GENETIC VARIATIONS IN LENGTH OF ACTIVE GROWTH PERIOD AMONG RACES OF DOUGLAS-FIR, PSEUDOTSUGA MENZIESII (MIRB.) FRANCO

by

HELGE IRGENS-MOLLER

A THESIS

submitted to

OREGON STATE COLLEGE

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1958

APPROVED:

Redacted for Privacy

Associate Professor of Botany and Plant Pathology

In Charge of Major

Redacted for Privacy

Chairman of Department of Botany and Plant Pathology

Redacted for Privacy

Chairman of School Graduate Committee

Redacted for Privacy

Dean of Graduate School

Date thesis is presented February 28, 1958

Typed by Carol Anderson

ACKNOWLEDGEMENT

The assistence and advice received throughout this study from Dr. William Chilcote is sincerely appreciated. His enthusiasm and interest has been of considerable value. I wish to express my sincere thanks for the help received in field work as well as in the numerous discussions with him.

Special acknowledgement is also due to members of my graduate committee; to Dr. S. M. Dietz for encouragement during the initial phases of the studies; to Dr. Frank H. Smith for valuable advice on the presentation of the data; to Dr. J. R. Cowan for guidance during the initial phase of the study; to Dr. W. K. Ferrell, and to Dr. H. P. Hansen for helpful comments and suggestions.

Grateful acknowledgement is due to The Forest Genetics Research Foundation, Berkeley, California for the financial assistance in form of two grants to the Forest Research Division of the Agricultural Experiment Station, Oregon State College. Without this aid the present study would have been impossible. Grateful acknowledgement is also given to Dr. W. F. McCulloch and Dr. G. H. Barnes of the School of Forestry who have given generously of their time for helpful discussions.

The assistance and encouragement received from the Pacific Northwest Forest and Range Experiment Station has been particularly helpful. I would like especially to express my thanks to Forest Geneticist Roy R. Silen for all the help and time he has spent with me in the field. Special thanks are also due to Mr. C. A. Rindt of the Timber Management Office, United States Forest Service, Portland, who gave me an opportunity for extensive travelling in the Pacific Northwest during the summer of 1955. The opportunities for studies of the geographical variations in Douglas-fir provided by this travelling has been of great help for this study.

Special acknowledgement is also due to Research Forester Bent Gerdes of Manning Seed Company, Seattle, for the donation of bonded seed from localities throughout the Pacific Northwest.

TABLE OF CONTENTS

Page

INTRODUCTION.................................... 1

LITERATURE REVIEW................................ 5

Studies of intra-specific diversity in length of active growth period.............. 6

The effect of photoperiod upon the time of initiation of height growth................. 23

Effect of photoperiod on the time of cessation of height growth................. 27

The locus of photoperiodic perception......... 29

Effect of temperature upon the time of initiation and cessation of height growth... 32

The interaction between responses to photoperiod and temperature...................... 34

The origin of genetically founded intra-specific diversity in time of height growth initiation and cessation............. 36

GENETIC DIFFERENCES WITH REGARD TO TIME OF BREAK OF DORMANCY................................... 39

Conclusions.................................. 66

THE INFLUENCE OF PHOTOPERIOD AND TEMPERATURE UPON THE TIME OF BREAK OF DORMANCY.................. 68

Conclusions.................................. 82

THE INFLUENCE OF VARYING DEGREES OF WINTER CHILLING ON THE TIME OF BREAK OF DORMANCY........ 84

Conclusions.................................. 92

GENETIC DIFFERENCES WITH REGARD TO THE TIME OF ONSET OF DORMANCY............................. 93

Conclusions.................................. 103

Page

THE INFLUENCE OF PHOTOPERIOD UPON THE TIME OF ONSET OF DORMANCY.................................. 105

Conclusions.................................. 124

THE CORRELATION BETWEEN THE TIME OF ONSET OF DORMANCY AND RESISTENCE TO FROST................ 125

Conclusions.................................. 132

THE CORRELATION BETWEEN DRY MATTER CONTENT OF NEEDLES AND RELATIVE LENGTH OF ACTIVE GROWTH PERIOD.. 134

Conclusions.................................. 135

DISCUSSION... 139

BIBLIOGRAPHY....................................... 147

APPENDIX... 154

LIST OF FIGURES

Figure Page

1. East-west transect in western Oregon along which eight localities were selected for observations on time of bud burst........... 41

2. Daily maximum and minimum temperatures at five localities along the east-west transect (see Fig. 1). Spring 1955......... 43

3. Daily maximum and minimum temperatures to which Douglas-fir seedlings for seven localities along the east-west transect were exposed during spring 1955............. 47

4. Dates of bud burst in Douglas-fir seedlings from seven different localities along the east-west transect when grown at Corvallis. Spring 1955.................................. 49

5. Dates of bud burst in Douglas-fir seedlings from seven localities along the east-west transect when grown at Corvallis, Oregon. Spring 1957.................................. 53

6. Mean dates of bud burst during 1955 and 1957 in Douglas-fir seedlings from seven localities along the east-west transect when grown at Corvallis....................... 55

7. Dates of bud burst in 3-month old progenies from seven different Douglas-fir trees at Browder Creek, Santiam Pass, Oregon when grown in greenhouse, spring 1957............ 60

8. Dates of bud burst in 3-month old progenies from five Douglas-fir trees in McDonald Forest, north of Corvallis, Oregon; and from two trees near Eddyville, Oregon. Greenhouse, spring 1957..................... 62

9. Dates of bud burst in three month old progenies of seven Douglas-fir trees from Browder Crrk, Santiam Pass, Oregon compared with those of three-month old progenies of five trees in McDonald Forest, north of Corvallis, Oregon. Greenhouse, spring 1957. 65

Figure Page

10. Temperatures and day-lengths employed in photoperiodic experiment with Douglas-fir seedlings from seven localities along the east-west transect. Spring 1956............ 72

11. Dates of bud burst in Douglas-fir seedlings from seven localities along the east-west transect when treated with photoperiods of nine and nineteen hours in temperature controlled cabinets. Spring 1956........... 74

12. Temperatures and day-lengths to which Douglas-fir seedlings from seven localities along the east-west transect were exposed. Spring 1956.................................. 76

13. Dates of bud burst in Douglas-fir seedlings from seven localities along the east-west transect when treated with normal and long days. Spring 1956.......................... 78

14. Dates of bud burst in three-month old Douglas-fir seedlings from high and low elevations when grown in the greenhouse since germination and treated with nine and nineteen hour photoperiods. Spring 1957.................. 81

15. Mean dates of bud burst in three to seven year old Douglas-fir seedlings from seven localities along the east-west transect when treated with various photoperiods and temperatures. Spring 1956.................. 87

16. Localities in the Pacific Northwest from which seed was obtained............................ 89

17. Dates of bud burst in chilled and unchilled one-year old Douglas-fir seedlings. For winter 1957.................................. 91

18. Time of cessation of height growth in ten months old Douglas-fir seedlings from nine different localities in the Pacific Northwest when grown at Corvallis................ 97

19. Comparisons between ten-month old Douglas-fir seedlings of different origins sown February 1957. October 1957......................... 99

Figure Page

20. Percentages of dormant and actively growing five-month old Douglas-fir seedlings from twenty localities in the Pacific Northwest when grown in Corvallis.................... 102

21. Three month old Douglas-fir seedlings grown under long days and short days since germination April 15, 1956................ 106

22. Three month old Douglas-fir seedlings from Bear Springs, Mt. Hood National Forest, Oregon, treated with long and short days since germination........................... 107

23. Three month old Doughlas-fir seedlings from Bohemia, Umpqua National Forest, Oregon, treated with long and short days since germination.................................. 107

24. Three month old Douglas-fir seedlings from Ashford, Snoqualmie National Forest, Washington, treated with long and short days since germination...................... 110

25. Three month old Douglas-fir seedlings from Rogue River National Forest, Oregon, treated with long and short days since germination.................................. 110

26. Three month old Douglas-fir seedlings from North Santiam Pass, Oregon, treated with long and short days since germination...... 112

27. Three month old Douglas-fir seedlings from high elevation in Linn County, Oregon, treated with long and short days since germination.................................. 112

28. Three month old Douglas-fir seedlings from Zig Zag, Mt. Hood National Forest, Oregon, when treated with long and short days since germination.................................. 114

29. Three month old Douglas-fir seedlings from Ashford, Snoqualmie National Forest, Washington, when treated with long and short days.................................. 114

Figure Page

30. Responses of Douglas-fir seedlings from eight localities in the Pacific Northwest when exposed to different photoperiods since germination February 1957.................. 120

31. Temperatures employed in three tests of resistence to frost in Douglas-fir seedlings from eight localities in the Pacific Northwest sown in the greenhouse on April 1, 1956............................. 128

32. The effect of nine-hour and nineteen-hour photoperiods on the resistence to frost of Douglas-fir seedlings from eight localities in the Pacific Northwest sown in the greenhouse on April 1, 1956......... 130

LIST OF TABLES

Table Page

1. (a) Multiple range F-test of mean dates of bud burst in Douglas-fir seedlings from seven different localities in Oregon when grown at Corvallis, Oregon, spring 1955... 50

   (b) Multiple range F-test of mean dates of bud burst in Douglas-fir seedlings from seven different localities in Oregon when grown at Corvallis, Oregon, spring 1957......... 50

2. Temperature data (F^o) from United States Weather Bureau's station at Oregon State College, Corvallis.......................... 51

3. Average number of leaves on three-month old Douglas-fir seedlings of different origins when treated with four different photoperiods.................................... 116

4. Analysis of variance of number of leaves on three-month old Douglas-fir seedlings of different origins when treated with four different photoperiods...................... 117

5. Percentages of actively growing Douglas-fir seedlings of different origins when treated with four different photoperiods for three months after germination.................... 122

6. Percentages of dormant plants among seedlings from six localities in the Pacific Northwest when grown under continuous illumination in the greenhouse from germination April 1, 1956 to September 5, 1956. For location of seed sources see Fig. 1......... 123

7. Percentages of dry matter in needles of Douglas-fir trees at nine localities along the east-west transect........................ 136

8. Percentages of dry matter in needles of twelve Douglas-fir trees at nine localities planted at McDonald Forest, Corvallis................ 137

Table Page

9. Percentages of dry matter in needles of six to ten year old Douglas-fir seedlings from seven localities along the east-west transect when grown at Corvallis for three years.. 137

GENETIC VARIATIONS IN LENGTH OF ACTIVE GROWTH PERIOD AMONG RACES OF DOUGLAS-FIR, *PSEUDOTSUGA MENZIESII* (MIRB.) FRANCO

INTRODUCTION

Resistance of perennial plants to adverse climate conditions such as frost or drought is correlated with their annual cycles of dormancy and active growth (26). Drought and frost resistance are often highest during the period of dormancy (26). The adaptation of a particular species to a particular area therefore includes the cessation of height growth well in advance of the onset of climatic conditions which would injure actively growing plants. Similarly, such adaptation also includes the characteristic of remaining dormant even though the period of unfavorable conditions for growth may be interrupted by short intervals of conditions favorable for growth.

The annual period favorable for active growth (the growing season) varies greatly with latitude and altitude. In the Douglas-fir region of the Pacific Northwest the number of frost-free days varies from 260 at the southern Oregon coast to less than 90 days in the Oregon Cascades at 4000 feet elevation (59). This diversity in length of active growth period may have resulted in the differentiation of ecotypes adapted to the length of growing season at the various localities. Such adaptation may result from the selective pressures exerted by the last killing frost in the fall.

On this assumption the conclusion may be drawn that trees native to a particular habitat are better adapted to that habitat than are trees introduced from other areas. However, this conclusion does not necessarily imply that native trees also produce a higher yield than introduced trees. Lindquist (27) has shown that Norway spruce (Picea abies (L.) Karst.) from certain areas in Germany gives a higher yield in southern Sweden than do Norway spruce native to southern Sweden. Similarly, Scots pine (Pinus silvestris L.) introduced to Europe from Latvia and Estonia performs better than Scots pine native to Europe (48,7).

The characteristics of a tree (its phenotype) result from an interaction between its genetic constitution (its genotype) and the environmental conditions under which it is and has been growing. The use of non-local seed may involve the introduction of seed into a type of environment different from that of the area in which it was collected. Consequently, changes in phenotypic expression may result. The degree to which the phenotypic expression of a particular genotype can be modified by changes in environment may be termed its range of reaction (51). All such modifications affect, in one way or other, the value of the ultimate crop.

A knowledge of the genetic differences with regard to length of active growth period appears important in the selection of a suitable seed source for re-forestation of any particular area. However, a knowledge of the degree to which the length of active growth period may be modified by certain environmental factors appears equally important.

The purpose of the present study was to obtain information on genetic differences in length of active growth period among Douglas-firs of different origins. Information was also sought as to the degree to which the length of active growth period may be modified by changes in photoperiod and temperature. The study was concerned primarily with the following:

(1) Genetic differences with regard to time of break of dormancy.

(2) The influence of photoperiod upon the time of break of dormancy.

(3) The influence of various degrees of winter chilling on the time of break of dormancy.

(4) Genetic differences with regard to the time of onset of dormancy.

(5) The influence of photoperiod upon the time of onset of dormancy.

(6) The correlation between the time of onset of dormancy and resistance to frost.

(7) The correlation between dry matter content of

needles and length of active growth period.

LITERATURE REVIEW

Intraspecific diversity in forest tree species has in the past largely been ascribed to environmental modifications. This is partly due to the fact that local seed usually was used in re-forestation programs. However, during the middle of the 18th century extensive re-forestation programs were initiated in Europe in which the seed often was collected considerable distances from the area in which it was used (2). This led to the observation that the success of the re-forestation often depended on the seed source. Thus, in 1755 D. G. Schreber observed that seed of larch from Tyrol, when used near Halle, Germany, gave rise to trees inferior to those from seed collected in certain other areas (48).

In 1760 Duhamel du Monceau pointed out (48) that the diversity in Scots pine (Pinus silvestris L.) could not be explained merely as environmental modifications. He based this on the observation that Scots pine from Latvia grew better than Scots pine from any other area when planted in southern France. Monceau was one of the first to realize that part of the diversity in Scots pine is of an hereditary nature.

During the middle of the 19th century Vilmorin in France started the first intensive study of the nature of this variation in Scots pine (48). He obtained seed from widely scattered areas in Europe and Russia from which he established plantations near Les Barres, France. In 1862 he reported (Exposé historique et descriptif de l'ecole forestiére des Barres. Memoires d'Agriculture. Paris 1862. Cited by 48) that striking differences were observed among the various sources with regard to growth rate and general appearance. His publication gave rise to numerous similar experiments and heated discussions as to the possible cause of the observed differences (48). Moraques in 1873 pointed out that they were due to hereditary differences: "Jamais je n'ai un des graines provenant de Geneve y produire un Pin de Riga, ni un Pin de Riga y produire un Pin de Geneve." (Cited by 48). This led many investigators to conclude that what Linnaeus had described as one species, Pinus silvestris, in reality was several closely related species or varieties. In the following years numerous taxonomic papers on Scots pine appeared (48).

Vilmorin's studies in Scots pine mark the beginning of a pericd of intensive studies of variability in forest tree species.

Studies of intra-specific diversity in length of active growth period.

With the increasing efforts toward re-forestation in Europe, convincing evidence accumulated as to the existence of hereditary variability within forest tree species, particularly with reference to the relative time of initiation and cessation of height growth.

In 1898 Örtenblad in Sweden observed that Scots pine from northern Sweden, planted near Stockholm, stopped height growth in August, whereas plants from southern Sweden planted adjacent to the former did not stop growth until fall frosts killed the terminal shoots. Örtenblad explained these differences as hereditary adaptations to the length of growing seasons in northern and southern Sweden (cited by 2).

These and similar findings elsewhere led to investigations to determine the magnitude and nature of such differences. One of the pioneers in this field was Cieslar in Austria. The purpose of his investigations was, in Cieslar's own words (4): "Es liegt in der Natur der Organismen dass sie sich den sie beinflussenden klimatischen Verhältnissen anpassen.........Uns interessiert heute vornehmlich die Frage, ob nicht eine physiologische Umstimmung unter dem Einflusse Jahrtausende langen Vegetierens auf einem und demselben Flecke eingetreten ist, welche die Tieflandsfichte von jener des Hochgebirges oder des Nordens unterscheidet." Like earlier investigators Cieslar believed in the inheritance of acquired characters, as is evident from the above quotation.

Cieslar found that Norway spruce from high altitudes or latitudes ceased height growth earlier than plants from low altitudes or latitudes when planted side by side in the lowland near Vienna. As a consequence of this the plants from high altitudes or latitudes attained smaller heights than those from low altitudes or latitudes.

Cieslar reported in two later publications (1899 and 1907, cited by 2) on the further development of the plants described in his first paper and on later established plantations at different elevations. At high elevations (1380 meters above sea level) the differences in height growth between plants from low and plants from high elevations were considerably less than in plantations at low elevations.

Cieslar's findings started some of the most heated discussions in European forestry literature. Particularly Mayr in Germany (30) criticized sharply Cieslar's conclusion that the different growth rates of high- and low-elevation plants were due to hereditary differences. The fact that the height differences almost disappeared at high elevations proved to Mayr that they were due only to environmental influences. He stated, that if the higher growth rate of the low-elevation plants was hereditary then it should also be maintained at high elevations. In other words, Mayr believed that only characteristics which were not modified by environmental changes could be termed hereditary. Mayr's paper appeared in 1908, a few years before Johannsen (51) coined the terms genotype and phenotype to describe the interaction between hereditary factors and the environment.

In Switzerland Engler (8) started similar experiments in 1898 and 1903. He obtained seed of Scots pine from 55 different localities from northern Scandinavia to southern France and from Scotland to the Ural mountains in eastern Russia. Plantations were established from this seed at eleven different localities in Switzerland at elevations ranging from 370 to 1980 meters above sea level. His findings were in agreement with those of Cieslar: "....die von Süd nach Nord und von den Tieflagen Mitteleuropas bis zur oberen Waldgrenze der Alpen auftretenden Formen dieser Holzart stellen zwei einander sehr ähnliche, kontinuerliche Reihen dar, deren Anfangs- und Endglieder durch eine grosse Zahl von Zwischengliedern verbunden sind." (8).

Of particular interest are Engler's observations on the relative time of height growth initiation and cessation in plants from different sources (9). In the plantations at low elevations (e.g., Adlisberg, 670 m) growth initiation occurred almost simultaneously in all sources. However, in the plantations at high elevations the trees from northern Scandinavia and those from high elevations in the Alps started growth considerably earlier than those from low elevations. Thus, in a plantation at 1800 meters elevation, plants from Belgium started growth around June 10, whereas those from Engadiner, Switzerland (1800 m.) almost had stopped growth at that time. This indicates, according to Engler, that the optimum temperature for height growth is lower for the plants from high elevations or northern latitudes than it is for plants from low elevations. Karschon (16, 17) has recently confirmed these findings.

Cessation of height growth, on the other hand, did not appear to be influenced by temperature conditions. Engler found (9) that the plants in the Adlisberg plantation (670 m.) could be grouped into three classes with regard to time of height growth cessation. Scandinavian and East-Russian plants stopped growth August 12-22. Plants from medium and high elevations in the Alps and southern French mountains stopped growth August 31 to September 20, and plants from the Swiss and German lowlands stopped growth September 27 to October 23. Similar differences were also found in the plantations at high elevations. The late growth of the plants from low elevations rendered them very susceptible to the early fall frosts at high elevations. The frost-killing of the immature terminal shoots was one of the reasons for the poor growth of low-elevation plants at high elevations.

In a study of the rate of shoot elongation in one of the lowland plantations Engler found (9) that the rate increased with increasing temperatures. However, this was more pronounced in plants native to the lowland than in plants from high elevations, since in the latter the period of shoot elongation had almost terminated when high temperatures occurred during July and August. Engler suggested that low-elevation plants require a higher temperature for shoot elongation than do high-elevation plants, and that the cold nights at high elevations may be another factor responsible for the poor growth of low-elevation plants at high elevations.

The hereditary nature of these differences in length of active growth period was well illustrated by Engler in a study of Norway spruce (9). He collected seed of lowland spruce which had been planted at high elevation (1750 m.) 30-40 years earlier. The trees in this plantation were, as would be expected, of rather slow growth and poor form. He also collected seed from native spruce in the vicinity at the same elevation. Both seed collections were sown in the lowland. The plants derived from the trees in the plantation developed into typical fast- and late-growing lowland spruces whereas the plants from the native trees developed into plants which stopped growth early in the season. Engler used these findings to emphasize that although the lowland spruces became strongly modified if planted at high elevations this should not, as Mayr suggested (30), be interpreted as being due to the lack of any hereditary differences between the two forms since: "....die in Hochgebirge verbrachten Tieflandsfichten im Alter von 30-40 Janren von schlechter Wuchsform sind und im Wachstum hinter den spontanen Hochgebirgsfichten zurückbleiben, so ist damit beweisen, dass gut ausgeprägte physiologische Fichtenrassen ihre Eigenschaften nicht so rasch verlieren."

In 1907 Schott (49) found great differences in time of initiation of height growth among Scots pine from various areas when grown at Knippelsheim, western Germany. The plants from Finland were the earliest, then followed the plants from Germany and Belgium. The latest were those from western Hungary and southern France which started growth at a time when all other sources had developed new shoots of one to three centimeters in length. Like Cieslar and Engler he found that the early cessation of height growth in plants from northern, continental, or high-elevation areas resulted in smaller plants than those from southern and maritime areas. At four years of age plants from the following sources had attained hieghts of:

Belgium	57.27 cm
Pfalz, Germany	56.66 cm
Western Hungary	36.78 cm
Southern French mountains	28.95 cm

Finland	14.80 cm

These findings were of particular importance in Sweden because of this country's great latitudinal extension (from 54°40' to 70°n. lat.). Re-forestation programs in northern Sweden during the period 1890-1900 proved to be complete failures with practically a 100% mortality during the first 5-10 years after planting or seeding (50). The reason, which became evident after Cieslar and Engler's work, was that the seed used came from southern Sweden or even Germany. Use of local seed was considered impractical and too costly because of the small and irregular seed crops at northern latitudes.

Schotte (50) in 1909 started collections of Scots pine seed from 24 localities throughout Sweden. From this he established plantations at seven different localities in central and northern Sweden. He found that the further north the plantations were established the greater became the differences between plants from the various sources with regard to survival. Thus, at a ten-year old plantation in Lappland at 67°n. lat. plants from Smaaland (57-58°n. lat.) suffered a mortality of 86 percent as opposed to 41 percent for plants from Lappland. The heavy mortality of the plants from southern Sweden was caused primarily by their failure to stop growth before the first severe fall frosts. Furthermore, the southern pines were highly susceptible to the snow mold, <u>Phacidium infestans</u>

Karst., and deer-browsing, as opposed to plants of northern origin.

Schotte concluded that only local seed should be used in northern Sweden. He divided Sweden into five climatic zones based on the mean temperatures during the period from June to September and recommended that all seed be used in the zone in which it was collected. Eneroth, in a later study (7), pointed out that Schotte's zones were much too large. From a study of the survival percentage at the various plantations he concluded that the variability in Scots pine was much greater than Schotte had indicated.

This variability in Scots pine became the object of what perhaps is the most extensive study ever made of any forest tree species. Although the study, which was reported by Langlet (24), was designed primarily to detect differences in frost hardiness among Scots pine from various localities in Sweden, the data presented also give valuable information as to variations in length of active growth period. In a preliminary study of the physiological nature of frost hardiness Langlet found that the dry matter content of the needles during the winter months (in percent of their fresh weight) was closely correlated with the degree of frost hardiness. The yearly changes in frost hardiness were followed closely by similar changes in dry matter content, both being highest during the period from November to February.

Langlet found that plants of northern origin had a significantly higher percentage of dry matter than those of southern origin. Since plants of northern origin start height growth earlier than those of southern origin when grown at the same locality (14,24,49) a correlation between the relative time of initiation of height growth and percentage of dry matter was demonstrated. Thus, in a plantation of 59°n. lat. containing plants from twenty-two different localities between the 56th and 69th northern parallels, Langlet found that the plants from 69°n. lat. were the earliest of all and their average dry matter percentage was 41.5. With decreasing latitude of origin the percentage of dry matter also decreased. Plants of the southernmost origin (56°n. lat.) were the latest with a dry matter percentage of only 35. The percentage of dry matter (determined during the winter months) thus appears indicative of the relative earliness of the plants.

In order to determine to what degree the percentage of dry matter content is modified by changes in environmental conditions Langlet established plantations at three different latitudes (56, 64, and 67°n. lat.) with plants from 26 different localities. Dry matter determinations made during the winter months showed that the plants of northern origin maintained about the same percentage of dry matter at all three latitudes. Plants of southern origin, on the other hand, showed a reduction in dry matter with increasing latitude. As pointed out by Langlet this situation reflects clearly the earlier observations (1,41) that plants of southern origin fail to reach maturity before winter at northern latitudes, i.e., immature needles are characterized by a low dry matter content compared to mature ones. Conversely, it had also been demonstrated earlier (4,49) that plants of northern origin moved to southern latitudes reach maturity before the growing season is over. Consequently their dry matter percentage during winter remained the same at all three latitudes.

Langlet found that the dry matter percentage of all the various sources investigated was a function of the latitude of seed source and the length of growing season at the seed source expressed in number of days with a mean temperature of 6°C. or over. At uniform elevations the latter is, of course, also a function of latitude.

Since the number of days with a mean temperature above 6°C. decreases in a more or less continuous manner with increasing latitude or altitude, Langlet implied that the variation in Scots pine also was of a more or less continuous nature. This implication was heavily criticized by Turesson (58) who re-analyzed Langlet's data and found that in the southern half of Sweden no correlation existed between the percentage of dry matter and latitude of seed source. He maintained that the southern form of Scots pine was clearly distinguishable from the northern form on both morphological and physiological characteristics, and that there existed only few intermediate forms. Turesson refers to some of his earlier publications (55, 56,57) in which he demonstrated discontinuous variation in a number of herbaceous species in Sweden. Some of this variation was also correlated with variations in edaphic factors, and he therefore found it unlikely that the variation in Scots pine should be correlated only with variations in mean temperatures.

Turesson (58) also pointed to the possibility that the differences in dry matter content might be the result of long-lasting modifications induced by the different climatic conditions under which the seed used had matured. Turesson cited results from an experiment with a pure line of barley in which it was shown that the yield was influenced by the climatic conditions under which the seed had matured. He pointed out that the proof of the hereditary nature of the differences in dry matter content could only be obtained if the seed was harvested from regions with similar climatic conditions.

An attempt to do this was described by Langlet in 1941 (25). He harvested seed from a 38-year old plantation, of Norway spruce of German origin in central Sweden and from native Swedish spruce in the vicinity.

He also imported seed from central Germany. Dry matter determinations of the seedlings from the German spruces, which had been growing in Sweden for 38 years, showed that they were similar to those from the imported seed. The seedlings from the native spruces, on the other hand, had a significantly higher dry matter content. Differences in dry matter content could thus not be ascribed to long-lasting modifications induced during seed ripening. Bornebusch had earlier made a similar investigation and reached the same conclusions (2).

The experiments described so far were primarily concerned with genetic differences between populations from widely separated areas. One of the first studies of genetic variability in small populations was reported by Raunkjaer in 1918 (43). He found that variations in time of growth initiation (defined as bud burst) within a small stand of European beech (*Fagus silvatica* L.) were due to genetic differences. The time of bud burst in progenies from selected early and late trees was well correlated with the time of bud burst of their mother trees. In Sweden Sylven (53) made observations over a period of three years on the time of bud burst in more than 300 trees of English oak (*Quercus robur* L.) in a single stand. He found considerable diversity from tree to tree. Generally, the same relative time of bud burst was recorded each year for each tree, but some fluctuations from year to year were noted.

