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Title: THE EFFECTS OF LOW TEMPERATURES ON DORMANCY

       RELEASE IN DOUGLAS-FIR (PSEUDOTSUGA MENZIESII

       (MIRB.) FRANCO) FROM WESTERN OREGON, WASHINGTON,

       AND CALIFORNIA

Abstract approved: Signature redacted for privacy.
                   H. Irgens-Moller

The effect of low temperatures given at different times and duration upon the time of bud burst, shoot elongation, number of needles developed and needle length in Douglas-fir plants from the Oregon Cascades and three coastal areas ranging from Washington to California were determined. The plants were grown outside in a lathhouse then chilled at 11-day intervals with three temperatures. These treatment combinations were applied early and late in the dormant period.

The most effective temperature treatment was 40°F followed by 45° and 50°F, in that order. All three temperatures hastened bud burst for the plants from low elevation as length of chilling increased; however, 45° and 50°F was ineffective when chilling was expanded

from 33 to 44 days for the high elevation.

If chilling is done early a longer period is required to break dormancy than if done late during the dormant period. Delay of chilling also increased shoot elongation and the number of needles developed remained fairly constant, altering only the needles per centimeter.

The Effects of Low Temperatures on Dormancy Release
in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)
From Western Oregon, Washington and California

by

Albert Itsuki Sugano

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INTRODUCTION

The buds of many perennial species require a period of chilling at low temperatures during the dormant period in order to resume normal growth. Plants that require chilling will not usually resume growth, unless chilling requirements are met even though growing conditions are favorable.

Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) is one of the species that has been found to require chilling. It is also a species which grows over an enormous geographic range and therefore can be expected to contain populations which have adapted to very diverse environmental conditions. Indeed, considerable variation among populations has been found in phenological characteristics, some of which could be quite closely related to chilling requirements. These include data of bud bursting (Silen, 1962), of time of cessation of height growth in seedlings (Irgens-Moller, 1967) and for growth responses to photoperiod and temperature (Irgens-Moller, 1957).

The purpose of the present study was to investigate the effect of chilling and its relationship to dormancy release of young Douglas-fir plants. The primary objective was to explore the effects of time

of chilling during dormancy. Secondarily, these effects were related to temperature, length of chilling and seed source. This study consisted of two experiments. Experiment I examined the effects of time of chilling using two sources from diverse climatic conditions, one coastal and one high elevation. Eight-month-old plants were chilled at three temperatures for 11 days, 22, 33 and 44 days. The average number of days until bud burst was used to evaluate the effects.

Because of the highly significant interactions among the components in Experiment I, Experiment II was designed to test four-month-old plants from three coastal sources at a constant temperature for 33, 44 and 55 days. In addition to average days to bud burst, height growth, number of needles and needle length were used to further evaluate the effects of time of chilling.

Localities sampled were a high elevation source in the Oregon Cascades and three coastal sources, one each from Washington, Oregon and California.

LITERATURE REVIEW

Dormancy

Five major reviews published during the past twenty years,

Doorenbos, 1953; Samish, 1954; Wareing, 1956; Romberger, 1963;

and Vegis, 1964, thoroughly discuss the published data describing

dormancy. These workers agree that the "dormant" period of most

temperate zone perennial plants may be divided into intergrading phys-

iological states of summer dormancy, correlated inhibition of winter

dormancy and rest.

Summer dormancy is a result of external conditions unfavorable

for growth, such as high temperatures and drought. The dormancy of

summer buds is readily broken by returning the plant to favorable

growth conditions, or by defoliation. If the unfavorable environment

is maintained, summer dormancy will gradually deepen until the plant

will not respond by resuming growth when returned to an environment

favorable to growth.

Plants whose growth is limited by internal rather than external

conditions are said to be in winter dormancy. It is a state of the

tissues themselves so that a normally favorable environment will not

cause breakage of dormancy. Samish (1954) further divides winter

dormancy into pre-rest, rest, and post-rest. These physiological

stages are distinguished by the degree of response resulting from some dormancy-breaking treatment such as ethylene chlorohydrin or warm baths. Under natural conditions, the transition from summer to winter dormancy may well be triggered by the lengthening nights of fall, decrease in night temperatures or a combination of both. In turn, winter dormancy is normally broken by the period of low temperature common to most temperate zone winters.

Instead of considering dormancy as an inhibition of elongation growth, Smith and Kefford (1964) have stressed that dormancy development involves a succession of processes. They suggest that three steady-state and three transitional phases follow each other. Chronologically they are:

1. The spring steady-state of elongation growth.

2. The transitional phase of dormancy development.

3. The dormant steady-state.

4. The transitional dormancy release.

5. The non-dormant state.

6. The transitional spring burst-state.

According to this scheme a dormant bud during a summer drought is quiescent, so also is a dormant bud in April. Physiologically however, they are in entirely different stages, therefore, they respond differently to the same environmental stimuli.

Forest Trees

The idea that increasing night length in late summer might be an important factor in inducing rest in woody plants was slow in gaining wide recognition. The work of Klebs, in 1914 (cited in Wareing, 1956) showed that European beech (Fagus sylvatica L.) could be induced to break dormancy readily in September, if exposed to long days. Wareing (1953) showed that this response of European beech is of a photoperiodic nature and that this species actually has no chilling requirement, and will not resume growth until the days reach a certain length (Wareing, 1956).

Garner and Allard (1920) had demonstrated the effects of day-length upon sexual reproduction in herbaceous plants. In 1923 they showed that the day-length was also an important regulating factor of vegetative growth in woody plants. 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. Other plants treated in a similar manner, but exposed only to normal length of day, remained dormant. Kramer (1936) showed that the duration of the growing season for yellow poplar may be partially regulated by the length of day. He brought dormant seedlings of yellow poplar indoors in early January and exposed them to short days (8-1/2 hours) and long days 14-1/2

hours). The plants exposed to long days resumed growth sooner than those exposed to short days.

Daylength may not be the controlling factor in bud break under natural conditions as demonstrated by Wareing (1949). He grew seedlings of yellow poplar, red gum (Liquidambar styraciflua L.), northern red oak (Quercus borealis var. maxima Ashe), white ash (Fraxinus americana L.) outdoors and exposed them to controlled photoperiods. The plants grown under short days resumed growth as soon as those under long days. Wareing concluded that when temperature has risen sufficiently to permit growth, the length of the natural day no longer was a limiting factor. In the event chilling requirement has been met, temperature determines time of bud break. Other investigators have found the same situation in other species (Olson, Nienstaedt, and Stearns, 1959; Ashby, 1962; Robert and Main, 1965).

Inadequately chilled plants on the other hand, show increased sensitivity to photoperiod (Wareing, 1951; Olmstead, 1951; Nienstaedt, 1958; Olson, Nienstaedt, and Stearns, 1959; Ashby, 1962; Robert and Main, 1965). The resumption of growth by unchilled plants under long photoperiods is earlier than under short ones, but later than in chilled plants. In addition, there is very little shoot elongation which indicates that chilling is necessary for normal resumption of growth.

The onset of dormancy under natural conditions is not

necessarily controlled by photoperiod alone even in species demon-
stratedly capable of photoperiodic response. For example, a photo-
periodic regimen may be effective in inducing dormancy within a
limited temperature range only (Moshkov, 1035, van der Veen, 1951).
Olmstead (1951) concluded that photoperiod frequently is not the dom-
inant factor in controlling bud dormancy in sugar maple. Unfavorable
temperature or light intensity may also induce dormancy in red maple
(Acer rubrum L.) in spite of photoperiodic conditions which, in them-
selves, favor continued growth (Perry, 1962).

Some forest tree species continue to grow in spite of prolonged
exposure to short photoperiod and may be capable of growth in late
fall or winter if the temperature permits (howard, 1910; Kramer,
1937; Nitsch, 1957). A few other forest tress species may be very
slow to become dormant under the influence of 8-hour photoperiods,
although they show a reduced growth rate. An example is American
elm (Downs and Borthwick, 1956).

Coville (1920) appears to have been the first to investigate chill-
ing requirements of a coniferous species. After ten years of experi-
mentation he arrived at several general conclusions, which, in part,
are still valid. (1) Most trees and shrubs of cold climates become
dormant in fall with requiring exposure to cold, but (2) lack of winter
chilling results in delayed bud break in spring, and (3) the effects of
cold exposure are limited to those parts of the plant actually chilled.

Gustafson (1938) found that three-year-old seedlings of red pine (Pinus resinosa Ait.) kept in a greenhouse during winter showed very little growth activity the following summer. He concluded that this was the result of lack of chilling, but noted that this could be overcome by subjecting the plants to 16-hour photoperiods. Three-year-old white spruce (Picea glauca (Moench)Voss.) seedlings, however, began growing when brought into the greenhouse in spite of short photoperiods. The red pine seedlings may have been quiescent, i.e. under the influence of reversible dormancy imposed by the external environment (Samish, 1954) and resumed growth under favorable long day conditions in the greenhouse. The possibility that the white spruce seedlings may not have a chilling requirement has been shown to be otherwise by Nienstaedt (1967). He reported that white spruce seedlings required some chilling in order to break dormancy under short day conditions while unchilled seedlings failed to resume growth under similar conditions.

Exposure to temperatures of from 33°F to 45°F for a sufficient number of hours is generally considered as good or better than sub-freezing temperatures in satisfying chilling requirement in several species of plants (Chandler, W. H. et al., 1937; Olmstead, 1951; Wareing, 1951). Vegis (1953) expanded from these investigations and concluded that when the temperature of resting buds is raised above a certain level the physiological effect increases the intensity and

duration of dormancy. If warm temperature is given immediately after dormancy has been broken by chilling, resumption of growth will occur in a narrow temperature range. If the upper limit of that range is exceeded for an appreciable time, dormancy will again be induced.

From this standpoint, the end of dormancy is not sharp but proceeds gradually into a state of "relative dormancy" (Vegis, 1964) which is temperature dependent. At first, bud break is possible only within a narrow temperature range above which dormancy is reinduced. As the dormant period progresses the range of temperature inducing bud burst becomes wider. Finally dormancy can no longer be re-induced by warm temperature.

Genetic Variation in Chilling Requirements of Forest Trees

It is obvious from the previous review that the various species differ genetically in their responses to photoperiod and chilling. These differences are further complicated by the existence of intra-specific genetic variation as deomonstrated by Perry and Chi Wu Wang (1960). They reported both racial and local variations in the chilling requirements of red maple (Acer rubrum L.). Plants from seeds collected from New York to southern Florida were grown in Florida for one year and then exposed to a combination of chilling treatments. The plants were then moved outdoors to a nursery where bud burst was observed. All unchilled plants from the southern

sources resumed growth rapidly while bud burst for the northern sources were delayed. The plants from southern Florida apparently have a low chilling requirement while plants from the northern sources require more.

One month of chilling was adequate to break dormancy in plants from all sources. This occurred earlier in the Florida plants than in plants from the northern sources. Increasing the chilling period to 2-1/2 months delayed bud burst approximately two weeks in the plants from Florida while it hastened bud burst in plants from northern sources. Despite this, the Florida plants still resumed growth earlier than the plants from the northern sources.

Eastern hemlock (Tsuga canadensis L. Carr) show similar patterns of genetic variation in chilling requirements (olson and Nienstaedt, 1957). Two-year-old seedlings representing a north-south transect and grown in New Haven, Connecticut were moved into a greenhouse under short and long day conditions. One group of seedlings was brought in early October without any chilling, a second group was moved in at the same time and chilled at 5°C for 5 to 15 weeks, and a third group was moved in early December after exposure to the cool natural autumn. Under all treatments plants native to areas with long frost-free seasons resumed growth earlier than plants native to areas with short seasons as observed in red maple (Perry and Chi Wu Wang, 1960).

Similar differences were found in sugar maple (Acer saccharum Marsh.) by Kriebel and Chi Wu Wang (1962) in a greenhouse experiment after various lengths of natural chilling out-of-doors. They also used the same provenances in field tests in central Florida and in northern Ohio. Seedlings exposed to a full winter in the field in Ohio flushed in a north-south sequence with regard to seed source indicating a lower spring flushing temperature requirement for the northern sources. However, the sequence was reversed in the field test in central Florida, indicating that plants from the northern sources probably did not receive enough chilling. The spring temperatures in Florida may also have been sufficiently high to mask the lower temperature requirement of plants from the northern sources.

Jensen and Gatherum (1965) also showed that southern sources of Scotch Pine (Pinus sylvestris L.) moved into three different photoperiods under two different temperatures in October consistently started growth earlier than seedlings from northern sources regardless of photoperiods. The delay in bud burst in the seedlings from the northern sources apparently was caused by the lack of chilling.

Chilling Requirements in Douglas-fir

Work on chilling requirements in Douglas-fir (Pseudotsuga menziesii (Mirb) Franco) under controlled environments have been few and fairly recent. Irgens-Moller (1958) 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 longer period when compared with plants left out of doors until January 15, and then moved into the greenhouse. He also found 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. He concluded that these differences may be due partially to differences in chilling requirements.

