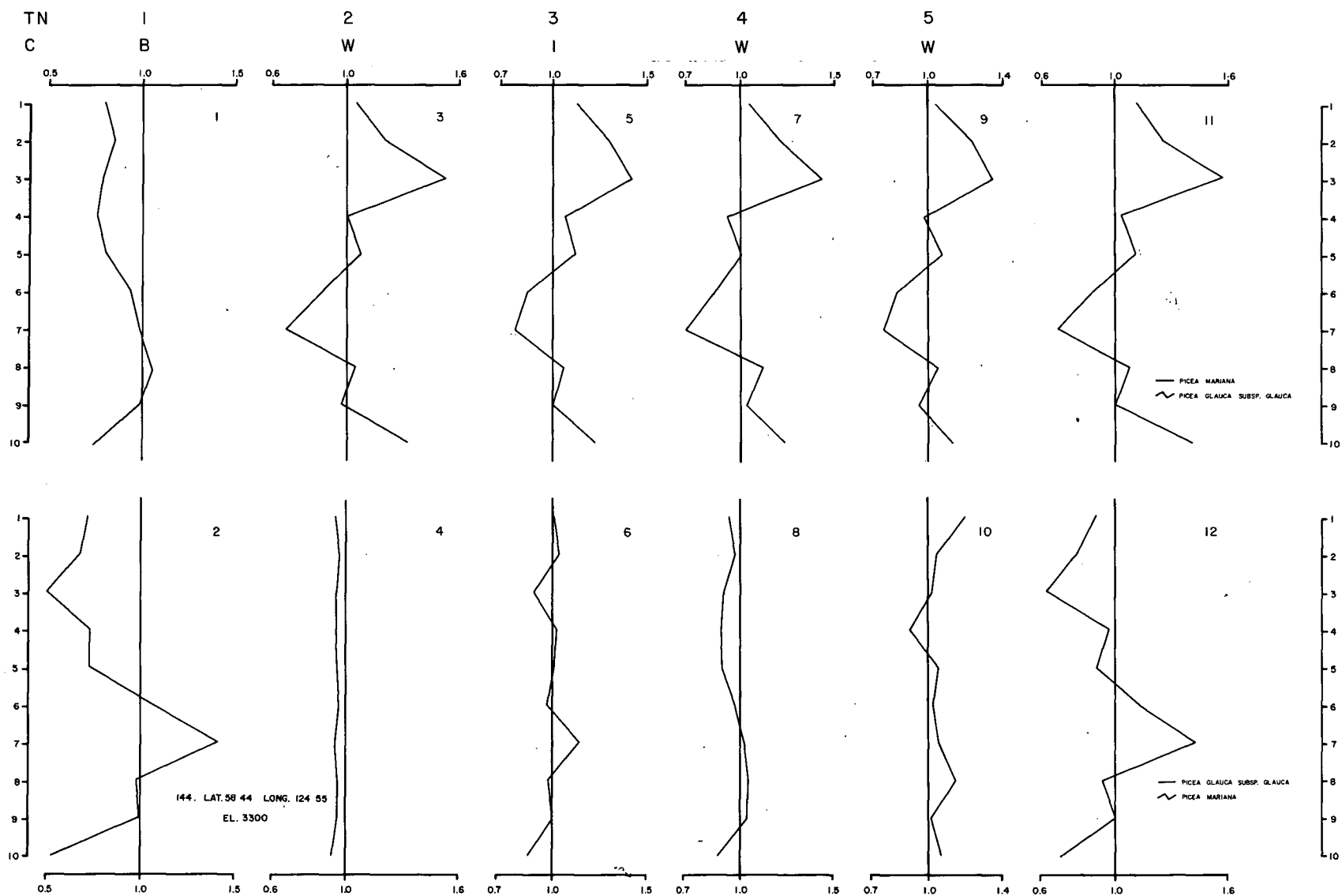


Fig. 41 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

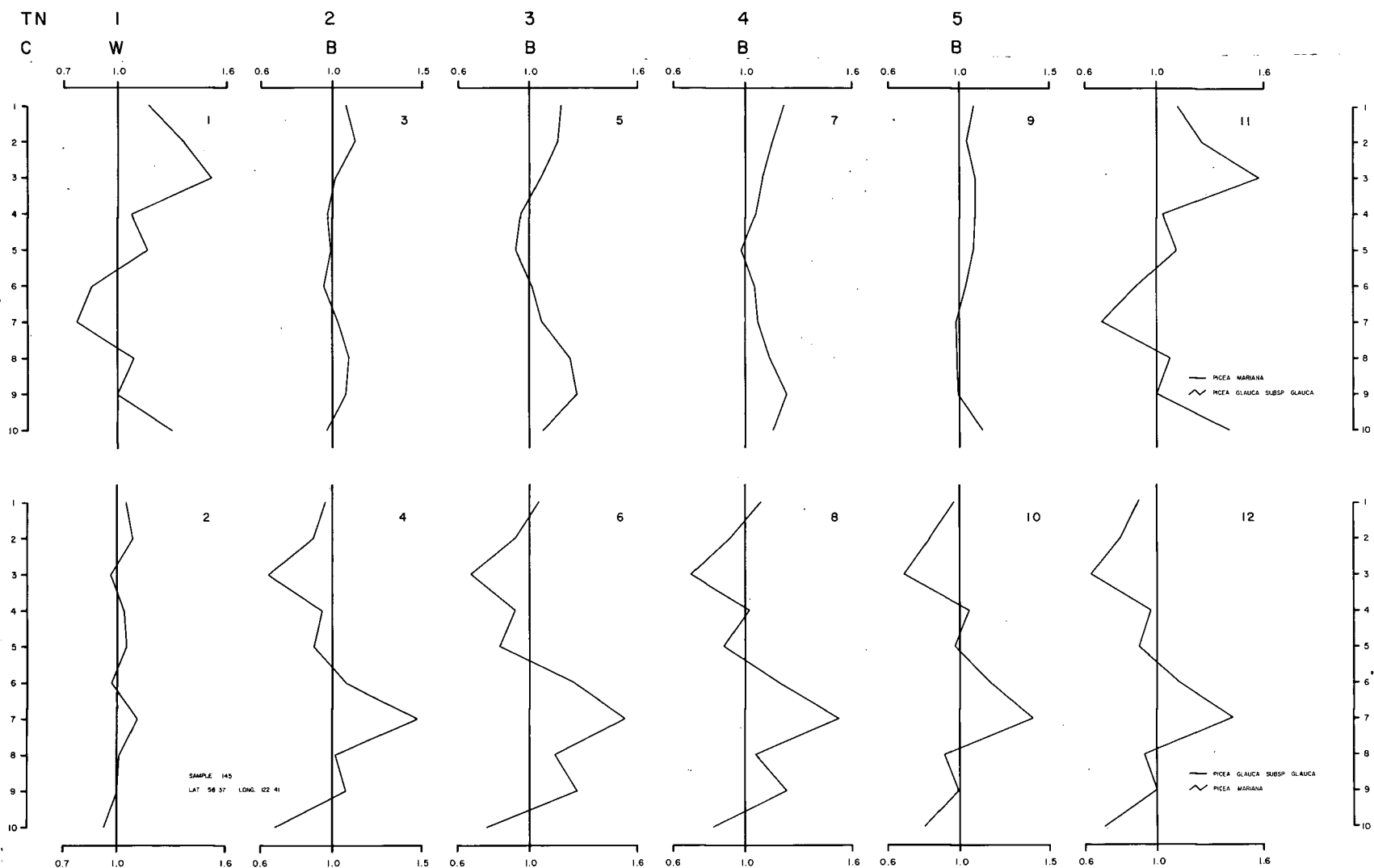