Rohmeder in Germany (46) found considerable differences in time of bud burst among the trees in a stand of Norway spruce. The genetic nature of this variation was well illustrated by the fact that a good correlation in time of bud burst was demonstrated between selected mother trees and their nine-year old progenies. Since the progenies were the result of uncontrolled pollinations there was, however, considerable variation withing each progeny.

Recently Kiellander in Sweden (19) reported on a study of the inheritance of relative time of bud burst in Norway spruce. He found that among trees of German origin certain individuals, after controlled pollinations, consistently transmitted genes for lateness to all their progenies with ensuing hardiness to late spring frosts. Kiellander found that such differences in time of bud burst were very little influenced by environmental factors and therefore well suited for genetic investigations.

Oksbjerg (36) found that trees which start growth late are of a distinct advantage in areas with late spring frosts. He found considerable variation in time of bud burst among the trees in a plantation of Norway spruce in western Denmark. Oksbjerg selected 500 early and 500 late trees and found that in a year with late spring frosts 310 of the early trees became heavily damaged while only 165 of the late trees were damaged. Oksbjerg suggested that selection in the nursery bed of seedlings which start growth late for planting in areas with late spring frosts would be of practical importance. He mentions that such is the practice in some English forest nurseries.

In 1925 Romell (47) reported on investigations of the length of active growth period of Norway spruce and Scots pine growing at ten different localities in Sweden from 56°n. lat. to 67°n. lat. Five young Scots pine and five young Norway spruces were selected among native trees at each locality and observed for three years. Romell found that the time of bud burst in Scots pine became increasingly later with increasing latitude as would be expected. For spruce, however, the variation was not of a continuous nature but varied widely and irregularly from locality to locality. The causes of this variability could not be determined. Romell suggested that edaphic factors no doubt played a major role. Although nothing can be concluded from this experiment with regard to the possible role of genetic differences as the cause of some of the irregularity, it appears likely from other studies (19, 36,46) that this is the case.

The speed of shoot elongation (i.e., the amount of elongation per week) was closely correlated with temperature conditions, with high temperatures increasing the speed. Mork in Norway (31) observed that the rate of shoot elongation in Norway spruce was reduced considerably during cold summers. The total amount of elongation, however, appeared unaffected by the temperature during the elongation period. Romell found that it was the temperature during the preceeding summer which influenced the total amount of elongation. This is in accordance with the findings of Wareing (63) and Hertz (13), and may be true of all conifers in which all internode primordia are formed in the apical meristem the summer previous to their emergence.

Although Norway spruces (which start growth late) are of a distinct advantage in areas with late spring frosts they suffer heavily in areas with early summer droughts as shown by Oksbjerg (37). During the period from May to September 1955 the weather in western Denmark was characterized by a cold and wet May and a cold and dry June, followed by an unusually long period of warm and dry weather lasting to the end of September. In a plantation of selected late and early trees described earlier he found that the trees starting growth late had suffered heavily from the drought. In many plants the terminal shoot had wilted and in some cases the whole plant had died. Practically none of the early trees were damaged. As pointed out by Oksbjerg, the damage was not only due to the length of the drought period but perhaps even more to the time in which it started. Observations during the early part of the drought period showed that the late trees had not yet stopped height growth and that the succulent new leaders therefore were very sensitive to water deficiencies. Oksbjerg suggested that the cold weather preceeding the drought period probably also contributed to the damage due to its retarding effect on shoot elongation.

Comparatively few investigations have been made on variations in the times of initiation and cessation of height growth in Douglas-fir. Munger and Morris (34) in 1933 and 1934 compared the times of bud burst in Douglas-fir from thirteen different localities west of the Cascade range from Darrington in northern Washington to Benton, near Corvallis, 250 miles to the south. Three plantations each containing plants from all thirteen localities were established in 1914 and 1916 at Wind River, Washington at 1100 feet elevation and near Mt. Hood, Oregon at 2800 and 4600 feet elevations. Morris and Munger found that at all three plantations trees from the same localities were the earliest in both years. These observations were repeated in 1955 by Morris, Silen, and Irgens-Moller (32) who found that the relative sequence in times of bud burst was the same as that twenty years earlier.

The effect of photoperiod upon the time of initiation of height growth.

In 1852 Henfrey suggested that the latitudinal variation in length of day may be an important factor in the distribution and development of plants (cited by 35). However, very little experimental evidence of the role of day-length upon the development of plants was available at this time. One of the first experiments on the effect of light upon initiation of height growth in forest trees was reported by Jost in 1894 (15). On March 10, 1892 he placed cut branches of European beech in water in a light-proof, dark box. By May 14 the tree from which the branches were cut had unfolded its leaves whereas the buds on the cut branches in the dark remained dormant. On June 21 Jost exposed the tip of one of the branches to the daylight through a hole in the box while the base of the branch remained in darkness. In a few weeks the exposed buds opened and normal leaves were developed while the basal buds in the dark remained dormant. On September 1 all the branches were removed from the dark with the result that all buds opened and new but somewhat smaller than normal leaves developed. Light thus appeared necessary for initiation of growth in beech. To eliminate any possible effect caused by the detachment of the branches from the mother tree Jost repeated the experiment with potted, 12-year old plants and obtained the same result as with cut branches. Jost's results were confirmed by Macdougal (28) in 1903 in an experiment designed to study the effect of etiolation upon the anatomy of a number of plant species.

In 1914 Klebs (20) reported on his classical experiments on the effect of light upon initiation of growth in beech. He showed that dormancy could be broken at any time during winter and even during the leafy stage of summer dormancy by exposure of the plants in the greenhouse to continuous illumination. Plants exposed to normal winter day-length in the same greenhouse failed to break dormancy.

Wareing (65) showed that the failure of beech to break dormancy under normal winter day-length in spite of high temperatures cannot be ascribed to lack of winter chilling. He found no difference between plants chilled for five months and unchilled plants in their response to light.

Wareing also showed (loc.cit.) that the effect of light upon the dormancy of beech is a photoperiodic phenomenon. Under day-lengths of less than twelve hours dormant beech seedlings moved into a greenhouse remained dormant in spite of high temperatures. He showed that this effect was governed by the length of the dark period, since if the latter was interrupted by one hour of illumination dormancy was broken. The photoperiodic nature of this response was further demonstrated by an experiment in which one group (A) of six dormant plants was exposed to two six-hour periods of light alternating with two six-hour periods of darkness while another group (C) of six dormant plants was exposed to twelve hours of light and twelve hours of darkness. Both groups thus received the same total amount of light and were exposed to the same temperatures. Yet, after 32 days of these treatments all the plants in group A had broken dormancy whereas all the plants in group C remained dormant. The periodicity of the light rather than the total amount of light was the governing factor.

Although high temperatures appear to have no effect on dormancy or beech exposed to day-lengths of less than about twelve hours they will hasten bud burst if the day-length exceeds twelve hours. This is borne out by Wareing's observation (loc.cit.) that under natural conditions in Great Britain bud burst occurs somewhat later than in the greenhouse.

Pauley (39) found that other members of the Fagaceae also failed to break dormancy in continuous darkness in spite of favorable temperatures (approximately 70°F.). The species tested were: red oak (Quercus borealis Michx. f.), white oak (Q. alba L.), black oak (Q. velutina Lam.), American beech (Fagus grandifolia Ehrh.), and American chestnut (Castanea dentata Borkh.).

The discovery and definition of photoperiodic responses in plants by Garner and Allard in 1920 (10) was based on experiments with induction of flowering in herbaceous plants exposed to various day-lengths. However, they also included few woody species in their experiments. They found (11) that yellow poplar (Liriodendron tulipifera L.) resumed height growth if moved into a greenhouse in September and given additional light from sunset to midnight. Plants moved to the same greenhouse but exposed only to normal length of day remained dormant.

In 1936 Kramer (21) found that sweet gum (Liquidambar styraciflua L.), red oak, and yellow poplar brought into a greenhouse in January broke dormancy earlier if exposed to day-lengths of 14 1/2 hours than if exposed to day-lengths of only 8 1/2 hours.

Phillips (42) found that dormancy in loblolly pine (Pinus taeda L.) and northern white cedar (Thuja occidentalis L.) could be broken almost immediately in November if the plants were exposed to an 18-hour day in the greenhouse. Control plants in the same greenhouse did not break dormancy until two and a half months later. Furthermore, red light (680 - 1400 millimicrons in wave-length) given from 8 pm to 1 pm as supplement to the normal length of day was as effective as full light. Blue light (380 - 510 millimicrons), on the other hand, had no effect on dormancy.

Wareing (67) has pointed out that although most plants respond to long photoperiods by initiating height growth the initiation of height growth in nature cannot be explained as a response of the plants to the increase in day-length during spring. He found that some forest tree species start growth independently of photoperiod if they have been exposed to low temperatures during the winter. Even continuous darkness did not prevent growth initiation in leafless, dormant seedlings of birch (Betula pubescens Ehrh.) chilled for six weeks at 5°C. The same situation exists in Populus as shown by Pauley and Perry (41). They exposed clones and progenies of various species of Populus representing all sections of the genus to continuous light, normal day-length, and continuous darkness for about three months during late winter and early spring of 1953. The temperature for all three treatments was maintained at approximately 70°F. No significant difference in time of break of dormancy was found between any of the treatments.

Effect of photoperiod on the time of cessation of height growth.

According to Wareing (67) over 60 species have been investigated with regard to the effect of photoperiod upon the time of cessation of height growth. In all but a few cases photoperiod had a marked influence. Exposure to a short photoperiod hastened cessation of height growth and consequently also reduced the total amount of height growth. Moshkov in Russia found that black locust (*Robinia pseudoacacia* L.) attained heights of only 3-5 cm during the first season of growth if exposed to short days from germination (cited by 67). Sylven (52) found that exposure to short days reduced height growth drastically in aspen (*Populus tremula* L.).

The effect of long days has in all cases proved to be a delay in cessation of height growth (67). Maksimov (29) reported that continuous illumination of English oak caused an increase in height growth of up to fourteen times that of the control plants (twelve hours illumination). During ten months of exposure to continuous illumination a height of 1.5 meter was attained and over 100 leaves per plant formed, while the control plants attained heights of only .06 to .10 meter with only four to six leaves. Up to nine "flushes" of growth occurred in the plants under continuous illumination as opposed to only one "flush" of growth in the plants exposed to twelve hours illumination.

Veen (61) demonstrated that day-lengths exceeding sixteen hours kept species of Populus growing continuously, whereas shorter day-lengths (9-12 hours) induced growth cessation after four to six weeks of growth.

Wareing (67) has stated that although most forest tree species respond to short days by ceasing height growth it cannot be concluded that cessation of height growth in nature represents a response to the decrease in day-length during late summer. He found that in genera like *Fagus*, *Quercus*, *Aesculus*, *Juglans*, *Pinus*, *Abies*, and others cessation of growth occurs in June or July before any appreciable reduction in day-length has occurred. In other genera such as *Alnus*, *Acer*, *Platanus*, and *Carpinus* cessation of growth occurs in July or August. Wareing is of the opinion that the reduction in day-length at this time of the year is too small to be considered as a limiting factor for further extension growth.

The locus of photoperiodic perception.

Wareing's recent experiments in England are probably the most extensive photoperiodic investigations in forest trees. He found (63) that Scots pine could be induced to resume growth during late summer by continuous illumination. Plants which had been dormant all winter were unaffected by such treatment. The dormancy during late summer in Scots pine is characterized by considerable activity of the apical meristem since it is during this period that the primordia of next season's shoot are formed (67). The failure of long days to break dormancy after the primordia have been formed (i.e., during winter) indicates, according to Warcing (loc. cit.) that photoperiodic induction of break of dormancy occurs via the active apical meristem and not via the leaves as is the case in herbaceous plants.

The important role of the apical meristem as the locus of photoperiodic perception has also been demonstrated in beech by Wareing (65). Light intensities as low as 20 Lux were sufficient to break dormancy rapidly if the bud scales were removed from the buds. Intact buds were not affected by such low intensities. De-scaled buds in continuous darkness did, however, also break dormancy, but only after a considerable length of time. This is never the case in intact buds. Wareing suggests that the bud scales may have an inhibitory effect which the meristem is able to overcome under long-day conditions.

In birch the apical meristem also appears to be the locus of photoperiodic perception. Wareing showed (66) that in leafy, dormant birch seedlings the buds must be exposed to continuous illumination or long days to break dormancy. Exposure of the mature leaves alone failed to break dormancy. However, leaves exposed to short days appear to have an inhibitory effect upon the activity of the apical meristem. Thus, if the buds were exposed to continuous illumination but the leaves kept under short days the plants remained dormant. The primary effect of exposing the leaves to continuous illumination appears to be to suppress the inhibitory effect which they exert on the apical meristem during long dark periods.

This inhibitory effect apparantly can be overcome by active apical meristems. Wareing found (loc. cit.) that if the leaves of actively growing birch seedlings were kept under short days no dormancy was induced if the apical meristem was maintained under continuous illumination.

English oak was found by Wareing to respond in essentially the same manner as birch to continuous illumination. However, the growth of oak differs from that of birch in that it does not take place continuously but in short periods of rapid internode extension ("flushes") alternating with periods characterized by the formation of a terminal bud. Wareing exposed dormant, leafy oak seedlings to continuous illumination and obtained a new "flush" of growth in less than four weeks. Plants in which the terminal buds were kept under short days (eight hours) and the leaves under continuous illumination did not produce new growth. If the terminal bud was kept under continuous illumination and the leaves under short days the plants remained dormant, as was the case with birch.

In sycamore maple (<u>Acer</u> <u>pseudoplatanus</u> L.) and black locust (<u>Robinia</u> <u>pseudoacacia</u> L.), on the other hand, the apical meristems appear insensitive to photoperiod.

Actively growing seedlings of these two species became dormant if the leaves were kept under short days even if the apical meristem was maintained under continuous illumination. Their photoperiodic insensitivity is shown by the fact that if the leaves were kept under continuous light and the active apical meristems under short days no dormancy was induced as in birch and oak but only a reduction of internode extension of the new shoot. Furthermore, dormant, leafy seedlings could not be induced to break dormancy by more than four weeks of continuous illumination.

These observations led Wareing to conclude (67) that the effect of long days on dormant, leafy seedlings of the species investigated (e.g., birch, oak, beech, and Scots pine) is primarily that of suppression of an inhibitory effect exerted by the leaves during long dark-periods and a direct growth stimulating effect upon the apical meristem. This latter effect is lacking in some species (i.e., black locust and sycamore maple).

Effect of temperature upon the time of initiation and cessation of height growth.

With the exception of beech (67) and other members of the Fagaceae (39) exposure to high temperatures always hasten initiation of growth in forest tree species (67). Olmsted (38) has shown that this response of dormant plants to high temperatures, is greatly influenced by past exposures to low temperatures. Olmsted found that the earliness of growth initiation (defined as bud burst) was correlated with the length of the period of exposure to low temperatures (chilling). After chilling outdoors until December 6 Olmsted brought groups of plants of sugar maple (Acer saccharum Marsh.) into the greenhouse at regular intervals until February 15. Growth started progressively earlier the longer the exposure to low temperatures until the last week in January when all plants apparently had received enough chilling. The effect of additional chilling in accelerating growth initiation was more pronounced in December than in January. Olmsted also found that short exposures to very low temperatures had an accelerating effect. For example, on December 13-14 the temperature outside the greenhouse went down to 10-18°F. for 23 hours. The mean date of bud burst for the plants brought into the greenhouse after this period was two weeks earlier than that for the plants brought in the day before the cold period.

Vegis (62) has demonstrated that high temperatures induce dormancy in the water plant Hydrocharis morsus-ranae L.. Temperatures above 25°C. invariably induced dormancy whereas at temperatures below 10°C. the plants remained actively growing almost indefinitely. Kramer (22) has recently shown a similar effect of high temperatures on seedlings of loblolly pine (Pinus taeda L.). Plants grown at 17°C. during night and 23°C. during day continued growth later in the season than did plants grown at a constant temperature of 23°C.

The interaction between responses to photoperiod and temperature.

Gustafson (12) has shown that the effect of chilling appears to be related to the effect of long days. He found that seedlings of red pine (Pinus resinosa Ait.) which had not been exposed to freezing temperatures during the winter made no growth or only slight growth during the following summer unless they were exposed to a day-length of more than approximately 16 hours. Similarly, Wareing (67) found that un-chilled, leafless and dormant seedlings of birch started growth earlier under long photoperiods than under short photoperiods, whereas chilled plants started growth independently of photoperiod. Black and Wareing found the same situation in birch seed. Long photoperiods were required for rapid germination in unchilled seed, whereas chilled seed germinated rapidly even in complete darkness. Olmsted (38) found that unchilled seedlings of sugar maple started growth earlier under 20-hour photoperiods than under eight-hour photoperiods which suggests that inadequate chilling may partly be compensated for by long photoperiods.

Vegis (62) has demonstrated a similar interaction between photoperiod and temperature during the growth period. He found that the dormancy-inducing effect of high temperatures on plants of Hydrocharis to a certain degree could be counter-acted by long photoperiods. The higher the temperatures the longer was the photoperiod required to keep the plants active. However, above 25°C. even continuous illumination could not prevent dormancy, whereas at temperatures below 10°C. the plants remained active almost indefinitely regardless of photoperiod. Even complete darkness did not induce dormancy.

On the basis of his findings in Hydrocharis Vegis attempted to explain the fact that northern ecotypes of forest trees stop growth in June or July if planted at southern latitudes. On the assumption that northern ecotypes have a lower optimum temperature for growth than southern ecotypes, he maintained (62) that the high temperatures during summer at southern latitudes exceeds the optimum temperature for growth of northern ecotypes. Consequently such plants go into dormancy earlier than plants native to southern latitudes. Furthermore, northern ecotypes planted at southern latitudes are also exposed to shorter photoperiods than those of their native habitat. This accentuates the dormancy-inducing effect of high temperatures.

Conversely, when southern ecotypes are moved to northern latitudes they may never be exposed to temperatures exceeding their optimum temperature for growth and therefore continue growth late. In addition they are exposed to photoperiods longer than those of their native habitat. This delays cessation of height growth.

The origin of genetically founded intra-specific diversity in time of height growth initiation and cessation.

As suggested by Pauley and Perry (41) adaptation to length of growing season in any particular area may come about by the selective pressures exerted by the last killing frosts during spring and the first killing frosts during fall. Only those plants which react to the prevailing conditions of the area in a suitable manner are capable of survival and reproduction.

Within any uniform day-length zone the growing season often varies considerably in length due to topography and other factors. If response to photoperiodic changes are one of the components of adaptation to length of growing season, then differences in such responses should be found among plants native to the same day-length zone. Pauley and Perry (41) have found such differences among plants of western balsam poplar (<u>Populus trichocarpa</u> Hook.) native to a zone between the 45th and 47th northern parallels extending from the Pacific Ocean to western Montana. While the length of growing season within this zone varies from 250 days to 90 days, the day-length regime is essentially the same throughout the zone. Plants collected from this zone were planted at Weston, Massachusetts (42^on. lat., length of growing season 148 days) and the time of height growth cessation noted for each plant. The plants from areas with a long growing season (250 days) stopped growth in early October while those from areas with a short growing season (90 days) stopped growth in early July.

Differences in photoperiodic responses was further demonstrated by Pauley and Perry (41) in the following experiment. They exposed about 100 clones of western balsam poplar from various elevations and latitudes to the natural day-length of Boston, Massachusetts and to a long-day regime corresponding to that of Juneau, Alaska (ca. 58^o 20'n. lat.) by way of supplemental electric light. Both treatments were given out-of-doors in a nursery. The long-day treatment was adjusted every third day so as to follow the natural changes in day-length at Juneau. Use of supplemental light was discontinued on September 30, when the day-length of Boston became greater than that of Juneau. Time of cessation of height growth for each clone under both treatments was observed. The differences between the two treatments were considerably greater in the clones from high elevations or latitudes (short growing seasons) than in those from low elevations at low latitudes (long growing seasons). Thus, in plants from 60°n. lat. the difference was 60 - 70 days whereas in plants from 44°n. lat. it was only 5 - 20 days. Two clones, both from 46°n. lat., but one from 5000 feet elevation, the other from 25 feet elevation, showed differerences of, respectively, 34 and 5 days.

Pauley and Perry (41) found that a clone native to approximately the same latitude as Boston, Massachusetts, stopped growth on October 6 if exposed to the day-length regime of Boston whereas it did not stop until November 11 if exposed to the day-length regime of Juneau. Clones from near Juneau, on the other hand, stopped growth August 28 when exposed to the day-length regime of Juneau and on June 20 if exposed to that of Boston. The clone from the latitude of Boston would thus quickly be eliminated by frost if planted near Juneau, while the clone from Juneau, if planted near Boston, soon would be overtopped by competing vegetation because it adds little to its height each season.

GENETIC DIFFERENCES WITH REGARD TO TIME OF BREAK OF DORMANCY

Bud burst [1] in Douglas-fir occurs in nature over a very wide period of time. In 1955 bud burst at the coast of Oregon, near Newport, occurred in late April, whereas in the Cascade range, at an elevation of 4000 feet, it did not occur until the last week of June. These observations refer in both cases to young plants (10-25 years) in which bud burst occurs up to three weeks earlier than in older plants.

These differences would appear to be an effect of the different length of growing seasons at the two localities. However, there is also the possibility that such differences are, in part, caused by genetic differences as demonstrated by Pauley(40) with altitudinal ecotypes of *Populus trichocarpa* Hook.

Plants at eight localities along an east-west transect from Santiam Pass in the Cascades to Tidewater near the coast were selected for study (Fig. 1). During the spring of 1955 temperatures at five of these localities were recorded (Fig. 2) by thermographs placed in shelters five feet above the ground in forest stands.

Temperature data for such a short period of time is of limited value for the interpretation of phenological

---

[1] Break of dormancy is in this study defined as bud burst, i.e., the emergence of the new shoot from the winter-bud.

Fig. 1. East-west transect in western Oregon along which eight localities were selected for observations on time of bud burst.

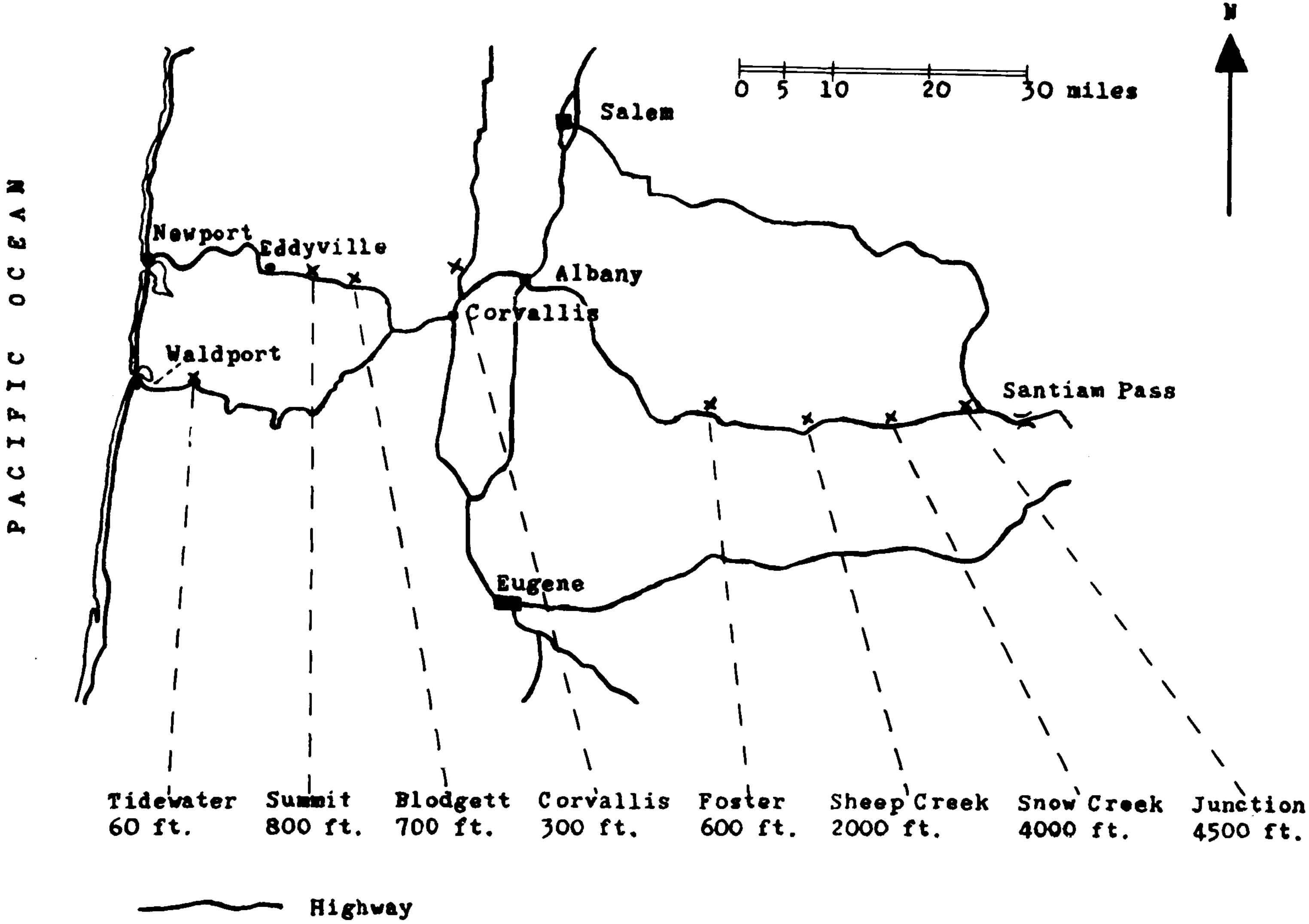
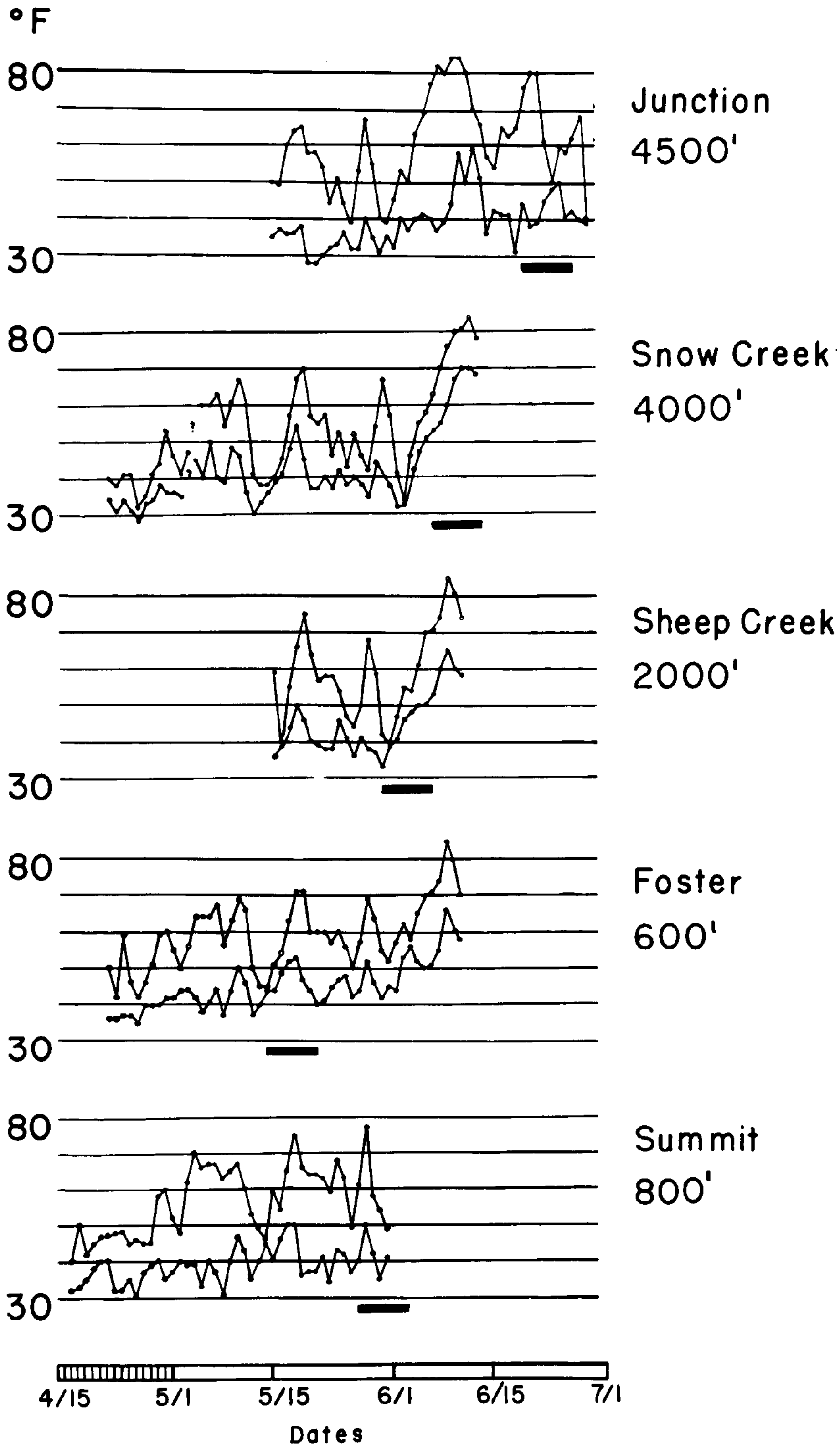

N
0 5 10 20 30 miles
PACIFIC OCEAN
Salem
Newport
Eddyville
Albany
Corvallis
Waldport
Santiam Pass
Eugene
Tidewater
60 ft.
Summit
800 ft.
Blodgett
700 ft.
Corvallis
300 ft.
Foster
600 ft.
Sheep Creek
2000 ft.
Snow Creek
4000 ft.
Junction
4500 ft.
Highway

Fig. 2. Daily maximum and minimum temperatures at five localities along the east-west transect (see Fig. 1). Spring 1955.



