EFFECT OF WINTER CHILLING AND PHOTOPERIOD ON GROWTH RESUMPTION IN DOUGLAS-FIR, PSEUDOTSUGA MENZIESII (MIRB.) FRANCO

by

DONALD EVERETT WOMMACK

A THESIS

submitted to

OREGON STATE COLLEGE

in partial fulfillment of
the requirements for the
degree of

MASTER OF SCIENCE

June 1960

APPROVED:

Redacted for privacy

Assistant Professor of Forest Management

In Charge of Major

Redacted for privacy

Head of Department of Forest Management

Redacted for privacy

Chairman of School Graduate Committee

Redacted for privacy

Dean of Graduate School

Date thesis is presented May 6, 1960

Typed by Janice Cram

ACKNOWLEDGMENT

The helpful advice and guidance received from Dr. Helge Irgens-Moller has been sincerely appreciated. His enthusiasm, interest, and encouragement throughout the study has been of immeasurable value. Sincere gratitude is also offered to Dr. Frank H. Smith for constructive criticism of the manuscript.

My appreciation is also offered to the Lewis W. and Maud Hill Foundation for financial assistance in the form of an assistantship and a fellowship. This aid has allowed me to continue my schooling and to complete this study.

To my wife, Anneliese Wommack, special appreciation is due for her constant encouragement.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
LITERATURE REVIEW	2
METHODS AND MATERIALS	13
EFFECT OF EXPOSURE TO WINTER CHILLING FOR TWO DIFFERENT PERIODS	18
Conclusions	21
GEOGRAPHIC VARIATION IN TIME OF GROWTH RESUMPTION	25
Understock	25
Scions	30
Conclusions	39
SCION AND UNDERSTOCK INTERACTION	40
Conclusions	43
EFFECT OF PHOTOPERIOD	44
Understock	44
Scions	49
Conclusions	63
DISCUSSION	64
BIBLIOGRAPHY	81

LIST OF FIGURES

Figure		Page
1.	East-west transect across western Oregon along which understocks and scions were selected	20
2.	Dates of bud burst in understocks of Douglas-fir from four different areas when the plants were brought into the greenhouse on January 29 and maintained on short days up to May 11.	27
3.	Dates of bud burst in scions of Douglas-fir from four different areas when the plants were brought into the greenhouse on January 29 and maintained on short days up to May 11	33
4.	Santiam Pass clone (D3) brought into the greenhouse on January 29, and maintained on short days. Eleven of the original 12 scions had resumed growth by May 11, 1959..	38
5.	Santiam Pass clone (D1) brought into the greenhouse on January 29, and maintained on short days. Eleven of the original 12 scions were still dormant on May 11, 1959	38
6.	Santiam Pass clone (D7) brought into the greenhouse on January 29, and maintained on short days. All of the original 12 scions were dormant on May 11, 1959. (One plant not shown)	38
7.	Dates of bud burst on understocks of Douglas-fir from four different areas when brought into the greenhouse on November 11 and maintained on short days until May 11 and normal days thereafter until August 25 (indicated by "S") or, maintained on short days until March 15 and long days thereafter until August 25 (indicated by "L")	55
8.	Plants of Corvallis clone (C6) brought into greenhouse on November 11, 1958, and maintained on short days until March 15, 1959. The plant on the left was exposed to long days starting March 15. The plant on the right was maintained on short days until May 11, and normal days thereafter. Arrows indicate the scion portion of the graft	57

Figure Page

9. Plants of Mary's Peak clone (B2) brought into greenhouse on November 11, 1958, and maintained on short days until March 15, 1959. The plant on the left was exposed to long days starting March 15. The plant on the right was maintained on short days until May 11, and normal days thereafter. Arrows indicate the scion portion of the graft 57

10. Dates of bud burst in scions of Douglas-fir from four different areas when brought into the greenhouse on November 11 and maintained on short days until May 11 and normal days thereafter until August 25 (indicated by "S"), or, maintained on short days until March 15 and long days thereafter until August 25 (indicated by "L") 59

11. Santiam Pass clone (D1) brought into greenhouse on January 29, and maintained on short days up to May 11, 1959. Arrows indicate the scion portion of the grafts. 62

12. Santiam Pass clone (D1) brought into greenhouse on January 29. The six plants on the right were exposed to long days starting May 11, and all broke dormancy. The five plants on the left were kept on short day-normal day treatment and were still dormant on August 25, 1959. Arrows indicate the scion portion of the grafts 62

13. Santiam Pass clone (D9) brought into the greenhouse on January 29, and maintained on short days. Note retention of leaves as of June, 1959. Arrows indicate scion portions of the grafts.. . . 70

14. Scion of Santiam Pass clone (D7) on plant brought into the greenhouse January 29, and maintained on short days to May 11. Exposed to long days from May 11, at which time it was dormant, the bud scales opened on May 20 to reveal new growth (arrow) with only little needle development and stem elongation. On May 25, vigorous growth and elongation had commenced.. 74

15. Same plant as in Figure 14 on November 4, 1959, after exposure to long days from May 11. The plant was actively growing and had been through three successive periods of shoot elongation . . . 76

Figure | Page

16. Scion of Santiam Pass clone (D7) brought into the greenhouse on January 29, and maintained on short days until May 11, at which time it was still dormant, and on normal days thereafter. On August 25 bud scales formed the previous fall opened to reveal new dormant bud, indicated by arrow, inside the old scales 78

17. Effect of lack of chilling and/or short photoperiod. There was little swelling of the bud, and little elongation of stem and needles on August 25, 1959. 80

18. Effect of lack of chilling and/or short photoperiod. There was little elongation of the stem on August 25, 1959. 80

LIST OF TABLES

Table		Page
1.	Plants (scion-understock combinations) used in chilling experiment. Capital letters designate area of origin of scion wood and small letters the area of origin of understock. A,a = Coast; B,b = Mary's Peak; C,c = McDonald Forest (Corvallis area); and D,d = Browder Creek (Santiam Pass area). Tree numbers refer to specific trees within a given area.	14
2.	Effects of exposure to short days and greenhouse conditions from November 11, 1958, and from January 29, 1959, upon bud burst in plants of Douglas-fir, up to March 15, 1959.	22
3.	Temperatures in greenhouse and out of doors from September, 1958 to March 15, 1959. Out of door temperatures are those of U. S. Weather Bureau's Climatological records for Corvallis, Oregon (17) .	24
4.	Mean dates of bud burst, total numbers, and percentages of plants which resumed growth before May 11 in understocks of Douglas-fir from four different areas. All plants were brought into greenhouse on January 29, 1959 and maintained on short days up to May 11, 1959	25
5.	Analysis of variance of mean dates of bud burst of Douglas-fir understocks from four different areas. All plants were brought into greenhouse on January 29, 1959 and maintained on short days to May 11, 1959	28
6.	T-tests comparing adjacent ranked mean dates of bud burst of Douglas-fir understock from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959. . . .	29
7.	Mean dates of bud burst, total numbers, and percentages of plants which resumed growth before May 11 in clones of Douglas-fir from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959. . . .	31

Table Page

8. Analysis of variance (hierarchical classification) of mean dates of bud burst of Douglas-fir clones from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959 34

9. T-tests comparing adjacent ranked mean dates of bud burst of Douglas-fir clones from different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959 35

10. Analysis of variance (hierarchical classification) of total number of plants to start growth in clones of Douglas-fir from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959. 36

11. Understock-Scion Interaction. Mean dates of bud burst of different understocks when grafted with different scions. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959. . . . 41

12. Scion-Understock Interaction. Mean dates of bud burst of different scions when grafted with different understocks. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959. . . . 42

13. Types of scions and number of plants by scion-understock combinations used in photoperiodic experiment. All plants were brought into the greenhouse on November 11, 1958, and were maintained on short days until March 15, 1959. Experiment was terminated August 25, 1959. 45

14. Effect of two different photoperiods on the breaking of dormancy in unchilled Douglas-fir understocks from four different areas. Long day treatment was started on March 15, 1959, and the experiment was terminated on August 25, 1959 . . . 48

Table | Page

15. Effect of two different photoperiods on the breaking of dormancy in unchilled Douglas-fir clones from four different areas. Long day treatment was started on March 15, 1959, and the experiment was terminated August 25, 1959 52

16. Effect of additional light after May 11, 1959, upon growth resumption in clones of Douglas-fir. All scions were brought into greenhouse on January 29, 1959, and maintained on short days until May 11, at which time they were still dormant. Experiment was terminated on August 25, 1959. 60

17. Comparison of average dates of bud burst of scion material and understocks from the same area moved in greenhouse January 29, 1959 and maintained on short days up to May 11, 1959. 67

18. Comparison of average dates of bud burst of unchilled scions and understocks from the same areas under normal days plus 2 hours of additional light up to August 25, 1959. 67

EFFECT OF WINTER CHILLING AND PHOTOPERIOD ON GROWTH RESUMPTION IN DOUGLAS-FIR, *PSEUDOTSUGA MENZIESII* (MIRB.) FRANCO

INTRODUCTION

Many species of woody plants native to temperate regions require a period of chilling during the winter months when the plants are dormant to permit break of dormancy and normal growth during spring and summer (4). In some of these species, lack of chilling may be compensated for by long photoperiods (7,14); in other species long photoperiods have little or no compensating effect (19).

A knowledge of chilling requirements is essential in experiments with woody plants conducted in a greenhouse since lack of chilling may bias the experimental results.

The purpose of this study was to determine (1) whether Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) requires chilling for normal growth; (2) geographic or local genetic differences in chilling requirements; and (3) possible compensatory effects of long photoperiods.

LITERATURE REVIEW

Howard, in 1910, showed that different species varied widely with respect to their length of resting period (9, p. 6-37). He brought cuttings from 234 different deciduous woody species into a warm greenhouse from October 28 to November 4, 1905. Only 18 percent of the species resumed growth during the first nine days and only a little more than half resumed growth before the experiment was terminated in the spring. However, when cuttings from the same species plus 49 additional species were brought into the greenhouse on January 10, 1906, 50 percent resumed growth during the first nine days and 86 percent resumed growth before the experiment was terminated in the spring. On February 26, 1906, cuttings from 63 species, primarily those that did not resume growth when collected earlier, were moved into the greenhouse. Of these, 77 percent resumed growth during the first nine days and 92 percent resumed growth before the experiment was terminated in the spring.

Howard concluded from these results that different species varied in their resting period. He found, for instance, that *Spiraea sorbifolia* (L.) A. Br. had one of the shortest resting periods of any of the species tested. It resumed growth very rapidly, even when brought into the greenhouse in late fall. European beech (*Fagus sylvatica* L.), on the other hand, had the longest resting period and did not resume growth until early spring, even when brought into the greenhouse in January or February.

Coville (4, p. 151) stated that trees and shrubs native to cold northern regions would not resume growth in the spring unless they had been exposed to a previous period of chilling.