Wommack (1960) used different clones of Douglas-fir from an east-west transect from the Oregon coast to Santiam Pass in the Cascades. The understocks used for the grafts were native seedlings from along the same transect. In early November, approximately half the plants of each type of scion-understock combination was brought into a warm greenhouse while the other half was brought into the same greenhouse in late January. The average daily temperature in the greenhouse was 74°F with a range of 50° to 90°F. Photoperiod in the greenhouse was maintained at approximately 9 hours and 40 minutes throughout the experiment.

By March 15, 20 percent of the scions and 67 percent of the understock brought in late January had resumed growth while none brought in early November had done so. The mean date of bud burst

for the understock from Corvallis was approximately eleven days earlier than the understock from Santiam Pass, and approximately eight days earlier than the understock from the Coast Range and the Coast.

Similarly, the clones from Corvallis were on the average five days earlier than the clones from the Coast Range, and eight days earlier than the clones from Santiam Pass. Wommack suggested that plants native to high elevations differ genetically from plants native to low elevations in that they require a longer exposure to winter conditions. These results also indicate that differences in chilling requirements become smaller with increasing age.

Wommack (1964) found that in general 40°F was more effective in satisfying chilling requirements for Douglas-fir seedlings than temperatures of 32°, 50° and 60°F or out-of-doors temperatures. Differences in effectiveness of the chilling temperatures decreased with increasing length of period. Three and four weeks of chilling were inadequate to break dormancy under nine-hour photoperiod regardless of the chilling temperature. Twelve weeks of chilling resulted in only small differences in time of bud burst between subsequent long and short day treatments indicating that chilling requirements had been met after twelve weeks.

The plants used by Wommack (1964) were from eight different localities ranging from Vancouver Island, B. C. (200 feet elevation)

to McDonald Pass, Montana (6320 feet). The seedlings native to the three continental areas resumed growth earlier than seedlings from coastal areas after twelve weeks of chilling at 40°F. This was also true after six weeks of chilling at 40°F; but after just three weeks of chilling there was some evidence of the reverse situation. Wommack suggested that these results may mean that seedlings from the continental areas require more chilling than three weeks but once they have received adequate chilling they break dormancy more rapidly than seedlings from coastal areas.

Although seedlings from continental areas may require more chilling, they also showed a greater sensitivity to photoperiod. Thus, in all long day treatments continental seedlings never resumed growth later than coastal seedlings. This was true for all chilling periods from three to twelve weeks.

Increased length of chilling period increased subsequent growth regardless of photoperiod. The 40°F treatment was generally the most effective followed by 32° and 50°F.

Lavender and Hermann (1970) observed that Douglas-fir plants grown outdoors at Corvallis, Oregon remained inactive prior to late October when moved into favorable conditions. By January it appears that Douglas-fir plants left outdoors have been adequately chilled and resumption of growth depends entirely upon the environmental conditions in the spring (Irgens-Moller, 1958; Wommack, 1960;

Lavender and Hermann, 1970). This stage of the plant development is referred to as the nondormant state by Smith and Kefford. Probably in late October or early November, effective chilling occurs until dormancy release which appears to be sometime in December prior to the nondormant state in January. Spring bud burst has been observed to occur from early April to late May (Irgens-Moller 1957; Silen, 1962; Sorensen, 1967) depending on the source of the plants. The same appear to be the case with the time of bud set which may occur between July and September (Irgens-Moller, 1957; Sorensen, 1967).

MATERIALS, METHODS AND PROCEDURES

Responses of Eight-Month-Old Plants to Early and Late
Chilling During the Dormant Period (Experiment I)

Douglas-fir seed used in this experiment was collected in the fall of 1968 from five trees at each of two locations, Cloverdale near the Oregon Coast and Government Camp in the Oregon Cascades (Figure 1). These two sources were selected in order to sample population from very different climatic zones (Table 1).

Table 1. Description of seed sources used in Experiment I
(Climatological Data 1949-1969)

Environmental Variable	Origin [1]	
	Cloverdale	Government Camp
Altitude (feet)	20	3980
Latitude	45° 13'N	45° 18'N
Annual precipitation (inches)	78.3	84.7
Growing season (days)	227	63
Date of last frost	4/5	6/27
Date of first frost	11/19	8/29

[1] Averages for both sources based on 20 years of records.

In early March, 1969, seed from both sources was soaked in water for 24 hours, then drained and placed in stratification at 35°F.
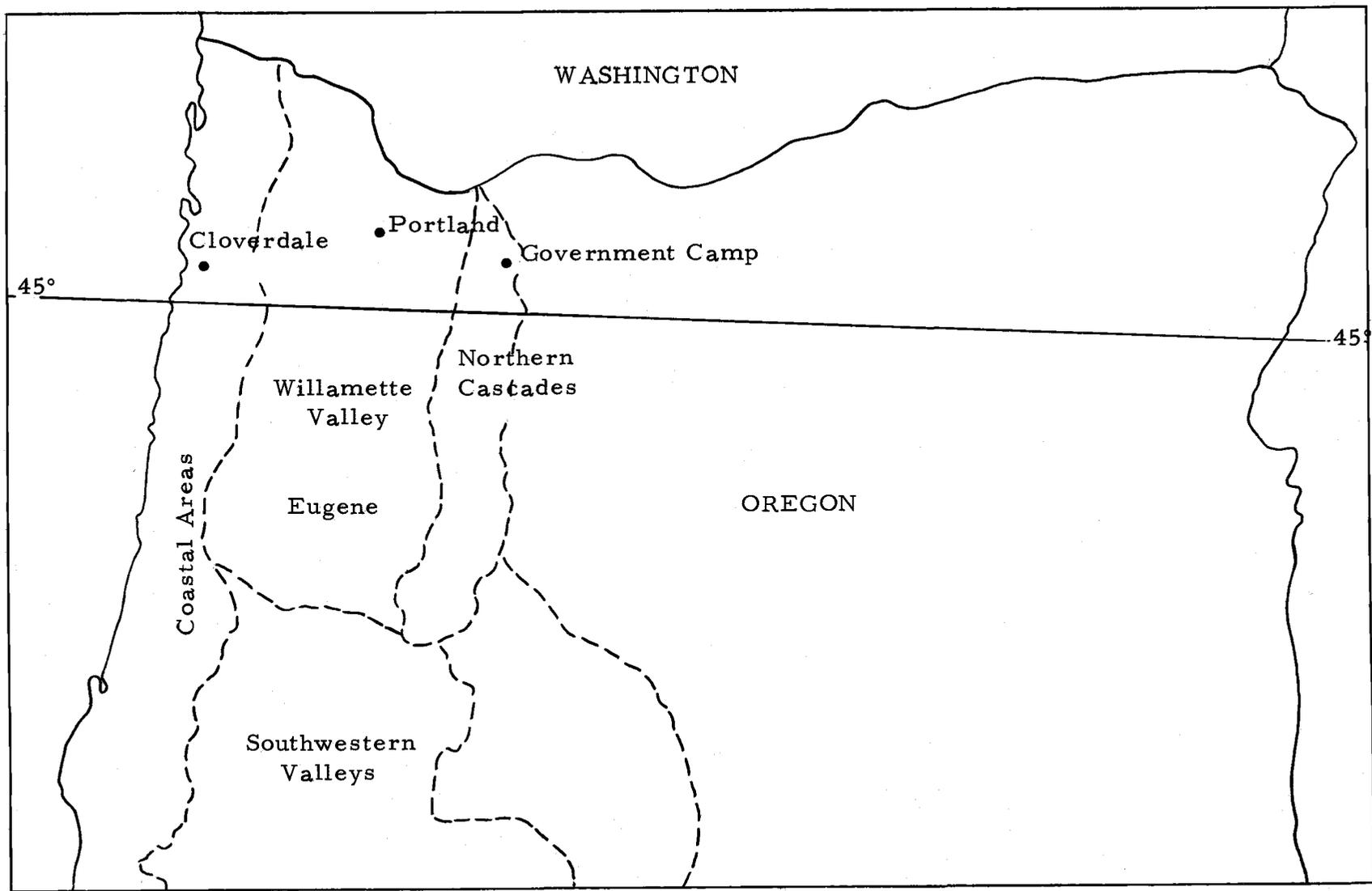
Figure 1.   Origin of Douglas-fir seed sources used in Experiment I.

After 14 days of stratification seed was germinated on moist filter paper in petri dishes in an incubator. Germination conditions were 86°F day/70°F night with 12 hour photoperiod and thermoperiod. Germinated seeds were planted six per pot in 4-1/2 inch black, pint plastic pots containing Willamette River bottom loam mixed with 1/3 peat by volume. Early losses were replanted to maintain six plants per pot.

Seedlings were grown in the greenhouse until late May, 1969, then moved outside under 50 percent shade. They were grown outside until they had all set terminal buds.

On September 15, all seedlings were moved into a growth chamber where they could be held in dormant conditions until the experimental treatments were applied. Conditions in the holding chamber were 70°F day/60°F night with nine hour photoperiod.

All plants were kept in the holding chamber until October 22 at which time plants on the first schedule were moved into chilling conditions (Figure 2). The schedule consisted of 216 pots, 108 each from Cloverdale and Government Camp. One-quarter of these were brought out of chilling after 11 days, one-quarter after 22, one-quarter after 33, and one-quarter after 44 days. A second schedule of 216 pots went into chilling after the first group on December 5. These also came out of chilling after intervals of 11, 22, 33 and 44 days. During both of these schedules, plants were chilled at three

Figure 2. Flow chart showing movement of plants into and out of the growth chambers and greenhouse used in Experiment I[1]

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[1] 216 pots/schedule; 9 pots/period treatment.

different temperatures, 40°, 45° and 50°F under nine hour photoperiod.

After the completion of each chilling period, the pots were placed in a warm greenhouse where long day (16 hours) conditions were maintained by using fluorescent tubes supplemented with incandescent bulbs. The temperature in the greenhouse was recorded during the experiment by thermographs placed among the plants. During the experiment the temperature never went above 80°F or below 65°F.

Date of bud burst was defined as the day when the terminal bud on the leader opened to expose the new needles. Bud burst was recorded for each individual plant by observations every 3-1/2 days and the results were subjected to analysis of variance based on pot means.

Responses of Four-Month-Old Plants to Early and Late
Chilling During the Dormant Period (Experiment II)

The plants used in this experiment were raised from seed collected in the fall of 1968 from five-tree collections made in three different maritime localities (Figure 3; Table 2).

In early June, 1970, seed from the three sources were stratified and germinated following similar methods and procedures used in Experiment I. Germinants were planted six per pot outside under 50 percent shade in mid-June. They were grown outside until September 8, when they were moved into a growth chamber and held in
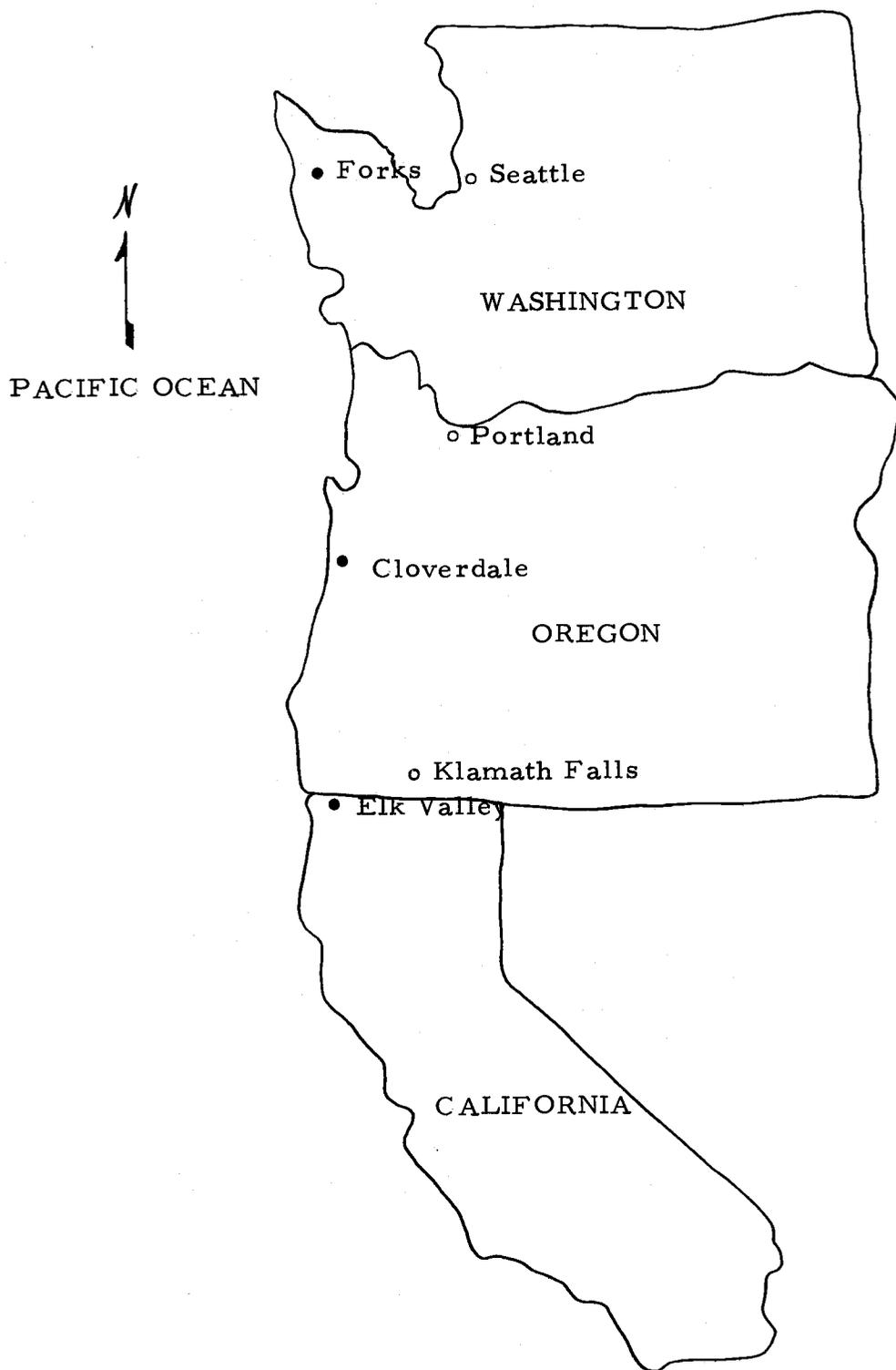
Figure 3. Origins of plants used in Experiment II.

dormant conditions as in Experiment I until experminental treatments were applied.