▬ = week during which bud bursting occurred.

observations. However, they do indicate that the daily temperature fluctuations are greater at high elevations in the Cascades than in the coastal range. Thus, at Santiam Pass (Junction, Fig. 2) the difference between day and night temperatures exceeded 40°F. on clear days while at the other locations considerably smaller differences were recorded.

The time of bud burst in younger plants (three to ten years old) was noted for each locality (Fig. 2). With increasing altitude bud burst occurred progressively later. Bud burst occurred at all localities in periods with no night frost.

During December of 1954 plants were collected from seven of the eight localities shown in Figure 1. No plants were collected from Junction, Santiam Pass. About 100 plants, three to six years old, were collected from each locality. All plants were brought to Corvallis and potted in four inch pots. Aiken silty loam from the Oak Creek area in McDonald Forest north of Corvallis was used for all the plants. The potted plants were placed randomly in cold-frames located on the campus of Oregon State College. All plants were thus exposed to the same winter conditions.

During the following spring the date of bud burst for each plant was noted. This date was defined as the day in which the needles of any bud, regardless of the position on the plant, first emerged from the bud scales. In most plants the terminal bud on the leader was the first to burst, but in a few plants buds on lateral branches were earlier than the terminal. Plants with a damaged terminal bud or leader were discarded since damage to, or removal of the leader may induce early bud burst. Temperature conditions in the cold frame were recorded by a thermograph (Fig. 3). Observations were made each day during the period of bud burst (Fig. 4).

A multiple range test as devised by Duncan (6) showed that the mean date of bud burst for the plants from Corvallis (20 days after April 1) was significantly different from any of the other means (Table 1a). The same was the case for the plants from Snow Creek (51 days after April 1). The plants from Tidewater (38 days) differed significantly from those from all other localities with exception of those from Blodgett (35 days). No significant difference was found among the plants from Foster (31 days), Summit (32 days), Sheep Creek (33 days), and Blodgett.

Twenty-five randomly selected plants from each locality were planted at the Botany and Plant Pathology farm east of Corvallis in 1956 for observations as to the consistency of the observed differences in time of bud burst (Fig. 4). Dates of bud burst for each of these

Fig. 3. Daily maximum and minimum temperatures to which Douglas-fir seedlings for seven localities along the east-west transect (Fig. 1) were exposed during spring 1955.

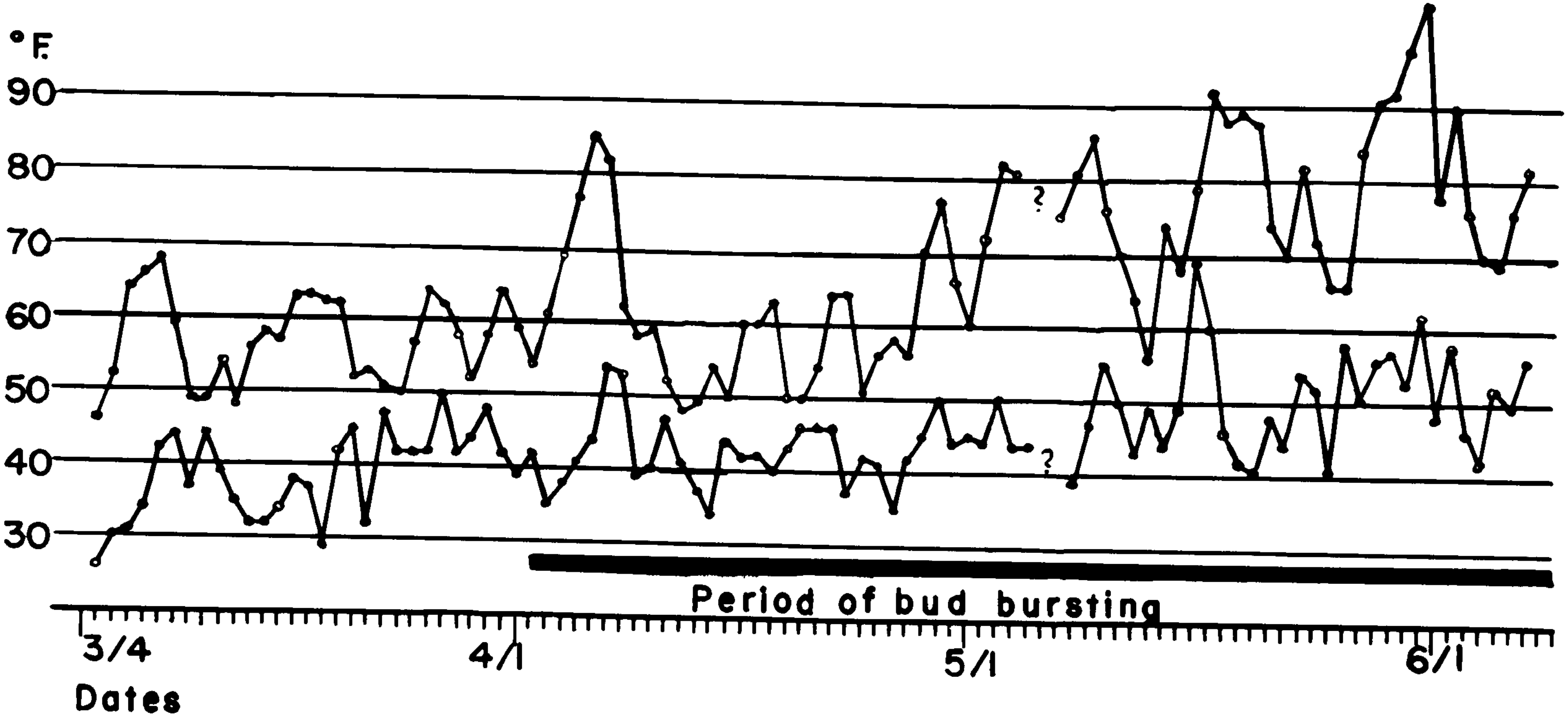

°F
90
80
70
60
50
40
30
?
?
Period of bud bursting
3/4
4/1
5/1
6/1
Dates

Fig. 4. Dates of bud burst in Douglas-fir seedlings from seven different localities along the east-west transect (Fig. 1) when grown at Corvallis. Spring 1955.


Origin and altitude
Snow Creek, 4000'
Sheep Creek, 2000'
Foster, 600'
Corvallis, 300'
Blodgett, 750'
Summit, 800'
Tidewater, 60'
0
5
10
75
Number of days after April 1
x = mean date
■ = one plant

Table 1a. Multiple range F- test of mean dates of bud burst in Douglas-fir seedlings from seven different localities (Fig. 1) in Oregon when grown at Corvallis, Oregon, spring 1955.

Origin:	Corvallis	Foster	Summit	Sheep Creek	Blodgett	Tidewater	Snow Creek
Number of days after April 1	20	31	32	33	35	38	51

Table 1b. Multiple range F- test of mean dates of bud burst in Douglas-fir seedlings from seven different localities (Fig. 1) in Oregon when grown at Corvallis, Oregon, spring 1957.

Origin:	Corvallis	Sheep Creek	Foster	Summit	Snow Creek	Blodgett	Tidewater
Number of days after March 20	16	20	23	24	25	29	29

Note: Any two means not underscored by the same line are significantly different. at the 5 percent level of significance.

Any two means underscored by the same line are not significantly different.

plants were noted during the spring of 1957 (Fig. 5). A multiple range test (Table 1b) showed that the plants from Corvallis were again in 1957 significantly earlier than any of the other plants (16 days after March 18). The plants from Snow Creek (25 days after March 18) were in 1957 significantly earlier than the plants from Blodgett and Tidewater (both 29 days after March 18).

In 1955 the difference between the mean dates of bud burst of the earliest and that of the latest plants was 32 days whereas in 1957 it was only 13 days. (Fig. 6). This drastic reduction in the length of the period of bud burst may be attributable to several factors. The higher temperatures during the spring of 1957 as compared to those of 1955 (Table 2) may be responsible for part of this reduction.

Table 2. Temperature data (°F) from United States Weather Bureau's station at Oregon State College, Corvallis (59).

Average Maximum		Average Minimum		Average		Highest		Lowest	
1957	1955	1957	1955	1957	1955	1957	1955	1957	1955
53.1	48.9	39.5	32.8	46.3	40.9	65	60	31	22
61.1	53.1	40.8	35.6	51.0	44.4	85	74	30	29
67.5	64.5	47.5	39.9	57.5	52.2	83	77	37	33
72.9	71.9	49.5	47.1	61.2	59.5	83	95	40	35

Note: Temperatures given for March, April, May, and June respectively.

Another factor may be the reduction in number of plants from each source. Thus, the 1955 observations were

Fig. 5. Dates of bud burst in Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) when grown at Corvallis, Oregon. Spring 1957.

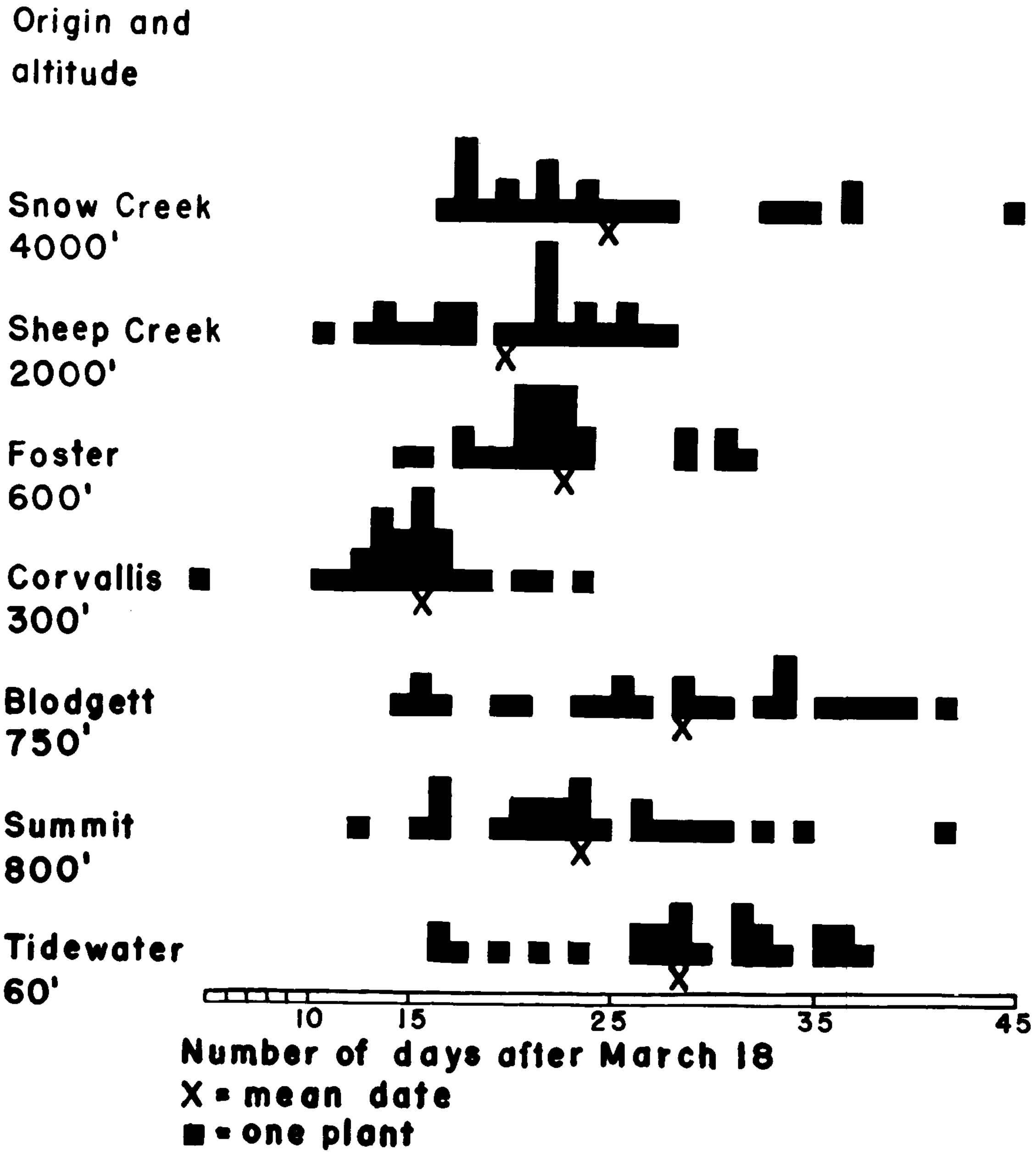
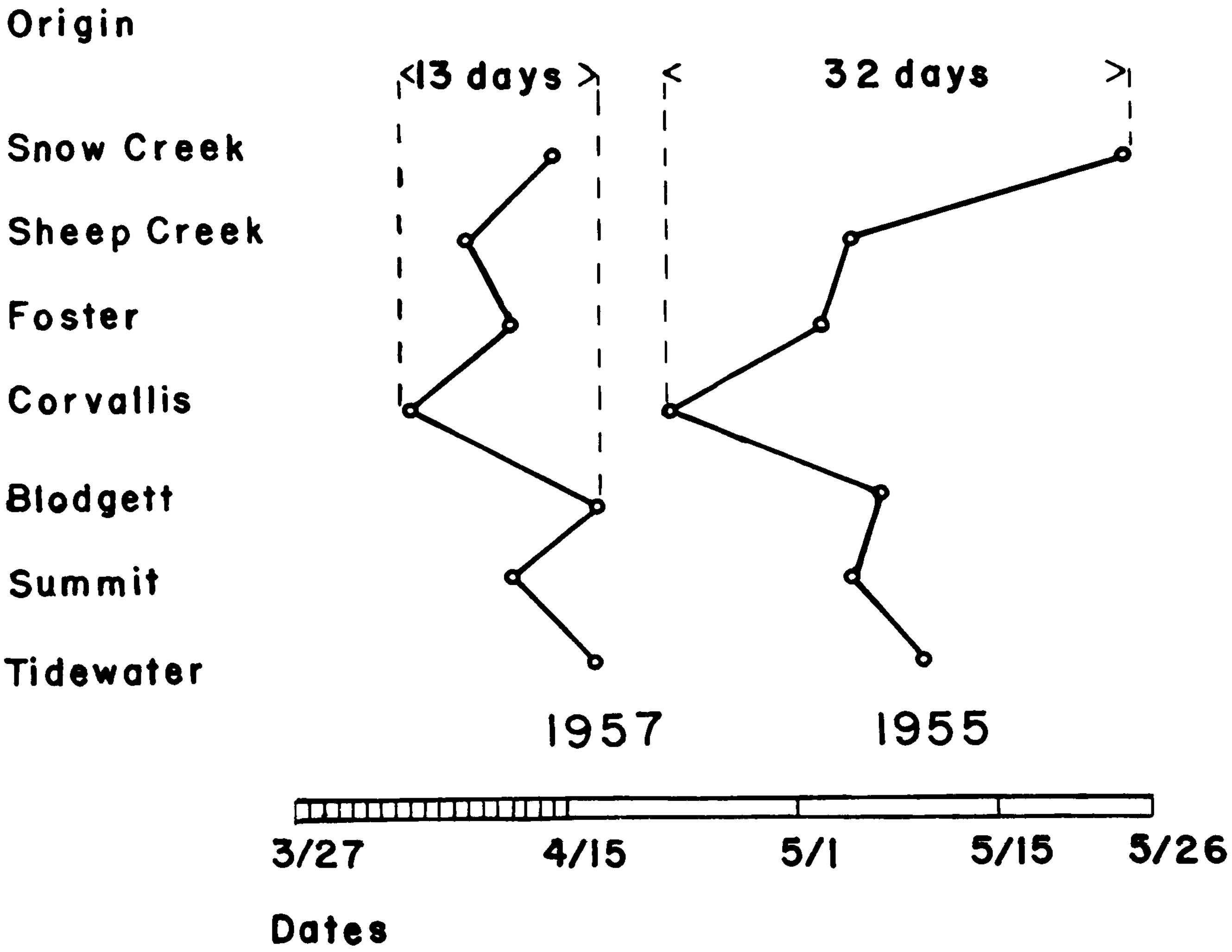

Origin and altitude
Snow Creek 4000'
Sheep Creek 2000'
Foster 600'
Corvallis 300'
Blodgett 750'
Summit 800'
Tidewater 60'
10
15
25
35
45
Number of days after March 18
X = mean date
■ = one plant

Fig. 6. Mean dates of bud burst during 1955 and 1957 in Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) when grown at Corvallis.


Origin
Snow Creek
Sheep Creek
Foster
Corvallis
Blodgett
Summit
Tidewater
13 days
32 days
1957
1955
3/27
4/15
5/1
5/15
5/26
Dates

based on 50 plants from each source as opposed to 25 in 1957.

Phenotypic adaptation (i.e., modifications) to the environmental conditions of the experimental area may also have contributed to the reduction of the differences in time of bud burst. This is evidenced by the fact that the plants from Corvallis maintained their relative position as the earliest plants in both years (Fig. 6). They were collected in an area close to the experimental areas, and were, consequently, not exposed to the modifying effects of a new environment. Conversely, the plants from Snow Creek were subjected to the greatest change in environmental conditions (i.e., moved from an elevation of 4000 feet to one of 200 feet). They also show the greatest change in relative time of bud burst during the two years they were grown in the valley (Fig. 6).

The seedlings employed in the above experiment represent a mixture of progenies from an unknown number of trees at each collection area. Seedlings were collected on the assumption that a better sample of the genotypes characteristic of each area would be obtained by collection of established seedlings than by collection of seed. Heterozygosity of the parent tree and genetic recombinations may result in seed of rather high genetic diversity of which only a part would be fitted for the conditions of the collection areas. The genotypes of seedlings derived from seed collected at each area and grown in a greenhouse may therefore not be characteristic of those of the collection areas.

By collection of seed from individual trees at each area some measure of local, genetic variation can be obtained by comparisons of progenies. Furthermore, collection of seed permits a uniform treatment of all plants from the time of germination whereas established seedlings collected at different localities have been exposed to different environmental conditions prior to their collection. Such differences may influence the subsequent development of the plants.

On the basis of these considerations it was found desirable also to study differences between seedlings which had been exposed to uniform conditions since germination. Seeds were therefore collected during the fall of 1956 from seven trees growing within an area of less than one half of a square mile near Browder Creek in Santiam Pass at 4000 feet elevation, from five trees in McDonald Forest, 10 miles north of Corvallis, at elevations ranging from 300 to 900 feet, and from two trees near Eddyville (Fig. 1) in the coastal range at 100 feet elevation. All seeds were stratified for two weeks at 5°C. and sown in November 1956 in pots in the greenhouse. Fifteen to thirty seedlings from each progeny were given additional light each day from 5 p.m. to 11 p.m. from four 40 Watt flourscent and one 40 Watt incandescent lamp suspended three feet above the plants. From December 15 the plants were treated with short days (nine hours) to induce dormancy. The plants were covered with black, light-proof cloth each day at 5 p.m. and uncovered at 8 a.m.. By February 1 all plants had formed a dormant, terminal bud. They were then treated with long days (nineteen hours) to induce bud burst. Date of bud burst was observed for each plant (Fig. 7). The mean dates of bud burst for the progenies from Browder Creek varied from 22 days (tree #93) to 35 days (tree #89) after February indicating a considerable local genetic variability. The fact that the progenies were derived from uncontrolled pollinations tends to emphasize the variability since it may be assumed that pollination occurred more or less at random among the trees of the area.

An even greater local difference was found between two trees growing within 100 feet from each other near Eddyville, Oregon (Fig. 8). The differences in mean dates of bud burst between their progenies was 22 days (24 and 46 days after February 1).

Progenies of the five trees from McDonald Forest, 10 miles north of Corvallis, showed mean dates of bud burst varying from 12 days to 21 days after February 1 (Fig. 8).

A comparison between the mean date of bud burst of all the progenies from McDonald Forest with that of all

Fig. 7. Dates of bud burst in 3-months old progenies from seven Douglas-fir trees at Browder Creek, Santiam Pass, Oregon when grown in greenhouse, spring 1957.

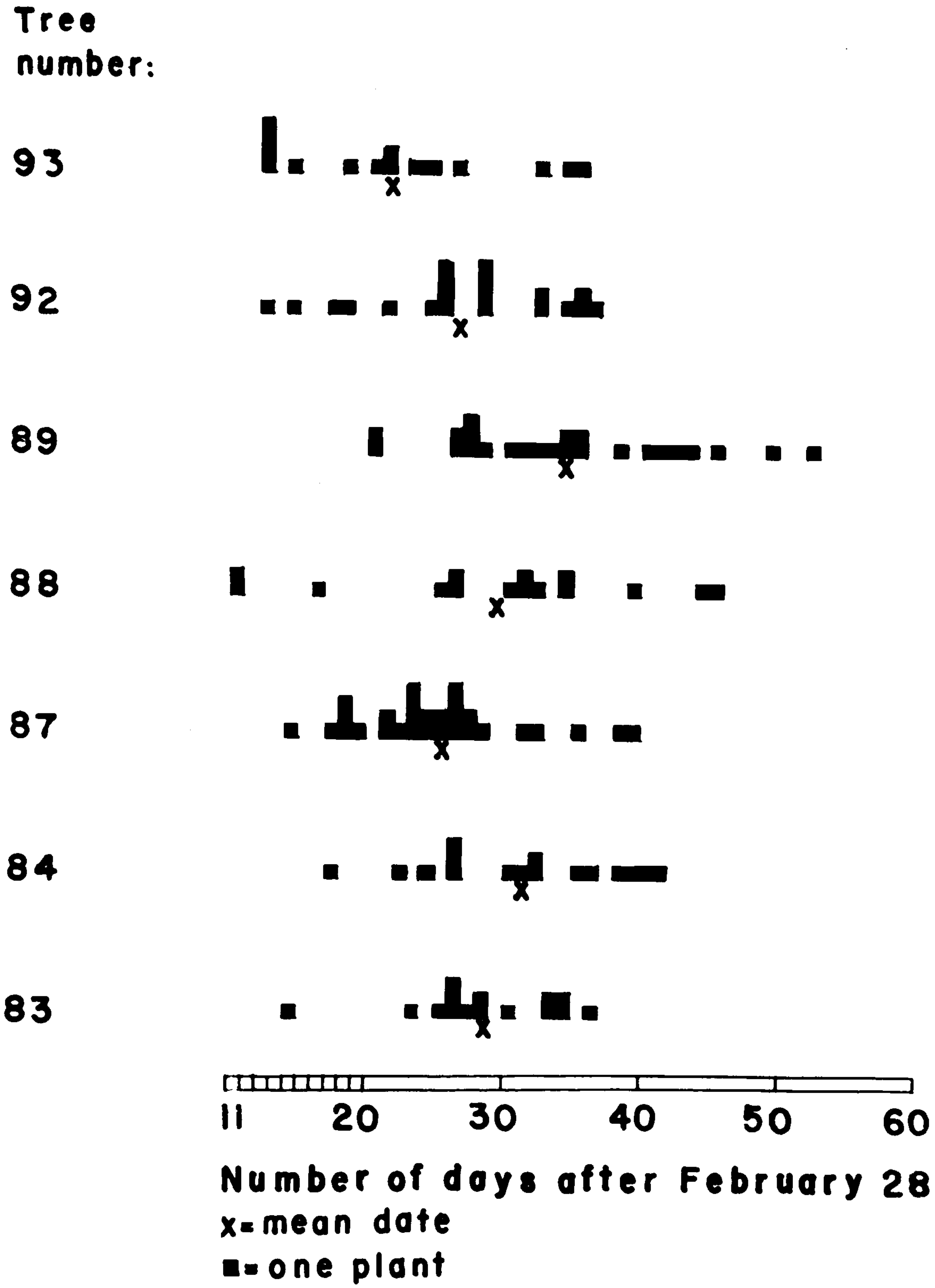
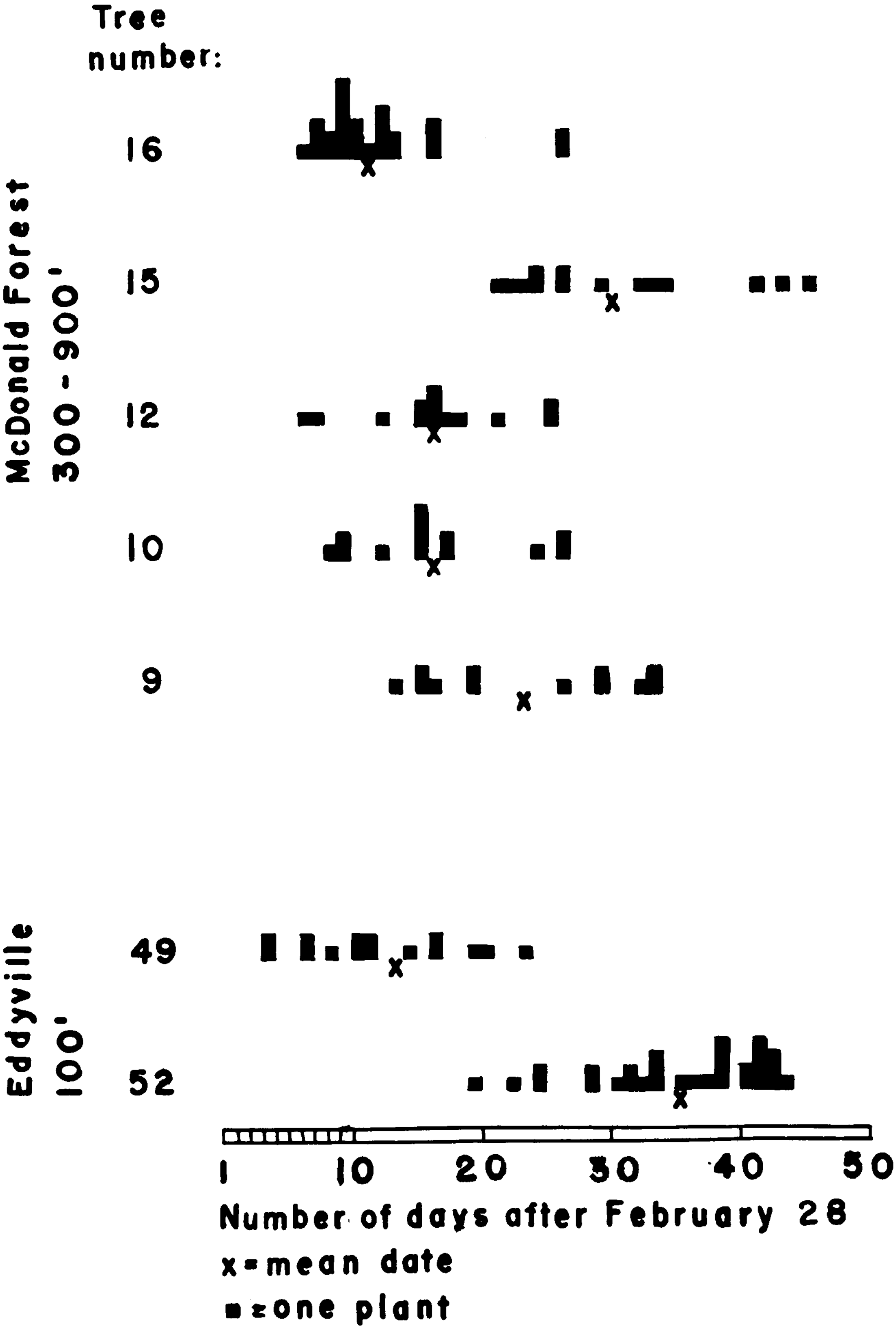