He found that cuttings of dormant blueberry (Vaccinium corymbosum L.) exposed to outdoor temperatures during the winter and put in cold storage on the first of March would eventually begin to grow, even if left in the cold storage for nine months with temperatures not above 34°F. Plants left out of doors during the winter and moved into the greenhouse on March 25 resumed growth shortly thereafter. In contrast, plants which received no winter chilling and were left in the greenhouse in March failed to resume normal growth during spring.

Coville (4, p. 152) also demonstrated that in blueberry the effect of chilling was limited to the portion of the plant chilled. Thus, if only one branch on a plant was exposed to chilling temperatures, only buds on that branch resumed normal growth during spring.

Coville was one of the first workers to investigate chilling requirements of a coniferous species (loc. cit.). One year old seedlings of tamarack (Larix laricina (Duroi) K. Koch.) broke dormancy by April 10 when chilled in a cold greenhouse at temperatures of 32°-40°F. during the winter; similar seedlings left in a warm greenhouse (55°-70°F.) during the winter failed to break dormancy during the spring.

In 1923, Garner and Allard introduced the term "photoperiodism". In an earlier report (5) they demonstrated the importance of day length as a factor influencing and regulating sexual reproduction in herbaceous plants. They also showed (6, p. 904) that photoperiod was an important factor controlling vegetative growth of woody species. Dormant seedlings of yellow poplar (*Liriodendron tulipifera* L.) moved into the greenhouse in September, and supplied with additional light from sunset to midnight, responded by breaking dormancy. Plants treated in a similar manner except for exposure to additional light remained dormant.

As mentioned previously (page 2), Howard concluded that European beech had the longest resting period of any species he studied. Growth was not resumed until spring regardless of the time at which it was moved into the greenhouse. Klebs, in 1914, (cited in 21, p. 196) observed that this species could be induced to break dormancy in September, before any chilling weather had occurred, if exposed to continuous light. In fact, he found that break of dormancy could be induced at any time during the winter by exposure to long days. Wareing (20, p. 70) proved these responses in European beech to be of a photoperiodic nature. He stated that this species actually has no chilling requirement, but rather is very sensitive to photoperiod and will not resume growth until the days reach a certain length (21, p. 208).

Hodgson (8, p. 152) made observations in the mild winter climate of Niles, California, on the time of growth resumption in 300 varieties of eight different species of deciduous fruit trees. By collecting cuttings at progressively later dates during the winter and exposing them to warm greenhouse temperatures he was able to determine that in most species some variation existed among the varieties in their chilling requirement.

Varieties of almonds were found to require very little chilling in order to break dormancy under warm greenhouse conditions and cuttings brought into the greenhouse on November 20 resumed growth almost immediately. However, different varieties of apricots, pears, plums, cherries, peaches, and apples all required two to three months of winter chilling before they would break dormancy in a normal manner when moved into the greenhouse.

Chandler, et al. (3, p. 3) stated that in areas where cold winter weather starts by the first of November the chilling requirement of the buds of deciduous orchard trees should be satisfied by about the first of February, and after this time they remain dormant only because the temperature is too low for growth. They reported that temperatures of from 33° to 40°F. are probably as good as freezing temperatures in satisfying the chilling requirement of these species. They also observed that plants in shade have their chilling requirement satisfied more rapidly and completely than plants in the sun, and suggested that this is the result of higher temperatures of the buds caused by insolation (3, p. 20).

Lammerts (12, p. 710) was able to bring embryo-cultured peach hybrids into flower two years after pollination. Seedlings from varieties with long chilling requirements were exposed to continuous light during the first growing season which was artificially prolonged. This was followed by hardening off and by exposure to six weeks of cold storage (40°F.) in a dark room. The seedlings were planted out in April and flowered abundantly. Other seedlings of the same varieties showed no flower buds when grown on short or normal days.

Bennett (1,2) found that if one-year-old Hardy pears were brought into a heated greenhouse in November, they would not resume growth in the spring and by August only a few terminal buds had opened and little elongation had occurred. Seedlings stored at 37°F. continuously for 52 or 71 days in a dark room responded in a manner similar to seedlings exposed to normal winter weather in California. However, plants removed from cold storage daily for six hours and exposed to either 73°F. and dim light, or to outdoor temperatures (mean of 64°F.) and direct sunlight, resumed growth later than the plants kept in cold storage continuously during each 24 hour cycle. Intermittent exposure to high temperatures appeared to reduce the effect of continuous exposure to low temperatures. He also found that growth resumption was delayed when the seedlings were stored at 37°F. continuously for only 19 or 42 days as compared to 52 or 71 days.

Gustafson (7, p. 655-658) reported that when three-year-old seedlings of white spruce (Picea glauca (Moench) Voss.) and red pine (Pinus resinosa Ait.) were moved into the greenhouse in early fall, the white spruce broke dormancy, while the red pine remained dormant. He also demonstrated that plants which had received inadequate chilling were very sensitive to photoperiod. Only 29.5 percent of red pine seedlings brought into a heated greenhouse (10° to 12°C.) in early fall and maintained on a normal photoperiod had resumed growth by May 21, as opposed to 87.5 percent in seedlings treated in a similar manner but exposed to a 16 hour photoperiod from March 5. Seedlings which remained out of doors in Michigan during the winter until March 5 under a normal photoperiod contained 87.6 percent actively growing plants by May 21. Gustafson concluded that red pine seedlings required chilling during the winter months for growth resumption during spring and that long photoperiods seemed to compensate for lack of chilling. He stated that if this were true, red pine would not be found in regions with no freezing temperatures during the winter.

Kramer (11, p. 130-132) brought dormant seedlings of various species (beech, yellow poplar, red gum, and red oak) indoors in early January. Some plants of each species were exposed to short days (8½ hours) and others to normal days plus additional light (14½ total hours). Plants of all species exposed to long days resumed growth sooner than those exposed to short days. Kramer concluded that the duration of the growing season of some tree species may be partially regulated by the length of day. However, if these plants were kept outdoors until spring and exposed to controlled photoperiods, the plants under short days resumed growth as soon as those under long days. Wareing (18, p. 214), commenting on these results, stated that "by the date when temperature has risen sufficiently to permit growth, the length of the natural day is no longer a limiting factor."

Wareing (19, p. 47-55) found that seedlings of Scots pine (<u>Pinus silvestris</u> L.) that were moved into a heated greenhouse (13°C.) in the fall remained dormant throughout the winter and showed little sign of breaking dormancy until early April. Plants which were left outdoors during winter and moved indoors the third week of February, all broke dormancy early in March. He also observed that if plants were exposed to continuous illumination early in September, they would resume growth in three weeks, while plants left on normal day remained dormant. However, if plants were exposed to continuous illumination from October 31, the plants remained dormant after three weeks and after eight weeks only about half the plants showed signs of breaking dormancy and very little shoot elongation followed. He concluded that after the buds became fully dormant, long photoperiod had little effect on breaking dormancy and that winter chilling was apparently needed for normal growth resumption (19, p. 55).

Olmsted (14, p. 372-393) reported that the sugar maple (Acer saccharum Marsh.) population in the Chicago, Illinois area with which he worked apparently needed several hundred hours of chilling to complete "bud rest." He demonstrated that unchilled seedlings failed to resume growth in a normal manner during spring if maintained on a nine hour photoperiod since by September 15, only 35 percent had resumed growth. Many more of the unchilled plants resumed growth when they were exposed to either normal spring and summer days (64 percent) or to 20-hour photoperiods (54 percent). He concluded that lack of adequate chilling can be partially compensated for by long photoperiods.

Olmsted brought groups of sugar maple seedlings into a warm greenhouse on December 6, and at intervals thereafter until February 16 (14, p. 381). He observed that the plants showed a proportionately earlier mean date of bud burst the longer they had been exposed to outdoor temperatures. The groups brought in after the last week in January, however, all resumed growth in about the same number of days. He concluded that the rest period was nearly completed by late January.

Exposure to temperatures of from 33° to 45°F. for a sufficient number of hours is generally considered as good or better than subfreezing temperatures in satisfying the chilling requirement of several species of plants (3,19,14, p. 367-368). Olmsted (14, p. 381-382), however, found some evidence that shorter periods of subfreezing temperatures may be much more effective than hitherto considered. On the night of December 12, the outside temperature near Chicago dropped to 8°F. and had risen only to 18°F. on the afternoon of December 13, at which time a group of seedlings was moved into a heated greenhouse. On the afternoon of December 14, another group was moved in while the temperature was still ranging between 10° and 18°F. This latter group was thus exposed to subfreezing temperatures for only 23 hours more than the group brought in on December 13. The group brought in latest did, however, resume growth approximately two weeks before the group brought inside 23 hours earlier. All other groups were brought in six to ten days apart, and yet none showed such wide divergence in mean dates of bud burst.

Olmsted suggested that geographic variation in chilling requirements of native populations might exist.

Nienstaedt (13), working with white spruce (*Picea glauca* (Moench) Voss.) grafted on rootstocks of white spruce or Norway spruce (*Picea abies* (L.) Karst.), found that unchilled scions almost completely failed to break dormancy in the spring if kept under short days (13 hours), but 73 percent of the grafts resumed growth if they were kept under long days (20 hours).

Nienstaedt found that chilling was more effective in inducing break of dormancy than long photoperiods, even if the plants were kept under short days. Not only was the average date of bud burst of unchilled scion material under long days delayed when compared with chilled scions under short days, but the amount of growth (elongation) was also reduced.

Olson, Nienstaedt, and Stearns (15, p. 47-60) demonstrated that seedlings of eastern hemlock (Tsuga canadensis (L.) Carr.) also required a period of chilling during the winter for break of dormancy during the spring. Unchilled plants could be induced to break dormancy by exposure to a 16 hour photoperiod, even though bud burst was delayed when compared with chilled seedlings. They found that chilled seedlings broke dormancy independently of the photoperiod. One-year-old seedlings of Carolina hemlock (Tsuga caroliniana Engelm.) broke dormancy even though unchilled and under short days. These results suggested to the authors (15, p. 48), "either that the chilling requirement was less than for Tsuga canadensis or that the photoperiod compensation for lack of chilling is greater in at least some individuals of this species."

Irgens-Moller (10, p. 84-92) reported that unchilled one-year-old seedlings of Douglas-fir on a 19-hour photoperiod broke dormancy in a very irregular manner and over a much longer period when compared with plants left out of doors until January 15 and then moved into the greenhouse. He also showed that when seedlings from different elevations along an east-west transect were brought into the greenhouse on February 1, and exposed to normal days, there was a much greater difference between mean date of bud burst of high and low elevation seedlings than when similar seedlings were left out of doors all winter. He concluded that these differences may be due partially to differences in chilling requirement.

No reference was found in the literature to possible chilling requirements of Douglas-fir.

METHODS AND MATERIALS

During the spring of 1958, grafts were made from sixteen trees selected from four areas along an east-west transect from the Oregon Coast at Yachats to Santiam Pass in the Oregon Cascades. The four areas are located: (A) on the coast near Yachats (at an elevation of 1300 feet); (B) on Mary's Peak in the Coast Range (3200 feet); (C) in McDonald Forest, ten miles north of Corvallis (300 feet); and (D) in the Browder Creek area in Santiam Pass (4000 feet, Fig. 1).