Fig. 42 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

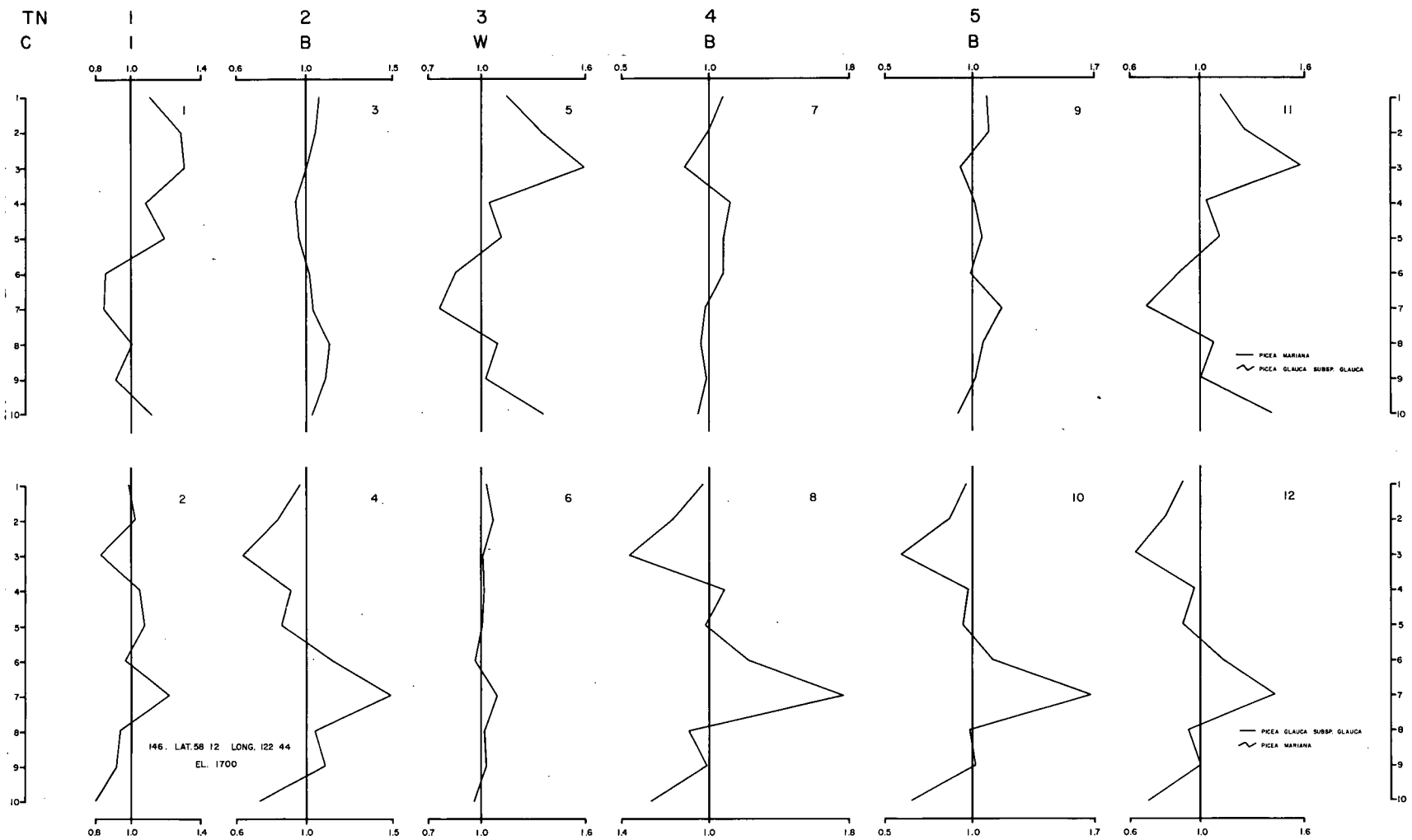


Fig. 43 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

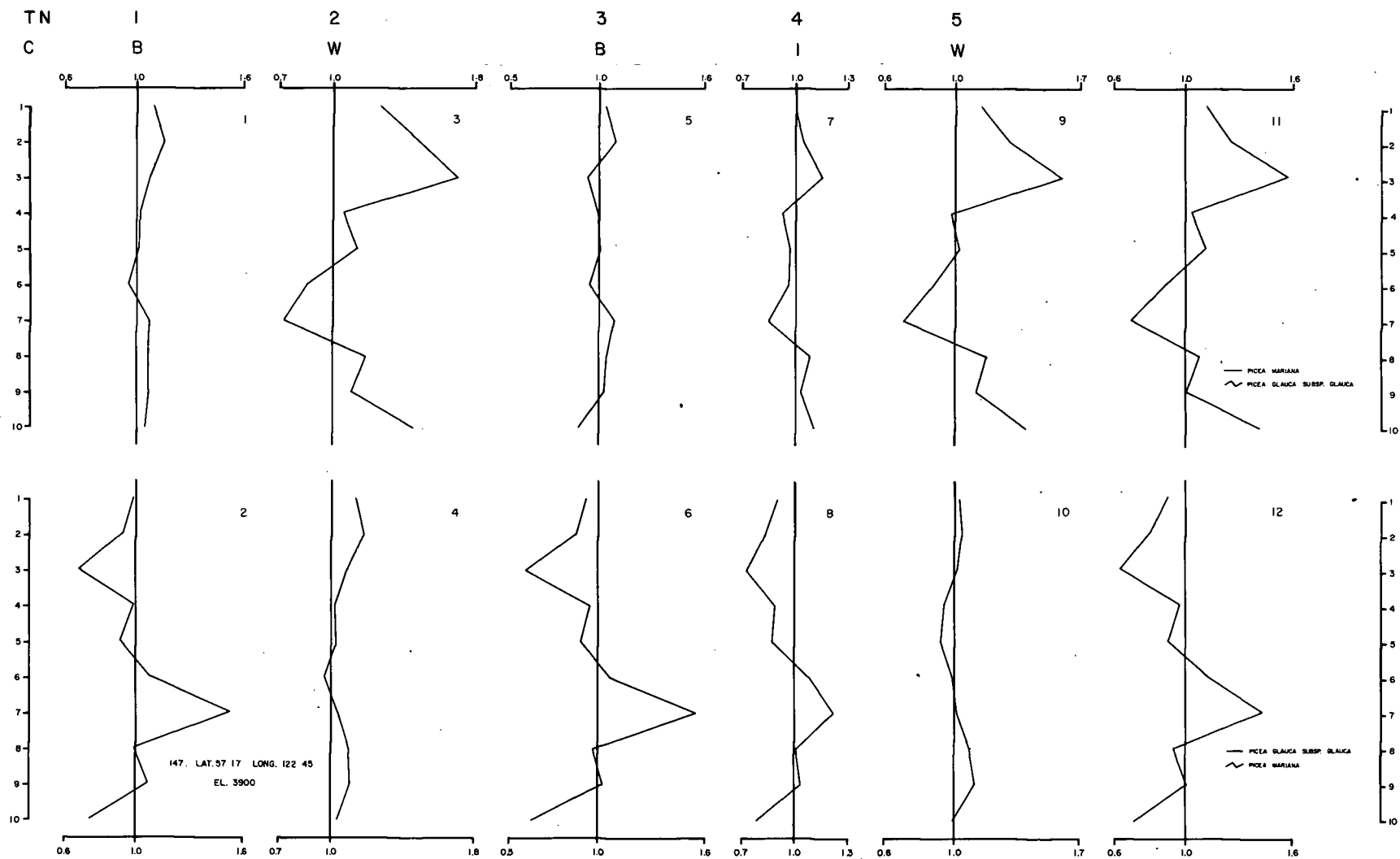


Fig. 44 Variation in cone scale morphology in a sympatric population of white and black spruce. 11 is the characteristic curve of pure white spruce on pure black. 12 is the characteristic curve of pure black on pure white. TN - tree number, C - classification, B - black spruce, W - white spruce, I - intermediate form.