Tree number:
93
92
89
88
87
84
83
11
20
30
40
50
60
Number of days after February 28
x = mean date
■ = one plant

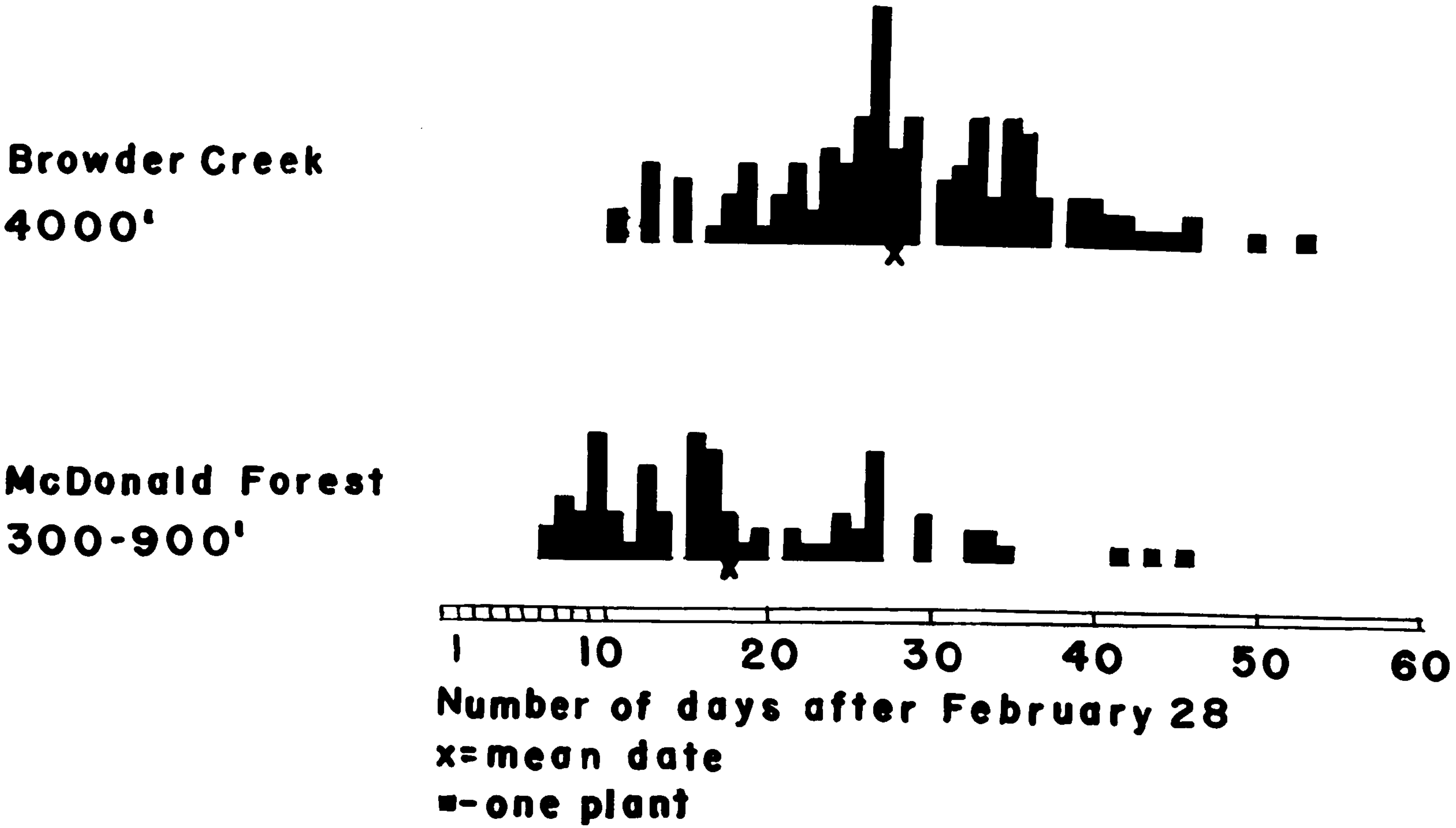
Fig. 8. Dates of bud burst in 3-month old progenies from five Douglas-fir trees in McDonald Forest, north of Corvallis, Oregon; and from two trees near Eddyville, Oregon. Greenhouse, spring 1957.


Tree number:
McDonald Forest 300 - 900'
16
15
12
10
9
Eddyville 100'
49
52
1
10
20
30
40
50
Number of days after February 28
x = mean date
■ = one plant

the progenies from Santiam Pass (Fig. 9) showed that the plants from McDonald Forest were earlier than those from Santiam Pass. The difference of 10 days is significant at the 5 percent level of significance ("t-test"). This confirms the earlier observation (Figs. 4 and 5) that plants from high altitudes start growth later than those from low altitudes when grown in the lowland.

Pauley (40), who described a similar situation in altitudinal ecotypes of western balsam poplar, found this earliness of the low altitude plants rather surprising since he anticipated that high altitude plants "would demonstrate a precosity similar to that which characterizes their high latitude cousins". This anticipation would appear justified since the length of the growing season at high altitudes often is comparable to that of high latitudes. Pauley's findings and the present findings in Douglas-fir are contrary to those of Karschon (16,17). He found that high-elevation ecotypes of Scots pine broke dormancy earlier than those from low elevation when both were grown at temperatures around 5°C. Karschon concluded that high-elevation plants have a lower optimum temperature for break of dormancy than do plants from low elevations. In other words, the differences in time of break of dormancy were due to differences in response to temperature increases during spring. This explanation does not appear valid for the situation in Douglas-fir and

Fig. 9. Dates of bud burst in three months old progenies of seven Douglas-fir trees from Browder Creek, Santiam Pass, Oregon compared with those of three-month old progenies of five trees in McDonald Forest, north of Corvallis, Oregon. Greenhouse, spring 1957,


Browder Creek
4000'
McDonald Forest
300-900'
1
10
20
30
40
50
60
Number of days after February 28
x=mean date
■-one plant

poplar.

The environmental conditions along the transect under study (Fig. 1) may be described as very heterogeneous. As pointed out by Thoday (54) natural selection in a heterogeneous environment tends to favor individuals with a high phenotypic flexibility (i.e., with wide reaction ranges) especially in organisms with a long life span. Many characteristics of Douglas-fir, including the relative time of bud burst, may therefore exhibit great flexibility. This phenotypic flexibility should not obscure the existence of genetic differences with regard to the time of bud burst among trees of different origins. Such differences may become of great importance when plants are moved to areas with adverse environmental conditions.

Conclusions

The observed variation in time of bud burst among altitudinal ecotypes of Douglas-fir growing under essentially uniform environmental conditions may be ascribed to genetic differences in their response to the environmental conditions of the experimental area. Plants native to high altitudes started growth later than those native to low altitudes. Except for minor changes, the relative sequence of time of bud burst was found to be the same over a period of two years. Comparisons between progenies of single trees from a restricted area indicate considerable local genetic diversity. Seedlings derived from seed collected at various altitudes and exposed to uniform conditions from germination showed differences similar to those of seedlings collected in their native habitats.

THE INFLUENCE OF PHOTOPERIOD AND TEMPERATURE UPON THE TIME OF BREAK OF DORMANCY

Break of dormancy represents a response of the plant to changes in the sum total of environmental conditions. Since the response to changes in one environmental factor never is independent of the status of all other environmental factors influencing the plant, any attempt to single out the environmental factors responsible for break of dormancy appears meaningless. Only the relative role of such factors can be determined. Such determinations may be made by changing the factor to be studied while keeping all other factors at a constant level.

Exposure to long photoperiods has been shown to hasten break of dormancy in a number of forest tree species (67). Pauley and Perry (41) have demonstrated that intra-specific diversity in time of onset of dormancy may, partly, be ascribed to intra-specific diversity in response to photoperiod. An experiment was set up in 1956 to determine whether the observed diversity in time of bud burst among altitudinal ecotypes of Douglas-fir (Figs. 4, 5, 7, 8, 9) was due to a diversity in response to photoperiod. On February 1 approximately twenty potted plants (three to seven years old) from each of the seven localities along the east-west transect (Fig. 1) were placed in temperature controlled compartments in the greenhouse. In compartment I the plants were exposed to normal daylight from 8 a.m. to 5 p.m. and covered with light-proof cloth from 5 p.m. to 8 p.m. In compartment II the plants were exposed to normal daylight from 8 a.m. to 5 p.m. and to artificial light from a 200 Watt incandescent lamp from 5 p.m. to 11 p.m. The temperature in both compartments was kept at 45°F. at night and 65-70°F. during the day. This was done to avoid any possible overriding effect of high temperatures upon the effect of the different photoperiods. The treatments are graphically illustrated in a generalized way in Figure 10.

Significant differences (at the five percent level, "t-test") was found between the responses to the two treatments in plants from all localities with the exception of those from the lowest elevations (Corvallis and Tidewater). Although long photoperiods did not significantly change the mean date of bud burst of the low-elevation plants, long days did hasten bud burst strikingly in the high-elevation plants (Fig. 11).

Approximately twenty plants from each of the same sources (three to seven years old) had been left in the cold-frame since their collection in 1954. During the spring of 1956 half of them were exposed to normal day, and the other half received additional light from 5 p.m. to 11 p.m. The temperatures to which these plants were exposed during the spring of 1956 are shown in Figure 12. The differences in mean dates of bud burst between the two treatments in this experiment are much smaller (Fig. 13) than in the previous experiment (Fig. 11). None of them are statistically significant. But, where there are differences it is consistently the long-day treated plants which have the earliest means. The smaller differences in this experiment may be due to the fact that the difference in day-length between the two treatments was less than in the previous experiment (cf. Fig. 10 and Fig. 12). The different temperature regimes under which the two experiments were conducted may be another reason for the smaller differences. The plants in the temperature controlled compartments were consistently exposed to 45°F. each night and to day temperatures between 65° and 70°F. The plants in the cold-frame, on the other hand, were seldom exposed to temperatures above 45°F. during the first month of the experiment (prior to March 10) while in the latter half of the experiment the temperature often went considerably above 70°F. and only occassionally down to 45°F. and then only for brief periods (Fig. 12).

The apparent high photoperiodic sensitivity of the high-elevation plants was confirmed by a second experiment during the spring of 1957. Seeds were collected from nine trees along Browder Creek at Santiam Pass at 4000 feet elevation and from six trees in McDonald Forest north of Corvallis at elevations ranging from 300 to 900 feet during the fall of 1956. The seeds were stratified for

Fig. 10. Temperatures and day-lengths employed in photoperiodic experiment with Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1). Spring 1956.

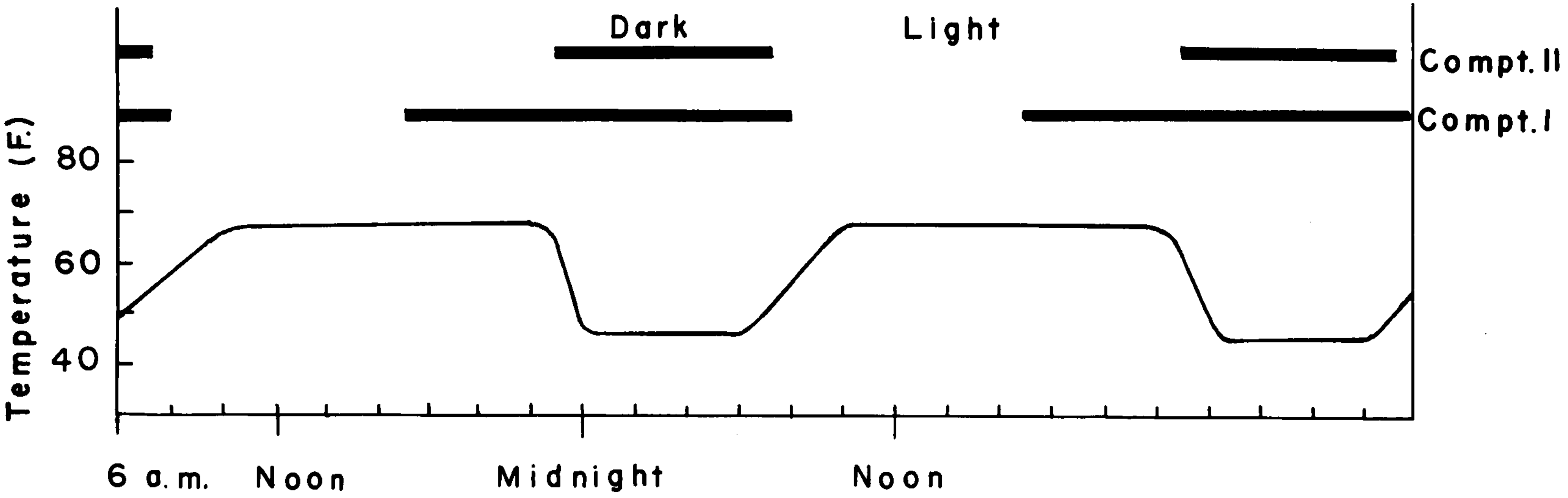

Dark
Light
Compt. II
Compt. I
Temperature (F.)
80
60
40
6 a.m.
Noon
Midnight
Noon

Fig. 11. Dates of bud burst in Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) when treated with photoperiods of nine hours (S) and nineteen hours (L) in temperature controlled cabinets (see Fig. 10); s-significant difference at the 5 percent level of significance ("t-test"). Spring 1956.

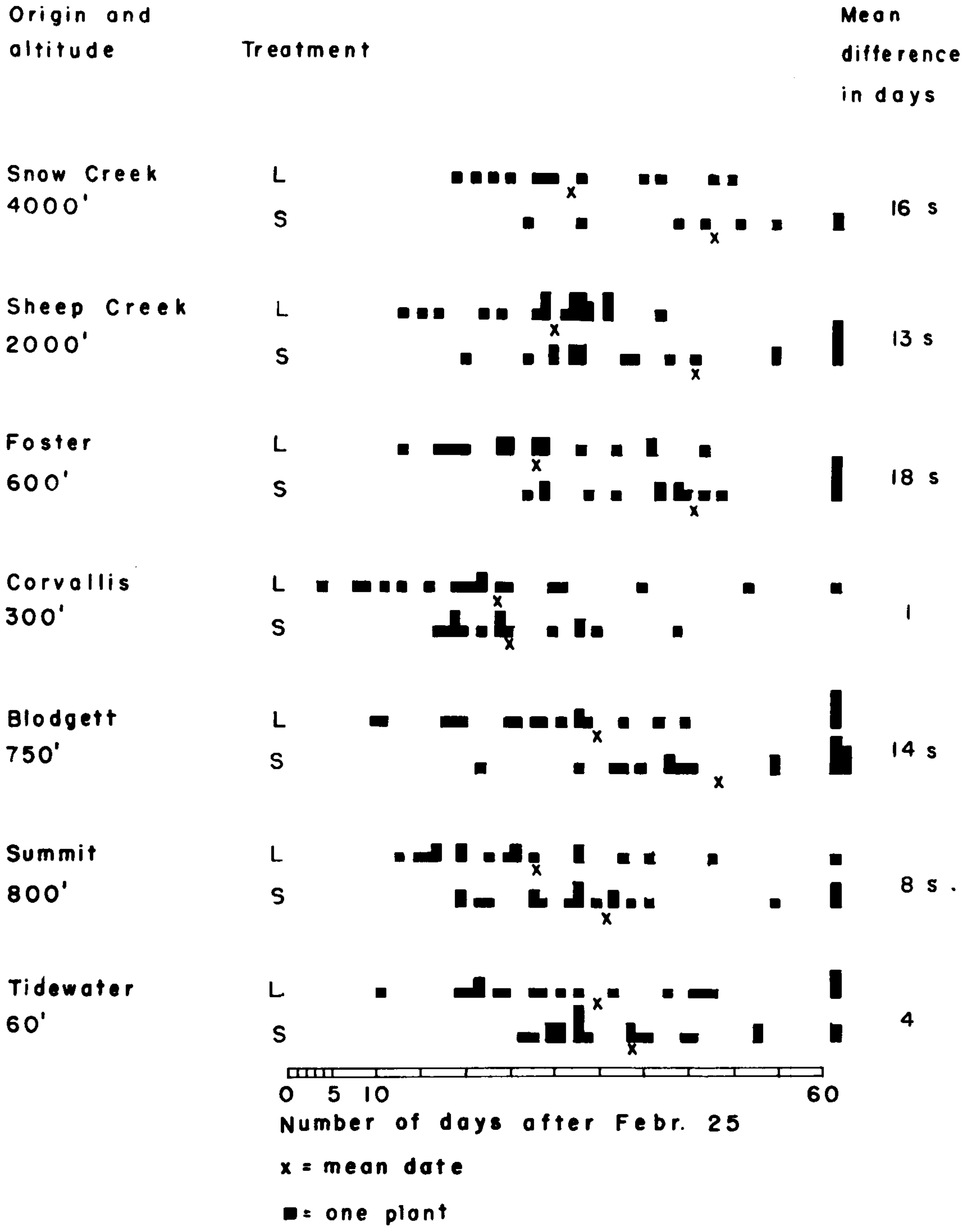

Origin and altitude
Treatment
Mean difference in days
Snow Creek 4000'
L
S
16 s
Sheep Creek 2000'
L
S
13 s
Foster 600'
L
S
18 s
Corvallis 300'
L
S
1
Blodgett 750'
L
S
14 s
Summit 800'
L
S
8 s
Tidewater 60'
L
S
4
x
0 5 10
60
Number of days after Febr. 25
x = mean date
■ = one plant

Fig. 12. Temperatures and day-lengths to which Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) were exposed. Spring 1956.

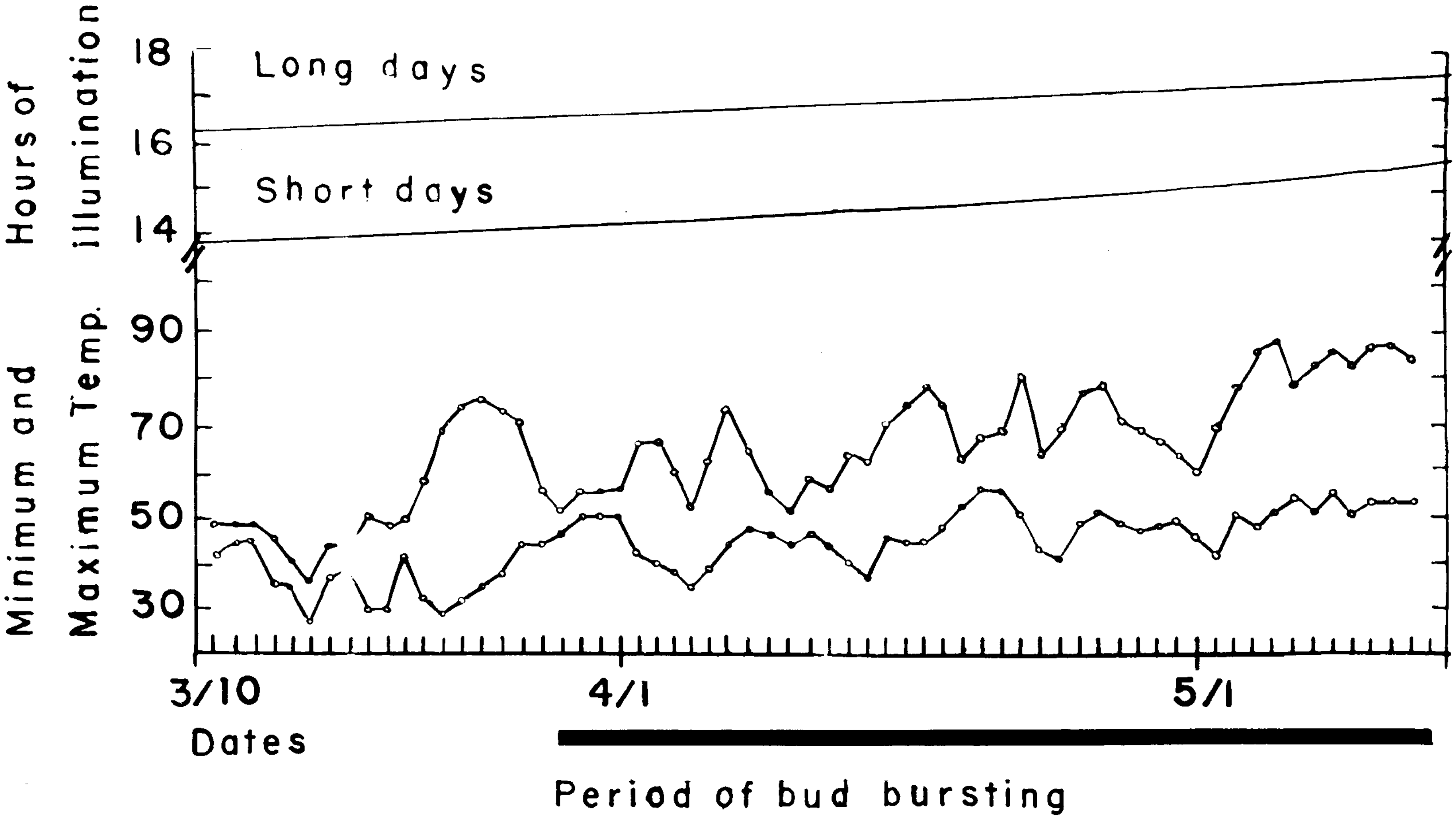
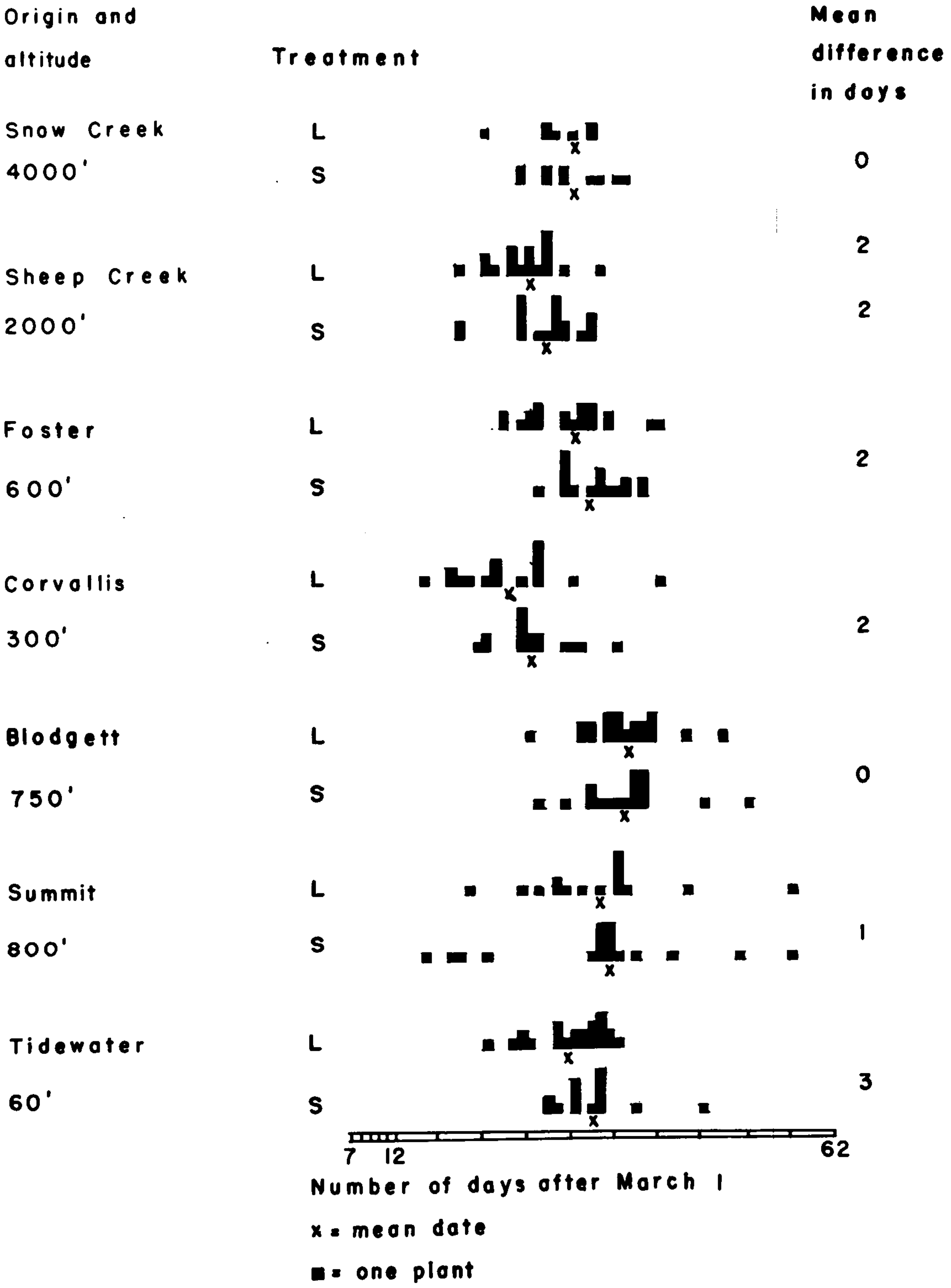
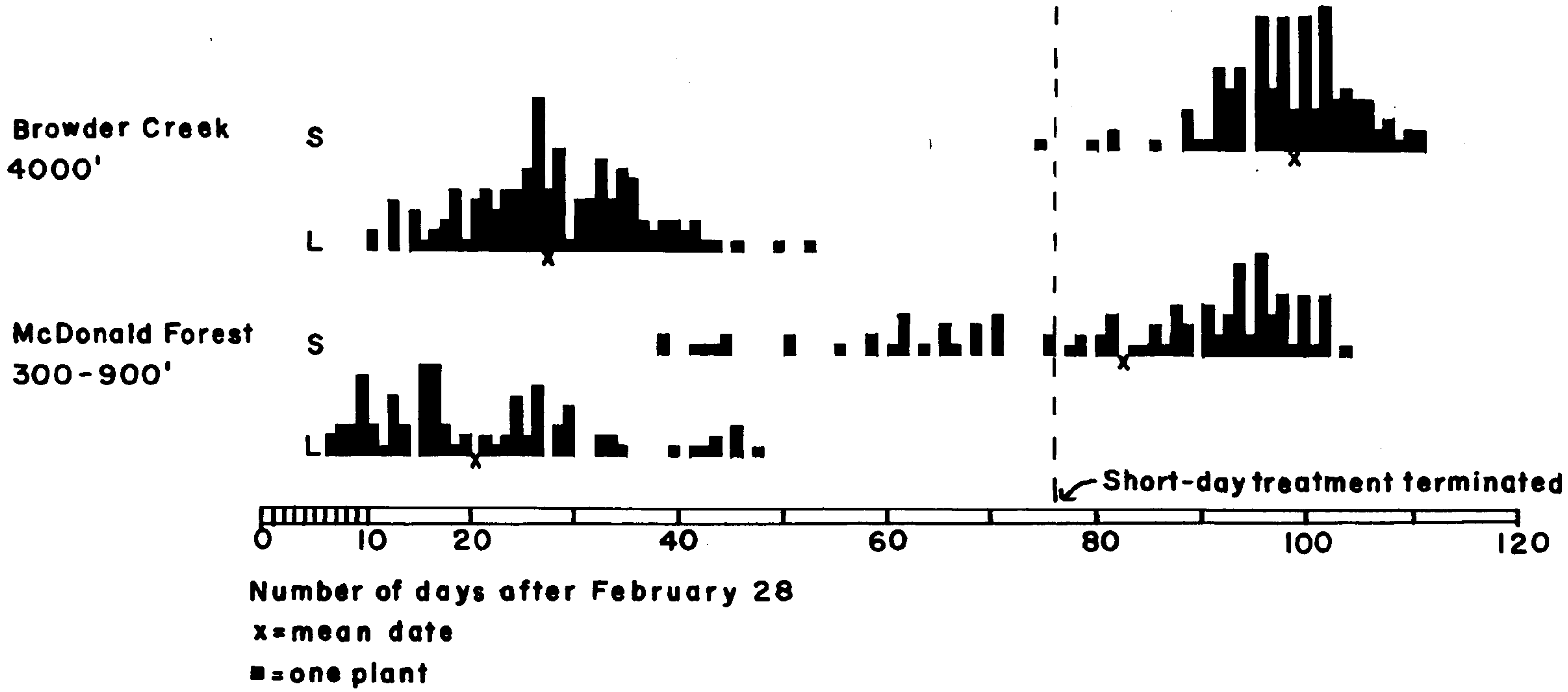

Hours of illumination
18
16
14
Long days
Short days
Minimum and Maximum Temp.
90
70
50
30
3/10
4/1
5/1
Dates
Period of bud bursting

Fig. 13. Dates of bud burst in Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) when treated with normal (S) and long (L) days as indicated in Figure 12. Spring 1956.