The understocks used for these grafts were native seedlings collected along road banks at each of the four locations mentioned above. Grafts from any one tree were made on all four types of understock (Table 1).

Only plants with healthy, vigorous appearing scions and understocks were used for the present study. Special care was taken to include only plants with several well-formed, dormant terminal buds both on scion and on understock branches. All plants were kept out of doors during the summer of 1958.[1]

On November 11, 1958, approximately half the plants of each type of scion-understock combination was brought into the greenhouse while the other half was brought into the same greenhouse January 29, 1959.

---

[1]Plants used in this study were part of a number of plants used for a Reciprocal Transplanting Study being conducted by Pacific Northwest Forest and Range Experiment Station, U. S. Forest Service, in cooperation with the Forest Research Division, Agricultural Experiment Station, Oregon State College.

TABLE 1. Plants (scion-understock combinations) used in chilling experiment. Capital letters designate area of origin of scion wood and small letters the area of origin of understock. A,a = Coast; B,b = Mary's Peak; C,c = McDonald Forest (Corvallis area); and D,d = Browder Creek (Santiam Pass area). Tree numbers refer to specific trees within a given area.

Origin of scion wood	Tree number	Origin of understock	Number of plants	Total in clone
A	4	a	6	
A	4	b	5	
A	4	c	6	
A	4	d	3	20
B	1	a	6	
B	1	b	6	
B	1	c	6	
B	1	d	6	24
B	2	a	6	
B	2	b	6	
B	2	c	6	
B	2	d	6	24
B	4	a	6	
B	4	b	6	
B	4	c	6	
B	4	d	6	24
C	1	a	6	
C	1	b	6	
C	1	c	6	
C	1	d	6	24
C	2	a	6	
C	2	b	6	
C	2	c	6	
C	2	d	6	24
C	3	a	6	
C	3	b	6	
C	3	c	6	
C	3	d	6	24

TABLE 1 (continued)

Origin of scion wood	Tree number	Origin of understock	Number of plants	Total in clone
C	6	a	6	
C	6	b	3	
C	6	c	6	
C	6	d	6	21
C	9	a	6	
C	9	b	6	
C	9	c	6	
C	9	d	6	24
C	10	a	6	
C	10	b	6	
C	10	c	6	
C	10	d	6	24
D	1	a	6	
D	1	b	6	
D	1	c	6	
D	1	d	6	24
D	2	a	6	
D	2	b	6	
D	2	c	6	
D	2	d	6	24
D	3	a	6	
D	3	b	6	
D	3	c	6	
D	3	d	6	24
D	4	a	6	
D	4	b	6	
D	4	c	6	
D	4	d	6	24
D	7	a	6	
D	7	b	6	
D	7	c	6	
D	7	d	6	24

TABLE 1 (continued)

Origin of scion wood	Tree number	Origin of understock	Number of plants	Total in clone
D	9	a	6	
D	9	b	6	
D	9	c	6	
D	9	d	5	23
		Total number of plants used in experiment	376	376

The length of day was approximately 9 hours and 40 minutes on November 11 when the first half of the plants was brought into the greenhouse and was approximately the same when the second group was brought inside on January 29. This day length was maintained after January 29 by covering the plants at 5:30 p.m. and uncovering them at 7:50 a.m. each day with black, light-proof cloth. By this means length of day was kept approximately constant throughout the experiment.

The temperature in the greenhouse was recorded during the experiment by a thermograph placed among the plants. The average daily maximum temperature was approximately 74°F., and the average daily minimum temperature was approximately 59°F. The temperature never went above 90°F. or below 50°F. during the experiment.

Through daily observations, the dates of bud burst for scion and understock of each individual plant were recorded. Date of bud burst was defined as the day when the terminal bud of any branch, regardless of position on the plant, opened to expose the new needles.

EFFECT OF EXPOSURE TO WINTER CHILLING FOR TWO DIFFERENT PERIODS

By March 15, 1959, bud burst had occurred in 37 (20 percent) of the scions and 124 (67 percent) of the understock brought in January 29 as opposed to none among the scion-understock combinations brought in November 11 (Table 2).

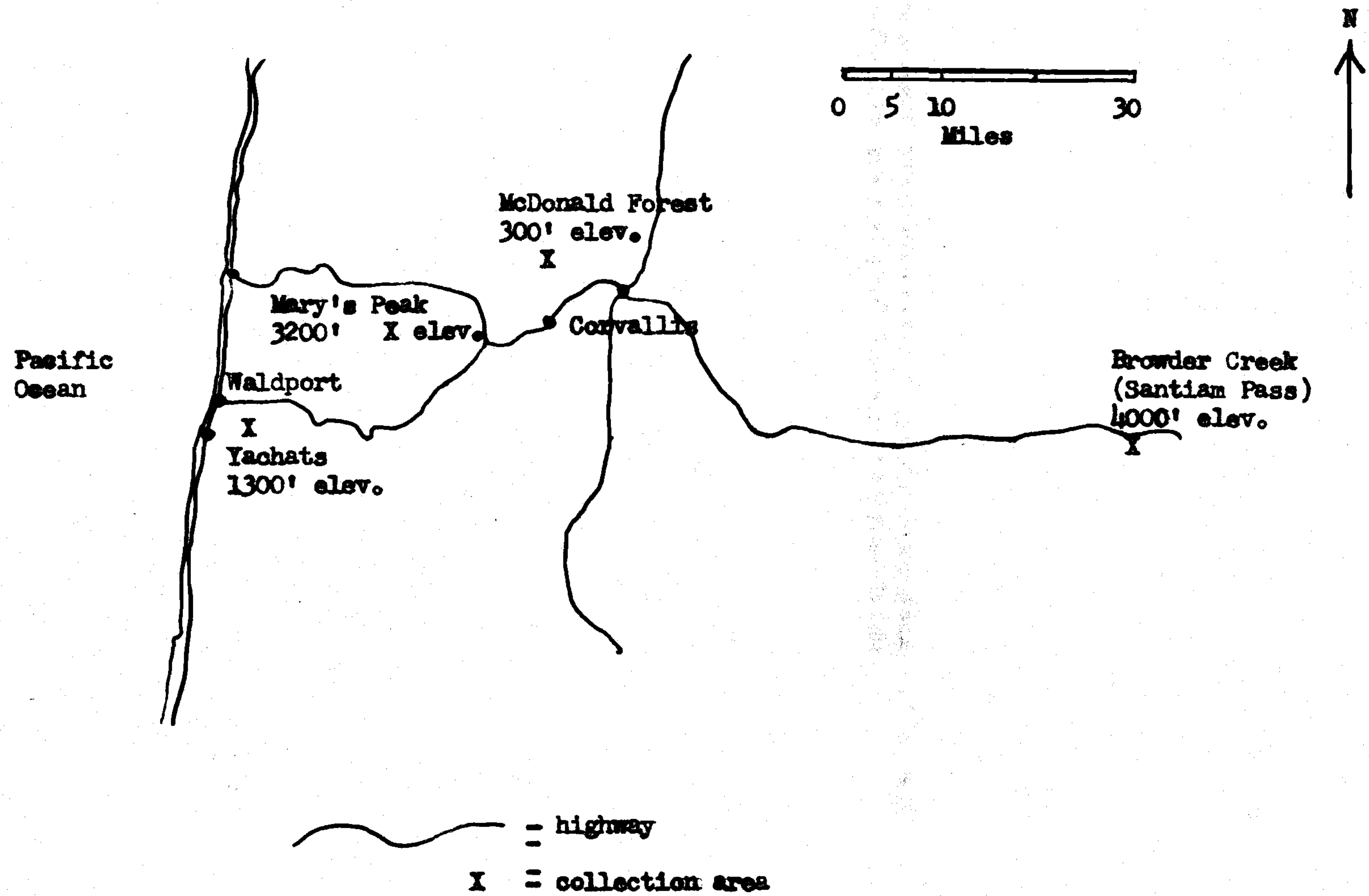
Four months of exposure to greenhouse conditions during the winter months (from November 11 to March 15) thus prevented growth resumption before March 15 in all of the clones used in the present experiment, as well as in all of the four types of understock used.[2] One and a half months of exposure (from January 29 to March 15) did not completely prevent growth resumption. Bud burst had occurred in approximately 20 percent of the scions by March 15, and in more than half of the remaining 80 percent the buds had swelled. Bud burst had occurred in 67 percent of the understock by March 15 while almost all of the remaining plants showed bud swelling.

Greenhouse conditions did not appear to affect the understocks to the same extent as the scions. This difference is no doubt due to the fact that the understocks were only four- to eight-year-old seedlings while the scions were collected from trees 30 to 50 years old. Young trees generally resume growth considerably earlier than older trees of similar hereditary constitution (21, p. 208).

---

[2]A clone is defined here as scions from a particular tree, regardless of the origin of rootstock.

Figure 1. East-west transect across western Oregon along which understocks and scions were selected.


N
0 5 10 30
Miles
McDonald Forest
300' elev.
X
Mary's Peak
3200' X elev.
Corvallis
Pacific
Ocean
Waldport
X
Yachats
1300' elev.
Browder Creek
(Santiam Pass)
4000' elev.
X
= highway
X = collection area

The mortality of scions was the same for both treatments (Table 2) and occurred only during the exposure to greenhouse conditions. The mortality of understock, however, was highest in the group brought in on November 11 (twelve as opposed to only three in the group brought in January 29).

Conclusions

The only variable factor in this experiment was the length of the period the plants were exposed to the greenhouse conditions, or, conversely, the length of exposure to outside winter conditions at Corvallis. The longer exposure to greenhouse conditions completely prevented resumption of growth before March 15. Temperature conditions represent, of course, the greatest difference between the outside and inside conditions (Table 3). Under a day length of 9 hours and 40 minutes, exposure to low temperatures during winter appears to be essential for growth resumption.

TABLE 2. Effects of exposure to short days and greenhouse conditions from November 11, 1958, and from January 29, 1959, upon bud burst in plants of Douglas-fir, up to March 15, 1959.

	Plants moved into greenhouse on November 11			Plants moved into greenhouse on January 29		
		Number of plants which			Number of plants which	
Origin of clones (scions)	Number of plants	started growth before March 15	died before March 15	Number of plants	started growth before March 15	died before March 15
A4	11	0	4	9	5	2
B1	12	0	1	12	0	1
B2	12	0	0	12	4	0
B4	12	0	0	12	1	0
Sub totals	36	0	1	36	5	1
C1	12	0	0	12	4	0
C2	12	0	1	12	3	0
C3	12	0	0	12	2	3
C6	11	0	1	10	2	0
C9	12	0	0	12	8	1
C10	12	0	0	12	2	0
Sub totals	71	0	2	70	21	4

TABLE 2 (continued)

Origin of clones (scions)	Plants moved into greenhouse on November 11: Number of plants	Number of plants which started growth before March 15	Number of plants which died before March 15	Plants moved into greenhouse on January 29: Number of plants	Number of plants which started growth before March 15	Number of plants which died before March 15
D1	12	0	1	12	0	0
D2	12	0	0	12	0	2
D3	12	0	1	12	6	0
D4	12	0	1	12	0	0
D7	12	0	1	12	0	0
D9	12	0	1	11	0	3
Sub totals	72	0	5	71	6	5
Grand totals	190	0	12	186	37	12

Origin of under-stock	Plants moved into greenhouse on November 11: Number of plants	Number of plants which started growth before March 15	Number of plants which died before March 15	Plants moved into greenhouse on January 29: Number of plants	Number of plants which started growth before March 15	Number of plants which died before March 15
a	48	0	2	48	32	0
b	47	0	6	45	28	2
c	48	0	3	48	41	1
d	47	0	1	45	23	0
Totals	190	0	12	186	124	3

TABLE 3. Temperatures in greenhouse and out of doors from September, 1958 to March 15, 1959. Out of door temperatures are those of U. S. Weather Bureau's Climatological records for Corvallis, Oregon (17).