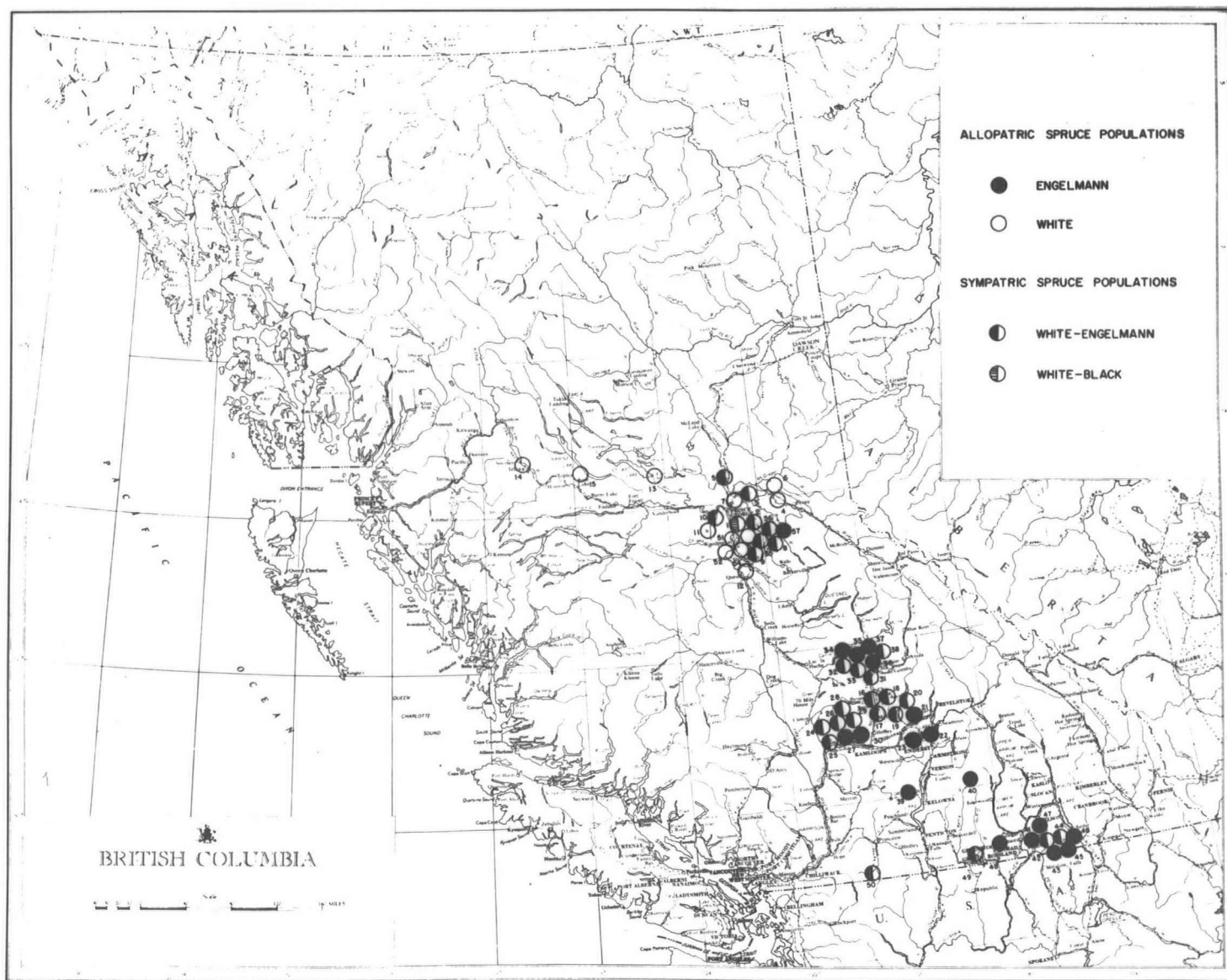


Fig. 45 Sympatric and allopatric spruce populations as indicated by discriminant function analysis of cone scale data. 1963 collection.