Origin and altitude
Treatment
Mean difference in days
Snow Creek 4000'
L
S
0
Sheep Creek 2000'
L
S
2
2
Foster 600'
L
S
2
Corvallis 300'
L
S
2
Blodgett 750'
L
S
0
Summit 800'
L
S
1
Tidewater 60'
L
S
3
7
12
62
Number of days after March 1
x = mean date
■ = one plant

two weeks at 5^{o}C. and sown in pots in the greenhouse in November. After germination the seedlings were given additional light each day from 5 p.m. to 11 p.m. from four 40 Watt flourescent and one 40 Watt incandescent lamp suspended three feet above the plants. From December 15 the plants were treated with short days (nine hours) to induce dormancy. The plants were covered with black, light-proof cloth each day at 5 p.m. and uncovered at 8 a.m. By February 1 all plants had formed a dormant, terminal bud. A total of 151 plants from Browder Creek and 95 from McDonald Forest were then treated with long days (nineteen hours) and 128 plants from Browder Creek and 111 from McDonald Forest were treated with short days (nine hours). The mean date of bud burst of the plants from McDonald Forest was significantly earlier than that of the plants from Browder Creek at the five percent level of significance ("t-test"). This was true under both long and short days (Fig. 14). The greater photoperiodic sensitivity of the plants from high elevations is evidenced by the fact that very few of the buds on plants from Browder Creek opened under short-day treatment, whereas the buds opened on several of the plants from low elevation (McDonald Forest). However, both high- and low-elevation plants showed a very abnormal type of growth. The emerging needles did not elongate fully and practically no internode extension took place. The opened buds

Fig. 14. Dates of bud burst in three-months old Douglas-fir seedlings from high and low elevations when grown in the greenhouse since germination and treated with nine hour photoperiods (S) and nineteen hour photoperiods (L). Spring 1957.


Browder Creek
4000'
S
L
McDonald Forest
300-900'
S
L
Short-day treatment terminated
0
10
20
40
60
80
100
120
Number of days after February 28
x=mean date
■=one plant

appeared as compact rosettes of short needles. A similar effect of short days on leaf elongation and internode extension was observed by Kramer (21) in red gum (*Liquidambar styraciflua* L.) and by Wareing (63) in Scots pine. By May 15, about a month after the buds on some of the plants under the short days had opened, no internode extension had yet taken place. Since there were no indications that the rest of the plants would start growth under short days this treatment was discontinued and the plants exposed to normal day-length. A month after the short-day treatment was discontinued all plants had started growth with normal internode extension and needle elongation.

Conclusion.

Photoperiod has a pronounced influence on time of bud burst in three to seven year old Douglas-fir seedlings. Long photoperiods (nineteen hours) hasten bud burst. This effect was found greatest in plants from high elevations. Short photoperiods (nine hours) almost completely prevented bud burst, particularly in plants from high altitudes.

The observed differences in time of bud burst among altitudinal ecotypes of Douglas-fir may tentatively be ascribed to genetic differences with regard to response to the natural increase in day-length during spring.

High-elevation plants may require a longer day for bud burst than low-elevation plants. However, the high photoperiodic sensitivity of the high-elevation plants may also be attributable to inadequate chilling during the winter months. Plants from high elevations may require a longer period of chilling than plants from low elevations. The chilling requirement of the high-elevation plants may not have been met by the short and mild winter at Corvallis which may result in increased photoperiodic sensitivity (67).

THE INFLUENCE OF VARYING DEGREES OF WINTER CHILLING ON THE TIME OF BREAK OF DORMANCY

Gustafson (12), Olmsted (38), and Wareing (68) showed that long days hasten break of dormancy in unchilled plants of a number of forest tree species whereas long days have little or no effect on chilled plants. Intra-specific variations in chilling requirements have been demonstrated in fruit trees (23). Similar intra-specific variations may be assumed to exist in forest tree species. High-elevation plants may require a longer period of winter chilling to break dormancy than plants from low elevations where the winters are shorter. Inadequate chilling of the high-elevation plants may explain the fact that long days hastened bud burst in these plants whereas long days had little or no effect on the low-elevation plants (Fig. 11). Comparisons between the mean dates of bud burst of the three- to seven-year old Douglas-fir seedlings collected along the east-west transect (Fig. 1) when treated with different photoperiods and temperatures illustrate well the effect of long photoperiods and/or chilling. The difference between the earliest and latest mean dates of bud burst of the plants from the temperature controlled cabinets (Fig. 10) was 24 days when exposed to nine-hour photoperiods and only 11 days when exposed to 15-16-hour photoperiods (Fig. 15 center). The long photoperiods may have hastened bud burst in the plants from high elevations because their chilling requirements were not met by the mild winters at Corvallis. This is further evidenced by the fact that plants brought into the greenhouse on February 1st and exposed to high temperatures (65-80°F. day and night) and normal day-length showed a difference of 27 days (Fig. 15, left) as compared to only 11 days for plants kept out-of-doors for the whole winter (Fig. 15, right.).

The effect of chilling was further demonstrated by the following experiment. On April 1, 1956 seeds from seven localities in the Pacific Northwest (Fig. 17) were sown in pots in the greenhouse. After germination twenty to thirty plants from each source were moved out-of-doors while another twenty to thirty plants from each source were kept in the greenhouse until January 15. On January 15, 1957 the plants kept out-of-doors were moved into the greenhouse adjacent to the plants kept in the greenhouse from germination. Both groups were then exposed to nineteen-hour photoperiods. The plants which had been kept in the greenhouse (i.e., no chilling) broke dormancy in a very irregular manner (Fig. 17) with the latest plants breaking dormancy up to 65 days after the earliest (e.g., the plants from Verlot, Mt. Baker National Forest). The plants which had been exposed to winter temperatures to January 15, on the other hand, broke dormancy during much shorter periods varying from ten to

Fig. 15. Mean dates of bud burst in three to seven years old Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) when treated with various photoperiods and temperatures. Spring 1956.

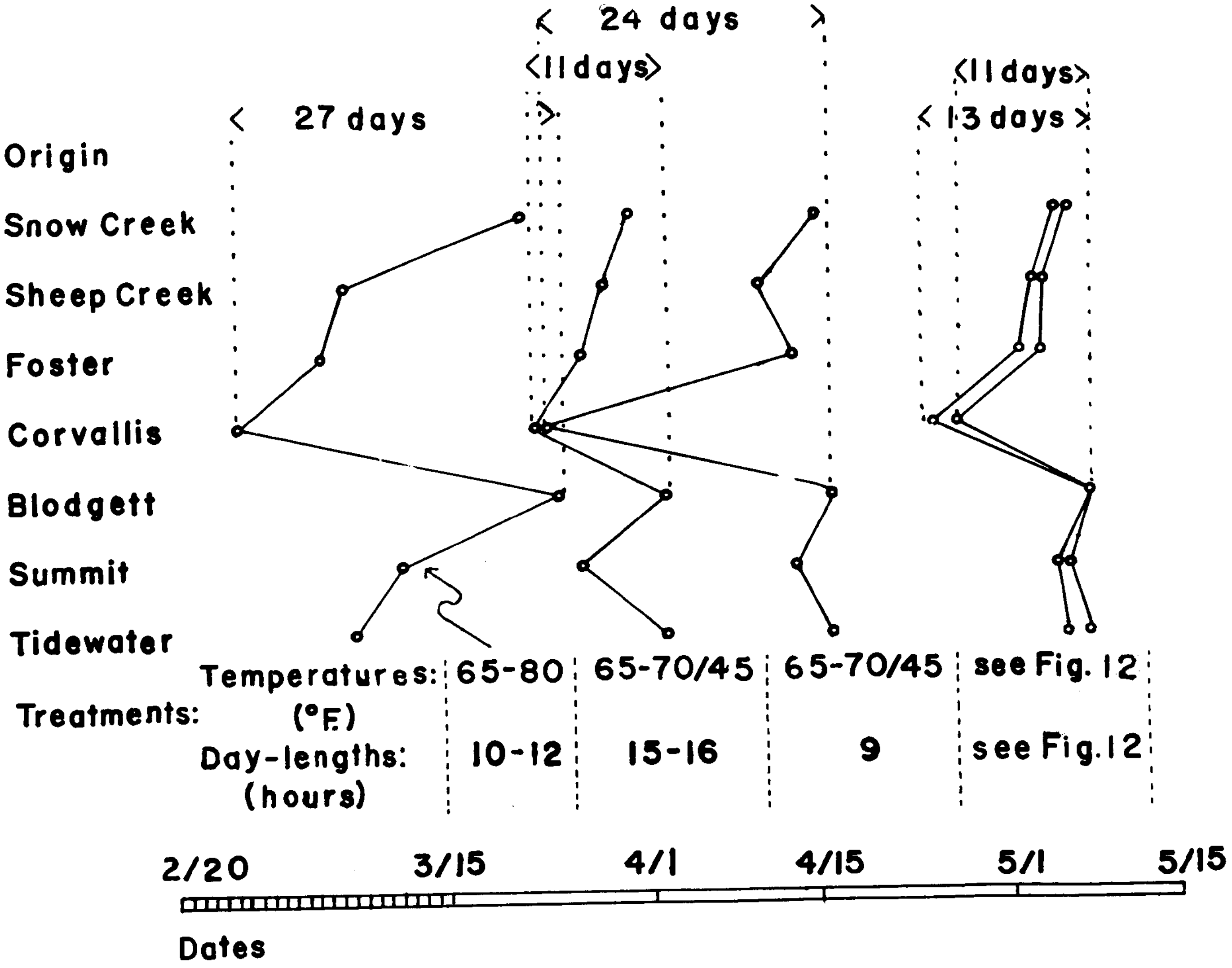

24 days
11 days
11 days
27 days
13 days
Origin
Snow Creek
Sheep Creek
Foster
Corvallis
Blodgett
Summit
Tidewater
Treatments:
Temperatures: (°F)
65-80
65-70/45
65-70/45
see Fig. 12
Day-lengths: (hours)
10-12
15-16
9
see Fig. 12
2/20
3/15
4/1
4/15
5/1
5/15
Dates

Fig. 16. Localities in the Pacific Northwest from which seed was obtained.

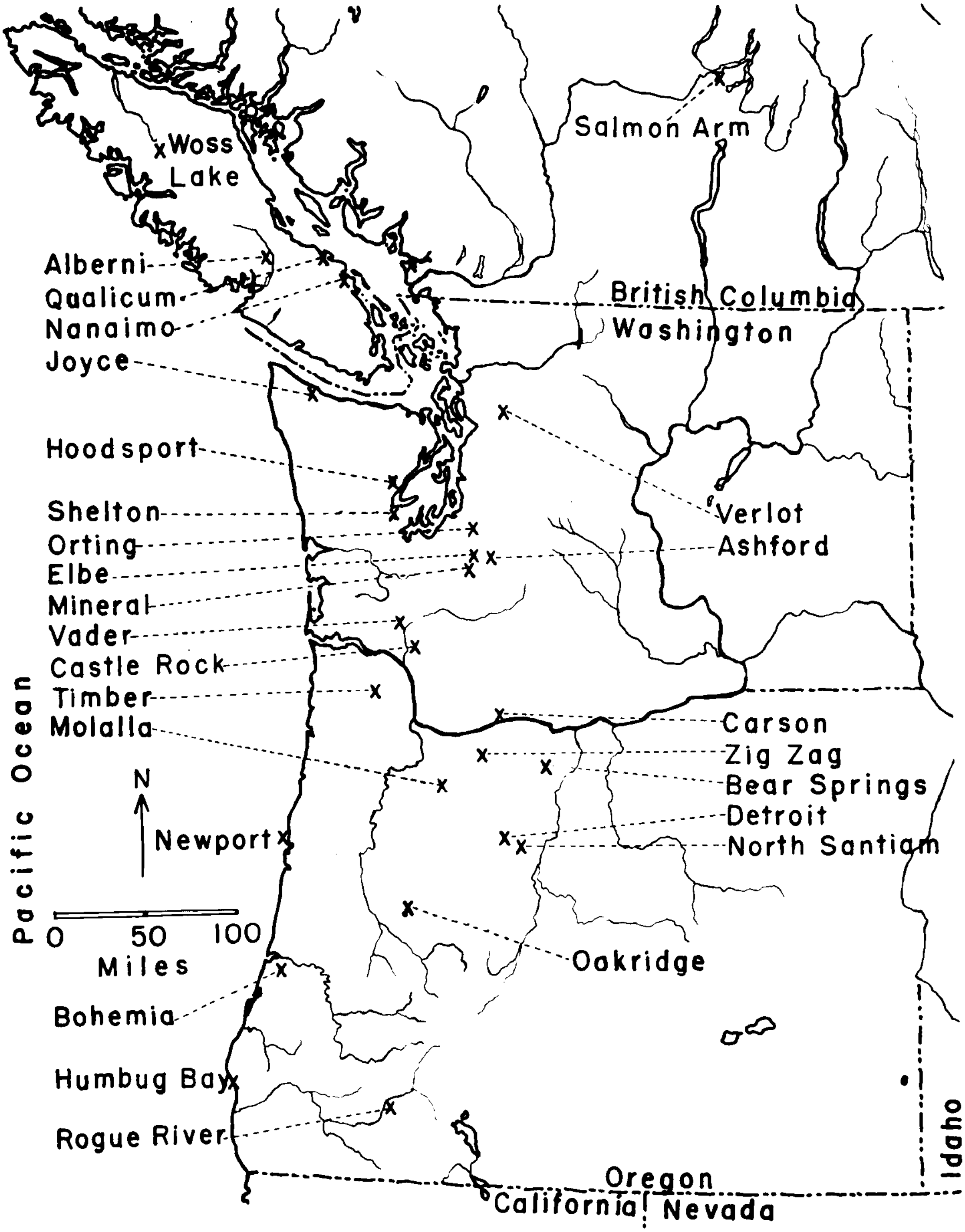
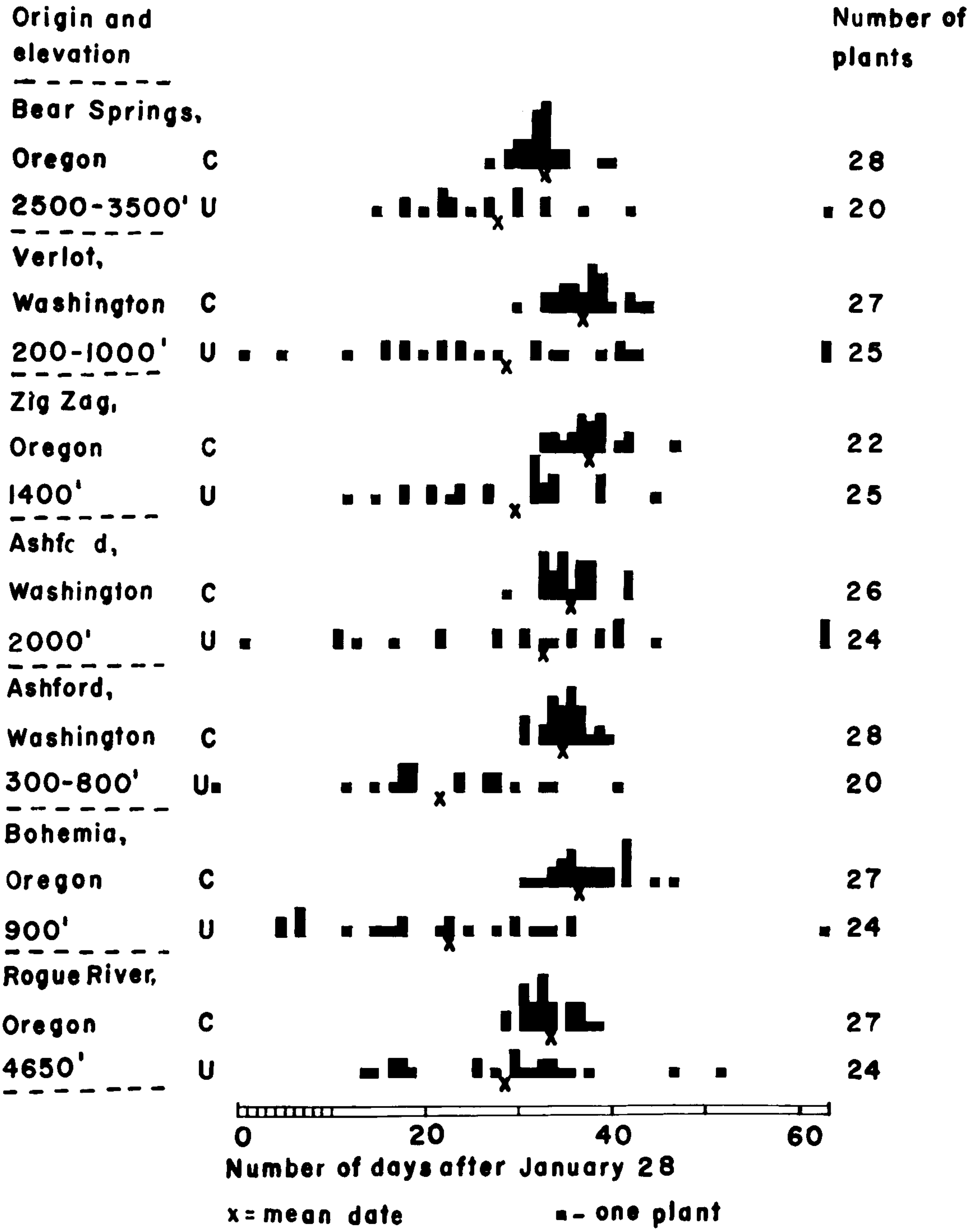

Woss Lake
Salmon Arm
Alberni
Qualicum
Nanaimo
Joyce
British Columbia
Washington
Hoodsport
Verlot
Shelton
Orting
Ashford
Elbe
Mineral
Vader
Castle Rock
Timber
Carson
Molalla
Zig Zag
Bear Springs
N
Detroit
Newport
North Santiam
Pacific Ocean
0 50 100
Miles
Oakridge
Bohemia
Humbug Bay
Rogue River
Idaho
Oregon
California
Nevada

Fig. 17. Dates of bud burst in chilled (C) and unchilled (U) one-year old Douglas-fir seedlings. For location of seed sources see Fig. 16. Winter 1957.


Origin and elevation
Number of plants
Bear Springs, Oregon 2500-3500'
C 28
U 20
Verlot, Washington 200-1000'
C 27
U 25
Zig Zag, Oregon 1400'
C 22
U 25
Ashford, Washington 2000'
C 26
U 24
Ashford, Washington 300-800'
C 28
U 20
Bohemia, Oregon 900'
C 27
U 24
Rogue River, Oregon 4650'
C 27
U 24
0
20
40
60
Number of days after January 28
x = mean date
■ - one plant

seventeen days (Fig. 18).

Conclusion.

High temperatures during the dormant period delay bud burst in Douglas-fir seedlings from high elevations as compared to plants from low elevations. This effect of high temperatures may partly be eliminated by long photoperiods (19 hours). The observed differences in the effect of long photoperiods upon high- and low- elevation plants, respectively, may therefore be ascribed partly to differences in chilling requirements. Similarly, the differences in the time of bud burst observed between high- and low-elevation plants grown under natural conditions at Corvallis (Fig. 4 and 5) may also be ascribed, at least partly, to differences in chilling requirements. The chilling requirements of the high-elevation plants may not have been met by the mild and short winters at Corvallis thus causing a delay in bud burst.

GENETIC DIFFERENCES WITH REGARD TO THE TIME OF ONSET OF DORMANCY

The onset of dormancy in Douglas-fir is characterized by a gradual reduction in growth rate and the formation of a terminal, dormant bud. Both of these processes extend over several weeks. The time of onset of dormancy (defined as cessation of height growth) is, consequently, difficult to determine with any great degree of exactness. However, the week during which height growth ceased may be determined by weekly height measurements.

Pauley and Perry have shown that plants of western balsam poplar (Populus trichocarpa Hook.) native to areas with a short frost-free period stop height growth earlier than plants native to areas with a long frost-free period. The greatest differences in time of cessation of height growth may therefore be expected between plants native to areas which differ greatly with regard to length of frost-free period. In the Pacific Northwest such areas are represented by high elevations in the Cascades with a frost-free period of less than 90 days and areas along the coast with a frost-free period of more than 200 days.(60)

During the fall of 1956 seed were obtained from the following areas with the object of determining differences in time of cessation of height growth:

1) Browder Creek, Santiam Pass, Oregon, (Fig. 1) at 4000 feet elevation with a frost-free period

of less than 90 days. Seeds from this area were collected from three single trees growing adjacent to each other.

2) Detroit, Oregon (Fig. 16), at 3600 feet elevation with a frost-free period of less than 90 days. This is a stand collection as are all the following collections.
3) Eddyville, Oregon (Fig. 1), at 100 feet elevation with a frost-free period of more than 200 days.
4) Salmon Arm, interior British Columbia (Fig. 16), at 1900-2120 feet elevation with a frost-free period of less than 90 days (18).
5) Qualicum, Nanaimo, and Alberni on southern Vancouver Island (Fig. 16), at elevations ranging from 180 to 690 feet and with a frost-free period of more than 200 days (18).

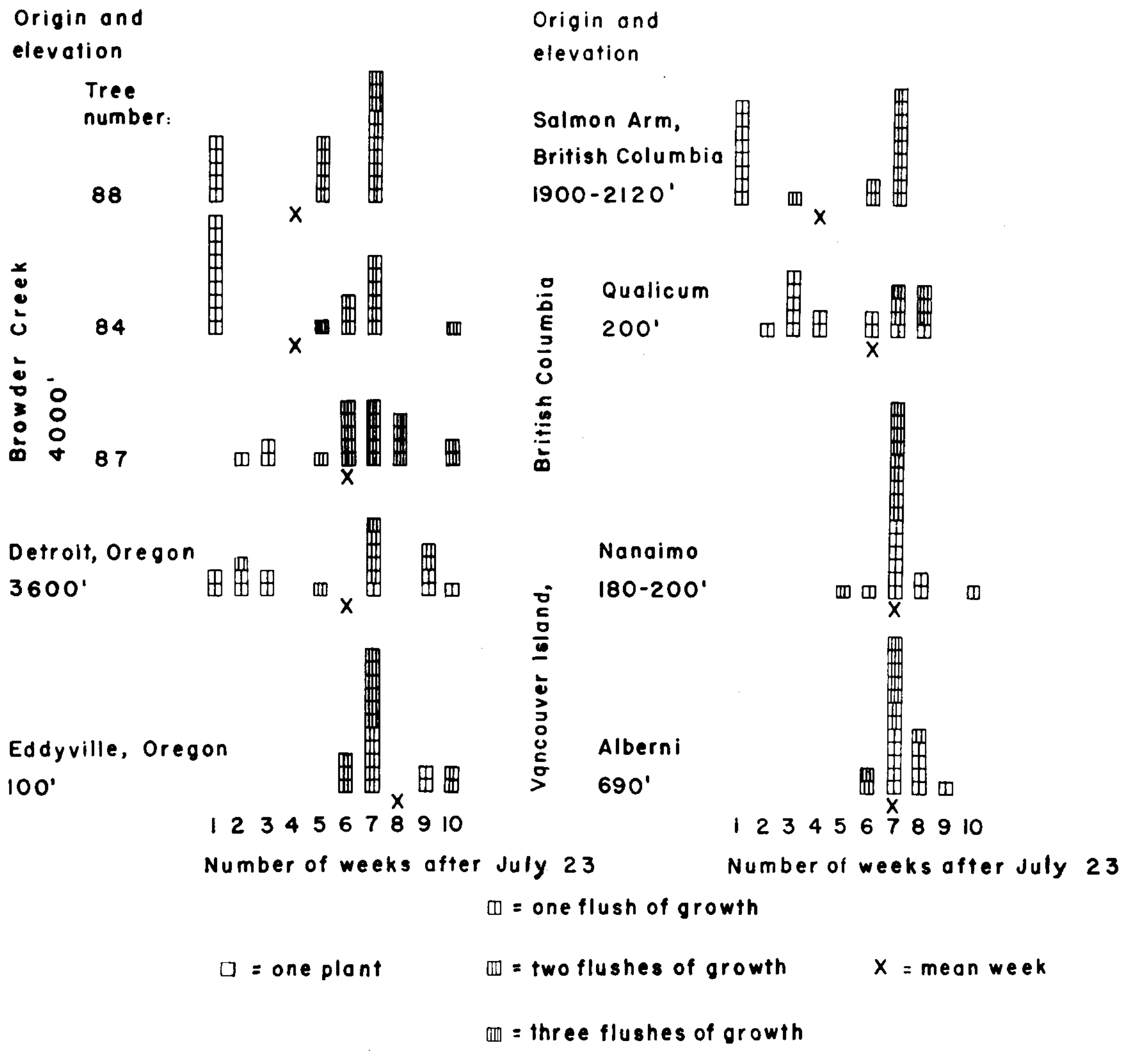
Seeds from these localities were sown in February 1957 in the greenhouse in four-inch pots. After germination the seedlings were thinned to two to three seedlings per pot. On April 2 the plants were moved out-of-doors and placed in cold-frames. Weekly height measurements were started on July 30. A piece of heavy wire was placed along each of twenty randomly selected plants from each source. The height of each plant above the cotyledonary node was marked on the wire each week. The week of cessation of height growth was defined as the week in which no increase in height from the previous week could be detected.