Table 2. Description of seed sources used in Experiment II (Climatological data 1949-1969)

| Environmental Variable | Origin[1] | | |
	Forks Washington	Cloverdale Oregon	Elk Valley California
Altitude (feet)	350	20	1711
Latitude	47° 57'N	45° 13'N	42° 00 N
Annual precipitation (inches)	117	78	38
Growing season (days)	180	227	129
Date of last frost	4/22	4/5	5/28
Date of first frost	10/20	11/19	10/4

[1] Averages for three sources based on 20 years of records.

The first schedule consisted of 36 pots, 12 each from Cloverdale, Elk Valley and Forks. On October 15, one-third of these were moved into chilling conditions, one-third 11 days later and one-third 22 days later and chilled for 55 days, 44 and 33 days, respectively (Figure 4). A second schedule of 36 pots was divided into three groups and chilled for 55, 44 and 33 days on December 9, 20 and 31, respectively. During both schedules plants were chilled at 45°F under 9-hour photoperiod.

After the completion of chilling, the pots were placed in a warm greenhouse. Plants in Schedules I and II were moved into the
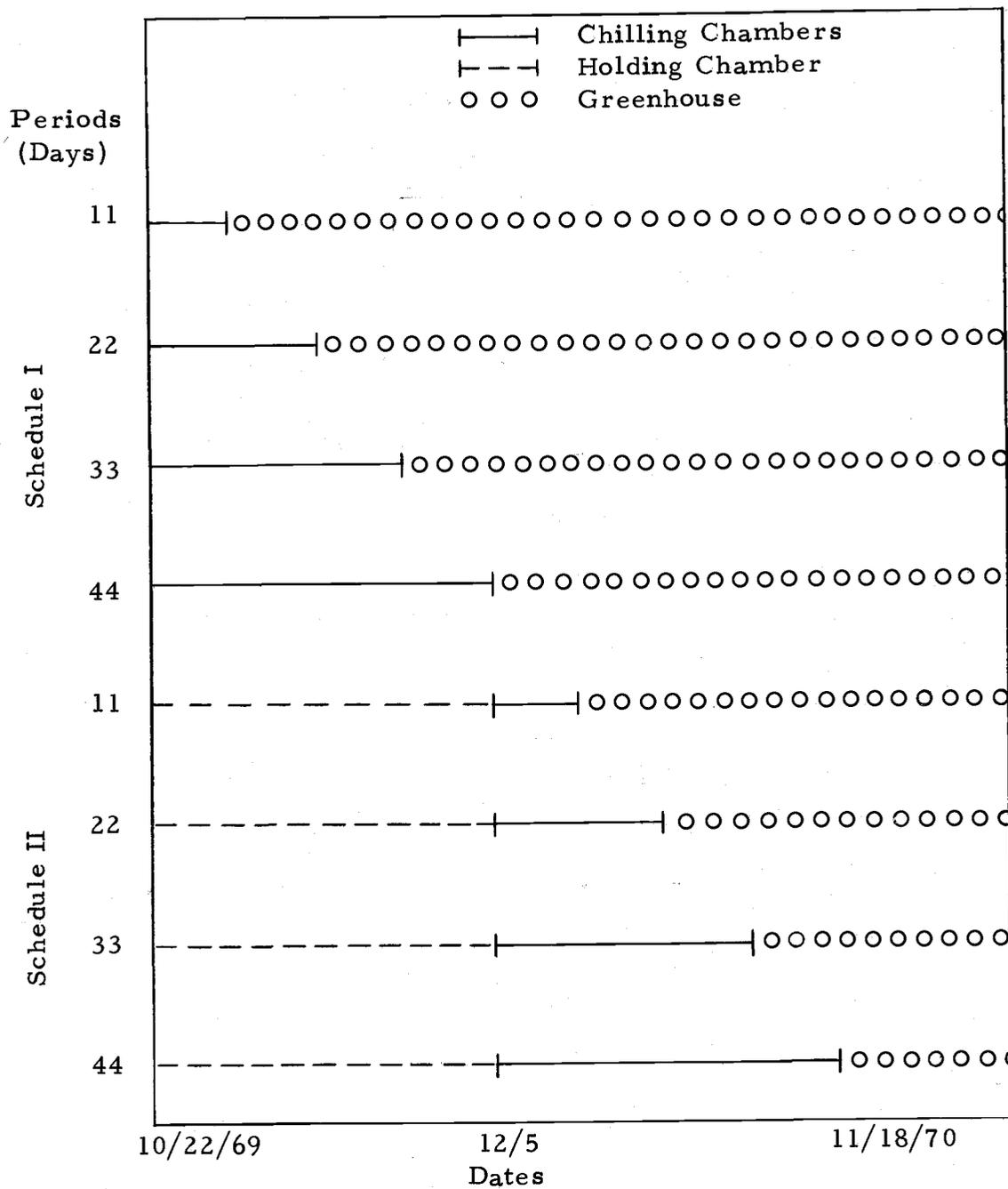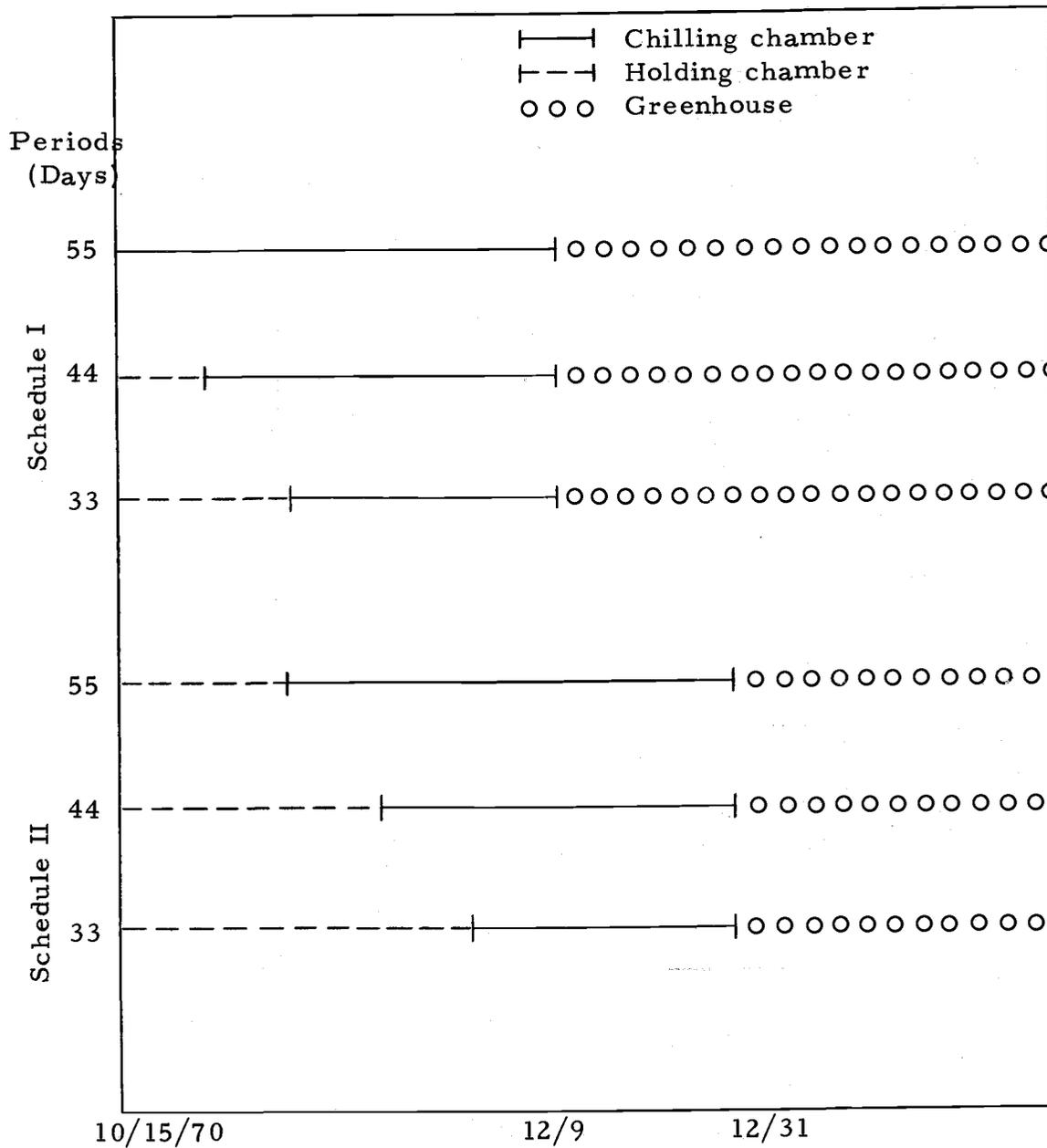
Figure 4. Flow chart showing movement of plants into and out of the growth chambers and greenhouse in Experiment II.[2]

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[2] 36 pots/schedule; 12 pots/period treatment.

greenhouse on December 9 and 31, respectively. Conditions in the greenhouse were kept as near as possible to conditions in Experiment I.

Date of bud burst was recorded for each individual plant every 3-1/2 days. In addition, total elongation, number of needles and needle length of the terminal shoot was made. The measurements were made after all plants had developed a terminal bud. The results were subjected to analysis of variance based on pot means.

RESULTS OF EXPERIMENT I

Interactions Involving Source and Other Factors

The temperature x sources interaction was highly significant
(Table 3). Raising the temperature to 45°F caused a larger delay in
bud burst for plants from Government Camp than for Cloverdale
plants, while raising it another 5 degrees caused no difference in
plants from Government Camp, but about the same delay as from 40°
to 45°F in Cloverdale plants (Figures 5 and 6). Chilling at 40°F was
more effective than 45° and 50°F in that order for Cloverdale and
Government Camp plants. Each additional 11 days of chilling for all
temperatures hastened bud burst in Cloverdale plants but it appears
that the last 11 days of chilling had no such effect in Government
Camp plants at 45° and 50°F (Figure 6).

Time of Chilling x Sources. Chilling during the latter part of
the dormant period (Schedule II) was more effective than earlier
(Schedule I) for the plants from Cloverdale while no such difference
was found in the plants from Government Camp (Figures 7 and 8).

In Schedule I the average number of days to bud durst for plants
from Government Camp was consistently lower than for Cloverdale
plants for every period-temperature combination (Figure 7). On the
average bud burst for Government Camp plants was approximately

Table 3. Analysis of variance of the average number of days to bud burst for two diverse sources of Douglas-fir plants chilled at different times and temperatures.