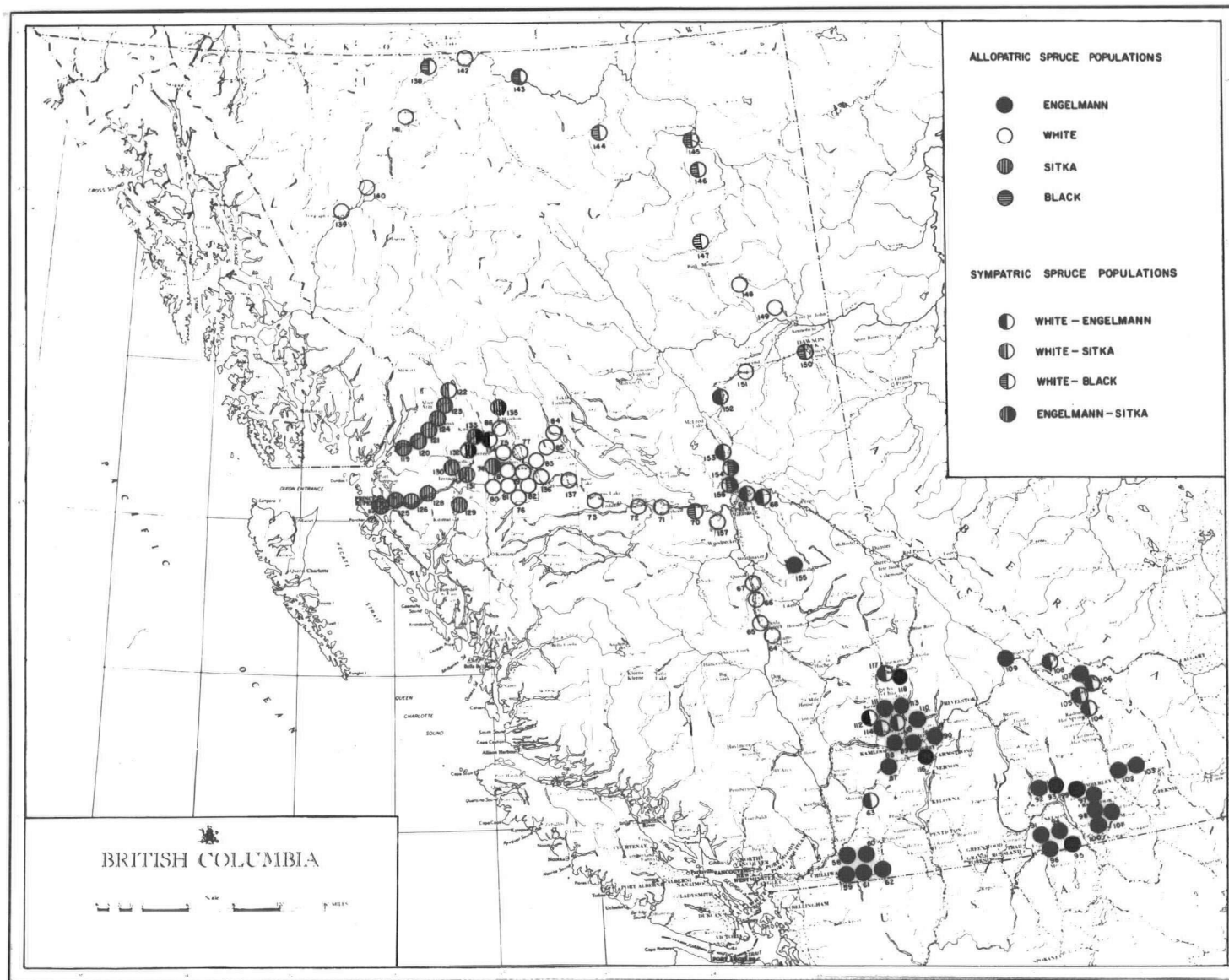


Fig. 46 Sympatric and allopatric spruce populations as indicated by discriminant function analysis of cone scale data. 1964 collection.