The plants native to areas with a short frost-free period (Browder Creek, Detroit, and Salmon Arm) stopped height growth considerably earlier than the plants native to areas with a long frost-free period (Vancouver Island and Eddyville). The mean weeks of cessation of height growth for the former varied from the fourth to the sixth week after the week of July 23, whereas for the latter the mean weeks varied from the sixth to the eigth week (Fig. 18). The greatest mean difference (four weeks) is between plants from high elevations and those from the coastal areas. This difference may actually be greater than indicated in Figure 18 since some of the selected plants had stopped height growth prior to July 30 when the measurements were started. This was particularly true for the plants from Salmon Arm, B.C.. The maximum average difference may therefore conservatively be estimated to be at least four weeks.

These differences in time of cessation of height growth may be ascribed to genetic differences in the response of the plants to the environmental conditions of the experimental area. Consequently, they are not necessarily of the same magnitude as those between the plants growing in their native habitats.

Each plant measured was also examined as to the

Fig. 18. Time of cessation of height growth in ten months old Douglas-fir seedlings from nine different localities in the Pacific Northwest when grown at Corvallis. The number of vertical lines through each square indicates the number of flushes of growth produced during the summer. The number of plants indicated to have stopped height growth during the first week after July 23 represents the number of plants which had stopped height growth prior to the first height measurement on July 30. For location of seed sources see Fig. 16 and 1.


Origin and elevation
Tree number:
88
84
87
Browder Creek 4000'
Detroit, Oregon 3600'
Eddyville, Oregon 100'
1 2 3 4 5 6 7 8 9 10
Number of weeks after July 23
Origin and elevation
Salmon Arm, British Columbia 1900-2120'
British Columbia
Qualicum 200'
Vancouver Island,
Nanaimo 180-200'
Alberni 690'
1 2 3 4 5 6 7 8 9 10
Number of weeks after July 23
□ = one plant
◫ = one flush of growth
⊞ = two flushes of growth
▥ = three flushes of growth
X = mean week

number of flushes of growth made during the summer (Fig. 18). The high elevation plants remained dormant for a longer period after the first flush of growth than did the low-elevation plants. For that reason the spread in time of cessation of height growth appeared greater in the high-elevation plants than in the low-elevation plants (Fig. 18). In the latter the flushes followed each other rapidly with only short periods of dormancy. Whereas the dormancy between flushes of growth in the high-elevation plants was characterized by the formation of a distinct, terminal bud, the buds formed in the low-elevation plants were indistinct, of short duration, and difficult to detect.

The differences in time of cessation of height growth among the various sources were reflected by the total heights of the seedlings at the end of the growing period. The plants which stopped growth early attained only small heights compared to those which continued growth late in the season (Fig. 19). Thus, the plants from Salmon Arm, B.C. attained an average height of only 22 mm as compared to 72 mm (Qualicum), 86 mm (Nanaimo), and 112 mm (Alberni) for the plants from Vancouver Island. Similarly, the plants from Browder Creek attained average heights of only 55 mm (tree #88), 75 mm (tree #87), and 35 mm (tree #84) as compared to 151 mm for the plants from Eddyville.

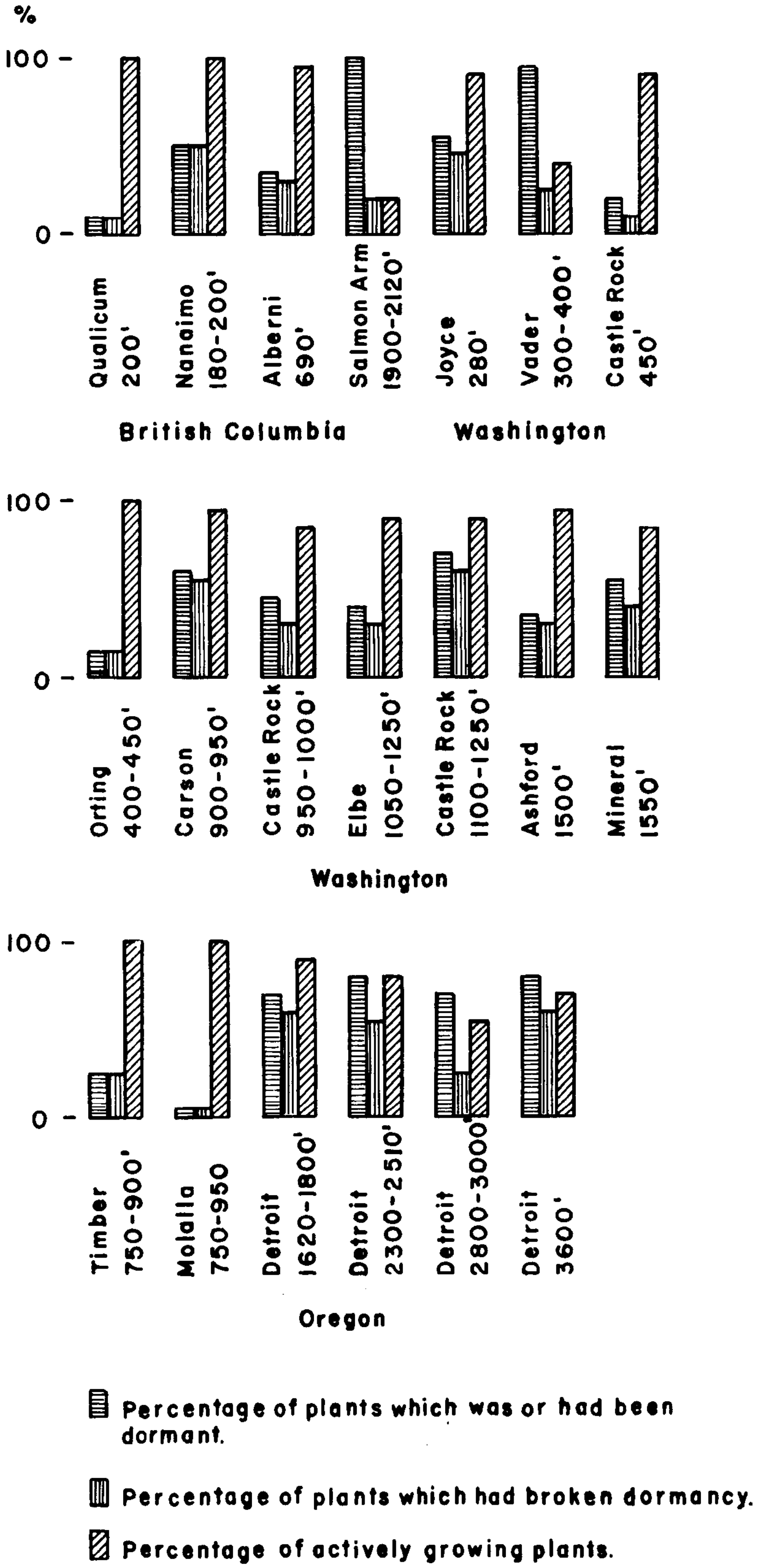
Fig. 19. Comparison between ten-months old Douglas-fir seedlings of different origins sown February 1957. From left to right: Salmon Arm, British Columbia, 1900-2120 feet elevation; Qualicum, Vancouver Island, 200 feet elevation; Browder Creek, Santiam Pass, Oregon, 4000 feet elevation (Tree #87); and Eddyville, Oregon, 100 feet elevation. For locations of seed sources see Figs. 1 and 16. October 1957.

The greatest differences in the time of cessation of height growth (and total height) are found between plants from coastal climates (Vancouver Island and Eddyville) and plants from more montane climates (Salmon Arm and Browder Creek). Although Eddyville is located more than 300 miles to the south of southern Vancouver Island the climatic conditions at these two localities are very similar and the frost-free periods are between 200 and 240 days, whereas at Browder Creek, only approximately 100 miles east of Eddyville, the climate is considerably more severe and the frost-free period less than 90 days.

Differences in time of cessation of height growth can also be detected simply by observations of the percentage of dormant plants at a certain date. Such observations were made on July 8th, 1957, on plants from twenty different sources (Fig. 20) sown in February 1957 in the greenhouse and placed out-of-doors in cold-frames on April 2. Twenty randomly selected plants from each source were observed as to dormancy, including earlier dormancies (i.e., some of the plants had at this time started a second flush of growth). The persistance of the bud scales or bud scale scars made such observations relatively easy.

All of the plants from interior British Columbia (Salmon Arm) had gone into dormancy once prior to July 8th and only twenty percent of these plants had started a

Fig. 20. Percentages of dormant and actively growing five-month old Douglas-fir seedlings from twenty localities in the Pacific Northwest when grown at Corvallis. For location of seed sources see Fig. 16.


%
100 -
0 -
Qualicum 200'
Nanaimo 180-200'
Alberni 690'
Salmon Arm 1900-2120'
Joyce 280'
Vader 300-400'
Castle Rock 450'
British Columbia
Washington
100 -
0 -
Orting 400-450'
Carson 900-950'
Castle Rock 950-1000'
Elbe 1050-1250'
Castle Rock 1100-1250'
Ashford 1500'
Mineral 1550'
Washington
100 -
0 -
Timber 750-900'
Molalla 750-950
Detroit 1620-1800'
Detroit 2300-2510'
Detroit 2800-3000'
Detroit 3600'
Oregon
▤ Percentage of plants which was or had been dormant.
▥ Percentage of plants which had broken dormancy.
▨ Percentage of actively growing plants.

second flush of growth (Fig. 20). Similarly, a high percentage of the plants from four localities at high elevations near Detroit, Oregon, was dormant on or prior to July 8th. Relatively few of the plants native to areas with a long frost-free period (Vancouver Island) had gone into dormancy and almost all of these had started a second flush of growth.

All of these plants were growing under essentially the same environmental conditions. The observed differences in time of cessation of height growth may therefore be ascribed to genetic differences.

Conclusion.

Genetic differences with regard to the time of cessation of height growth among Douglas-fir seedlings of different origins have been demonstrated. Plants native to areas with a short frost-free period stopped growth at least four weeks earlier than plants native to areas with a long frost-free period.

Plants native to areas with a short frost-free period were characterized by a long period of dormancy between the first and second flush of growth, whereas in plants native to areas with a long frost-free period the flushes of growth followed each other rapidly with only short periods of dormancy.

The early cessation of height growth in the plants native to areas with a short growing season is reflected by their short heights at the end of the season compared to the three to four times greater heights attained by the plants native to areas with a long growing season.

THE INFLUENCE OF PHOTOPERIOD UPON THE TIME OF ONSET OF DORMANCY

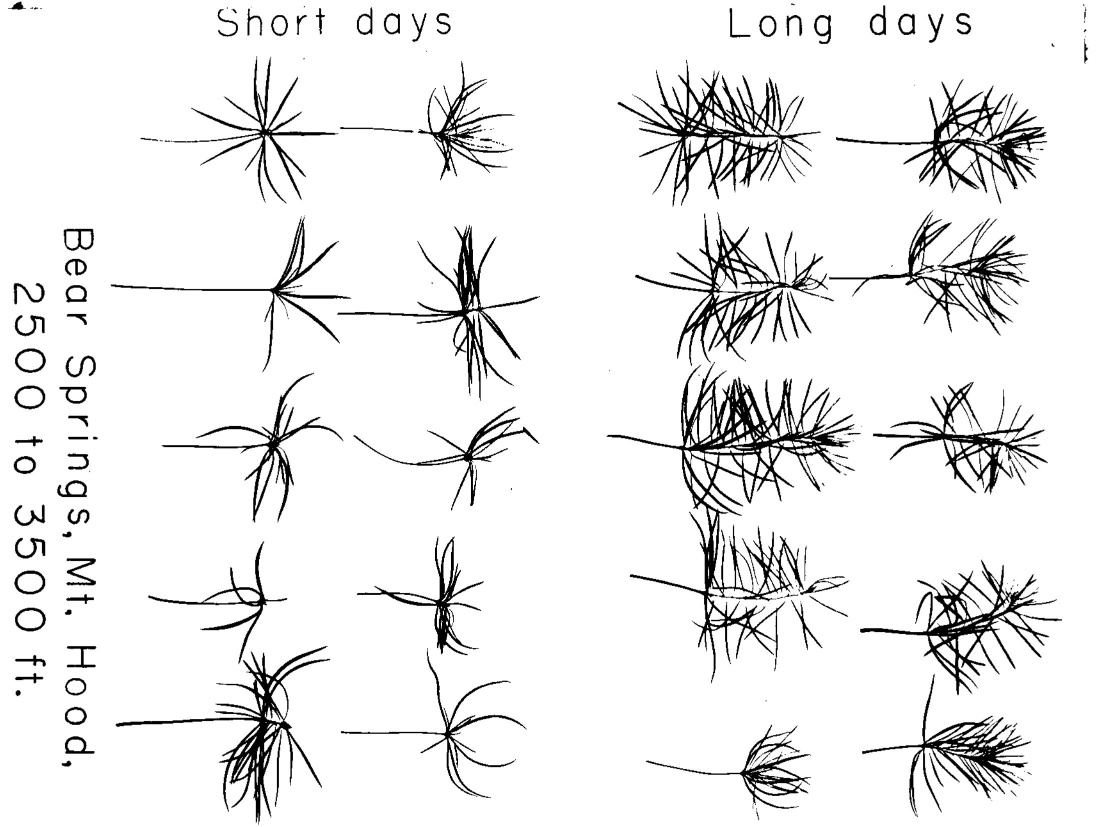
Short photoperiods hasten onset of dormancy in a number of forest tree species. An experiment was set up in 1956 to determine the effect of short photoperiods upon the time of onset of dormancy in Douglas-fir seedlings.

Seeds from nine different localities in the Pacific Northwest were sown in cans in the greenhouse on April 1st 1956. Half of the plants from each locality was grown under a nine-hour photoperiod and the other half under a nineteen-hour photoperiod. The experiment was repeated in two different greenhouses. On July 1st the plants exposed to the short photoperiods had all stopped height growth and formed a dormant, terminal bud whereas the plants exposed to the long photoperiods were still actively growing (Fig. 21). For comparative purposes random samples of five plants from each locality and experiment were dried in a plant press and photographed (Figs. 22-29). The plants exposed to short photoperiods had produced fewer needles than those exposed to long photoperiods. Furthermore, the difference in number of leaves between plants exposed to short photoperiods and plants exposed to long photoperiods appeared to vary with the seed source (cf. Fig. 22 with Fig. 29) indicating a diversity in response to photoperiod.

Fig. 21. Three months old Douglas-fir seedlings grown under long days (19 hours) and short days (9 hours) since germination April 15, 1956. Photographed July 15, 1956.

Fig. 22. Three months old Douglas-fir seedlings from Bear Springs, Mt. Hood National Forest, Oregon, treated with long and short days since germination.

Fig. 23. Three months old Douglas-fir seedlings from Bohemia, Umpqua National Forest, Oregon, treated with long and short days since germination.


Short days
Long days
Bear Springs, Mt. Hood, 2500 to 3500 ft.

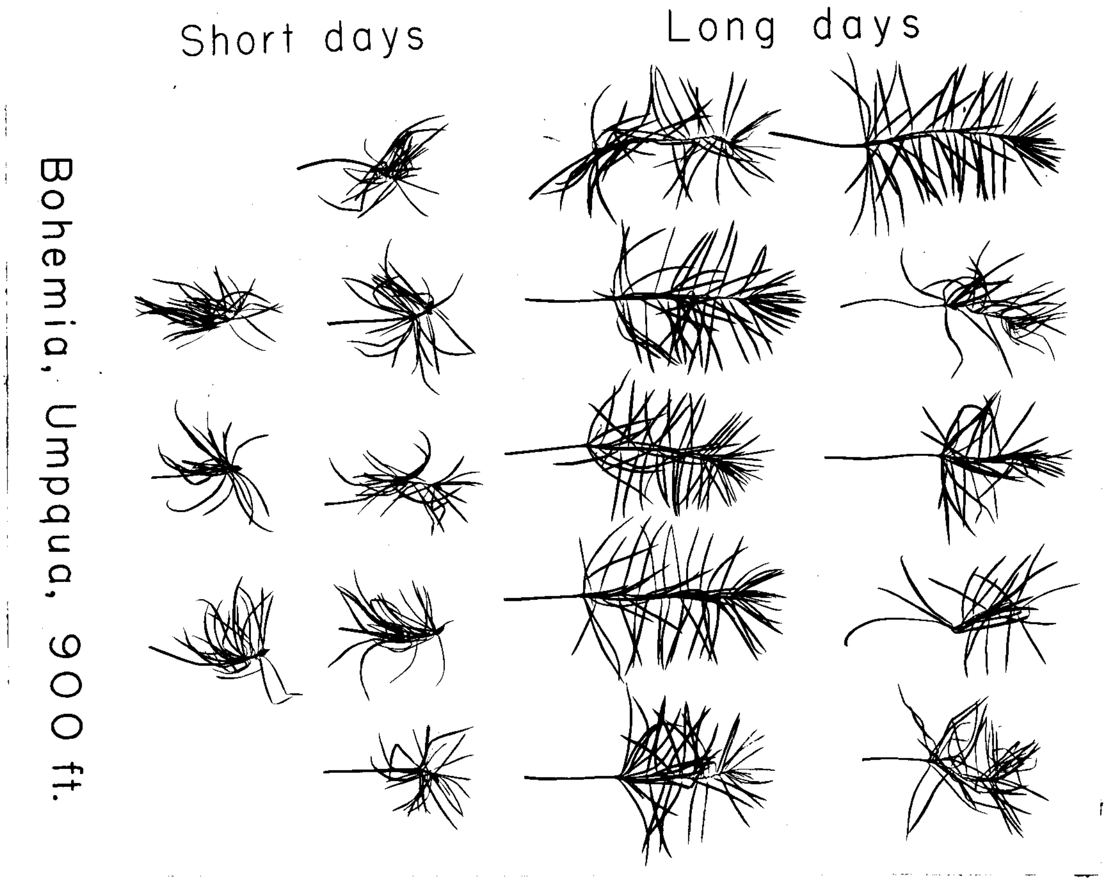
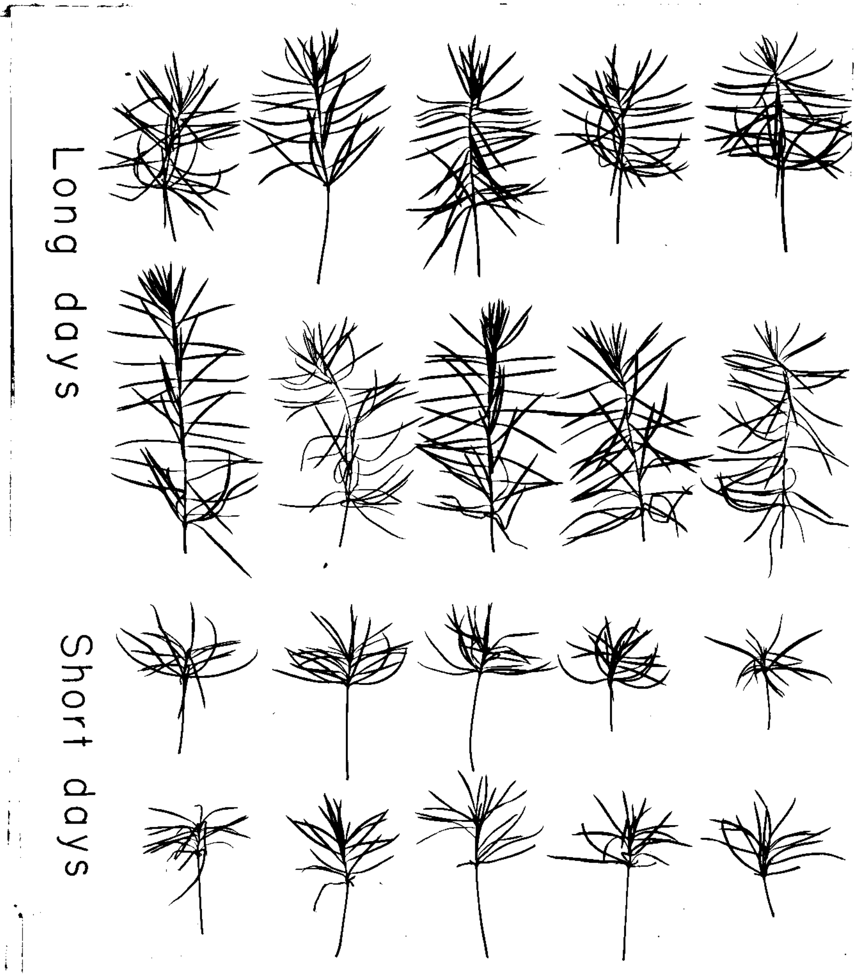

Short days
Long days
Bohemia, Umpqua, 900 ft.

Fig. 24. Three months old Douglas-fir seedlings from Ashford, Snoqualmie National Forest, Washington, treated with long and short days since germination.

Fig. 25. Three months old Douglas-fir seedlings from Rogue River National Forest, Oregon, treated with long and short days since germination.

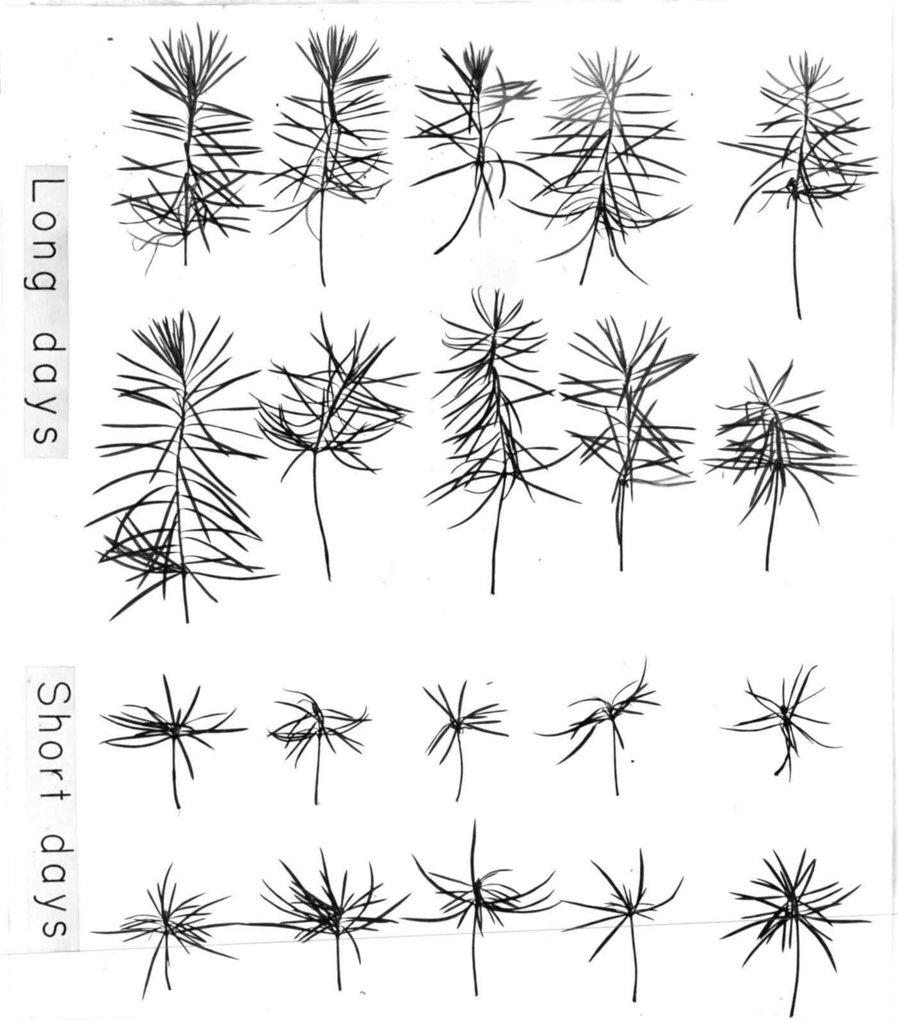
Rogue River, 4650 ft.



Ashford, Snoqualmie, 2000 ft.

Fig. 26. Three months old Douglas-fir seedlings from North Santiam Pass, Oregon, treated with long and short days since germination.

Fig. 27. Three months old Douglas-fir seedlings from high elevation in Linn County, Oregon, treated with long and short days since germination.