Source of Variation	d.f.	M.S.	F-values
Periods (P)	(3)	2643.07	170.37**
P_L	1	7880.24	507.94**
Remainder	2	24.38	
Temperature (T)	(2)	2129.09	137.24**
T_L	1	3504.167	225.87**
T_Q	1	754.014	48.60**
Schedules (R)	(1)	3864.69	249.11**
Sources (S)	(1)	890.03	57.37**
P x T	(6)	30.29	1.95NS
P x R	(3)	24.77	1.60NS
P x S	(3)	38.92	2.51NS
T x R	(2)	62.30	4.02*
$T_Q R$	1	117.556	7.58**
Remainder	1	7.04	
T x S	(2)	335.59	21.63**
$T_L S$	1	337.50	21.76**
$T_Q S$	1	333.70	21.51**
R x S	(1)	2352.25	151.62**
P x T x S	(6)	24.76	1.60NS
Error	(94)	15.51	
Total	143		

** = Sig. at 1% Level   NS = Not Sig. at 5% Level
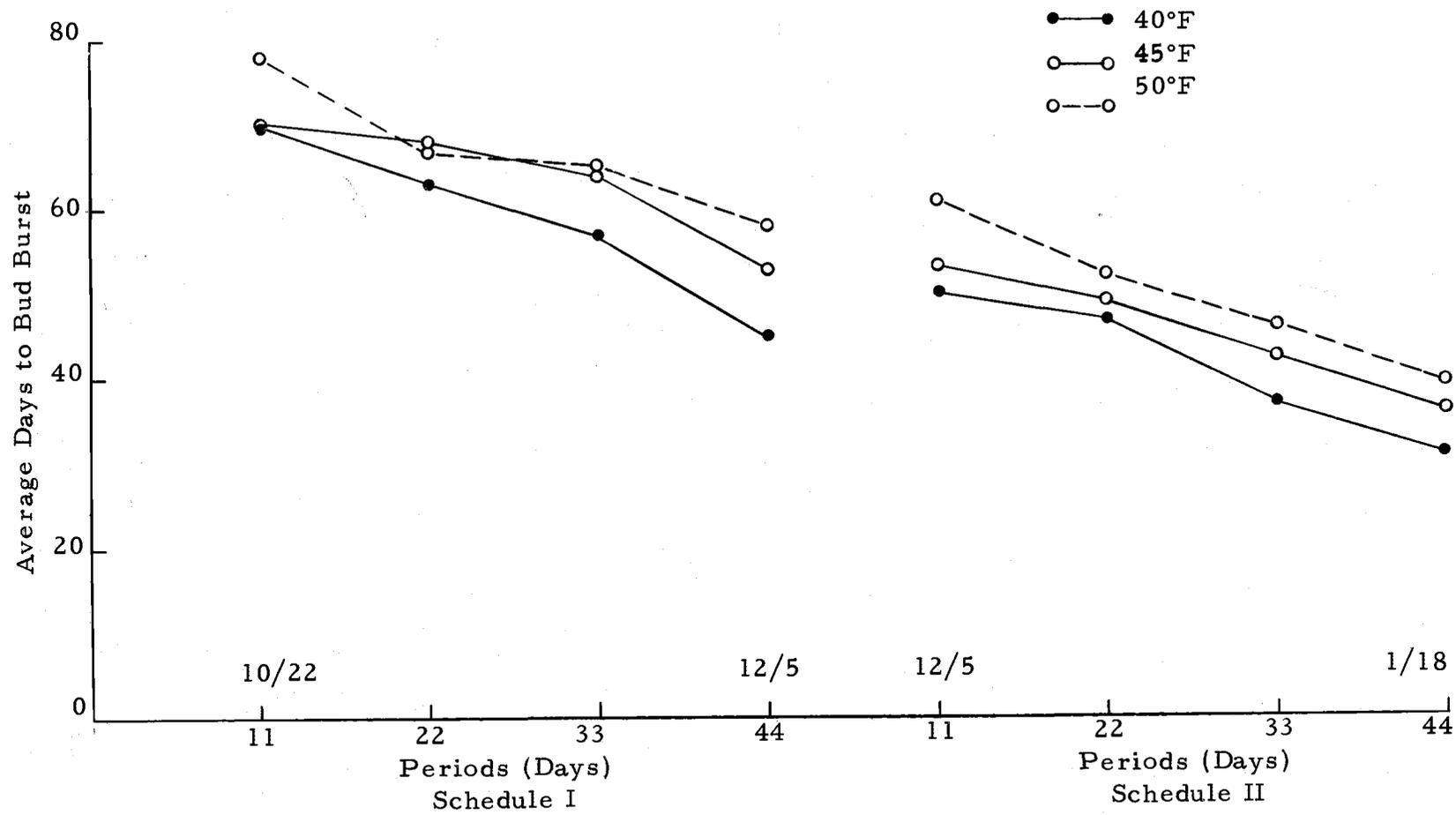
Figure 5. Average number of days to bud burst for plants from Cloverdale after chilling
at different temperatures.
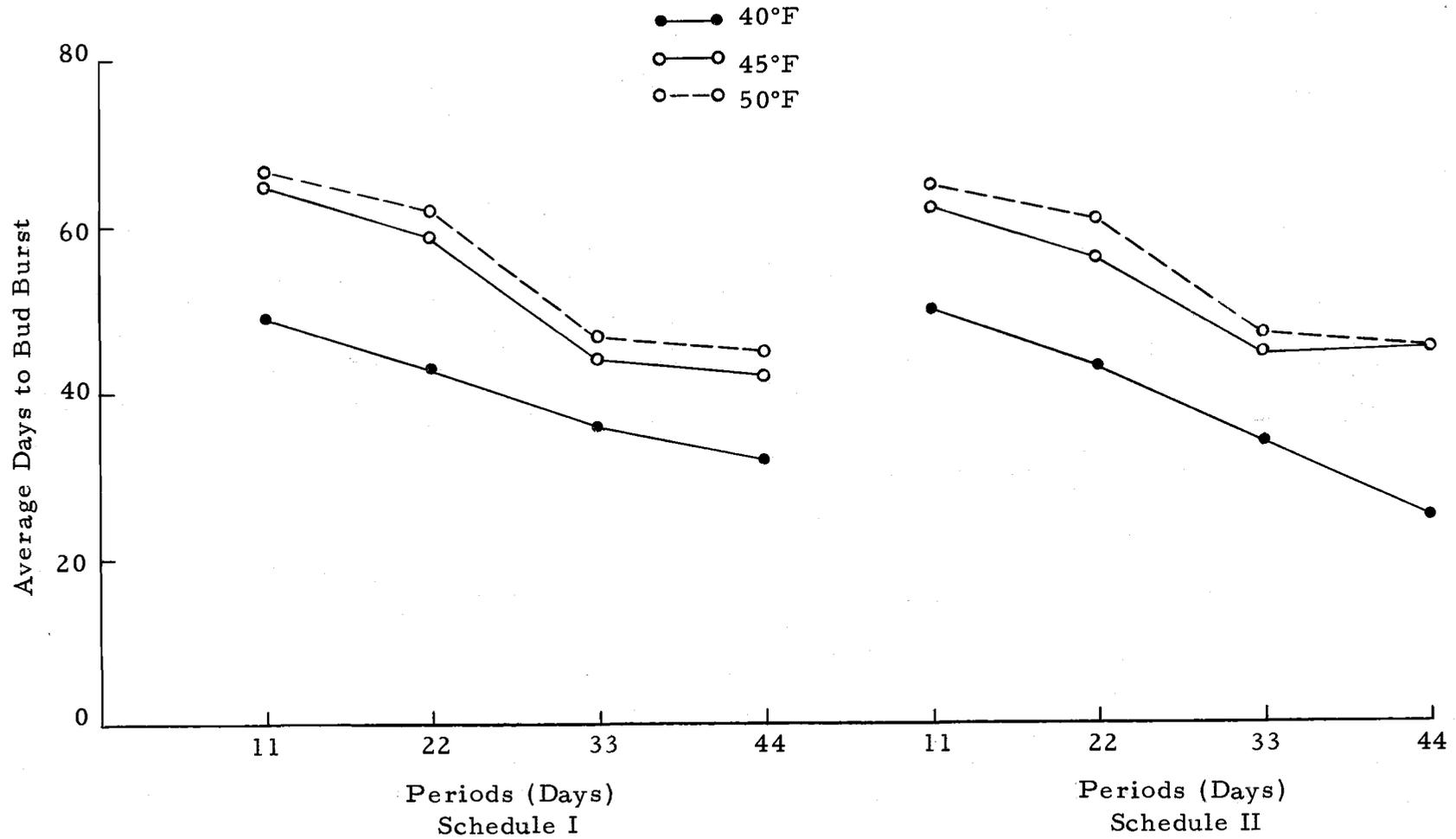
Figure 6.   Average number of days to bud burst for plants from Government Camp after chilling at different temperatures.
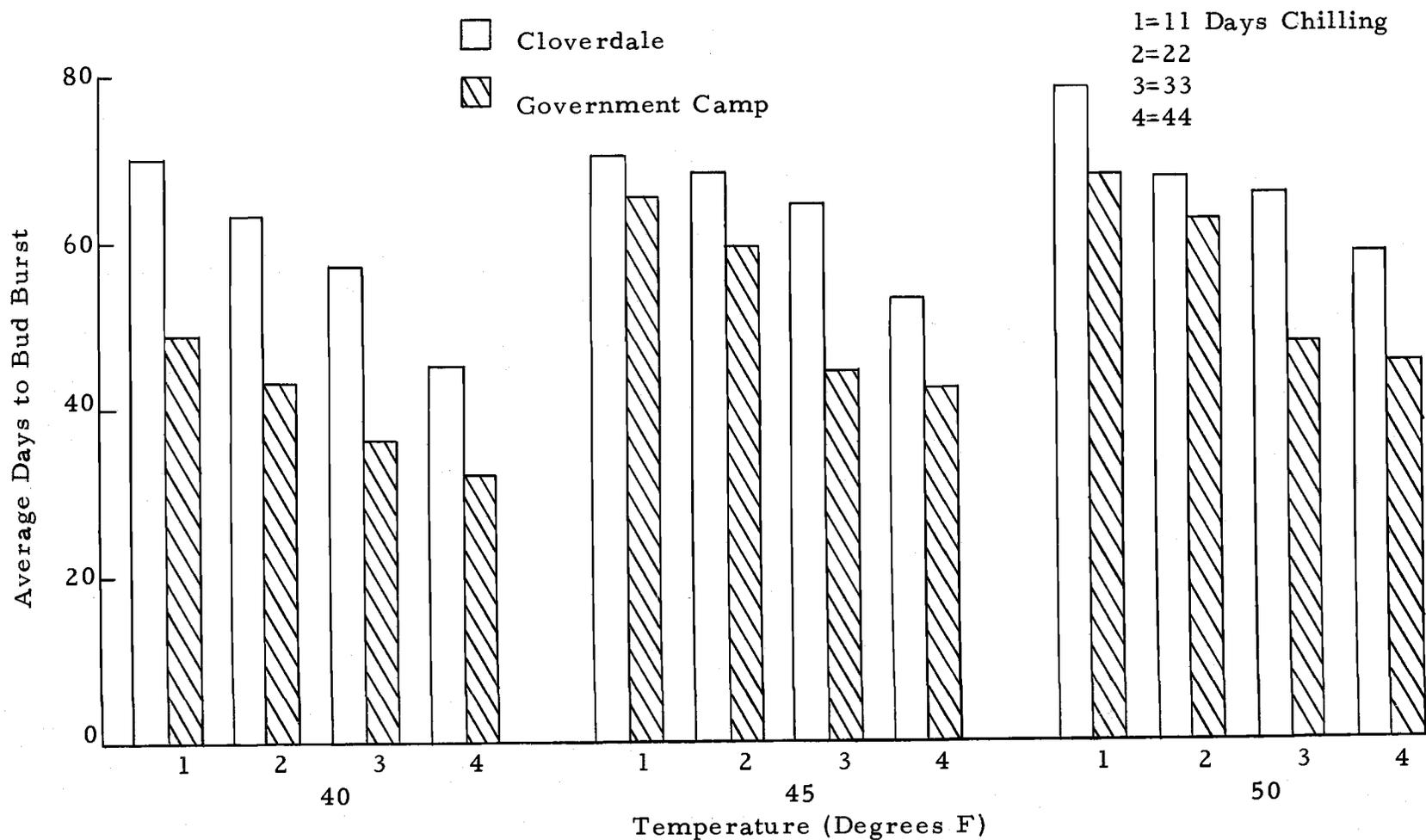
Figure 7. Average days to bud burst for plants from Cloverdale and Government Camp in Schedule I. Bud burst was observed in a warm greenhouse where plants were maintained on long days (16 hours). Each bar represents an average of 50 plants.
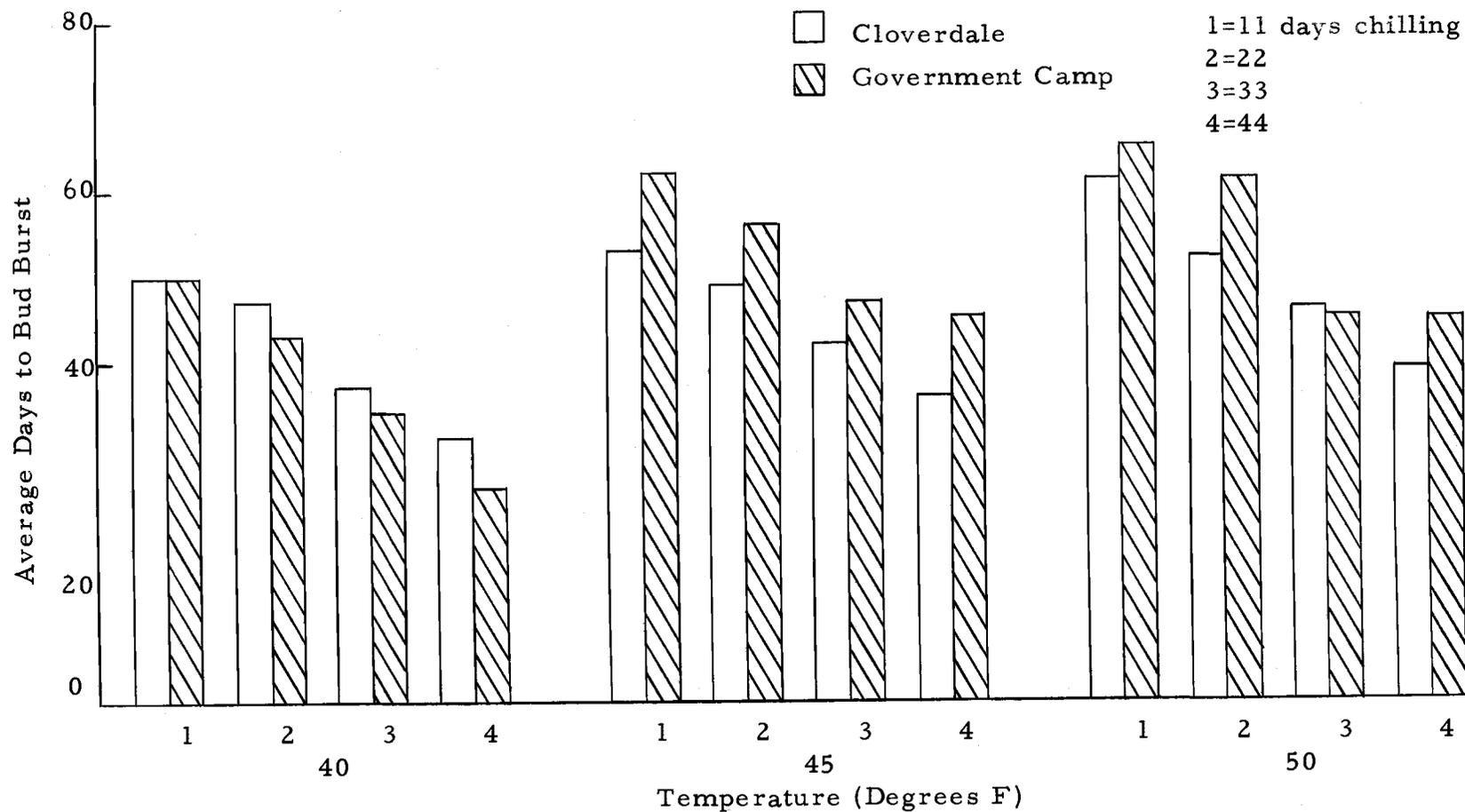
Figure 8. Average days to bud burst for plants from Cloverdale and Government Camp in Schedule II. Bud burst was observed in a warm greenhouse where plants were maintained on long days (16 hours). Each bar represents an average of 50 plants.

