

RESEARCH NOTE

No. 71

1975



FLUSHING RESPONSE OF DOUGLAS FIR BUDS TO CHILLING AND TO DIFFERENT AIR TEMPERATURES AFTER CHILLING

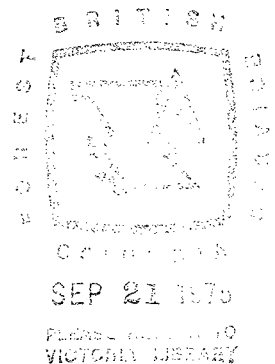
by

R. van den Driessche

634.9097
11
BCMF
RES
RN 71
1975



BRITISH COLUMBIA FOREST SERVICE
Research Division
Victoria, B.C.



ACDV

11/2
136891
~~0149759~~
12198

FLUSHING RESPONSE OF DOUGLAS FIR
BUDS TO CHILLING AND TO DIFFERENT
AIR TEMPERATURES AFTER CHILLING

by

R. van den Driessche

ABSTRACT

Two-year old Douglas fir plants were exposed to varying amounts of chilling under artificial conditions at about 2°C, and under natural conditions. Duration of exposure to all temperatures below 4.4°C., within the range encountered under natural conditions, seemed a satisfactory measurement of chilling as it was comparable with duration of chilling under artificial conditions. Chilling requirements of three Douglas fir provenances were all reasonably well satisfied by 2,000 hours at temperatures below 4.4°C, as measured by time taken for buds to flush after chilling. There was clear indication that provenances differ in their exact chilling requirements, and the response of terminal buds and lateral buds to chilling did not show the same differences in each provenance.

Evidence was obtained that interruption of chilling conditions with periods of high temperature (24°C) could offset the dormancy breaking effect of chilling.

Plants which had received 1,250 hours of chilling below 4.4°C flushed quite rapidly at 24°C, but slowly at a mean daily temperature of 13°C. Flushing was rapid, however, at a mean daily temperature of 12.8°C after plants had received 2,070 hours chilling.

Higher mean daily temperature increased the speed of flushing after chilling, and it appeared that flushing of Douglas fir buds was also influenced by the range of daily temperature.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
METHODS	2
RESULTS	5
DISCUSSION	15
ACKNOWLEDGEMENTS	19
LITERATURE CITED	19
APPENDICES	21

INTRODUCTION

Many woody perennials will only break dormancy and continue normal growth after exposure to chilling (Samish 1954, Vegis 1963, 1964). This necessity for chilling has also been specifically demonstrated for certain conifers (Romberger 1963, Nienstaedt 1966, 1967, Nagata 1967, Worrall and Mergen 1967). According to Lavender and Hermann (1970), Wommack, in 1964, showed that Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) had a chilling requirement which could be satisfied by 8-12 weeks at a temperature between 3 and 6°C. Under natural conditions, of course, plants which have a chilling requirement usually have this need fully satisfied by the time spring arrives (c.f. Lavender *et al.* 1973). Now that forest tree seedlings are frequently removed from natural conditions during fall and winter, however, either by being placed in cold storage, or grown in containers inside greenhouses, it is necessary to pay attention to whether their chilling requirements are adequately met. This may be especially important in relation to present practice since Lavender and Wareing (1972) have suggested that chilling may not only overcome bud dormancy in Douglas fir, but also improve ability of seedlings to survive cold storage.

There is also circumstantial evidence which suggests adequate chilling is necessary for satisfactory cold storage (at 2-5°C) of Douglas fir, because it has been found that storage prior to mid-November is unsuccessful in Oregon (Hermann *et al.* 1972), and in Holland lifting for storage is not recommended until mid-January (Oldenkamp *et al.* 1969).

The work reported here was confined to measuring chilling requirements necessary to overcome bud dormancy in Douglas fir, and examining the effect of temperature conditions on flushing after chilling.

METHODS

Experiment 1

Two-year old nursery grown Douglas fir, of three provenances (Table 1), were potted into a 1 peat : 1 nursery soil mixture in early September 1971. Three blocks, each containing 80 plants of each provenance, were arranged in the open, away from any source of artificial light. Provenances were randomly arranged in rows of 20 plants within a block. A Stevenson screen, containing a thermograph and thermometer, was placed adjacent to the blocks at ground level to obtain a continuous temperature record.

On each of four lifting dates, (1) 4 October, 1971 (2) 1 November, 1971, (3) 6 December, 1971, and (4) 6 February, 1972, 60 plants of each provenance were removed from the three blocks and groups of 15 were subjected to one of four treatments: (1) no chilling, (2) two weeks chilling, (3) four weeks chilling, and (4) eight weeks chilling. Chilling consisted of exposure to a temperature of about 2°C, but occasional extreme variation between 0°C and 10°C occurred. Temperature was continuously recorded in the chilling room. Eight-hour photoperiods of 3,745 lux were maintained with incandescent lamps during chilling. On completion of the chilling treatment plants were placed into a greenhouse where the temperature was close to 24°C, and a 16-hour photoperiod was imposed. Condition of terminal bud and condition of lateral buds were determined when plants were placed in the greenhouse and subsequently at two-week intervals for 18 weeks. Terminal buds were recorded either as not flushed, or flushed, and plants were given a score of 1, 2, or 3, according to whether there were no lateral buds flushed, some lateral buds flushed, or all lateral buds had flushed.