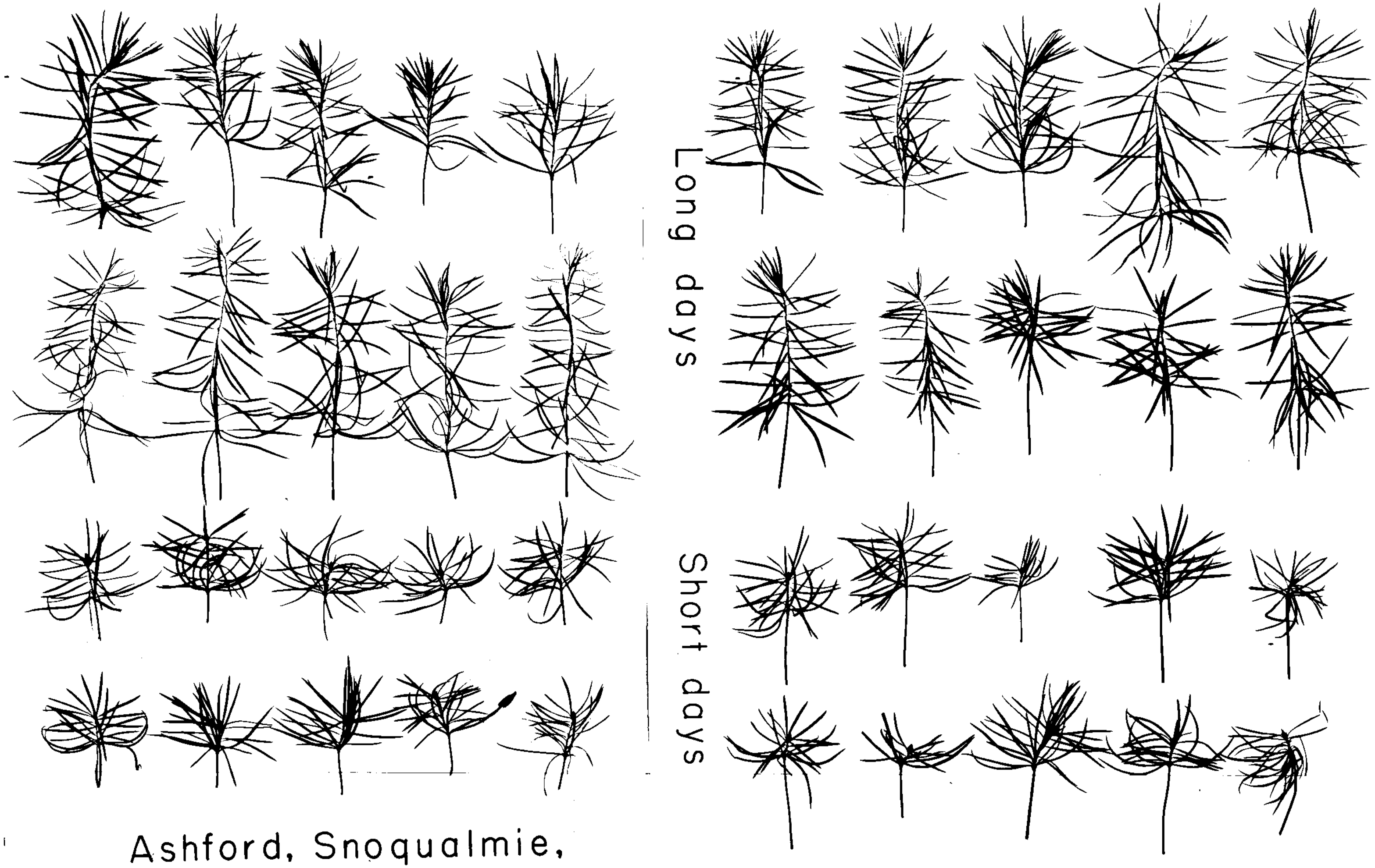


Linn County, 3500 to 4000 ft.

North Santiam Pass, 3600 ft.

Fig. 28. Three months old Douglas-fir seedlings from zig zag, Mt. Hood National Forest, Oregon, when treated with long and short days since germination.

Fig. 29. Three months old Douglas-fir seedlings from Ashford, Snoqualmie National Forest, Washington, when treated with long and short days.



Ashford, Snoqualmie,
300 to 800 ft.

Zigzag, Mt. Hood, 1400 ft.

Diversity in response to photoperiod was further indicated by the following experiment:

Seed from eight different localities in the Pacific Northwest (Table 3) were stratified for two weeks at 5°C. and sown on February 26 in pots in the greenhouse. Plants from each source were exposed to each of the following different photoperiods:

1) 8 a.m. to 5 p.m. -- 9 hours
2) 8 a.m. to 5 p.m. with a "light-break" from 9 p.m. to 10:30 p.m. -- 10½ hours
3) 8 a.m. to 5 p.m. with a "light-break" from 2 a.m. to 3:30 a.m. -- 10½ hours
4) 4 a.m. to 11 p.m. -- 19 hours

All light given in addition to the daylight from 8 a.m. to 5 p.m. was given from a 40 Watt incandescent lamp suspended three feet above the plants. Each source was represented twice in each treatment.

On May 25 twenty plants from each source and treatment were cut off at the soil surface and dried in a plant press. This was done to facilitate the counting of leaves.

The plants from treatment 1 were in all sources the smallest with an average number of leaves of only 14.55 (Table 3). Additional light from 9 p.m. to 10:30 p.m. (treatment 2) increased the average number of leaves to 21.34. If the additional light was given from 2 a.m. to 3:30 a.m. the average number of leaves was increased to 25.16. Thus, although the same total amount of light was

Table 3. Average number of leaves on three-month old Douglas-fir seedlings of different origins when treated with four different photoperiods.

Origin	Treatments								Source Averages
	1		2		3		4		
	Samples		Samples		Samples		Samples		
	1	2	1	2	1	2	1	2	
Oakridge, Oregon	13.4	10.9	21.9	20.3	24.0	25.0	26.1	29.3	
2500-3000 ft.	12.15		21.10		24.50		27.70		21.36
Mineral, Washington	15.9	17.5	20.5	20.0	28.0	26.0	27.0	29.7	
1550 ft.	16.70		20.25		27.00		28.35		23.07
Ashford, Washington	20.5	15.7	20.1	18.3	24.5	25.4	26.2	24.6	
1500 ft.	18.05		19.20		24.95		25.90		22.02
Elbe, Washington	13.9	17.1	26.4	27.5	27.2	26.0	25.5	28.6	
1050-1250 ft.	15.50		26.95		26.60		27.05		24.02
Nanaimo, Vancouver Island	17.1	15.8	19.4	22.4	26.6	24.9	28.3	25.7	
180-200 ft.	16.45		20.90		25.75		27.00		22.52
Nanaimo, Vancouver Island	14.8	17.2	24.4	26.2	24.9	27.3	24.0	24.6	
0-500 ft.	16.00		25.30		26.10		24.30		22.92
Salmon Arm, B. C.	10.1	13.3	19.3	22.4	27.8	24.6	23.5	23.1	
1900-2120 ft.	11.70		20.85		26.20		23.30		20.51
Shuswap Lake (Salmon Arm)	10.8	8.9	16.7	15.6	20.1	20.2	26.5	22.7	
B. C., 1000-1500 ft.	9.85		17.15		20.15		24.60		17.69
Treatment Averages	14.55		21.34		25.16		26.03		

Note: Underlined numbers denote averages of the two samples from each treatment and source. For location of seed sources see Fig. 16.

given in treatments 2 and 3 a greater effect was obtained if the "light-break" was given during the latter half of the dark-period than during the first half. Long-day treatment increased the number of leaves to only 26.03 (treatment 4). A light-break during the latter half of the dark period is thus almost as effective as a long photoperiod. The statistical significance of these results was tested by an analysis of variance (Table 4).

Table 4. Analysis of variance of number of leaves on three-month old Douglas-fir seedlings of different origins when treated with four different photoperiods.

Treatments	Sums of Squares	Degrees of freedom	Mean Squares	F
Treatments (T)	1310.1942	3	436.7314	166.30*
Sources (S)	217.3699	7	31.0528	11.82*
T x S	174.2720	21	8.2986	3.16*
Samples in T x S	84.0350	32	2.6261	
Total	1785.8711	64		

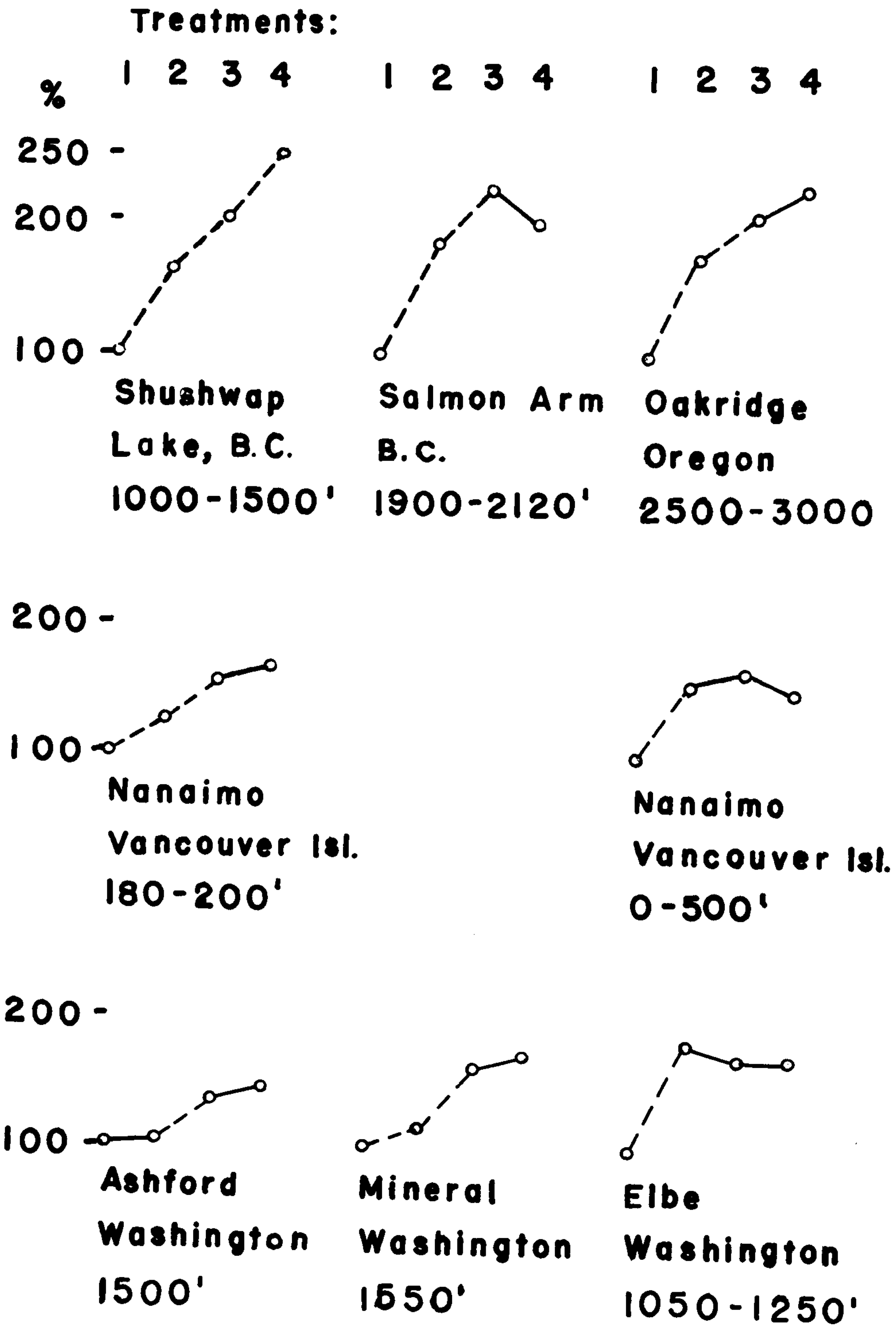
Both the responses to treatments and the sources differ significantly at the five percent level of significance. The least significant difference between the treatment means (LSD) is $\sqrt{\frac{2 \times 2.6261}{8}} \times 2.04 = 1.65$. Since the means appear in order of increasing magnitude in Table 3 any difference between adjacent means greater than 1.65 may be considered as significant at the five percent level. The fact that the responses to treatments 2 and 3 differ significantly even though the total amount of light given was the same in both treatments proves that the periodicity rather than the total amount of light was the governing factor. The responses to the four treatments are therefore of a photoperiodic nature.

Plants from the various localities respond differently to the same treatment as indicated by the significance of the treatment-source interaction in the analysis of variance (Table 4.). The least significant difference between responses to the various treatments within any one group of plants from the same source is $\sqrt{\frac{2 \times 2.6261}{2}} \times 2.04 = 3.30$. The number of leaves developed under the various photoperiods (expressed as percentages of the number of leaves developed under the nine-hour photoperiods) varies widely with the seed source (Fig. 30). Plants from areas with short frost-free periods and continental climates showed a greater response to photoperiod (Shuswap Lake and Salmon Arm, interior British Columbia) than plants from areas with a coastal climate (Nanaimo, Vancouver Island). No direct correlation appears to exist between the length of frost-free period at the seed source and the magnitude of response to photoperiod. This is evidenced from the fact that plants from Nanaimo, Vancouver Island, with a frost-free period of more than 200 days (18) showed almost as great a response to treatment 3 and 4 as did plants from Ashford, Mineral,

Fig. 30. Responses of Douglas-fir seedlings from eight localities in the Pacific Northwest (Fig. 16) when exposed to the following photoperiods since germination February 1957:

1) 8 a.m. to 5 p.m. -- 9 hours
2) 8 a.m. to 5 p.m. with a "light-break" from 9 p.m. to 10:30 p.m. -- 10½ hours
3) 8 a.m. to 5 p.m. with a "light-break" from 2 a.m. to 3:30 a.m. -- 10½ hours
4) 4 a.m. to 11 p.m. -- 19 hours

The number of leaves developed under the various photoperiods is expressed as percentage of number of leaves developed under the nine-hour photoperiod (treatment 1). Broken lines indicate significant differences at the five percent level of significance. For location of seed sources see Fig. 16. May 25, 1957.


Treatments:
1 2 3 4
1 2 3 4
1 2 3 4
%
250
200
100
Shushwap
Lake, B.C.
1000-1500'
Salmon Arm
B.C.
1900-2120'
Oakridge
Oregon
2500-3000
200
100
Nanaimo
Vancouver Isl.
180-200'
Nanaimo
Vancouver Isl.
0-500'
200
100
Ashford
Washington
1500'
Mineral
Washington
1550'
Elbe
Washington
1050-1250'

and Elbe in Washington with frost-free periods of from 140 to 160 days (60). On the other hand, plants from Oakridge, Oregon with a frost-free period of about 180 days (60) showed a much greater response to treatments 3 and 4 than the plants from the three localities in Washington.

The differences in number of leaves between the treatments and sources reflect differences in time of cessation of height growth. The small number of leaves on the plants from treatment 1 is due to the fact that only 34 percent of the seedlings were actively growing at the time of sampling (Table 5). The seedlings from treatment 2 on the other hand, contained 75 percent actively growing seedlings. The corresponding percentages for treatments 3 and 4 were 92 and 98, respectively. Comparisons between plants from different sources <u>within</u> any one treatment clearly reflects the differences in photoperiodic sensitivity, particularly among the plants treated with short days (treatment 1). The plants from interior British Columbia had all stopped growth at the time of sampling. The plants from Vancouver Island, on the other hand, contained 65 to 73 percent actively growing seedlings. A few of the plants treated with long days (treatment 4) from interior British Columbia had stopped growth at the time of sampling whereas all the plants from all the other sources were actively growing. This may indicate that a photoperiod longer than nineteen hours is required to keep

Table 5. Percentages of actively growing Douglas-fir seedlings of different origins when treated with four different photoperiods for three months after germination.

Origin	Treatments								Source Averages
	1		2		3		4		
	Samples		Samples		Samples		Samples		
	1	2	1	2	1	2	1	2	
Oakridge, Oregon	10	0	95	95	95	100	100	100	
2500-3000 ft.	5.0		95.0		97.5		100		74.38
Mineral, Washington	50	40	100	100	100	100	100	100	
1550 ft.	45.0		100		100		100		86.25
Ashford, Washington	45	65	85	85	100	100	100	100	
1500 ft.	55.0		85.0		100		100		85.00
Elbe, Washington	35	25	100	100	100	100	100	100	
1050-1250 ft.	30.0		100		100		100		82.50
Nanaimo, Vancouver Island	70	60	85	100	100	100	100	100	
180-200 ft.	65.0		92.5		100		100		89.38
Nanaimo, Vancouver Island	65	80	95	100	95	100	100	100	
0-500 ft.	72.5		97.5		97.5		100		91.88
Salmon Arm, B. C.	0	0	65	45	90	90	90	85	
1900-2120 ft.	0		55.0		90.0		87.5		58.13
Shuswap Lake, B. C.	0	0	80	55	35	65	100	95	
	0		42.5		50.0		97.5		53.75
Treatment Averages	34.06		74.65		91.88		98.13		

Note: Underlined numbers denote averages of the two samples from each treatment and source. For location of seed sources see Fig. 16.

plants from interior British Columbia actively growing. However, even under continuous illumination plants from interior British Columbia stopped height growth earlier than plants from other localities as indicated by the following experiment. On April 1 seed from six localities in the Pacific Northwest were sown in greenhouse. After germination the plants were exposed to continuous illumination from four 40 Watt fluorescent and one 40 Watt incandescent bulb suspended three feet above the plants. On September 5 a higher percentage of dormant plants was found among the plants native to areas with a continental or montane climate than among plants native to areas with a coastal climate (Table 6).

Table 6. Percentages of dormant plants among seedlings from six localities in the Pacific Northwest when grown under continuous illumination in the greenhouse from germination, April 1, 1956 to September 5, 1956. For location of seed sources see Fig. 1.

Source	Total Number of plants	Percentage of dormant plants
Salmon Arm, British Columbia 2000 feet elevation	22	91
North Santiam, Oregon 3600 feet elevation	29	79
Rogue River, Oregon 3600 feet elevation	27	57
Bohemia, Oregon 900 feet elevation	27	66
Ashford, Washington 2000 feet elevation	25	28

Table 6. Continued.

Source	Total Number of plants	Percentage of dormant plants
Zig Zag, Oregon 1400 feet elevation	28	36

The persistence of differences in time of cessation of height growth even under continuous light indicates that such differences are not due solely to differences in response to photoperiod.

Conclusion.

Photoperiod has a pronounced influence on the time of cessation of height growth in seedlings of Douglas-fir. Short photoperiods (nine hours) hasten cessation of height growth and long photoperiods (nineteen hours) delay cessation of growth. This effect varies with the seed source. Plants from continental climates (interior British Columbia) are more sensitive to changes in photoperiods than plants from coastal climates (Vancouver Island).

THE CORRELATION BETWEEN THE TIME OF ONSET OF DORMANCY AND RESISTENCE TO FROST

Resistence to frost in plants is correlated with the developmental stage of the plants and is often highest during the dormant period (26). Differences in resistence to frost at any given time among plants of different origins may therefore partly be due to differences in developmental stages.

Seed from eight different sources (Fig. 32) were sown in cans in the greenhouse on April 1, 1956. After germination plants from each source were divided into two groups one of which was exposed to nine-hour photoperiods, and the other to nineteen-hour photoperiods. The experiment was replicated in two different greenhouses.

On May 1st, while all plants were actively growing, a preliminary test of frost resistence was made on the plants from each source and treatment were cut off at the soil surface and placed in two-and-a-half inch vials containing a piece of wet cotton. The vials were stoppered tightly with corks. A thermometer was inserted through the cork in three of the vials. All vials were then placed in a shallow dish containing a saturated sodium chloride solution. The vials were placed in a horizontal position in the dish to avoid temperature gradients from the top to the bottom inside the vials. The dish with the vials was placed in the freezing compartment of a household refrigerator and the temperature in the vials brought down to 32°F. during the first 28 hours. During the next twelve hours the temperature was gradually brought down to 18°F. The dish with the vials was then removed from the refrigerator and allowed to warm up at room temperature. The temperature in the vials was recorded at frequent intervals throughout the experiment (Fig. 31). When the ice in the salt solution had melted the plants were removed from the vials and placed on newspaper at room temperature. During the course of a few hours of exposure to room temperature many seedlings lost their turgidity and attained a dull, greenish-brown color while a few remained turgid and fresh-green for more than 24 hours. Three vials had been removed from the refrigerator before the temperature in the vials went below freezing. Seedlings from such vials remained turgid and fresh-green for more than 24 hours. Loss of turgidity and discoloration may thus be ascribed to injury because of exposure to temperatures below freezing.

All seedlings subjected to this test were actively growing. Consequently, most of the seedlings suffered from frost damage. All seedlings treated with long photoperiods were damaged (Fig. 32). Similarly, almost all seedlings treated with short photoperiods were damaged. The only exceptions were some plants from Rogue River and North Santiam Pass (Fig. 32).

Fig. 31. Temperatures employed in three tests (on May 1, June 2, and July 2) of resistence to frost in Douglas-fir seedlings from eight localities in the Pacific Northwest sown in the greenhouse on April 1, 1956.

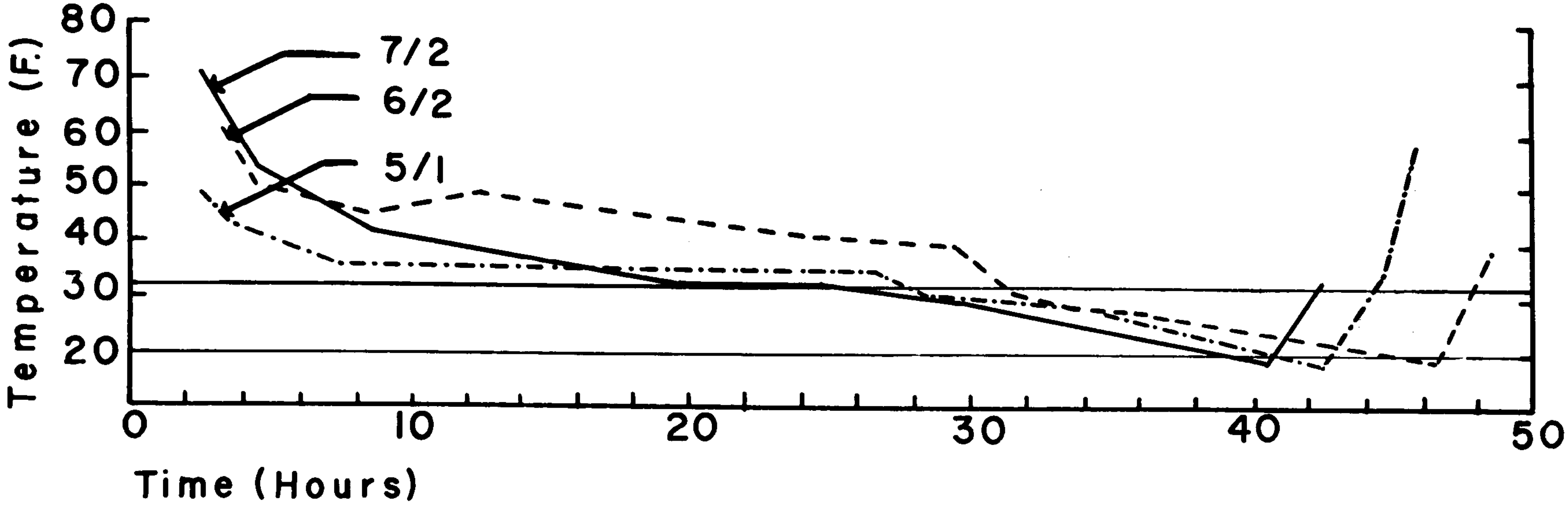
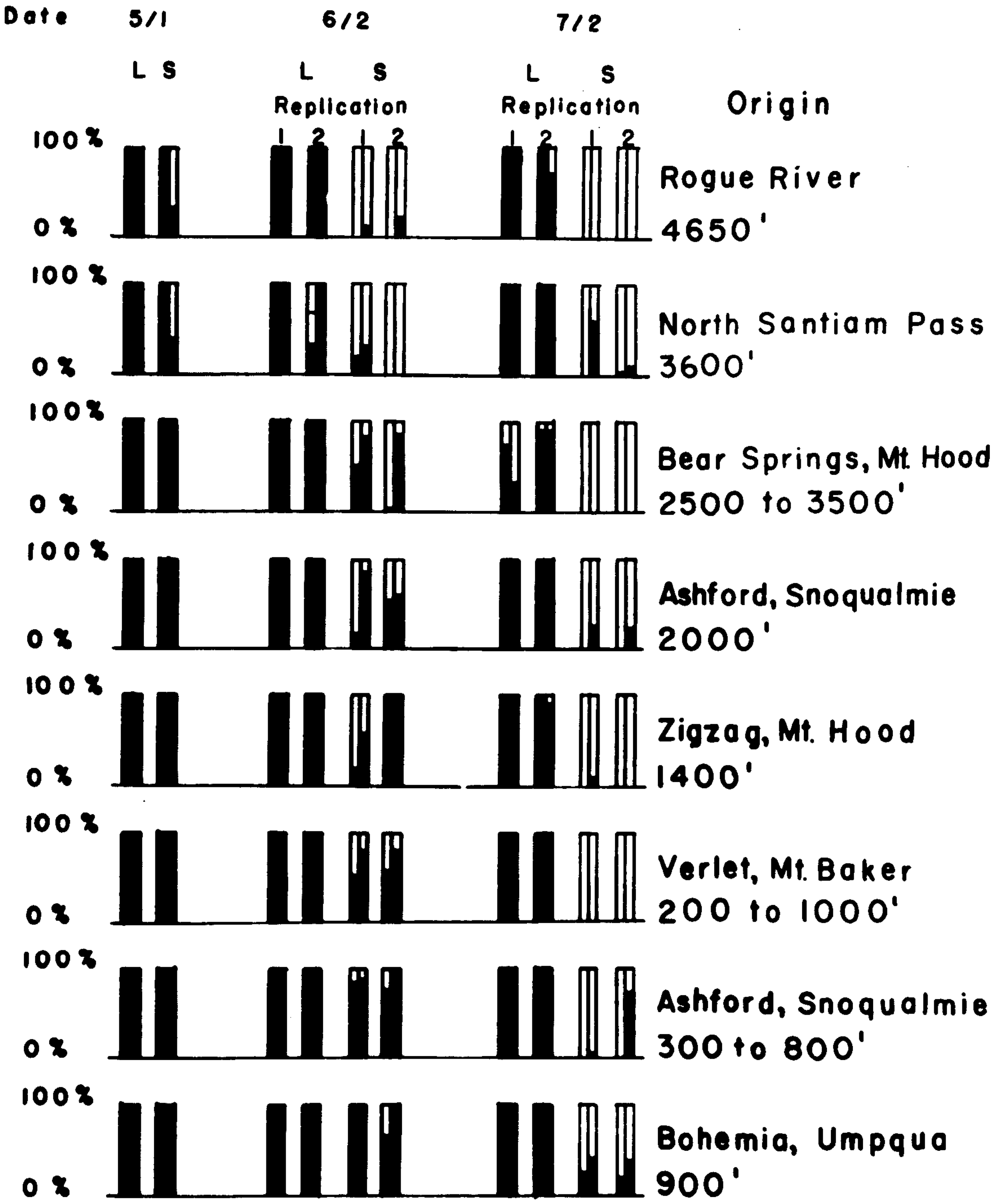

80
70
60
50
40
30
20
Temperature (F.)
7/2
6/2
5/1
0
10
20
30
40
50
Time (Hours)

Fig. 32. The effect of nine-hour photoperiods (S) and nineteen-hour photoperiods (L) on the resistence to frost of Douglas-fir seedlings from eight localities in the Pacific Northwest sown in the greenhouse on April 1, 1956. Tests of resistence to frost were made on May 1, June 2, and July 2, 1956. The left half of each column denotes percentage of actively growing seedlings. The right half denotes percentages of seedlings damaged by frost. For location of seed sources see Fig. 16.


Date
5/1
6/2
7/2
L S
L S
L S
Replication
Replication
1 2 1 2
1 2 1 2
Origin
100%
0%
Rogue River
4650'
North Santiam Pass
3600'
Bear Springs, Mt. Hood
2500 to 3500'
Ashford, Snoqualmie
2000'
Zigzag, Mt. Hood
1400'
Verlet, Mt. Baker
200 to 1000'
Ashford, Snoqualmie
300 to 800'
Bohemia, Umpqua
900'

Although all plants in both treatments from these two sources were actively growing and apparently in the same developmental stage, those treated with short photoperiods were more resistent to low temperatures than those treated with short photoperiods. Moshkov (33) found similar differences in frost resistence between long-day and short-day treated plants of several woody species in spite of no apparent external difference in developmental stage.

On June 2 a similar test was made on a larger scale. Twenty randomly selected plants from each source, treatment and replication were cut off at the soil surface and placed in vials as described above. Some difficulty was encountered in exposing the plants to exactly the same temperatures as in the previous experiment. However, the small differences between the three treatments (Fig. 31) probably does not affect the validity of comparisons between sources within each treatment.