19 days earlier than for Cloverdale plants for all chilling periods at 40°F and approximately 11 days and 12 days earlier at 45° and 50°F respectively.

In Schedule II the average number of days to bud burst was less for the plants from Government Camp when chilled at 40°F than for Cloverdale plants but at 45° and 50°F it was reversed (Figure 8). On the average plants from Government Camp were approximately four days earlier than Cloverdale plants for chilling periods at 40°F while Cloverdale plants were approximately eight and five days earlier than Government Camp at 45° and 50°F respectively.

Interactions Not Involving Sources

The temperature x time of chilling (schedule) interaction was significant as was the $T_Q R$ comparison indicating that raising the temperature to 45°F in early chilling caused a larger dealy in bud burst than in late chilling, while raising it another five degrees caused virtually no difference in early chilling but a slight delay in late chilling (Figure 9). There were no other significant two-factor interactions and no significant three-factor interactions.
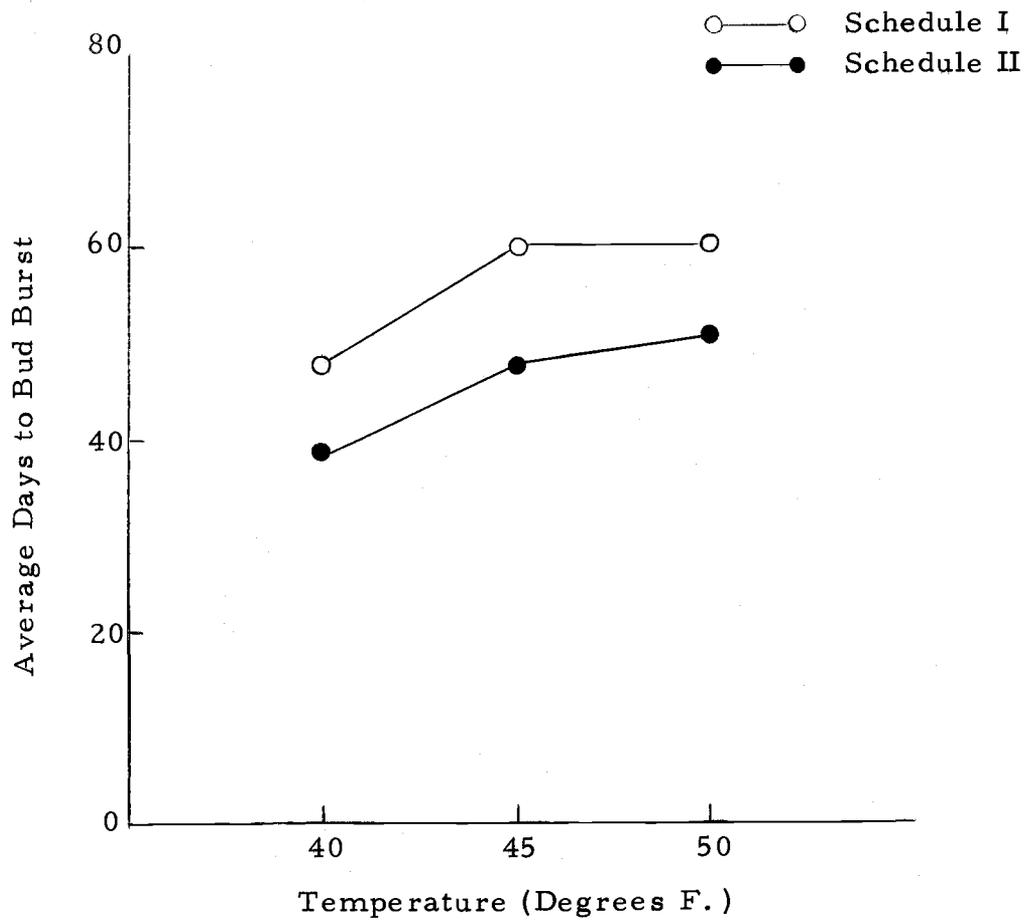
Figure 9. Average number of days to bud burst in relationship to the temperature schedule interaction.

CONCLUSIONS (EXPERIMENT I)

Chilling temperatures of 5 degrees and 10 degrees above the optimum of 40°F (Wommack, 1964) diminishes in effectiveness sooner in the Government Camp plants than in the Cloverdale plants (Figures 5 and 6). All three chilling temperatures, 40°F, 45°F and 50°F appear to hasten bud burst in the Cloverdale plants (Figure 5). Although chilling at 40°F when expanded from 33 to 44 days still hastened bud burst in plants from Government Camp, this did not appear to be the case for the same periods of chilling at 45° and 50°F (Figure 6). It therefore appears that a decrease in temperature below 45°F is necessary to further hasten bud burst.

The highly significant F-value (151.62) for the interaction between time of chilling and sources indicates that chilling requirements apparently vary during the dormant period for the two sources tested in this experiment. Dormancy for each source occurred at different times and therefore the plants were chilled at different stages of their physiological development (Table 4). Bud set for the Government Camp plants was completed five weeks earlier than for the plants from Cloverdale.

The high interaction significance also indicates that there may be genetic differences in chilling requirements over and above the fact that genetic differences also cause a different time course of

development stages. If plants from the two sources were treated so that they were chilled at exactly the same development or physiological stages, differences in chilling requirements would probably still exist.

Table 4. Sequence of events by dates for plants from Cloverdale and Government Camp.

Sequence of Events	Date	Number of Days From Event 1
1. Completion of bud set		
Government camp	10 August 1969	
Cloverdale	18 Sept. 1969	
2. Seedlings moved into holding chamber	20 Sept. 1969	
Government Camp		41
Cloverdale		2
3. Start of Schedule I	22 Oct. 1969	
Government Camp		73
Cloverdale		34
4. Start of Schedule II	5 Dec. 1969	
Government Camp		117
Cloverdale		79
5. End of Schedule II	18 Jan. 1970	
Government Camp		161
Cloverdale		123

An attempt was made to estimate when the plants from this experiment had reached the dormant state as described by Smith and Kefford (1964). During the early and latter part of each schedule, plants from both sources were chilled for 11 days at 40°F, hereafter called Experiment IA (Figure 10). There was virtually no difference
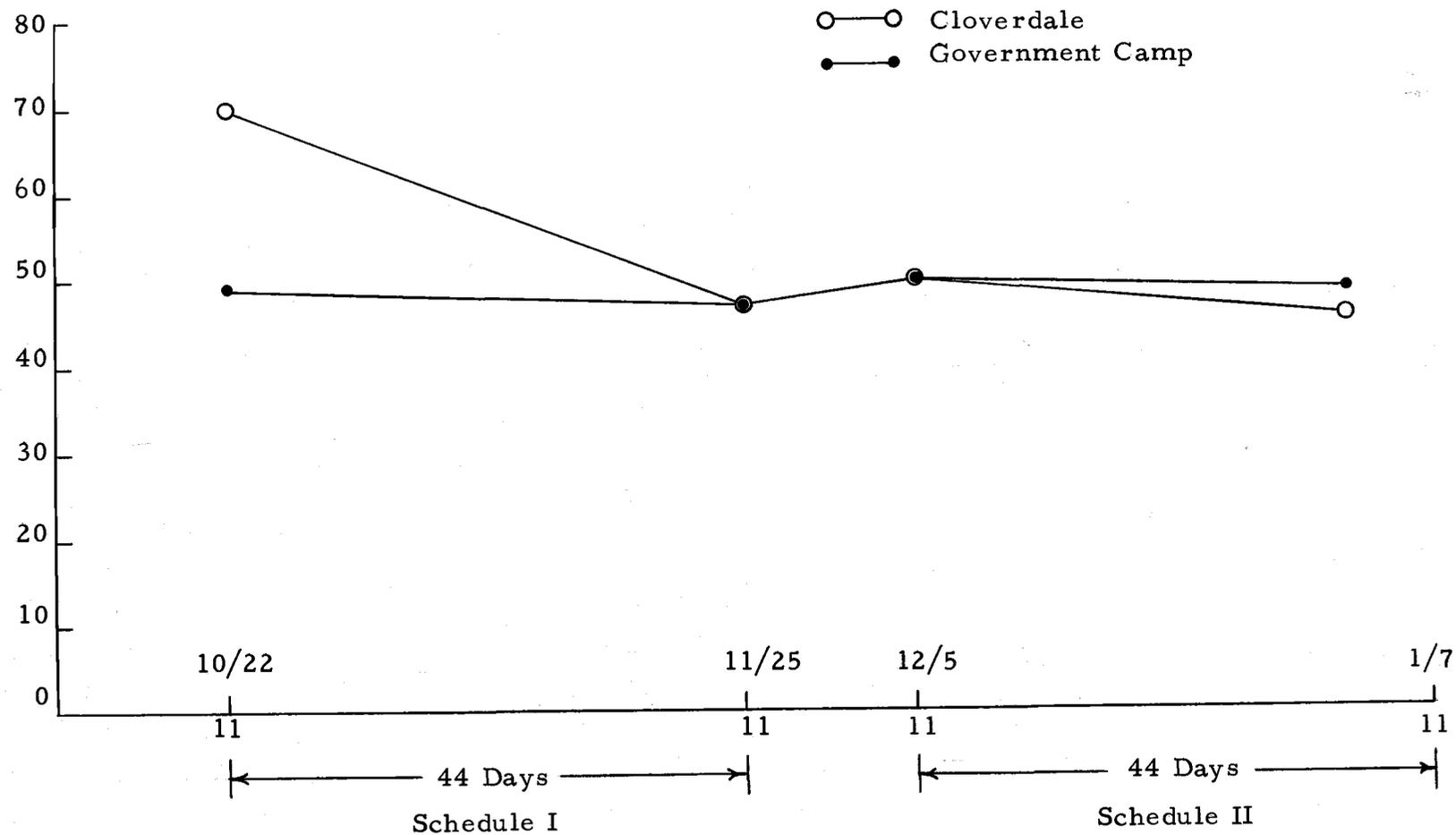
Figure 10. Average days to bud burst for plants from Cloverdale and Governement Camp. Each dot represents 50 plants chilled for 11 days at 40°F (Experiment IA). Dates on abscissa denotes the start of each 11 days of chilling.

between these treatments for the Government Camp plants. Previously it was also shown that there was no difference in days to bud burst between early and late chilling in plants from this source (Figure 6). Both of these results indicate that they had reached the dormant state sometime prior to the beginning of Schedule I (October 22).