Average Daily Maximum-Minimum Temperatures

Month	Greenhouse			Out of doors			
	Maximum	Minimum	Difference in maximum-minimum	Maximum	Minimum	Difference in maximum-minimum	No. days below 32°F.
September				75	49	26	0
October				67	41	26	0
November	70	51	19	53	39	14	9
December	70	59	11	51	38	13	6
January	71	60	11	48	36	12	7
February	77	59	18	49	34	15	11
March 1-15	81	59	22	55	35	20	6

GEOGRAPHIC VARIATION IN TIME OF GROWTH RESUMPTION

Differences in the time of bud burst among the clones and the four kinds of understocks appeared in the plants brought in January 29 (Table 2). In order to study these differences, the plants were kept under the controlled photoperiod until May 11, 1959.

Understock

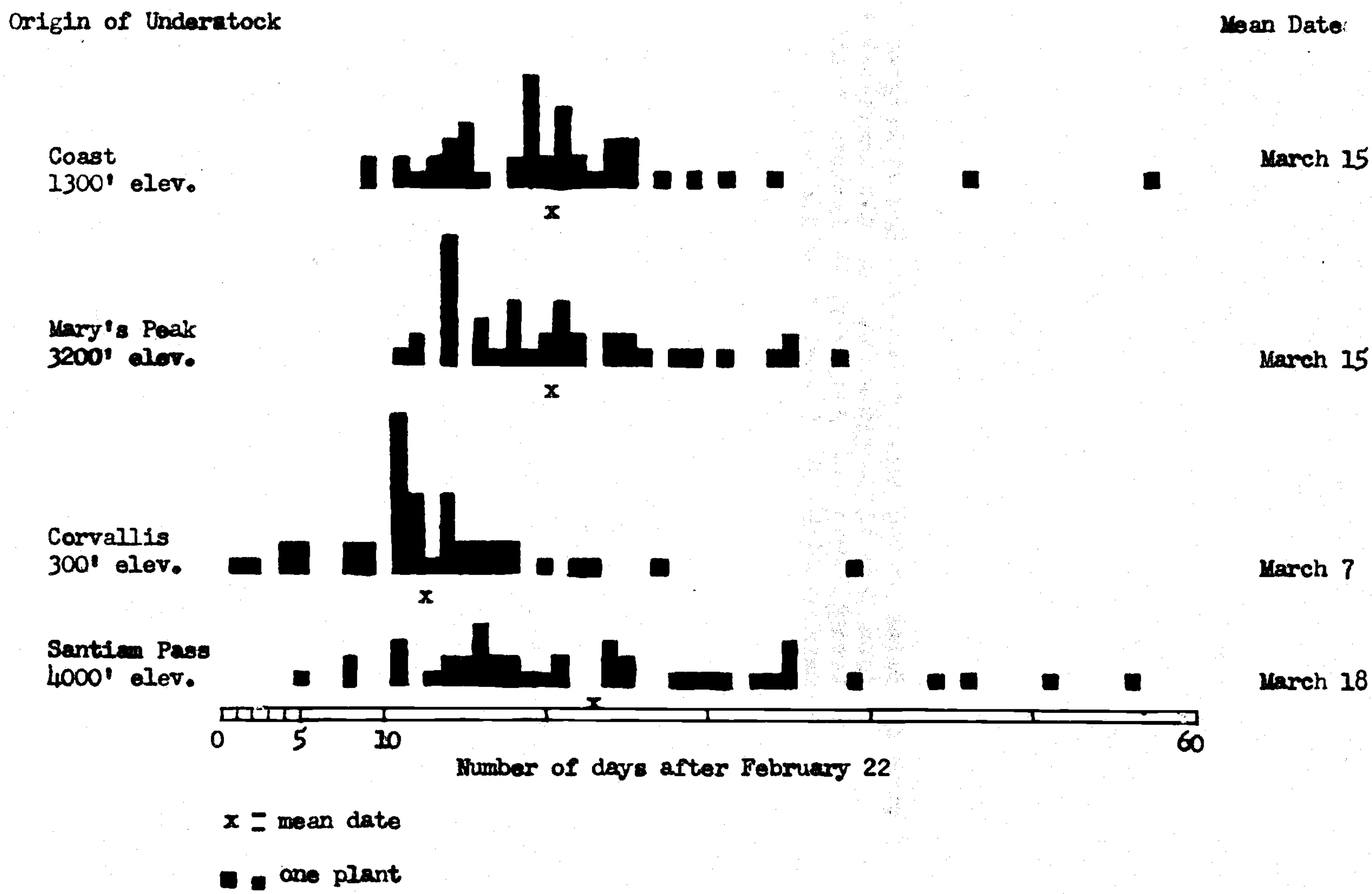
The mean date of bud burst for the understock from Corvallis was approximately eleven days earlier (March 7) than the mean date for the understock from Santiam Pass (March 18), and approximately eight days earlier than the mean dates for the understock from Mary's Peak and the Coast (March 15) (Fig. 2, Table 4).

TABLE 4. Mean dates of bud burst, total numbers, and percentages of plants which resumed growth before May 11 in understocks of Douglas-fir from four different areas. All plants were brought into greenhouse on January 29, 1959 and maintained on short days up to May 11, 1959.

Origin of understock	Number of plants alive at end of experiment	Number of plants which started growth	Percentage which started growth	Mean date of bud burst*
Coast	48	46	96%	20.61
Mary's Peak	43	40	93%	20.63
Corvallis	46	44	96%	12.98
Santiam Pass	45	42	93%	23.52
Total understock	182	172	95%	

*Number of days after February 22.

Figure 2. Dates of bud burst in understocks of Douglas-fir from four different areas when the plants were brought into the greenhouse on January 29 and maintained on short days up to May 11.


Origin of Understock
Mean Date
Coast
1300' elev.
March 15
Mary's Peak
3200' elev.
March 15
Corvallis
300' elev.
March 7
Santiam Pass
4000' elev.
March 18
0
5
10
60
Number of days after February 22
x = mean date
■ = one plant

Analysis of variance (Table 5) showed significant differences among the mean dates of bud burst for the four kinds of understock. Further analysis (t-tests comparing adjacent ranked means, Table 6) showed that the understock from Corvallis was significantly earlier than the understock from the Coast; that the understock from the Coast was not significantly earlier than understock from Mary's Peak; and that understock from Mary's Peak did not differ significantly from Santiam Pass understock with regard to time of bud burst. From these results it can be inferred that the Corvallis understock also differs significantly from the Mary's Peak and Santiam Pass understock.

TABLE 5. Analysis of variance of mean dates of bud burst of Douglas-fir understocks from four different areas. All plants were brought into greenhouse on January 29, 1959 and maintained on short days to May 11, 1959.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-value
Among areas	2,656.40	3	885.46	11.34*
Understock within an area	13,115.78	168	78.07	
Total	15,772.18	171		

*Significant at the 5 percent level of significance.

TABLE 6. T-tests comparing adjacent ranked mean dates* of bud burst of Douglas-fir understock from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Ranked mean dates of bud burst

Corvallis (c)	Coast (a)	Mary's Peak (b)	Santiam Pass (d)
12.98	20.61	20.63	23.52

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

T-test comparisons	T-values
Corvallis vs. Coast understock	-4.09 with 168 degrees of freedom**
Coast vs. Mary's Peak understock	-0.00 " " " " "
Mary's Peak vs. Santiam Pass understock	-1.48 " " " " "

*Number of days after February 22.
**Significant at the 5 percent level of significance.

Scions

The mean date of bud burst of the clones from Corvallis (Table 7; Fig. 3) was five days earlier (March 20) than the mean date for the clones from Mary's Peak (March 25), and eight days earlier than the mean date for the clones from Santiam Pass (March 28). These differences are consistent with the differences in mean date of bud burst found among the understocks from the same areas (Table 4). The mean for the single clone from the Coast was two days earlier (March 18) than the mean for the clones from the Corvallis area; however, this difference is based on only seven plants within one clone which is too small a sample to permit any conclusions.

A hierarchical classification analysis of variance (Table 8) revealed that mean dates of bud burst for clones from the four areas did not differ significantly. This lack of significant difference in date of bud burst should be viewed critically because of the fact that only one clone from the Coast area and only three from the Mary's Peak area were available for the experiment, while six clones from each of the other two areas were available. Furthermore, in only three of the six clones from the Santiam Pass area did a sufficient number of plants start growth (bud burst) before termination of the experiment (Table 7).

TABLE 7. Mean dates of bud burst*, total numbers, and percentages of plants which resumed growth before May 11 in clones of Douglas-fir from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Origin of clones	Total number of plants at end of experiment	Number to resume growth	Percentage to resume growth	Mean date of bud burst
Coast				
A4	9	7	78%	17.00
Mary's Peak				
B1	12	7	58%	25.43
B2	12	6	50%	12.17
B4	12	12	100%	29.58
Total	36	25	69%	24.24 General mean
Corvallis				
C1	12	9	75%	16.89
C2	12	9	75%	24.22
C3	12	9	75%	23.78
C6	10	10	100%	18.10
C9	12	9	75%	9.56
C10	12	10	83%	24.60
Total	70	56	80%	19.59 General mean
Santiam Pass				
D1	12	1	8%	25.00
D2	12	6	50%	34.50
D3	12	11	91%	14.91
D4	12	6	50%	43.00
D7	12	0	0%	---
D9	11	1	8%	36.00
Total	71	25	35%	27.60 General mean
Grand total	186	113	61%	

*Number of days after March 1.

Figure 3. Dates of bud burst in scions of Douglas-fir from four different areas when the plants were brought into the greenhouse on January 29 and maintained on short days up to May 11.