Several of the plants treated with short days had formed dormant, terminal buds (left half of each bar in Fig. 32 indicates percentage of plants actively growing). Consequently, a greater percentage of the plants escaped frost damage on June 2 than on May 1. A higher percentage of actively growing plants was found among plants from low elevations than among plants from high elevations (cf. short-day treated plants from Rogue River and Bohemia Fig. 32). Consequently the frost damage was greatest among the plants from low elevations. All long-day treated plants were actively growing with the exception of some of the plants from North Santiam Pass. Although some of the plants from this source had formed dormant buds under long-day treatment they were all damaged by frost. The long-day treatment apparently increased sensitivity to frost irrespective of the developmental stage. This finding, and the earlier finding that plants in the same developmental stage but treated with different photoperiods showed differences in frost resistence, indicates that photoperiod effects frost resistence not only through its effect on the time of cessation of height growth but also through an effect on some other, yet undetermined processes.

On July 2 a third and similar test of frost resistence was made. At this time all plants treated with short days had formed dormant, terminal buds with the exception of some of the plants from the southernmost source (Bohemia, Fig. 32). Consequently, only few plants suffered frost damage. All plants treated with long photoperiods were still actively growing with the exception of a few from Bear Springs. Almost all long-day treated plants were damaged by frost.

Conclusion.

Photoperiod has a pronounced influence on the resistence to frost in Douglas-fir seedlings. Long photoperiods (nineteen hours) decrease the frost resistence. This is partly due to the retarding effect on cessation of height growth. However, the fact that dormant plants treated with long photoperiods also show a reduction in frost resistance as compared to dormant plants treated with short photoperiods (nine hours) indicates that long photoperiods also reduce frost resistence through their effect on some other unknown process.

Differences in resistence to frost among seedlings from different sources may be ascribed partly to their differences in response to photoperiods, resulting in differences in time of cessation of height growth.

THE CORRELATION BETWEEN DRY MATTER CONTENT OF NEEDLES AND RELATIVE LENGTH OF ACTIVE GROWTH PERIOD

Langlet (24) has demonstrated that Scots pine native to northern latitudes in Sweden is characterized by a higher percentage of dry matter in the needles than in Scots pine native to southern Sweden.

During the last week of December 1955 samples of twigs were collected from nine different localities along the east-west transect (Fig. 1 and Table 7) in an effort to determine possible correlations between percentage of dry matter and altitude. At each locality twigs were collected from ten trees (10-30 years old) from the lower part of the crown. The twigs were placed in polyethylene bags with moist cotton immediately after collection and stored in a household refrigerator for one night. Five grams of the current years needles were removed from each sample of twigs and placed in small, open paper bags in an oven kept at 50°C. After drying to constant weight (about three days) the dry weight of each sample was calculated as percentage of fresh weight. The needles of plants at high elevations was found to have a higher percentage of dry matter than those from the low elevations (Table 7). A multiple range test showed that the needles of plants from Junction and two miles east of Snow Creek differed significantly from any of the other samples.

Samples were also taken from twelve trees of an eighteen years old clone planted at McDonald Forest (Table 8). The variation in percent of dry matter (from 36.8 to 39 percent) among these trees of genetic uniformity indicates that the percentage of dry matter may be modified considerably by environmental factors.

During November of 1957 dry matter determinations were made of needles from plants from seven localities along the east-west transect (Fig. 1) which had been growing near Corvallis for three years (Table 9). No significant differences in percentage of dry matter were found between plants from different sources. The lack of any such differences between plants from different sources but growing under similar environmental conditions indicates that the differences in percentages of dry matter observed between plants growing along the east-west transect (Table 7) primarily were due to environmental modifications.

Conclusion.

Differences in percentages of dry matter in needles of trees growing along the east-west transect (Fig. 1) have been demonstrated. Needles from trees at high elevations had a significantly higher percentage of dry matter than needles from trees at low elevations. Determinations of dry matter of needles from twelve clonal trees showed considerable variations within the clone

Table 7. Percentages of dry matter in needles of Douglas-fir trees at nine localities along the east-west transect (Fig. 1).

Locality and elevation	Tree number										Mean
	1	2	3	4	5	6	7	8	9	10	
Junction, 4500'	42.7	43.2	43.8	44.5	44.2	43.7	43.3	44.1	42.9	44.2	43.6
Snow Creek, 4000'	37.2	44.3	43.1	39.8	41.3	38.5	40.9	40.9	37.8	41.1	40.5
Two miles west of Snow Creek, 3500'	40.4	44.2	45.3	43.1	47.8	47.8	46.5	41.8	43.2	47.1	44.7
Two miles west of Sheep Creek 1800'	38.7	41.9	38.5	35.7	36.8	41.8	35.2	38.8	37.1	38.4	38.3
Five miles west of Blodgett, 500'	39.6	38.1	35.7	40.9	38.4	41.6	38.3	39.4	42.2	42.6	39.7
Summit, 600'	37.4	40.3	40.3	40.4	39.2	42.2	38.4	38.2	49.1	40.6	40.6
Eddyville, 100'	36.8	37.3	39.4	40.6	36.5	39.2	41.1	41.4	41.8	40.9	39.5
Pioneer Mt. 13 miles east of Newport, 350'	34.8	38.1	38.2	38.2	39.2	38.4	38.9	38.9	38.4	37.3	38.1
Newport 20'	37.7	37.5	37.3	36.8	42.0	36.3	33.9	35.7	36.2	35.2	36.9

Table 8. Percentages of dry matter in needles of twelve Douglas-fir trees at nine localities planted at McDonald Forest, Corvallis.

Tree number		Tree number	
1	37.5	7	37.9
2	37.7	8	37.5
3	37.9	9	39.8
4	39.2	10	37.3
5	38.0	11	39.1
6	36.8	12	37.6

Table 9. Percentages of dry matter in needles of six to ten year old Douglas-fir seedlings from seven localities along the east-west transect (Fig. 1) when grown at Corvallis for three years.

Origin and elevation	Seedling number:					Mean
	1	2	3	4	5	
Snow Creek, 4000'	42.7	42.7	47.0	45.3	44.8	44.5
Sheep Creek, 2000'	41.0	48.8	44.7	42.2	41.5	43.6
Foster, 600'	43.9	41.5	42.2	42.6	44.1	42.8
Corvallis, 300'	48.7	40.4	46.7	41.8	38.9	43.3
Blodgett, 750'	43.2	38.6	40.8	41.7	44.9	41.9
Summit, 800'	46.6	41.4	44.5	42.3	46.5	44.3
Tidewater, 60'	43.6	43.8	41.6	42.8	43.6	43.1

suggesting environmental modifications. This was further confirmed by the lack of any significant differences in percentage of dry matter among trees from seven localities along the east-west transect which had been growing at Corvallis for three years.

DISCUSSION

The diversity in environmental conditions throughout the Douglas-fir region is reflected by the genotypic diversity in relative time of initiation and cessation of height growth among Douglas-fir seedlings of different origins. One of the difficulties in the evaluation of this diversity is the great susceptibility of these characteristics to environmental modifications. As pointed out by Clausen, Keck, and Hiesey (5) the range of modification varies with different species, different races within the species, and even with different individuals, within the same local population. Determinations of genetic differences in the time of initiation and cessation of height growth are therefore of limited value unless they are supplemented by some determinations of the degree to which they may be modified by environmental factors. Since initiation and cessation of height growth may be considered as a response of the plant to changes in the sum total of all environmental factors influencing the plant, such determinations have obvious limitations if used to explain the diversity as it occurs among plants in their native habitats. However, the determination (under controlled environmental conditions) of the diversity in the response to various levels of one environmental factor may be of great value for the study of the pattern of ecotypic variation within a widely distributed species such as Dougls-fir. Photoperiod is one of the environmental factors which lends itself best to this purpose because of the ease with which it can be controlled.

The response of dormant seedlings to long photoperiods (nineteen hours) varies not only with the seed sources but also with the temperature to which the plants have been exposed during the dormant period. Plants from the high Cascades in Oregon respond to long photoperiods by initiating height growth considerably earlier than plants from the same locality exposed to short days (nine hours), whereas plants from the Willamette Valley and the Oregon coast show very little difference in responses to long and short photoperiods. The effect of the temperatures to which the plants have been exposed during the dormant period is illustrated by the fact that plants from the high Cascades in Oregon which are kept at temperatures of 60-70°F. in the greenhouse during the dormant period show a great difference in responses to long and short photoperiods whereas if the plants are kept at lower temperatures (out-of-doors) during the dormant period the difference in responses to short and long photoperiods is considerably smaller.

Young seedlings just emerging from the cotyledon stage are better suited for studies of genotypic diversity in response to photoperiods than are dormant seedlings. This is primarily because of the fact that the number of leaves formed in such seedlings is greatly influenced by photoperiod, whereas in seedlings which have been dormant earlier the number of leaves formed is predetermined by the conditions at the time the leaf primordia were formed (i.e., the conditions during the previous period of shoot elongation).

Long photoperiods increase the number of leaves formed in young seedlings just emerging from the cotyledon stage by prolonging the period of active growth, whereas short photoperiods decrease the number of leaves formed by shortening the period of active growth. The relative difference in number of leaves formed between plants grown under short and plants grown under long photoperiods is greater in plants from montane or continental climates than in plants from coastal climates. The photoperiodic nature of these differences is evident from the fact that plants exposed to nine-hour photoperiod supplemented by a one-and-a-half hour illumination during the latter part of the dark-period produce more leaves than plants exposed to the same total amount of light but with the supplementary light given during the first half of the dark-period.

The genotypic diversity in response to photoperiod among young seedlings of different origins may explain part of the diversity in the time of cessation of height growth. Since short photoperiods induce early cessation of height growth the diversity in time of cessation of height growth may be explained partly as due to diversity in response to the natural reduction in day-length during the summer. The selective advantage of this response to reduction in day-length is evident from the fact that photoperiod is the only environmental factor which changes in a consistent manner from year to year, whereas the first killing frost occurs at a date which varies widely from year to year. A high sensitivity to the natural reduction in day-length during summer would appear to be of selective advantage in areas where the change from summer to winter is abrupt and severe. In such areas only those plants which respond to the natural reduction in day-length by ceasing height growth well in advance of the first severe frost are capable of survival and reproduction. This may explain the fact that plants from interior British Columbia (Salmon Arm) respond more vigourously to photoperiod than plants from the coastal climates of Vancouver Island where the change from summer to winter is gradual and less severe.

The fact that differences in the time of cessation of height growth persist even under continuous illumination shows that cessation of height growth represents a response also to factors other than photoperiod. Vegis

(62) found that high temperatures induced cessation of growth in the water plant Hydrocharis morsus-ranae L.. Similarly, Kramer (22) found that seedlings of loblolly pine (Pinus taeda L.) stopped growth earlier when grown under high temperatures than when grown under low temperatures. Particularly the night temperature was important in this respect. Genotypic differences in response to photoperiod may, therefore, also contribute to differences in the time of cessation of height growth. The great diversity in thermoperiod throughout the Douglas-fir region has probably lead to the differentiation of ecotypes which differ in their response to thermoperiod. The experimental detection of such differences necessitates facilities by which temperatures can be rigidly controlled. Future studies of this nature will no doubt reveal considerable genotypic variations in response to thermoperiod.

Differences in response to thermoperiod may explain the early cessation of height growth in plants from interior British Columbia (Salmon Arm) when grown at Corvallis. Plants from this source stopped height growth before any appreciable reduction in the natural day-length had occurred (before July 23).

The diversity in time of initiation and cessation of height growth among young Douglas-fir seedlings may be reduced with age due to phenotypic flexibility as indicated by the findings of Bornebusch (2). This is further indicated by the fact that the differences in the time of initiation of height growth among plants from high and low elevations grown at Corvallis was reduced considerably over a period of three years. Continued observations over a period of several years will reveal to what extent these differences may be considered as due to juvenile characteristics.

Although plants from montane or continental climates generally show the greatest differences between responses to various photoperiods than plants from coastal climates several exceptions exist. Plants from Blodgett in the coastal range in Oregon (750' elevation), for example, show almost as great a difference between responses to long and short photoperiods as do plants from the high Cascades (Snow Creek, 4000' elevation). Although the climatic conditions at these two localities differ widely insofar as length of frost-free period is concerned, the differences between the responses to long and short photoperiods in plants from these localities are almost identical. This may be attributed to factor-compensation but may also be due to similarities in evolutionary history of the stands at these two localities. The distinctness of plants from the area around Blodgett with reference to their late initiation of height growth is illustrated by an experiment started in 1914 and 1916 by the United States Forest Service. Plantations each containing plants from the same 13 sources in the Pacific Northwest were established at Wind River, Washington (at 1100 feet elevation) and near Mt. Hood, Oregon at 2800 and 4600 feet elevations. Observations over a period of more than twenty years showed that plants from an area near Blodgett (Benton, 700 feet elevation) consistently were among the latest plants to initiate height growth at all three plantations (32).

Treatment with short photoperiods increase the frost resistence of three month old Douglas-fir seedlings. This effect of short photoperiods has been utilized successfully in forest nurseries. Robak (44) in Norway reported that the survival of seedlings of Japanese larch (Larix leptolepis (Sieb. et Zucc.) Gord.) may be increased several times by covering the seed beds with light-proof material from 9 p.m. to 7 a.m. each day during the period from July 10 to September 1.

Langlet (24) has demonstrated a correlation between percentage of dry matter in the needles of Scots pine and the relative time of initiation and cessation of height growth. No such correlation was found in seedlings collected along an east-west transect across western Oregon and grown for two years at Corvallis. However, the transect sampled may be considered as too short for the detection of such differences. If plants from the eastern part of the natural range of Douglas-fir (Idaho, Montana, Wyoming) had been included in the study significant differences in percentage of dry matter might have been found.

Determinations of responses to photoperiod of Douglas-fir seedlings of different origins appear to present excellent opportunities for a detailed study of the pattern of genotypic variation in a species which occur naturally over a wide variety of habitats. The present studies have shown that plants from montane or continental climates show a greater response to photoperiod than plants from coastal climates. Extension of these studies may reveal genotypic differences in response to photoperiod between plants native to steep south slopes and plants native to north slopes. Furthermore, differences in response to photoperiod may prove to be correlated with differences in other characteristics such as frost or drought endurance which are considerably more difficult to determine experimentally. The determination of differences in response to photoperiod between seedlings of different origins, whether widely separated geographically or from different ecological habitats in the same general area (north slopes versus south slopes etc.) may prove to be of value in the selection of a seed source for reforestation of a particular area.

BIBLIOGRAPHY

1. Black, M. and P. W. Wareing. Growth studies in woody species. VII. Photoperiodic control of germination in Betula pubescens Ehrh. Physiologia Plantarum 8:300-316. 1955.

2. Bornebusch, C. H. Proveniensforsög med rödgran. Det forstlige forsögsväsen i Danmark 13:325-378. 1935.

3. Bunning, E. Entwicklungs- und Deweguhgsphysiologie der Pflanze. Berlin, Springer Verlag, 1948. 464 p.

4. Cieslar, A. Über die Erblichkeit des Zuwachsvermögens bei den Waldbäumen. Centralblatt für das gesammte Forstwesen 21:7-29. 1895.

5. Clausen, Jens, David D. Keck and William M. Hiesey. Experimental studies on the nature of species.I. Effect of varied environments on western North American plants. Washington D. C., Carnegie Institution of Washington, 1940. 452 p. Publication 520.

6. Duncan, David B. Multiple range and multiple F-tests. Biometrics 11:1-42. 1955.

7. Eneroth, O. Studier över risken vid användning av tallfrö av för orten främmande proveniens. Meddelanden fran Statens Skogsförsöks-anstalt, Stockholm 23:1-62. 1927.

8. Engler, A. Tatsachen, Hypothesen und Irrtümer auf dem Gebiete der Samen-Provenienz-Frage. Forstwissenschaftliches Centralblatt 30:295-314. 1908.

9. _______________. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. Mitteilungen der Schweizerischen Centralanstant für das forstliche Versuchswesen 10:187-386. 1913.

10. Garner, W. W. and H. A. Allard. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Journal of Agricultural Research 18:553-606. 1920.

11. _______________. Further studies in photoperiodism, the response of the plant to relative length of day and night. Journal of Agricultural Research 23:871-920. 1923.

12. Gustafson, F. C. Influence of the length of day on the dormancy of tree seedlings. Plant Physiology 13:655-658. 1938.

13. Hertz, M. Beobachtungen über die jährlichen und täglichen Perioden im Längenwachstum der Kiefer und Fichte. Acta Forestalia Fennica 34:(18) 1-26. 1929.

14. Irgens-Moller, Helge. Forest-tree genetics research: Quercus L.. Economic Botany 9:53-71. 1955.

15. Jost, L. Ueber den Einfluss des Lichtes auf das Knospentreiben der Rothbuche. Berichte der deutschen botanischen Gesellschaft 12:188-197. 1894.

16. Karschon, R. Untersuchungen über die physiologische Variabilität von Föhrenkeimlingen autochtoner Populationen. Mitteilungen der Schweizerischen Astalt für das forstliche Versuchswesen 26:205-244. 1949.

17. _______________. Photopériodicité et thermoperiodicite chez le pin sylvestre. Schweizerische Zeitschrift fur Forstwesen 102:268-275. 1951.

18. Kendrew, W. G. The climates of the continents. 4th ed. Oxford, Clarendon Press, 1953. 607p.

19. Kiellander, C. L. Uber eine spättreibende Rasse von Picea Abies in Schweden und eine Schwierigkeit bei der Plusbaumauswahl. Zeitschrift für Forstgenetik und Forstpflanzenauchtung 5:181-185. 1956.

20. Klebs, G. Ueber das Treiben Einheimischen Bäume speziell der Buche. Abhandlungen Heidelberger Akademie der Wissenschaften (Mathematisch-Naturwissenschaftliche Klasse) 3:1-116. 1914.

21. Kramer, P. J. The effect of variation in length of day on the growth and dormancy of trees. Plant Physiology 11:127-137. 1936.

22. ______________. Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. Forest Science 3:45-55. 1957.

23. Lammerts, W. E. Effect of photoperiod and temperature on growth of embryo-cultured peach seedlings. American Journal of Botany 30:707-711. 1943.

24. Langlet, O. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Meddelanden fran Statens Skogsförsöksanstalt, Stockholm 29:219-470. 1937.

25. ______________. Kulturförsök med tysk gran av första och andra generationen. Meddelanden fran Statens Skogsförsöksanstalt 32:361-380. 1941.

26. Levitt, Jacob. The hardiness of plants. New York, Academic Press, 1956. 278p.

27. Lindquist, Bertil. Genetics in Swedish forestry practice. Stockholm, Svenska Skogsvardsföreningens Förlag, 1948. 173p.

28. Macdougal, D. T. The influence of light and darkness upon growth and development. Memoirs of the New York Botanical Gardens 2:1-319. 1903.

29. Maksimov, N. A. and V. M. Leman. (Culture of woody seedlings in electric light). Doklady, Moskovskaya Ordena Lenina sel'skoknozyaystvennaya Akademiya imeni K. A. Timiryazeva 3:46-51. 1946 (Abstracted in Forestry Abstracts 10:1796. 1949).

30. Mayr, H. Die Variationen der Holzgewächse, ihre Entsehung und ihre Bedeutung für die Praxis. Forstwissenschaftliches Centralblatt 30:1-16. 1908.

31. Mork, Elias. Om sambandet mellom temperatur og vekst. Meddelelser fra det norske skogforsöksvesen, Oslo 8:1-89. 1941.

32. Morris, W. G., R. R. Silen and H. Irgens-Moller. Consistency of bud bursting in Douglas-fir. Journal of Forestry 55:208-210. 1957.

33. Moshkov, B. S. Photoperiodismus und frosthärde ausdaurnder Gewächse. Planta 23:774-803. 1935.

34. Munger, Thornton T. and William G. Morris. Growth of Douglas-fir trees of known seed source. Washington, U. S. Government Printing office, 1936. 40p. (U.S. Department of Agriculture. Technical Bulletin 537).

35. Murneek, A. E. and R. O. Whyte. Vernalization and Photoperiodism. Waltham, Mass., Chronica Botanica, 1948. 196p.

36. Oksbjerg, E. Om udspringstid og skudsträkning i grankulturer. Hedeselskabets Tidsskrift, Denmark 75:49-55. 1954.

37. ______________. Sommervejret 1955 paa en midtjydsk lokalitet, og törkens virkning paa parceller med tidligt- og sentudspringende rödgraner. Dansk Skovforenings Tidsskrift 41:273-302. 1956.

38. Olmsted, C. N. Experiments on photoperiodism. Dormancy and leaf age and abscission in sugar maple. Botanical Gazette 112:365-390. 1951.

39. Pauley, Scott S. Influence of light on break of dormancy in various tree species. Records of the Genetics Society of America 23:60. 1954.

40. ______________. Variations on time of break of dormancy among altitudinal ecotypes of *Populus trichocarpa*. Records of the Genetics Society of America 23:60. 1954.

41. Pauley, Scott S. and Thomas O. Perry. Ecotypic variation of the photoperiodic response in *Populus*. Journal of the Arnold Arboretum 35:167-188. 1954.

42. Phillips, J. E. Effect of day length on dormancy in tree seedlings. Journal of Forestry 39:55-59. 1941.

43. Raunkjär, C. Om lovspringstiden hos afkommet af böge med forskellig löspringstid. Botanisk Tidsskrift 36:197-203. 1918.

44. Robak, H. Litt om aarsakene til daarlig overvintring hos japansk lerk i kystplanteskolerne. Aarskrift for norske Skogplanteskoler 1953: 34-40. 1954 (Abstracted in Forestry Abstract 15:3502. 1954).

45. Rohmeder, E. Beobachtungen über früh - und spätanstreibende Buchen. Forstwissenschaftliches Centralblatt 56:517-523. 1934.

46. _______________. Die Vererbung der Austreibe Fichteneinzelstämmen. Forstwissenschaftliches Centralblatt 67:32-38. 1948.

47. Romell, Lars-Gunnar. Växttidsundersökninger a tall och gran. Meddelanden fran Statens Skogsförsöksanstalt, Stockholm 22:45-123. 1925.

48. Schott, P. K. *Pinus sylvestris* L., Die gemeine Kiefer. Forstwissenschaftliches Centralblatt 26:123-141, 306-324, 436-449, 514-536, 587-606. 1904.

49. _______________. Rassen der gemeinen Kiefer. Forstwissenschaftliches Centralblatt 29:199-218, 262-278. 1907.

50. Schotte, Gunnar. Tallfröets proveniens,- Norrlands viktigaste skogsodlingsfraga. Meddelanden fran Statens Skogsforsoksanstalt, Stockholm 20:305-400. 1924.

51. Sinnot, Edmund W., L. C. Dunn and Th. Dobzhansky. Principles of Genetics. 4th ed. New York, McGraw-Hill, 1950. 505p.

52. Sulven, N. Lang- och kortdagstyper av de svenska skogsträden. Svensk Papperstidning 43:317-324. 1940.

53. _______________. Om ekens lövspricknings- och lövfäldningsdata. Ett bidrag till kännedomen om ekens mangformighet. Svensk Pappers Tidning 47:167-174. 1944.

54. Thoday, J. M. Components of fittness. Symposia of the Society for Experimental Biology 7:96-113. 1953.

55. Turesson, Göte. The species and the variety as ecological units. Hereditas 3:100-113. 1922.

56. ______________. The genotypical response of the plants species to the habitat. Hereditas 3:211-350. 1922.

57. ______________. The plant species in relation to habitat and climate. Hereditas 6:147-236. 1925.

58. ______________. Rassenokologie und Planzengeographie. Einige kritische Bemerkungen. Botaniska Notiser för ar 1936:420-437. 1936.

59. U. S. Department of Commerce, Weather Bureau. Climatological Data, Oregon Section Vol. 61 and 63. 1955 and 1957.

60. U. S. Dept. of Agriculture. Climate and Man, the Yearbook of Agriculture, 1941. Washington, U. S. Government Printing Office, 1941. 1248p.

61. Veen, R. van der. Influence of day-length on the dormancy of some species of the genus Populus. Physiologia Plantarum 4:35-40. 1951.

62. Vegis, Auseklis. Uber den Einfluss der Temperatur und der täglichen Licht-Dunkel-Periods auf die Bildung der Ruheknospen zugleich ein Beitrag zur Entstehung des Ruhezustandes. Symbolae Botanicae Upsalienses 14:1-175. 1955.

63. Wareing, P. P. Growth studies in woody species. II. Effect of day-length on shoot-growth in Pinus silvestris after the first year. Physiologia Plantarum 3:300-314. 1950.

64. ______________. Growth studies in woody species. III. Further photoperiodic effects in Pinus silvestris. Physiologia Plantarum 4:41-56. 1951.

65. ______________. Growth studies in woody species. V. Photoperiodism in dormant buds of _Fagus sylvatica_ L. Physiologia Plantarum 6:692-706. 1953.

66. ______________. Growth studies in woody species. VI. The locus of photoperiodic perception in relation to dormancy. Physiologia Plantarum 7:261-277. 1954.

67. ________________. Photoperiodism in woody plants. Annual Review of Plant Physiology 7:191-214. 1956.

APPENDIX

The following seed was furnished by Manning Seed Company, Seattle, Washington. (Stand and lot numbers are those of Manning Seed Company).

Qualicum, Vancouver Island, Stand No. 100, B 13. 200 ft.

Nanaimo, Vancouver Island, Stand 101, B 14. 180-200 ft.

Alberni, Vancouver Island, Stand 28, B 13. 690 ft.

Salmon Arm, B. C., Stands No. 102 and 31, B 22. 1900-2120 ft.

Elbe, Washington, Stand No. 202, 78. 1050-1250 ft.

Mineral, Washington, Stand No. 203, 78. 1550 ft.

Ashford, Washington, Stand No. 204, 78. 1500 ft.

Carson, Washington, Stand No. 217, 75. 900-950 ft.

Castle Rock, Stand No. 219, 79. 1100-1250 ft.

Castle Rock, Stand No. 208, 79. 450 ft.

Castle Rock, Stand No. 209, 79. 950-1000 ft.

Joyce, Washington, Stand No. 200, 11. 280 ft.

Orting, Washington, Stand No. 207, 78. 400-450 ft.

Vader, Washington, Stand No. 213, 77. 300-400 ft.

Detroit, Oregon, Stand No. 306, 87. 2800-3000 ft.

Detroit, Oregon, Stand No. 305, 87. 1620-1800 ft.

Detroit, Oregon, Stand No. 301, 87. 2300-2550 ft.

Detroit, Oregon, Stand No. 3, 87. 3600 ft.

Molalla, Oregon, Stand No. 300, 85. 750-950 ft.

Timber, Oregon, Stand No. 32, 82. 750-900 ft.

Certified Seed:

Shuswap Lake, B. C. Lot No. 22. 1000-1500 ft.

Nanaimo, Vancouver Island, Lot No. B 14. 0-500 ft.

Oakridge, Oregon, Lot No. 89. 2500-3000 ft.

The following seed was furnished by the Regional Office, Region 6, U. S. Forest Service, Portland, Oregon.

Mt. Baker National Forest, Verlot, 200' to 1000' elevation

Snoqualmie National Forest, Ashford, 2000' elevation

Snoqualmie National Forest, Ashford, 300' to 800' elevation

Mt. Hood National Forest, Bear Springs, 2500' to 3500' elevation

Mt. Hood National Forest, Zig Zag, 1400' elevation

Rogue River National Forest, 4650' elevation

Umpqua National Forest, Bohemia, 900' elevation