It appears that sometime prior to the latter 11 days of chilling (November 25) of Experiment IA, the Cloverdale plants had completed dormancy development and reached the dormant state (Figure 10). Attainment of the dormant state by the Cloverdale plants is further confirmed by the earlier bud burst in Schedule II (early December) than in Schedule I (late October) Figure 5.

The Cloverdale plants required approximately 8 to 9 weeks to reach the dormant state. This is calculated from time of bud set to sometime prior to the latter 11 days of chilling (November 25) in Schedule I of Experiment IA (Table 4; Figure 10). The Government Camp plants as previously discussed had apparently reached the dormant state prior to Schedule I (late October).

It would be reasonable to expect that plants from Government Camp, characterized by long and severe winters, require more chilling than plants from Cloverdale, characterized by mild winters. However, based on results of this experiment, when the plants from both sources reached approximately the same physiological stage of development (dormant state), large differences in chilling requirements

apparently do not exist.

Both early and late chilling treatments showed that 45° and 50°F apparently became ineffective when expanded from 33 to 44 days for the Government Camp plants (Figure 6). This consistency indicates that the forces of natural selection operating in high elevations may have favored plants that require chilling temperatures lower than 45°F to satisfy their chilling requirements (plants chilled at 40°F used as a source for comparison). This seems to be in order for Government Camp having average monthly temperatures during the dormant period (late August to late May) considerably lower than the temperatures used in this study (Tables 1 and 5).

All three chilling temperatures (40°F, 45°F and 50°F) hastened bud burst for the Cloverdale plants up to 44 days of treatment (Figure 5). During the dormant period (late November to late April) these plants are exposed to monthly average temperatures that are within the range of temperatures used in this study (Tables 1 and 5). Natural selection operating in Cloverdale may have selected plants that do not require temperatures below 50°F to satisfy their chilling requirements.

Table 5. Location of weather stations at seed collection points. Temperature averages for the stations and their corresponding seed sources. (Climatological Data, 1949-1969)

Location	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
Cloverdale	56	50	44	42	45	47	50	51	56	59	61	59
Government Camp	48	37	33	30	31	34	40	41	50	58	55	52

RESULTS OF EXPERIMENT II

Effects on Bud Burst

The effects of length and time of chilling were essentially similar to those found in Experiment I. Both effects were again highly significant (Table 6). The average number of days to bud burst under long days after chilling decreased with longer exposure to chilling irrespective of origin (Figure 11). Thus, for both schedules combined the average number of days until bud burst was 27, 26 and 22 after 33, 44 and 55 days of chilling, respectively.

As in Experiment I the early chilling was less effective than the later. Average number of days to bud burst was 28 for plants exposed early in the dormant period and 22 for plants exposed later.

The only significant interaction was between length and time of chilling (Table 6). As the chilling period increased in length the differences between early and late chilling decreased significantly after 55 days regardless of source (Figure 12). Average number of days until bud burst during early in the dormant period was 32, 28 and 22, while during late in the dormant period they were 22, 23 and 20 after 33, 44 and 55 days of chilling, respectively.

Table 6. Analysis of variance of the average number of days to
bud burst for three maritime sources of Douglas-fir
plants chilled at different times during the dormant period.

Source of Variation	d.f.	M. S.	F-values
Sources (S)	2	1.58	1.41 NS
Periods (P)	2	102.58	91.59 **
Schedules (R)	1	277.78	248.02 **
S x P	4	.67	.59 NS
S x R	2	.86	.86 NS
P x R	2	45.86	40.95 **
S x P x R	4	.44	.39 NS
Error	18	1.12	
Total	35	430.89	

NS = Not Sig. at 5% Level   ** = Sig. at 1% Level

Effects on Height Growth

With respect to the amount of growth, all three main effects,
sources, length and time of chilling were highly significant while there
were no significant interactions (Table 7). The average heights for
the three sources in all treatment combinations were 6.5, 6.1 and
5.1 centimeters for Cloverdale, Forks and Elk Valley, respectively.

Increased length of chilling increased growth of plants from all
three sources. Thus, plants from Cloverdale grew 5.5, 6.7 and 7.3
centimeters while plants from Forks grew 5.1, 6.4 and 6.8

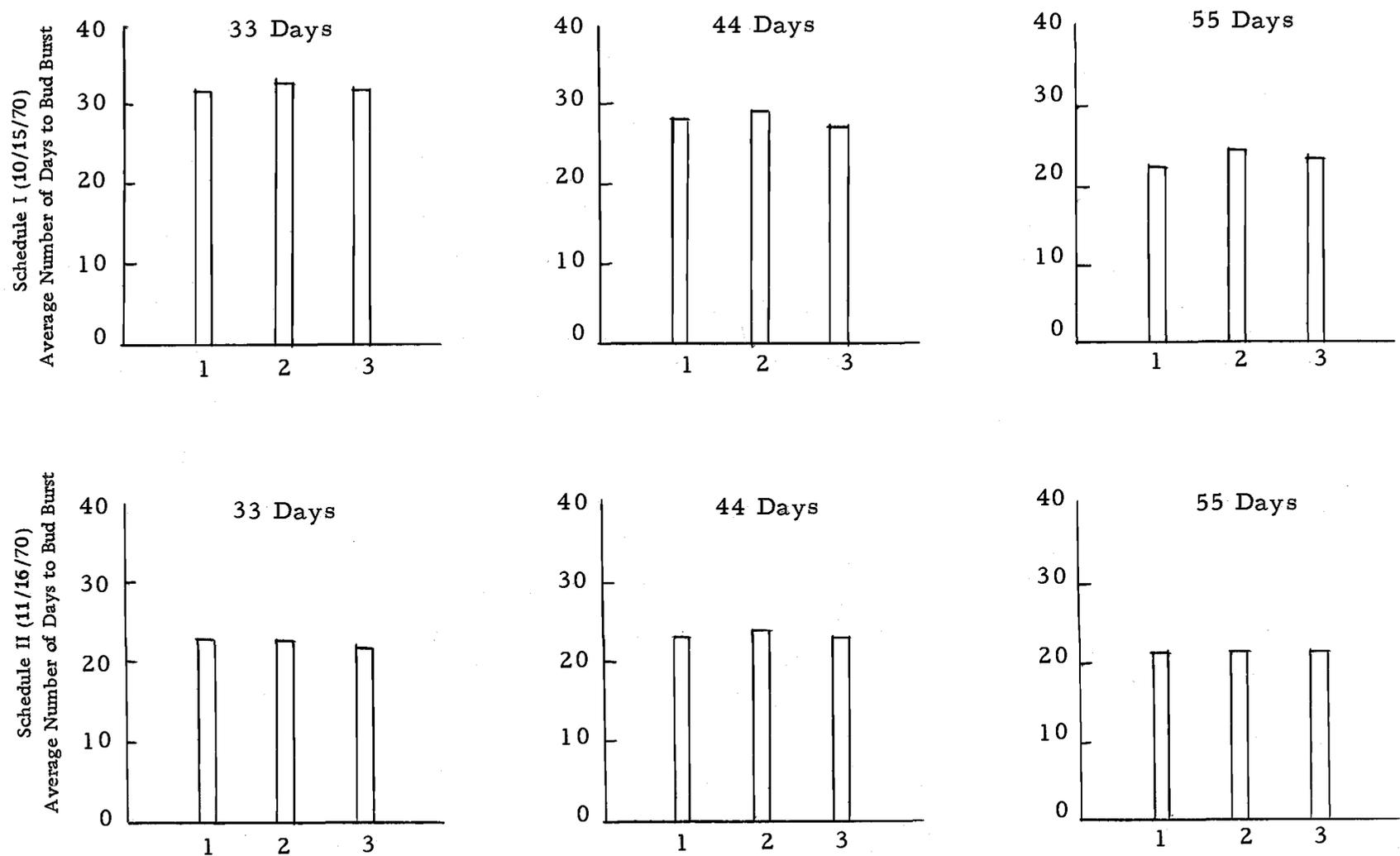Figure 11. Average number of days to bud burst of Douglas-fir plants from three maritime areas after chilling at 45°F for the indicated number of days and different times.

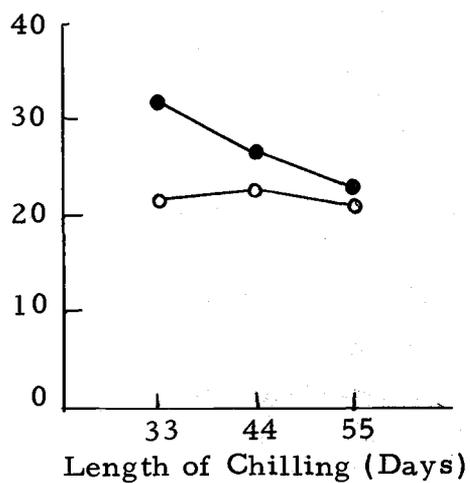Sources: 1-Cloverdale, Oregon; 2-Elk Valley, California; 3-Forks, Washington.
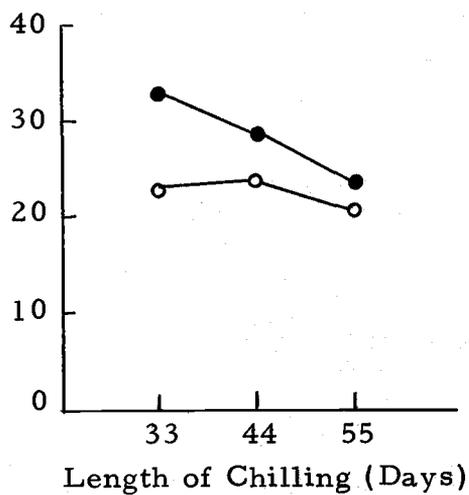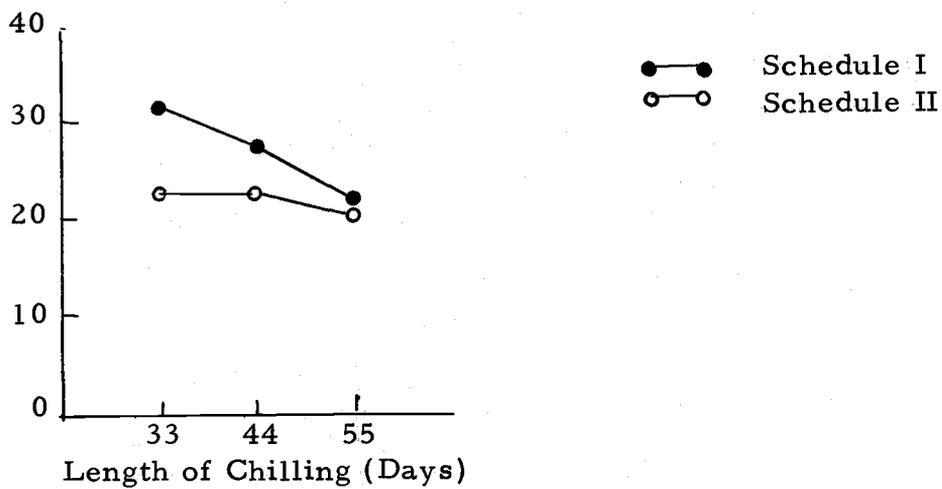
Figure 12. Average number of days to bud burst after early (Oct. 15) and late (Nov. 6) chilling. All plants were chilled at 45°F then placed under long days in the greenhouse.

centimeters and plants from Elk Valley grew 4.1, 5.4 and 5.9 centimeters after 33, 44 and 55 days respectively.

Table 7. Analysis of variance of the average amount of growth (in centimeters) for three maritime sources of Douglasfir plants after early and late chilling.

Source of Variation	d.f.	M. S.	F-Values
Sources (S)	2	5.81	132.1 **
Periods (P)	2	10.13	230.2 **
Schedules (R)	1	5.44	123.7 **
S x P	4	.01	< 1
S x R	2	.00	< 1
P x R	2	.04	< 1
S x P x R	4	.02	< 1
Error	18	.04	
Total	35	21.49	

Plants chilled late in the dormant period grew considerably more than plants chilled early. The average amount of growth for plants chilled early and late were 5.5 and 6.3 centimeters, respectively. Each source grew consistently more when exposed to late chilling for the same length of chilling (Figure 13).