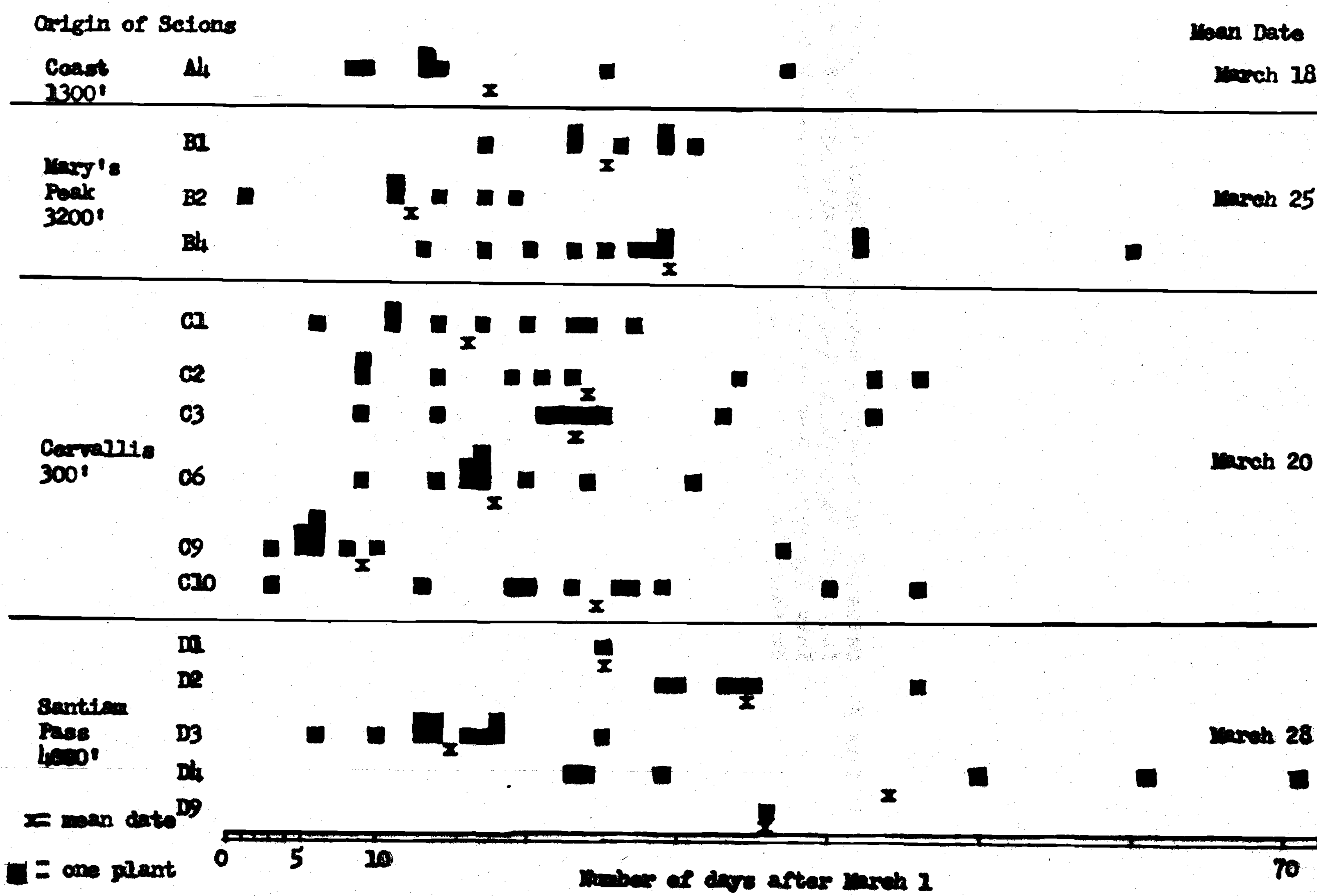

Origin of Scions
Mean Date
Coast
1300'
A4
March 18
Mary's
Peak
3200'
B1
B2
B4
March 25
Corvallis
300'
C1
C2
C3
C6
C9
C10
March 20
Santiam
Pass
D1
D2
D3
D4
D9
March 28
x = mean date
■ = one plant
0
5
10
70
Number of days after March 1

TABLE 8. Analysis of variance (hierarchical classification) of mean dates of bud burst of Douglas-fir clones from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-value
Among the four areas	1,403.90	3	467.96	0.80
Clones within an area	6,380.71	11	580.06	5.34*
Scions within clones	10,643.39	98	108.60	
Total	18,428.01	112		

*Significant at the 5 percent level of significance.

Clones within a particular area, however, differed significantly in mean date of bud burst (Table 8). Further analysis (t-tests on adjacent ranked means, Table 9) showed that among the clones from Mary's Peak, clone B2 was significantly earlier (March 13) than clone B1 (March 26). None of the adjacent ranked means of the clones from Corvallis differed significantly. Among the clones from Santiam Pass (Fig. 4), clone D3 was significantly earlier (March 15) than clone D2 (April 5). Clone D1 and D9 were not included in the test because only one observation was obtained from each of these clones.

Differences in the percentage of plants which started growth before May 11 were also evident. In the six Corvallis clones, an average of 80 percent of the plants had started growth as opposed to only 35 percent for the clones from Santiam Pass. The corresponding figure for the clones from Mary's Peak was

TABLE 9. T-tests comparing adjacent ranked mean dates* of bud burst of Douglas-fir clones from different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Mary's Peak Clones

Ranked mean dates

B2	B1	B4
12.17	25.43	29.58

T-test comparisons	T-value
Clone B2 versus clone B1	-2.36 with 22 degrees of freedom**
Clone B1 versus clone B4	-0.86 with 22 degrees of freedom

Corvallis Clones

Ranked mean dates

C9	C1	C6	C3	C2	C10
9.56	16.89	18.10	23.78	24.22	24.60

T-test comparisons	T-value
Clone C9 versus clone C1	-1.51 with 50 degrees of freedom
Clone C1 versus clone C6	-0.25 with 50 degrees of freedom
Clone C6 versus clone C3	-1.20 with 50 degrees of freedom
Clone C3 versus clone C2	-0.91 with 50 degrees of freedom
Clone C2 versus clone C10	-0.08 with 50 degrees of freedom

Santiam Pass Clones

Ranked mean dates

D3	D2	D4
14.91	34.50	43.00

T-test comparisons	T-value
Clone D3 versus clone D2	-3.42 with 20 degrees of freedom**
Clone D2 versus clone D4	-1.30 with 20 degrees of freedom

*Number of days after March 1.
**Significant at the 5 percent level of significance.

Note: Any two adjacent ranked means not underscored by the same line differ significantly at the 5 percent level of significance. Any two adjacent ranked means underscored by the same line do not differ significantly.

69 percent. The variation in percentage of plants to start growth among the clones from any given area differed greatly. For the six Corvallis clones, this percentage varied from 75 to 100 percent, while for the six Santiam Pass clones the corresponding figures were 0 to 91 (Fig. 4,5,6), and for the three Mary's Peak clones, 50 to 100.

An analysis of variance (hierarchical classification) revealed that the clones from the four different areas did not differ significantly with respect to the number of plants which started growth within any given area; however, it was found that the clones within a particular area differed significantly in number of plants which started growth (Table 10).

TABLE 10. Analysis of variance (hierarchical classification) of total number of plants to start growth in clones of Douglas-fir from four different areas. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-value
Among the four areas	7.75	3	2.58	3.19
Clones within an area	9.71	12	0.80	5.11*
Scions within clones	26.88	170	0.15	
Total	44.34	185		

*Significant at the 5 percent level of significance.

Again these results should be viewed critically due to the unequal number of clones from the different areas.

Figure 4. Santiam Pass clone (D3) brought into the greenhouse on January 29, and maintained on short days. Eleven of the original 12 scions had resumed growth by May 11, 1959.*

Figure 5. Santiam Pass clone (D1) brought into the greenhouse on January 29, and maintained on short days. Eleven of the original 12 scions were still dormant on May 11, 1959.

Figure 6. Santiam Pass clone (D7) brought into the greenhouse on January 29, and maintained on short days. All of the original 12 scions were dormant on May 11, 1959. (One plant not shown).

*Arrows indicate the scion portion of the graft. Note complete loss of all old needles on scions in clones D3 and D1. Scions in clone D7 show no defoliation.

Conclusions

All plants brought in on January 29, 1959 had been growing under essentially similar conditions since May, 1958. For that reason, the observed variation may be ascribed tentatively to genetic differences.

Lack of exposure to low temperatures was shown to result in delay in, or lack of, resumption of growth (Table 2). The understocks from the three highest elevations (Coast, Mary's Peak, and Santiam Pass) were the latest to start growth (Table 4). Similarly, the clones from the two highest elevations (Mary's Peak and Santiam Pass) contained a higher percentage of plants which failed to start growth (Table 7).

This would suggest that plants native to high elevations, or areas characterized by long and severe winters, differ genetically from plants native to low elevations with mild winters in that they require a longer exposure to winter conditions. The differences found among clones native to the same area (Table 9) suggest that considerable local genetic variation also exists.

SCION AND UNDERSTOCK INTERACTION

The average date of bud burst of understock (Table 11), regardless of origin, when grafted with scions from Mary's Peak, was earlier (March 9) than understock grafted with scions from Corvallis (March 13) or from Santiam Pass (March 15).

The amount of influence of the different scions upon the understocks appears to differ among the four types of understock. Thus, excluding the effect of scions from the Coast because of inadequate samples, the greatest differences are found among the understocks from Santiam Pass (11 days) and the smallest among understocks from Corvallis (3 days).

The average date of bud burst of scions, regardless of origin, when grafted onto Santiam Pass understock, was four and five days later (March 26) than scions grafted onto Mary's Peak (March 22) and Corvallis understock (March 21), respectively.

The amount of influence of different understocks upon scions also appears to differ among the four types of scions (Table 12). Thus, again excluding the Coast scions, the greatest differences are found among the scions from Santiam Pass (16 days), while the differences for the scions from Mary's Peak and from Corvallis are only six and five days, respectively. This variation is similar to that found among the understocks.

TABLE 11. Understock-Scion Interaction. Mean dates of bud burst* of different understocks when grafted with different scions. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Source of scion material	Coast understock		Mary's Peak understock		Corvallis understock		Santiam Pass understock		Average	Number of plants
	Mean date	No. of plants	Mean date	No. of plants	Mean date	No. of plants	Mean date	No. of plants		
Coast	13.00	2	16.00	1	19.50	2	56.00	1	22.83	6
Mary's Peak	19.11	9	15.89	9	11.44	9	15.14	7	15.41	34
Corvallis	19.41	17	17.33	12	11.53	17	26.50	16	18.68	62
Santiam Pass	23.73	15	25.44	16	14.05	15	20.87	15	21.10	61
Greatest differences	5		9		3		11			

*Number of days after February 22.
Understocks with dead scions are excluded.

TABLE 12. Scion-Understock Interaction. Mean dates of bud burst* of different scions when grafted with different understocks. All plants were brought into the greenhouse on January 29, 1959, and were maintained on short days up to May 11, 1959.

Source of understocks	Coast scions		Mary's Peak scions		Corvallis scions		Santiam Pass scions		Average	Number of plants
	Mean date	No. of plants	Mean date	No. of plants	Mean date	No. of plants	Mean date	No. of plants		
Coast	11.50	2	25.57	7	24.47	15	24.57	7	23.90	31
Mary's Peak	10.50	2	22.29	7	15.77	13	31.29	7	20.72	29
Corvallis	19.00	2	28.00	6	17.20	15	19.83	6	20.10	29
Santiam Pass	37.00	1	20.60	5	20.85	13	36.00	5	24.63	24
Greatest differences			7		5		16			

*Number of days after March 1.