Incidentally, plant height growth initiation occurred earlier and the rate of growth (average daily height growth) was greater after

Cloverdale

Schedule I
Schedule II

Length of Chilling (Days)

Elk Valley

Length of Chilling (Days)

Forks

Length of Chilling (Days)

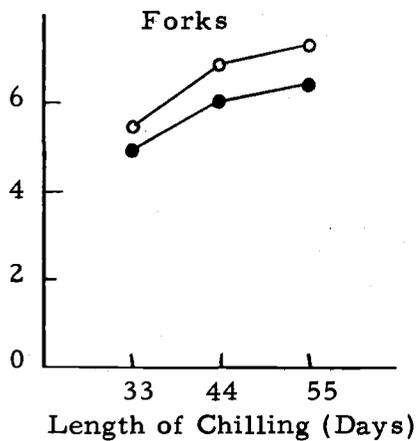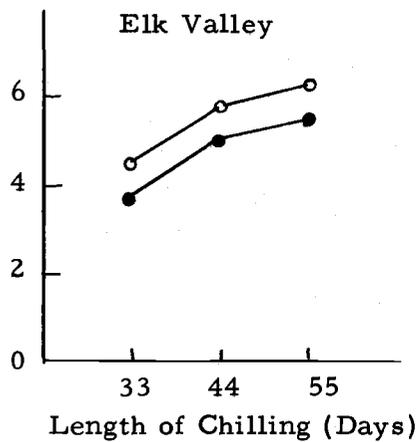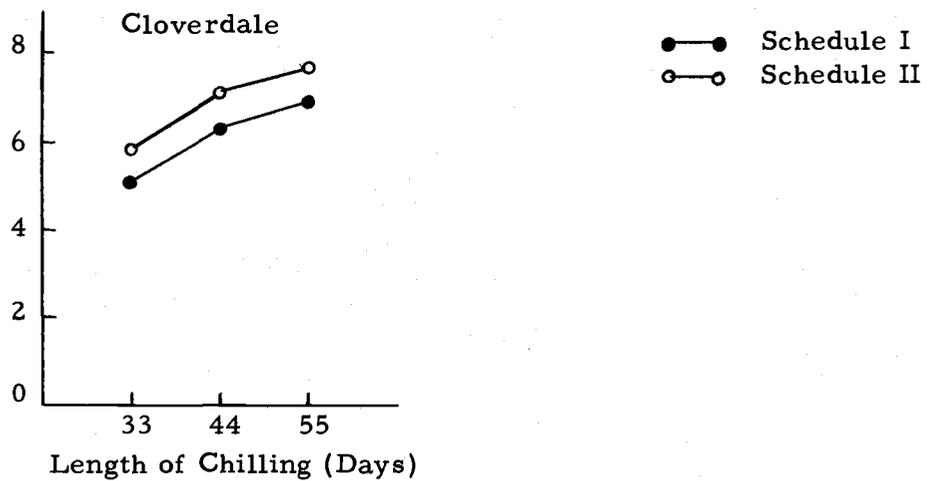Figure 13. Height growth (in centimeters) of plants chilled early and late in the dormant period. Plants were chilled at 45°F for the indicated lengths of chilling.

late chilling (Figure 14). This was also the case with increased

length of chilling. Cloverdale and Forks plants had a higher rate than

Elk Valley (Figure 15 and Table 8).

Table 8. Effects of early and late chilling, length of chilling and
seed source on rate of height growth (c m/day).[1]

Seed Source	Schedule I			Schedule II		
	Length of Chilling (Days)					
	33	44	55	33	44	55
Cloverdale	.16	.22	.30	.24	.28	.34
Elk Valley	.10	.16	.22	.18	.23	.28
Forks	.14	.20	.26	.24	.27	.32

[1] Mean daily height growth rate was calculated for the period of
most active growth, between average day to bud burst and 66 days
after the plants had been moved into the greenhouse.

Intermitten growth was particularly pronounced in plants from

Elk Valley (Table 9). This phenomenon consists of the formation of a

small, green terminal bud with distinct bud scales, which, however,

soon resumes growth again. Formation of these terminal buds occur-

red once for all of the the observed plants.
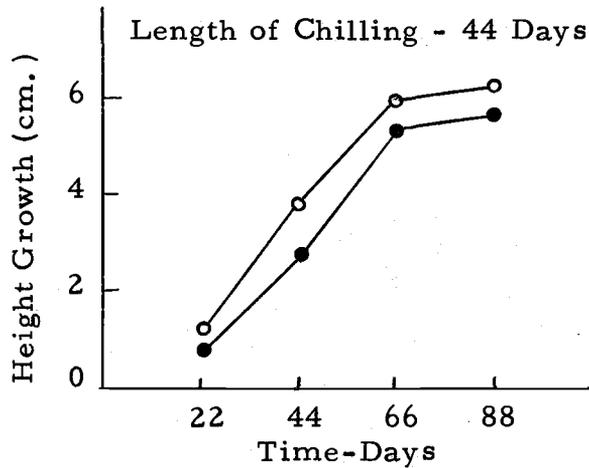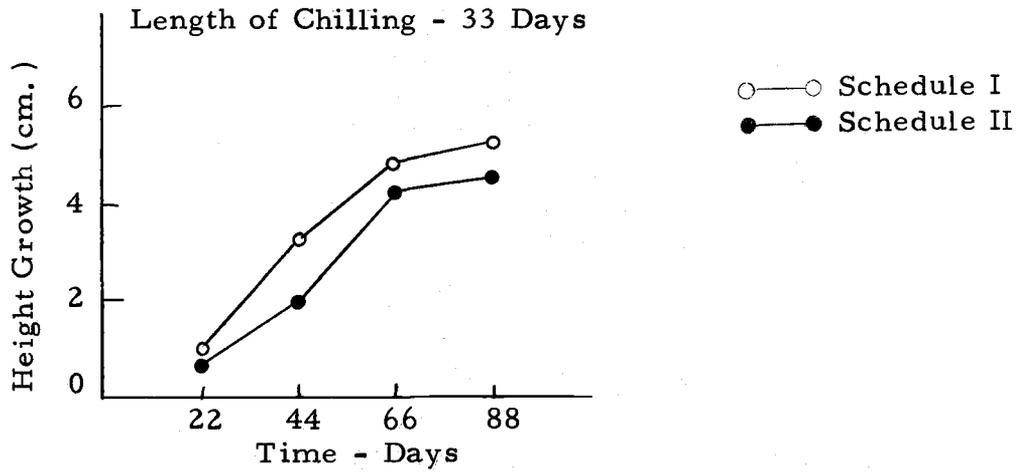
Figure 14.   Effects of length of chilling and time of chilling on height
growth patterns, seed sources pooled.

Length of Chilling - 33 Days

Length of Chilling - 44 Days

Length of Chilling - 55 Days

1- Cloverdale, Oregon
2- Elk Valley, California
3- Forks, Washington
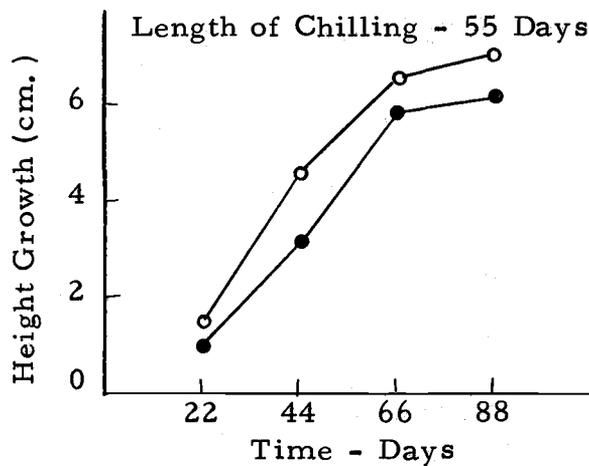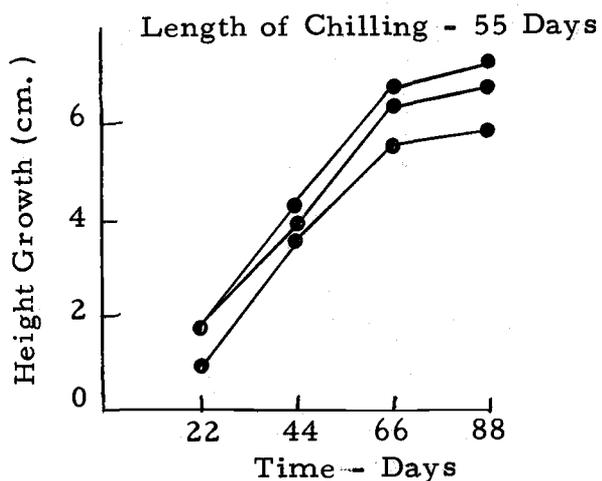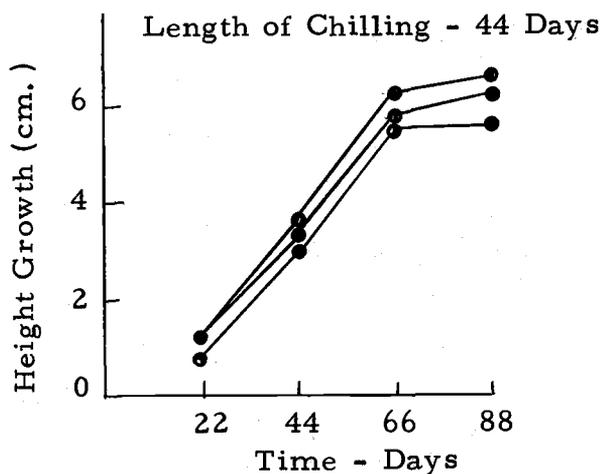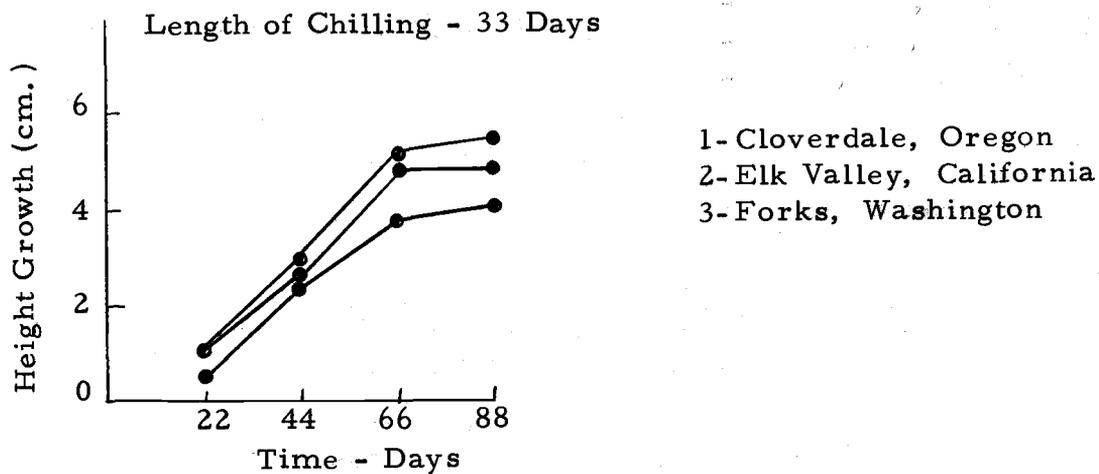
Figure 15.   The effects of length of chilling and seed sources on height growth patterns, early and late chilling results pooled.

Table 9. Number of plants for each source that demonstrated intermittent growth after early and late chilling.

Seed Source	Schedule I			Schedule II			Total Number of Plants
	Length of Chilling (Days)						
	33	44	55	33	44	55	
Cloverdale	6	4	5	5	6	7	33
Elk Valley	18	19	17	16	18	17	105
Forks	5	6	4	8	6	4	33

Effects on Number of Needles

The average number of needles developed after late chilling was significantly higher than the number developed after early chilling (Table 10). Differences among sources were also highly significant with plants from Cloverdale and Forks having an average of 126 and 125 needles, respectively while the plants from Elk Valley had an average of 100 needles (Table 11). There were no other significant factors in the analysis of variance.

The number of needles per centimeter of stem were greater after late chilling than after early chilling and decreased as chilling increased (Table 12).

Effects on Needle Length

The average needle length increased significantly as chilling

increased for all three sources (Table 13 and Figure 16). Differences among sources was highly significant with the plants from Cloverdale and Forks having greater needle lengths than Elk Valley within any specific treatment combination. The differences in needle length between Cloverdale and Forks were almost nil. Time of chilling was non-significant.

Table 10. Analysis of variance of the average number of needles developed during height growth. [1]

Source of variation	d. f.	M. S.	F-values
Sources (S)	2	2738.78	947.71**
Periods (P)	2	9.69	3.42
Schedules (R)	1	3885.44	1344.44**
S x P	4	3.40	1.21
S x R	2	5.80	2.08
P x R	2	.53	< 1
S x P x R	4	5.82	2.08
Error	18	2.89	
Total	35	6652.35	

[1] Analysis was based on using the average number of needles developed on four plants per treatment.

Table 11. Effects of early and late chilling, length of chilling and seed source on the average number of needles developed during height growth. [2]

Seed Source	Schedule I			Schedule II		
	Length of Chilling (Days)					
	33	44	55	33	44	55
Cloverdale	113	114	117	138	141	138
Elk Valley	92	93	96	108	108	107
Forks	114	117	116	136	140	139

[1] Each average represents height growth from eight plants (four plants per replication).

Table 12. Effects of early and late chilling, length of chilling and seed source on number of needles developed per centimeter of height growth.

Seed Source	Schedule I			Schedule II		
	Length of Chilling (Days)					
	33	44	55	33	44	55
Cloverdale	22.2	18.1	16.9	23.8	19.9	17.9
Elk Valley	24.9	23.3	17.5	25.4	24.3	18.1
Forks	23.8	19.5	18.1	25.2	20.3	19.0

Table 13. Analysis of variance of the average needle lengths (in MM.) for three maritime sources of Douglas-fir plants after early and late chilling. [1]

Source of variation	d.f.	M.S.	F-values
Sources (S)	2	149.53	316.81**
Periods (P)	2	364.36	777.22**
Schedules (R)	1	.028	< 1
S x P	4	1.41	2.89
S x R	2	.528	1.10
P x R	2	.528	1.10
S x P x R	4	.278	< 1
Error	18		
Total	35	516.66	

[1] Analysis based on the average of 120 needle lengths per treatment. Average needle length was determined by measuring five needles at mid-height of each shoot elongation.
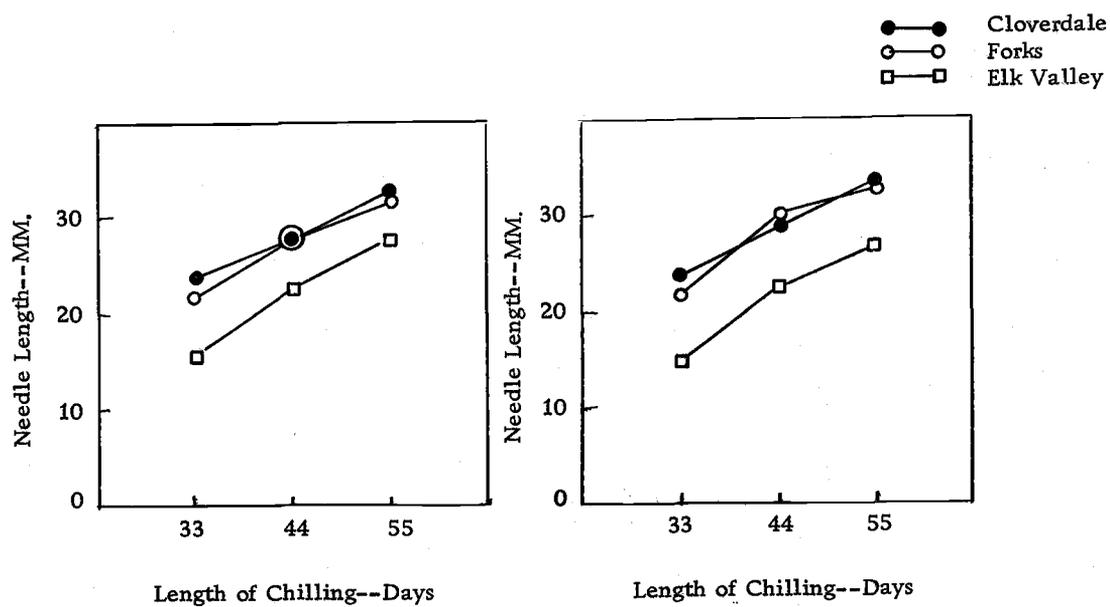
Figure 16. Effects of time of chilling, length of chilling and seed
source on mean needle length of Douglas-fir plants.
I. Early chilling; II. Late chilling.

CONCLUSIONS (EXPERIMENT II)

Although only 21 days separated the early and late chilling, the effect was statistically significant. The absence of the source x time interaction indicates that all three sources were affected similarly by early and late chilling. In addition, there were no significant interaction between source and length of chilling. The conclusion is drawn, that the six treatment combinations and the one condition after chilling failed to demonstrate any genetic differences in chilling requirements. It is also concluded that the various chilling treatments differ with respect to the degree that they satisfy the chilling requirements of the plants.

The average number of days to bud burst of the plants from all three areas was influenced significantly by the length at which they were chilled. There was clear evidence that plants chilled for 55 days resumed growth earlier than those chilled for 44 and 33 days (Figure 11). All three chilling treatments were more effective during the latter part of the dormant period with the longest period being the most effective.

Fifty-five days of chilling eliminated any differences between effects of early and late chilling while this was not the case for 33 days (Figure 12). It is concluded that as the length of chilling is increased, the time effect becomes less significant.

The amount of growth for each source was also affected by the time of chilling. The greater height after late chilling is related to a faster growth rate and a longer growth period resulting from earlier bud burst (Figure 14 and Table 8). Growth also increased as length of chilling increased.

Within any specific treatment combination, height growth differences among the seed sources was related to the rate of growth but not to the length of the growth period (Figure 15).

In Table 2 it was shown that Elk Valley has a short growing season (129 days) as compared to 180 days for Forks and 227 days for Cloverdale. Also, Figure 17 shows Elk Valley has the least annual precipitation and much less during the summer months than Forks and Cloverdale. These environmental variables are reflected in the early cessation of height growth for the plants from Elk Valley and the fact that these plants showed intermittent height growth may conceivably permit plants to remain dormant even early in the season if for some reason the growing conditions became unfavorable, for example, low soil moisture, and yet resume growth quickly as the conditions became favorable.

The increased growth after late as compared to early chilling could come about in two ways: either by increased elongation without any increase in number of needles, or: by an increase in number of leaf primordia produced. The latter appears to be the case in this

Seed Source and Annual Precipitation

Elk Valley, California 39"

Cloverdale, Oregon 78"

Forks, Washington 117"

Inches of Precipitation
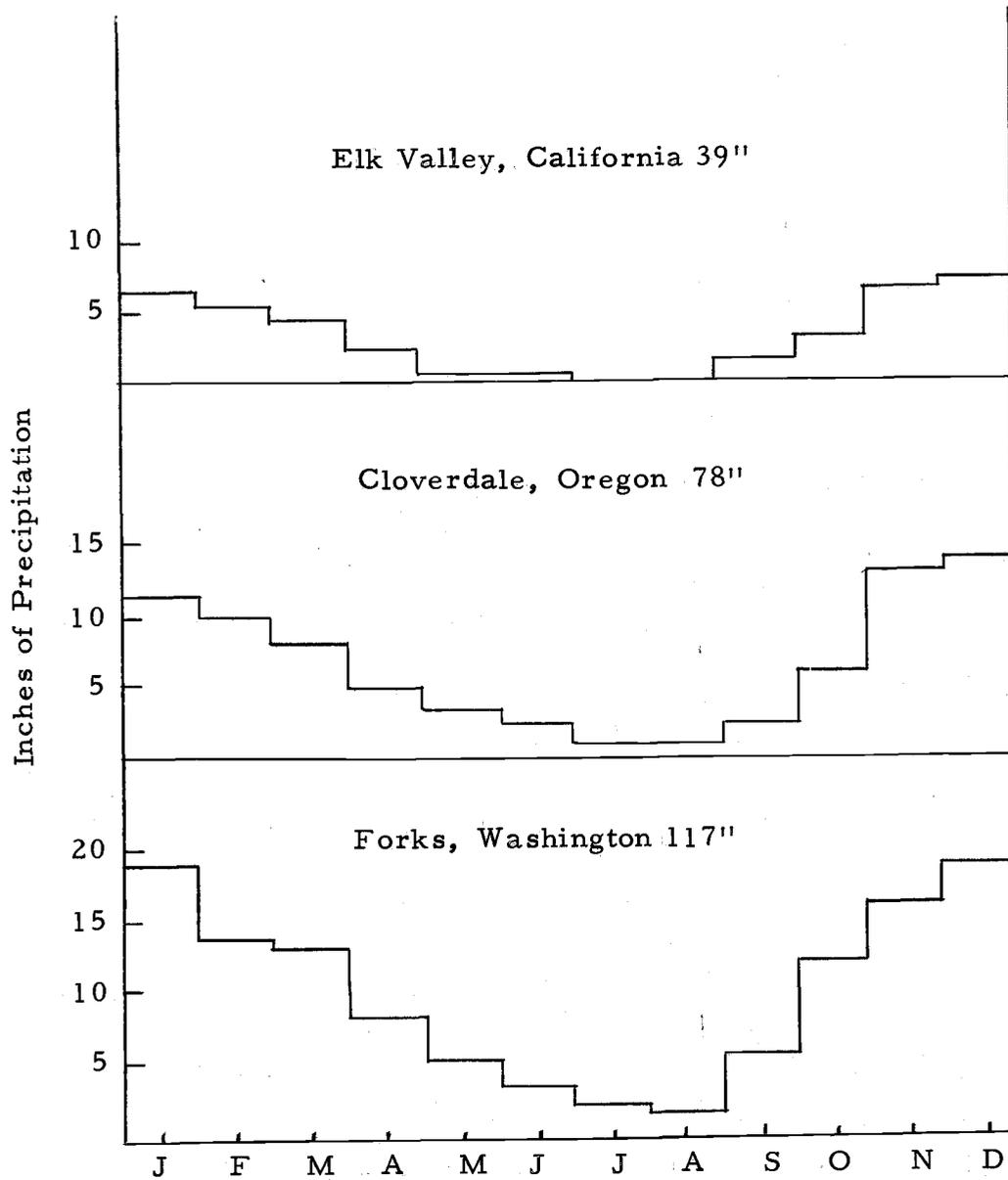
J F M A M J J A S O N D

Figure 17. Distribution of monthly precipitation in inches for
the seed collection areas. (Climatological Data
1949-1969)

experiment. After late chilling the number of needles were significantly higher than after early chilling. Furthermore, the number of needles per centimeter stem was slightly higher after late chilling (Table 12).

However, comparing the effect of length of chilling within early or late chilling it is also clear that increased length increases elongation without increasing the number of needles. Thus, in all cases the number of needles per centimeter stem was lowest after the longest period of chilling (Table 12).

There were almost no differences in needle length between Cloverdale and Forks while needle length for Elk Valley was significantly less than these two sources. Time of chilling was non-significant which indicates that delay of chilling did not affect needle length. This in contrast to the results for bud burst, height growth and number of needles developed. Needle length of all sources was greater after the longer chilling periods.

DISCUSSION

The results of this study clearly show that both the time and the length of chilling influences subsequent time of growth resumption and the amount of growth in young Douglas-fir plants from coastal areas.

The influence of time of chilling is probably a direct effect of the low temperatures upon the rate of initiation of leaf primordia. The earlier the chilling the fewer primordia has been initiated prior to the beginning of the chilling and subsequent primordia initiation is delayed directly by the low temperature. That this is so is clear not only from the fact that late chilling always resulted in more needles but also when the coastal sources are compared with the inland source (Government Camp). In the latter source bud formation and beginning dormancy occurred five weeks prior to that of the coastal sources as would be expected. It is therefore not surprising that no difference was found in plants from this source between the effect of early and late chilling since leaf primordia formation no doubt had ceased even before the time of early chilling.

When comparing chilling requirements and/or responses to various chilling treatments of plants from coastal versus inland sources it is therefore important to keep in mind that the different selective forces during the past (primarily length of frost-free period and annual distribution of precipitation) have resulted in plants with

different annual cycles of growth and dormancy and that the effect of chilling varies greatly with the physiological stage.

Besides the direct effect on number of leaf primordia on plants where leaf primordia initiation has not yet been completed at the time of chilling there are other effects. It is for instance clear that increasing the length of chilling period increases the amount of stem elongation but does not affect the number of leaf primordia. In other words, increasing the chilling period from say 33 to 44 days increases height growth but not the number of needles (i.e., a decrease in the number of needles per centimeter stem). The mechanism of this effect remains obscure.

Another effect other than on the number of leaf primordia initiated is the increase in needle length when chilling is increased. This is not surprising considering time of growth resumption was hastened and stem elongation increased as the chilling period was extended.

An interesting side line is the intermittent growth of the plants from Elk Valley. Elk Valley is located approximately 25 miles inland on the northern California coast. It has a short growing season (129 days) and its annual distribution of precipitation is much less than the distribution of the other coastal sources used in this study. From May to late August precipitation is almost nil with undoubtedly very high soil moisture tensions. This finding shows how careful one

must be in delineating seed zone areas, but above all that direct com-
parisons of chilling requirements of different sources can only be
made if the treatments are given when the plants are in the same phy-
siological stage. Such experimental conditions are difficult to obtain
with our present knowledge of the annual cycles of physiological
changes. It should therefore caution against too rigid conclusions on
chilling requirements when comparing plants native to widely different
habitats.

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