Conclusions

Since the present experiment was not originally designed to study scion-understock interactions, the above data should probably be viewed critically. However, it appears that scions from Santiam Pass delay bud burst in understocks, regardless of the origin, and similarly, that understocks from Santiam Pass delay bud burst in scions, regardless of origin.

No definite conclusions should be drawn until larger experiments specifically designed to study such interactions have been made. However, in view of the fact that other types of scion-understock interactions are known from other woody species (16), it is felt that further investigations are warranted.

EFFECT OF PHOTOPERIOD

The plants brought into the greenhouse on November 11, 1958 showed no signs of bud burst on March 15, 1959 after having been exposed to greenhouse temperatures and to a day length of approximately nine hours and 40 minutes for over four months.

On March 15, these plants were divided into two groups, with each group containing approximately six of the original twelve plants of each clone (Table 13). One group was kept under a nine hour and 40 minute photoperiod until May 11 after which date the plants were exposed to normal day length. The other group was placed on a bench in the same greenhouse and exposed to normal day length, and two hours of artificial light from 1 a.m. til 3 a.m. by means of four fluorescent tubes and one 150 watt incandescent lamp suspended four feet above the plants. Thermographs placed among plants under each of the two treatments showed that temperature differences caused by the lamps were negligible.

Understock

The experiment was terminated on August 25. By that date only 36 percent of the understocks under the short day-normal day treatment had resumed growth while 63 percent, or almost twice as many, of the plants receiving additional light had resumed growth (Table 14). Mortality under the short day-normal day treatment was 54 percent as opposed to 33 percent under the additional light treatment.

TABLE 13. Types of scions and number of plants by scion-understock combinations used in photoperiodic experiment. All plants were brought into the greenhouse on November 11, 1958, and were maintained on short days until March 15, 1959. Experiment was terminated August 25, 1959.

Scion	Understock	Normal days plus 2 hours additional light: No. of plants	Normal days plus 2 hours additional light: Total for scions	Short days until May 11, normal days thereafter: No. of plants	Short days until May 11, normal days thereafter: Total for scions
A4	a	1		1	
A4	b	1		0	
A4	c	1		1	
A4	d	1	4	1	3
B1	a	1		2	
B1	b	1		1	
B1	c	2		1	
B1	d	1	5	2	6
B2	a	2		1	
B2	b	2		1	
B2	c	1		2	
B2	d	1	6	2	6
B4	a	1		2	
B4	b	2		1	
B4	c	1		2	
B4	d	2	6	1	6
C1	a	2		1	
C1	b	1		2	
C1	c	2		1	
C1	d	1	6	2	6
C2	a	1		2	
C2	b	1		1	
C2	c	1		2	
C2	d	2	5	1	6
C3	a	2		1	
C3	b	1		2	
C3	c	2		1	
C3	d	1	6	2	6

TABLE 13 (continued)

Scion	Under-stock	Normal days plus 2 hours additional light: No. of plants	Normal days plus 2 hours additional light: Total for scions	Short days until May 11, normal days thereafter: No. of plants	Short days until May 11, normal days thereafter: Total for scions
C6	a	1		2	
C6	b	1		1	
C6	c	0		2	
C6	d	2	4	1	6
C9	a	2		1	
C9	b	1		2	
C9	c	2		1	
C9	d	1	6	2	6
C10	a	1		2	
C10	b	2		1	
C10	c	1		2	
C10	d	2	6	1	6
D1	a	2		1	
D1	b	2		1	
D1	c	1		1	
D1	d	1	6	2	5
D2	a	1		2	
D2	b	1		2	
D2	c	2		1	
D2	d	2	6	1	6
D3	a	1		2	
D3	b	1		1	
D3	c	2		1	
D3	d	1	5	2	6
D4	a	2		1	
D4	b	1		1	
D4	c	2		1	
D4	d	1	6	2	5
D7	a	1		1	
D7	b	2		1	
D7	c	1		2	
D7	d	2	6	1	5

TABLE 13 (continued)

Scion	Under-stock	Normal days plus 2 hours additional light		Short days until May 11, normal days thereafter	
		No. of plants	Total for scions	No. of plants	Total for scions
D9	a	2		1	
D9	b	1		2	
D9	c	2		1	
D9	d	1	6	1	5
Total plants		89	89	89	89

TABLE 14. Effect of two different photoperiods on the breaking of dormancy in unchilled Douglas-fir understocks from four different areas. Long day treatment was started on March 15, 1959, and the experiment was terminated on August 25, 1959.

Origin of understock	Normal days plus 2 hours additional light				Short days until May 11, normal days thereafter			
	Number of plants	Percentages of plants which: Started growth	Died	Remained dormant	Number of plants	Percentages of plants which: Started growth	Died	Remained dormant
Coast	24	71	25	4	23	61	39	0
Mary's Peak	21	57	43	0	20	30	55	15
Corvallis	23	56	35	9	22	36	59	5
Santiam Pass	21	67	28	5	24	17	62	21
Totals	89	63	33	4	89	36	54	10

Scions

By August 25, when the experiment was terminated, only about three percent (3 of 89) of the scions under the short day-normal day treatment had resumed growth as opposed to 50 percent (45 of 89) of those receiving additional light (Table 15; Fig. 8,9). The corresponding figures for mortality were 64 and 42 percent, respectively.

The six clones from Santiam Pass and Corvallis appeared to respond equally well to additional light in terms of percentage of scions which resumed growth (60 and 55 percent, respectively), while only 35 percent of the scions from the three Mary's Peak clones resumed growth.

Meaningful comparisons of mean date of bud burst and number of scions to resume growth between clones from within any given area could not be made because of the small number of plants per clone. When all clones from a given area are grouped together, however, the average date of bud burst for the scions from the Corvallis area clones was ten days earlier than for the scions from the Santiam Pass clones, being 94 and 104 days, respectively, after the start of the long day treatment (Fig. 10). This difference is comparable to the difference of 7 days found between the Corvallis and Santiam Pass understocks under the long day treatment, the average dates being 54 and 61 days, respectively, after the start of the long day treatment (Fig. 7). The average date of bud burst for the scions from the Mary's

Peak clones was 102 days after the start of the long day treatment; however, only six scions from this area resumed growth which is an inadequate sample for comparisons.

Differences in mortality and in number of scions which lived but remained dormant appeared between the clones from the Santiam Pass area and the clones from the Mary's Peak and Corvallis areas under the short day-normal day treatment. Only 44 percent of the scions from the Santiam Pass area died and 53 percent lived but remained dormant. The corresponding figures for the scions from the Corvallis area were 80 and 14 percent, respectively, and for the scions from the Mary's Peak area, 67 and 33 percent, respectively.

The percentages of plants which resumed growth or died did not differ greatly among the four types of understock receiving additional light. Under the short day-normal day treatment, however, 61 percent of the Coast understock resumed growth while only 36, 30, and 17 percent of the understock from Corvallis, Mary's Peak, and Santiam Pass, respectively, resumed growth. Mortality was lowest in Coastal understock (39 percent) and highest in Santiam Pass understock (63 percent).

The understock from Santiam Pass showed the greatest difference in response to the two treatments. Only 17 percent of this understock under the short day-normal day treatment resumed growth while 67 percent of those receiving additional light resumed growth. Noticeable differences between treatments also existed for the Corvallis and Mary's Peak understock, but for the Coast understock the difference was only 10 percent (61 and 71 percent resumed growth under short days-normal days and under long days, respectively).

The dates of bud burst under the two treatments show certain characteristic pattern irrespective of the origin of the plants (Fig. 7). Thus, under the short day-normal day treatment the spread between the earliest and latest plants was 117 days, whereas under additional light the corresponding figure was 67 days. Additional light thus not only induced early bud burst (mean date 54 days after start as opposed to 100 days for the short day-normal day treatment), but also reduced the spread between individual plants.

Due to the small percentages of plants which started growth in some of the short day treated plants no meaningful comparisons can be made among the mean dates of bud burst of the four kinds of understock under this treatment.

Some of the clones brought into the greenhouse on January 29, 1959 had not yet resumed growth when the experiment was terminated on May 11. This was particularly the case with three of the Santiam Pass clones (D1, D7, and D9).

All dormant, healthy plants in each clone were divided into two groups. One group was exposed to normal days while the other group received additional light from 1 a.m. til 3:00 a.m.

TABLE 15. Effect of two different photoperiods on the breaking of dormancy in unchilled Douglas-fir clones from four different areas. Long day treatment was started on March 15, 1959, and the experiment was terminated August 25, 1959.

Origin of clones	Normal days plus 2 hours additional light				Short days until May 11, normal days thereafter			
	Total number of plants	Number of plants which			Total number of plants	Number of plants which		
		Started growth	Died	Remained dormant		Started growth	Died	Remained dormant
Coast								
A4	4	0	4	0	3	0	2	1
Mary's Peak								
B1	5	1	4	0	6	0	3	3
B2	6	4	2	0	6	0	4	2
B4	6	1	5	0	6	0	5	1
Total for area	17	6	11	0	18	0	12	6
Percentages	100	35	65	0	100	0	67	33
Corvallis								
C1	6	4	2	0	6	0	5	1
C2	5	2	3	0	6	0	6	0
C3	6	2	4	0	6	0	4	2
C6	4	3	1	0	6	1	5	0
C9	6	4	1	1	6	0	4	2
C10	6	3	3	0	6	1	5	0
Total for area	33	18	14	1	36	2	29	5
Percentages	100	55	42	3	100	6	80	14

TABLE 15 (continued)

Origin of clones	Normal days plus 2 hours additional light: Total number of plants	Number of plants which: Started growth	Died	Remained dormant	Short days until May 11, normal days thereafter: Total number of plants	Number of plants which: Started growth	Died	Remained dormant
Santiam Pass								
D1	6	3	1	2	5	0	3	2
D2	6	5	1	0	6	1	0	5
D3	5	1	3	1	6	0	5	1
D4	6	4	2	0	5	0	3	2
D7	6	3	1	2	5	0	3	2
D9	6	5	0	1	5	0	0	5
Total for area	35	21	8	6	32	1	14	17
Percentages	100	60	23	17	100	3	44	53
Total for all areas	89	45	37	7	89	3	57	29
Percentages	100	50	42	8	100	3	64	33

Figure 7. Dates of bud burst on understocks of Douglas-fir from four different areas when brought into the greenhouse on November 11 and maintained on short days until May 11 and normal days thereafter until August 25 (indicated by "S") or, maintained on short days until March 15 and long days thereafter until August 25 (indicated by "L").

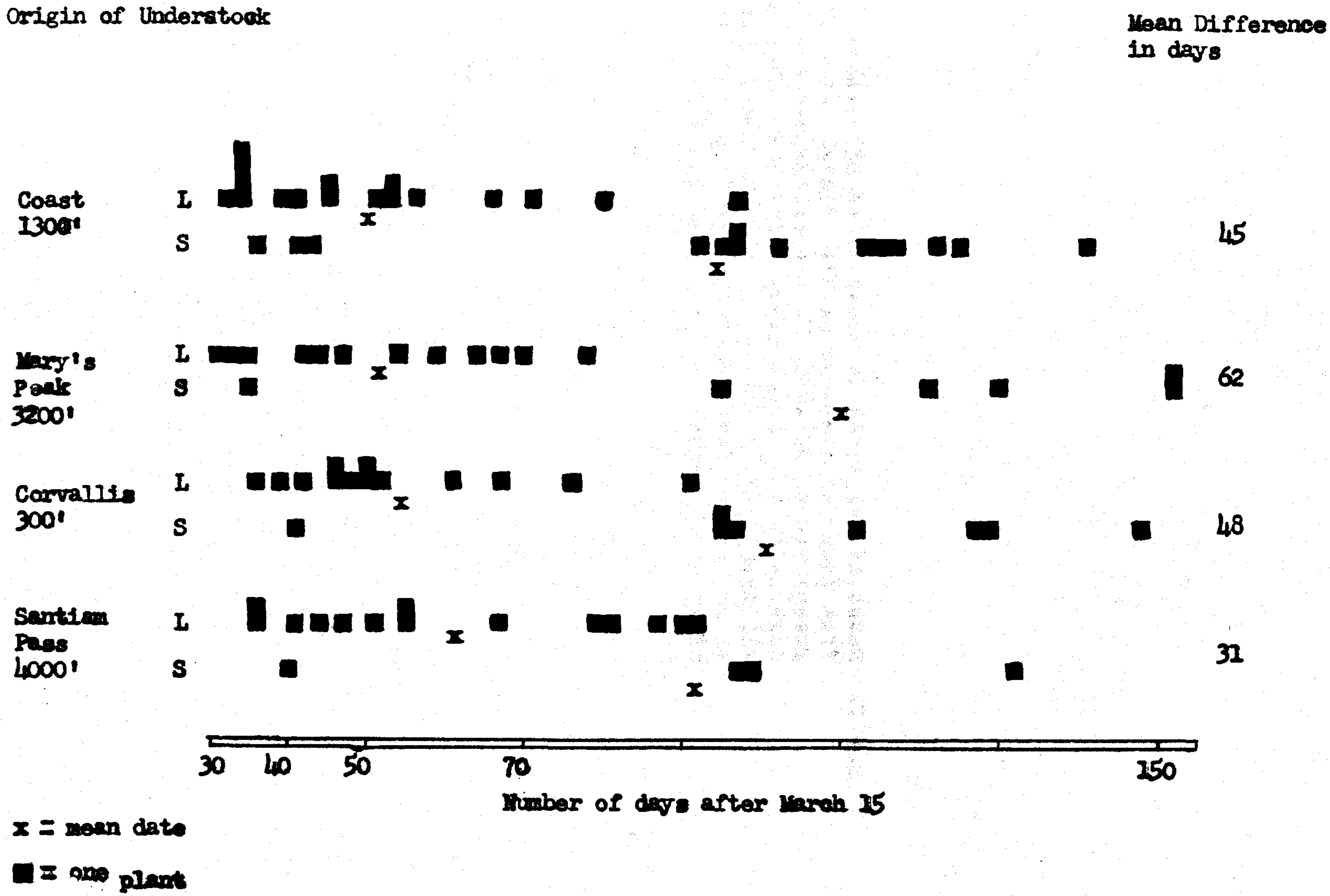
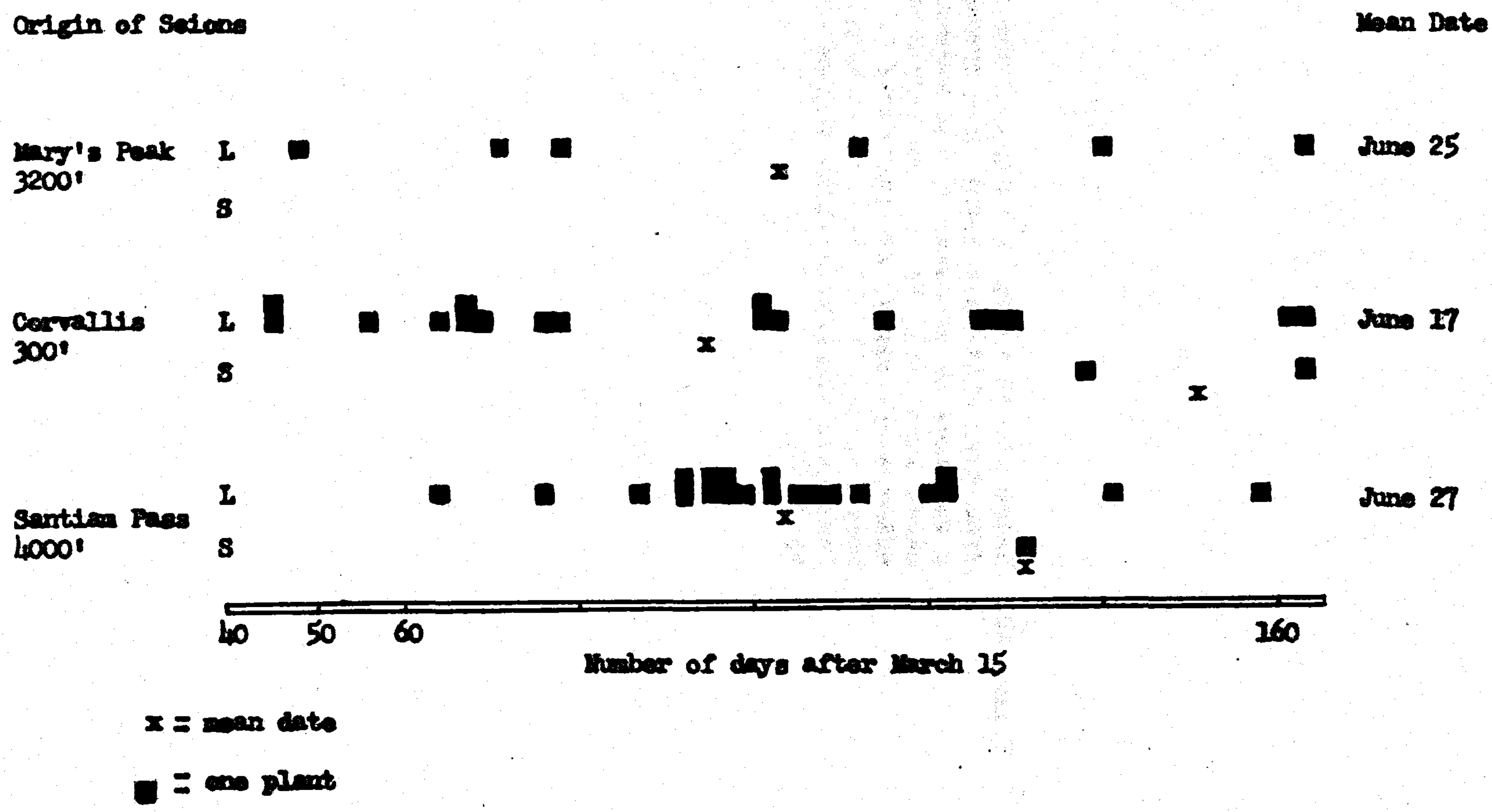

Origin of Understock
Mean Difference in days
Coast 1300'
L
S
45
Mary's Peak 3200'
L
S
62
Corvallis 300'
L
S
48
Santiam Pass 4000'
L
S
31
30
40
50
70
150
Number of days after March 15
x = mean date
■ = one plant

Figure 8. Plants of Corvallis clone (C6) brought into greenhouse on November 11, 1958, and maintained on short days until March 15, 1959. The plant on the left was exposed to long days starting March 15. The plant on the right was maintained on short days until May 11, and normal days thereafter. Arrows indicate the scion portion of the graft.

Figure 9. Plants of Mary's Peak clone (B2) brought into greenhouse on November 11, 1958, and maintained on short days until March 15, 1959. The plant on the left was exposed to long days starting March 15. The plant on the right was maintained on short days until May 11, and normal days thereafter. Arrows indicate the scion portion of the graft.

Figure 10. Dates of bud burst in scions of Douglas-fir from four different areas when brought into the greenhouse on November 11 and maintained on short days until May 11 and normal days thereafter until August 25 (indicated by "S"), or, maintained on short days until March 15 and long days thereafter until August 25 (indicated by "L").


Origin of Scions
Mean Date
Mary's Peak
3200'
L
S
June 25
Corvallis
300'
L
S
June 17
Santiam Pass
4000'
L
S
June 27
40
50
60
160
Number of days after March 15
x = mean date
= one plant

By August 25, when the experiment was terminated, 23 of the 26 scions on the long day treatment had resumed growth while only 5 of the 25 on the normal day treatment had resumed growth (Table 16; Fig. 11 and 12).

TABLE 16. Effect of additional light after May 11, 1959, upon growth resumption in clones of Douglas-fir. All scions were brought into greenhouse on January 29, 1959, and maintained on short days until May 11, at which time they were still dormant. Experiment was terminated on August 25, 1959.

Clones	Normal day plus 2 hours additional light		Normal days	
	Total number of plants	Number of plants to resume growth	Total number of plants	Number of plants to resume growth
B1	1	1	2	0
B2	3	3	2	2
Total	4	4	4	2
C1	1	1	1	0
C3	1	0	1	0
C9	1	0	1	0
Total	3	1	3	0
D1	6	6	5	1
D2	2	2	2	0
D3	1	1	0	-
D4	2	1	2	0
D7	5	5	5	2
D9	3	3	4	0
Total	19	18	18	3
Grand total	26	23	25	5
Percentage	100%	89%	100%	20%

Figure 11. Santiam Pass clone (D1) brought into greenhouse on January 29, and maintained on short days up to May 11, 1959. Arrows indicate the scion portion of the grafts.

Figure 12. Santiam Pass clone (D1) brought into greenhouse on January 29. The six plants on the right were exposed to long days starting May 11, and all broke dormancy. The five plants on the left were kept on short day-normal day treatment and were still dormant on August 25, 1959. Arrows indicate the scion portion of the grafts.

Conclusions

Exposure to two hours of additional light during the middle of the dark period induced growth resumption in plants which had received only little exposure to winter conditions, prior to November 11; or inadequate exposure, prior to January 29. Since plants treated similarly except for the exposure to additional light failed to resume growth, it may be concluded that additional light compensates to some extent for lack of exposure to winter conditions.

No explanation is offered for the high mortality of the unchilled plants (Tables 14 and 15). However, since in almost all cases death occurred before bud burst, it seems that lack of chilling and/or short days are the cause of the mortality. In the unchilled plants that received additional light, the mortality was less than in the unchilled plants kept on short days-normal days. This would appear to be an effect of the additional light. High mortality in unchilled plants has been reported in other studies (7,14,15).

DISCUSSION

The failure of Douglas-fir plants to break dormancy in a normal manner when moved into a warm greenhouse in November confirms earlier reports (4,7,14,15) that many of the woody species native to temperate regions require a period of exposure to low temperatures before growth may be resumed. This is further confirmed by the fact that some of the plants exposed to low temperatures until the end of January did break dormancy when moved into the greenhouse, as opposed to none of the plants that were moved in during November (Table 2).

The observed differences in mean dates of bud burst and in number of plants to resume growth (Tables 4 and 7) may be ascribed, at least in part, to genetic differences in response to some environmental factor of the experiment. Such genetic differences may be the result of the differences in selective forces among the four areas of origin.

One of the greatest differences among the four areas, with respect to environmental conditions, is the duration and severity of winter temperatures. At high elevations the winters are longer than along the Coast or in the Willamette Valley (22). The fact that several of the scions from the Willamette Valley (Corvallis area) did resume growth when exposed to winter temperatures until late January, as opposed to very few scions from high elevations (Mary's Peak and Santiam Pass), indicates that the duration and severity of winter may be the selective force responsible for the apparently greater chilling requirements of the clones from high elevations (Table 7). This is also indicated by the fact that in those plants which resumed growth, mean date of bud burst was earlier for Willamette Valley understock and scions than for understock and scions from high elevations (Tables 4 and 7).

Unchilled scions failed almost completely to break dormancy. However, if they were exposed to long days, almost as high a percentage resumed growth as in scions chilled until January 29, being 50 and 61 percent, respectively (Tables 7 and 15). While only 61 percent of the chilled scions broke dormancy before May 11, 89 percent of those which had not resumed growth by that time did so when exposed to long days as compared to only 20 percent under normal days (Table 16).

Of considerable interest is the fact that 73 percent of the scions which failed to break dormancy after chilling until January 29 were from Santiam Pass, which indicates a high chilling requirement for plants from this area. Approximately 95 percent of these plants started growth under long days compared with only 17 percent under short days (Table 16). This large difference suggests that response to photoperiod may be used as an indication of the degree to which chilling requirements have been met. The greater the effect of long days upon growth resumption, compared with that of short days, the greater the unsatisfied chilling requirement appears to be.

Understocks and scions differed with regard to mean date of bud burst under the various treatments. Scion material from the Coast has been disregarded here due to an inadequate sample. Understocks and scions that were moved into the greenhouse January 29 and maintained on short days, differed 10 to 13 days in mean date of bud burst (Table 17). Understocks and scions moved in November 11 and subjected to long days starting March 15, differed 40 to 50 days in mean date of bud burst (Table 18). In all cases, the understocks resumed growth before the scions. Similarly, the difference between the percentage of understocks and scions brought in November 11 which resumed growth was greater under short days than when additional light was given (Table 14, 15). Under short days, 36 percent of the understocks but only 3 percent of the scions resumed growth. With additional light, 63 percent of the understocks and 50 percent of the scions resumed growth.

These results indicate either that the chilling requirement of the scions was greater than the chilling requirement of understock from the same area, or that the scions from a particular area were more sensitive to photoperiod than understock from the same area. However, since the scions used in this experiment were collected from trees 30 to 50 years old, while the understocks were three- to eight-year-old seedlings, these results probably reflect Wareing's observation (21, p. 208) that in a particular area seedlings resume growth before older trees in the same area.

TABLE 17. Comparison of average dates of bud burst of scion material and understocks from the same area moved in greenhouse January 29, 1959 and maintained on short days up to May 11, 1959.

Area of origin	Understock	Scion material	Difference
Coast	March 15	March 18	3 days
Mary's Peak	March 15	March 25	10 days
Corvallis	March 7	March 20	13 days
Santiam Pass	March 18	March 28	10 days

TABLE 18. Comparison of average dates of bud burst of unchilled scions and understocks from the same areas under normal days plus 2 hours of additional light up to August 25, 1959.

Area of origin	Understock	Scion material	Difference
Coast	May 4	---	---
Mary's Peak	May 6	June 25	50
Corvallis	May 8	June 17	40
Santiam Pass	May 15	June 27	43

This study yielded no information as to the relative importance of the level of low temperatures compared to the length of time of exposure. The plants left out of doors until January 29 received approximately three more months of chilling than those brought in on November 11. During this period, the daily minimum temperatures averaged around 38°F. and the daily maximum temperatures averaged around 50°F. (Table 3). On only 22 days during this period did the temperature drop below freezing.

Several interesting observations were made during this study that may merit further investigation. For instance, among clones brought into the greenhouse on November 11, many of the scions dropped their needles during January. On closer examination it became apparent that this defoliation was limited to certain clones. In the plants brought in January 29, defoliation did not occur until March, and was again confined to certain clones. All the scions in clones D1, D3, C6, and B2 were completely defoliated but there was no defoliation in clones D7, D9, and D2 (Fig. 4,5,6,8,9,13).

Defoliation did not cause mortality or prevent breaking of dormancy. In clone D1, for instance, all twelve scions which received winter chilling became defoliated, but growth was resumed in August in the six plants exposed to long days after having been defoliated for over five months. The five plants which did not receive long-day treatment remained dormant and were still alive April, 1960, after having been defoliated for over one year and dormant for about 19 months. Scions of clone D7 which did not resume growth were still dormant in April, 1960 but had not become defoliated. No explanation is offered as to why certain clones were defoliated while others retained their leaves.

Lack of bud burst was not always an indication of dormancy of the apical meristem. Scions of clone D7 which received winter chilling were still dormant on May 11, although at least a few buds showed some swelling. At that time the clone was divided

Figure 13. Santiam Pass clone (D9) brought into the greenhouse on January 29, and maintained on short days. Note retention of leaves as of June, 1959. Arrows indicate scion portions of the grafts.

into two groups, one of which was exposed to long days, while the other was kept on normal days. One week after the long day treatment was started, the scales on the swollen buds opened to reveal another poorly developed terminal bud on a very short shoot with abnormally short and closely spaced needles (Fig. 14). After another two weeks of exposure to long days, needle and stem elongation occurred (Fig. 14,15).

About August 23 the swollen buds of the scions exposed to short days opened to reveal a well formed dormant bud within the bud scales formed the preceding fall (Fig. 16). These observations suggest that needle development and stem elongation can be retarded by lack of adequate chilling and/or short photoperiods.

A similar retardation was found also in unchilled plants, but it was more evident in the plants left on short days than in those that received long days (Fig. 17 and 18).

Due consideration of chilling requirements is important in research involving Douglas-fir. In greenhouse and laboratory experiments where plants may be moved in and out at different times during the dormant period, the experimental results may be affected if the plants have not received adequate chilling, or if they vary in their chilling requirements.

The apparent geographic variation in chilling requirement is perhaps of even greater importance in the selection of a seed source for a given area. The time of growth resumption would appear to be of great importance for the ability to withstand early summer droughts. Since lack of chilling delays growth resumption, it may very well be that plants with a high chilling requirement that are planted in areas with mild winters and early summer droughts, such as the central Willamette Valley, would be at a great disadvantage. Growth in such a situation would not start until very late and maturation of the new growth would not occur before the onset of drought.

Studies including a wider variety of seed sources and conducted under more rigidly controlled conditions than was possible in the present study would appear necessary to further clarify the problems raised by this study. This would apply especially to the possible scion-understock interaction that was observed (Tables 11 and 12).

Figure 14. Scion of Santiam Pass clone (D7) on plant brought into the greenhouse January 29, and maintained on short days to May 11. Exposed to long days from May 11, at which time it was dormant, the bud scales opened on May 20 to reveal new growth (arrow) with only little needle development and stem elongation. On May 25, vigorous growth and elongation had commenced.

Figure 15. Same plant as in Figure 14 on November 4, 1959, after exposure to long days from May 11. The plant was actively growing and had been through three successive periods of shoot elongation.

Figure 16. Scion of Santiam Pass clone (D7) brought into the greenhouse on January 29, and maintained on short days until May 11, at which time it was still dormant, and on normal days thereafter. On August 25 bud scales formed the previous fall opened to reveal new dormant bud, indicated by arrow, inside the old scales.

Figure 17. Effect of lack of chilling and/or short photoperiod. There was little swelling of the bud, and little elongation of stem and needles on August 25, 1959.

Figure 18. Effect of lack of chilling and/or short photoperiod. There was little elongation of the stem on August 25, 1959.

BIBLIOGRAPHY

1. Bennett, J. P. Temperatures and bud rest period. California Agriculture 3(11):9,12. 1949.

2. Bennett, J. P. Temperature and bud rest period. Blue Anchor 27(1):17,31. 1950.

3. Chandler, W. H. *et al*. Chilling requirements for opening of buds on deciduous orchard trees and some other plants in California. Berkeley, 1937. 63 p. (California. Agriculture Experiment Station. Bulletin no. 611)

4. Coville, Frederick V. The influence of cold in stimulating the growth of plants. Journal of Agricultural Research 20(2):151-161. 1920.

5. 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(11):553-606. 1920.

6. ______________ Further studies in photoperiodism, the response of the plants to the relative length of day. Journal of Agricultural Research 23:871-920. 1923.

7. Gustafson, Felix G. Influence of the length of day on the dormancy of tree seedlings. Plant Physiology 13:655-658. 1938.

8. Hodgson, Frank R. Observations on the rest period of deciduous fruit trees in a mild climate. American Society of Horticulture Science, Proceedings 20:151-155. 1923.

9. Howard, W. L. An experimental study of the rest period in plants. Columbia, 1910. 105 p. (Missouri. Agricultural Experiment Station. Bulletin no. 1)

10. Irgens-Moller, Helge. Genetic variations in length of active growth period among races of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Ph.D. thesis. Corvallis, Oregon State College, 1958. 156 numb. leaves.

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

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

13. Nienstaedt, Hans. The effect of rootstock activity on the success of fall grafting of spruce. Journal of Forestry 57(11):828-832. 1959.

14. Olmsted, Charles E. Experiments on photoperiodism, dormancy, and leaf age and abscission in sugar maple. Botanical Gazette 112(4):365-393. 1951.

15. Olson, J. S., Hans Nienstaedt and F. W. Stearns. Eastern hemlock seeds and seedlings--response to photoperiod and temperature. New Haven, 1959. 70 p. (Connecticut. Agricultural Experiment Station. Bulletin 620)

16. Rogers, W. S. and Beryl Beakbane. Stock and scion relations. Annual Review of Plant Physiology 8:217-236. 1957.

17. U. S. Department of Commerce, Weather Bureau. Climatological Data, Oregon Section 64:148-162. 1958; 65:2-36. 1959.

18. Wareing, P. F. Photoperiodism in woody species. Forestry 22(2):211-221. 1949.

19. ______________ Growth studies in woody species. III. Further photoperiodic effects in _Pinus silvestris_. Physiologia Plantarum 4:41-56. 1951.

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

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

22. Wells, Edward L. Climates of the states (Oregon). In: U. S. Department of Agriculture. Climate and Man; the Yearbook of Agriculture, 1941. p. 1075-1086.