Experiment 2

Fifteen two-year old Douglas fir, from each of three provenances (Table 1), were transplanted into wooden boxes, measuring 45 x 30 x 15 cm, in a known random sequence in August. Ten such boxes were allocated in pairs to five chilling treatments so that 30 plants of each provenance were subjected to each treatment

Table 1 Sources of provenances used in experiments 1 and 2

Name	Seed lot number	Place	Elevation m	Lat.	Long.
Experiment 1					
Great Central Lake	510	Block 769	457	49 ⁰ 20'	125 ⁰ 15'
Pemberton	1261	Poole Creek	457	50 ⁰ 28'	122 ⁰ 40'
Golden	1707	Hospital Creek	915	51 ⁰ 19'	116 ⁰ 58'
Experiment 2					
Sechelt	1284	Halfmoon Bay	609	49 ⁰ 30'	123 ⁰ 55'
Pemberton	1009	Green Lake	762	50 ⁰ 12'	122 ⁰ 55'
Chehalis River	1215	Vaughn Creek	762	49 ⁰ 21'	121 ⁰ 58'

from the beginning of October. Treatments consisted of imposing either low temperature of 2°C under an 8 hour photoperiod of 3,200 lux intensity (referred to as "C"), or high temperature of 24°C under 8-10 hour photoperiods of daylight in a greenhouse (referred to as "G"), in various combinations. These combinations were (1) 8 weeks G, (2) 4 weeks G/4 weeks C, (3) 2 weeks G/6 weeks C, (4) 8 weeks C, (5) 2 weeks G/2 weeks C/2 weeks G/2 weeks C. At the end of the 8 week treatment period trees were placed in a greenhouse under 16 hour photoperiods, at 24°C, and a record of terminal bud flushing was kept at weekly intervals over the following 11 weeks. The length of new terminal shoot extension was also measured after 11 weeks.

Experiment 3

On 26 January four groups of 36 plants were selected for uniformity of height and appearance from 500 potted two-year old Douglas fir of coastal provenance (Goldstream, Vancouver Island). Each group of plants was put into one of four growth chambers which all had a 12 hour photoperiod providing light intensity of 29,000 lux at plant tops. A different temperature regime was applied in each growth chamber and these regimes were, for 12-hour day and 12-hour night periods respectively: (1) 18.5°C/7.5°C, (2) 13°C/13°C (3) 24°C/2°C, and (4) 24°C/24°C. Consequently over each 24 hour period the mean temperature in regimes 1 to 3 was 13°C, and the mean temperature in regime 4 was, of course, 24°C.

A record of bud flushing was made three times a week during the 84 days the plants were in the growth chambers. Terminal buds were recorded as flushed or not flushed according to whether needles were exposed from the bud scales or not. The number of lateral buds flushing was recorded up to a total of 5, and beyond that the plant was given an arbitrary score of 8 when all buds had flushed. Consequently the lateral bud data are distorted, though not unduly, because once a few lateral buds had flushed the remainder did so in a relatively short time.

At the end of the experiment total length of main stem and length of new main stem growth were measured, and then dry weights of old shoot, new shoot growth and roots were determined.

Exposure to temperatures below 4.4°C experienced by these plants between 1 October and placement into growth chambers was determined from thermograph records.

Experiment 4

An experiment of similar design to the previous one (experiment 3) was done. The plants used were of the same Goldstream provenance, and, on 24 April, were placed under the following 24-hour temperature regimes: (1) 6 hours at 18.3°C and 18 hours at 10.9°C, (2) 14 hours at 18.3°C and 10 hours at 5.0°C, (3) 6 hours at 18.3°C and 18 hours at 14.6°C, and (4) 14 hours at 18.3°C and 10 hours at 11.7°C. The mean temperature over each 24 hours period was 12.8°C for regimes 1 and 2, and 15.5°C for regimes 3 and 4. Photoperiods were of 12 hours and the middle of the high temperature period coincided with the middle of the photoperiod. Measurements were made as described for experiment 3, and this experiment was terminated after 52 days.

RESULTS

Experiment 1

The average time taken for terminal and lateral buds to flush was determined for each treatment from the raw data. Length of time during which plants were exposed to temperatures below 4.4°C, as well as degree hours below 4.4°C to which plants were exposed, was also estimated for each treatment from thermograph records. The time to flush was then regressed over each of the two measurements of low temperature exposure for both terminal and lateral buds of each provenance. A straight line and a second degree polynomial were fitted to each set of data by multiple regression and it was found that in all sets, except that of lateral buds in provenance 1, the polynomial was a significantly better fit (Fig. 1, 2, Appendix I). In some instances these fitted curves turn upwards after having reached a minimum. This does not imply that time required to flush will increase again after a large amount of chilling, but merely that the polynomial model employed is unrealistic at this point.

Correlation coefficients were high for the relationships between time for buds to flush and both measures of low temperature exposure (Table 2). Use of hours exposure below 4.4°C as the independent variable resulted in slightly higher correlation coefficients than use of degree hours below 4.4°C. Furthermore, plotting time taken for flushing over degree hours below 4.4°C showed a discontinuity in the trend between the fourth lifting date and the remainder of the data. For these reasons, and because duration of exposure to temperature below 4.4°C was the simplest of the two low temperature exposure measurements to make, this independent variable seemed the most suitable for determining chilling received by Douglas fir plants.

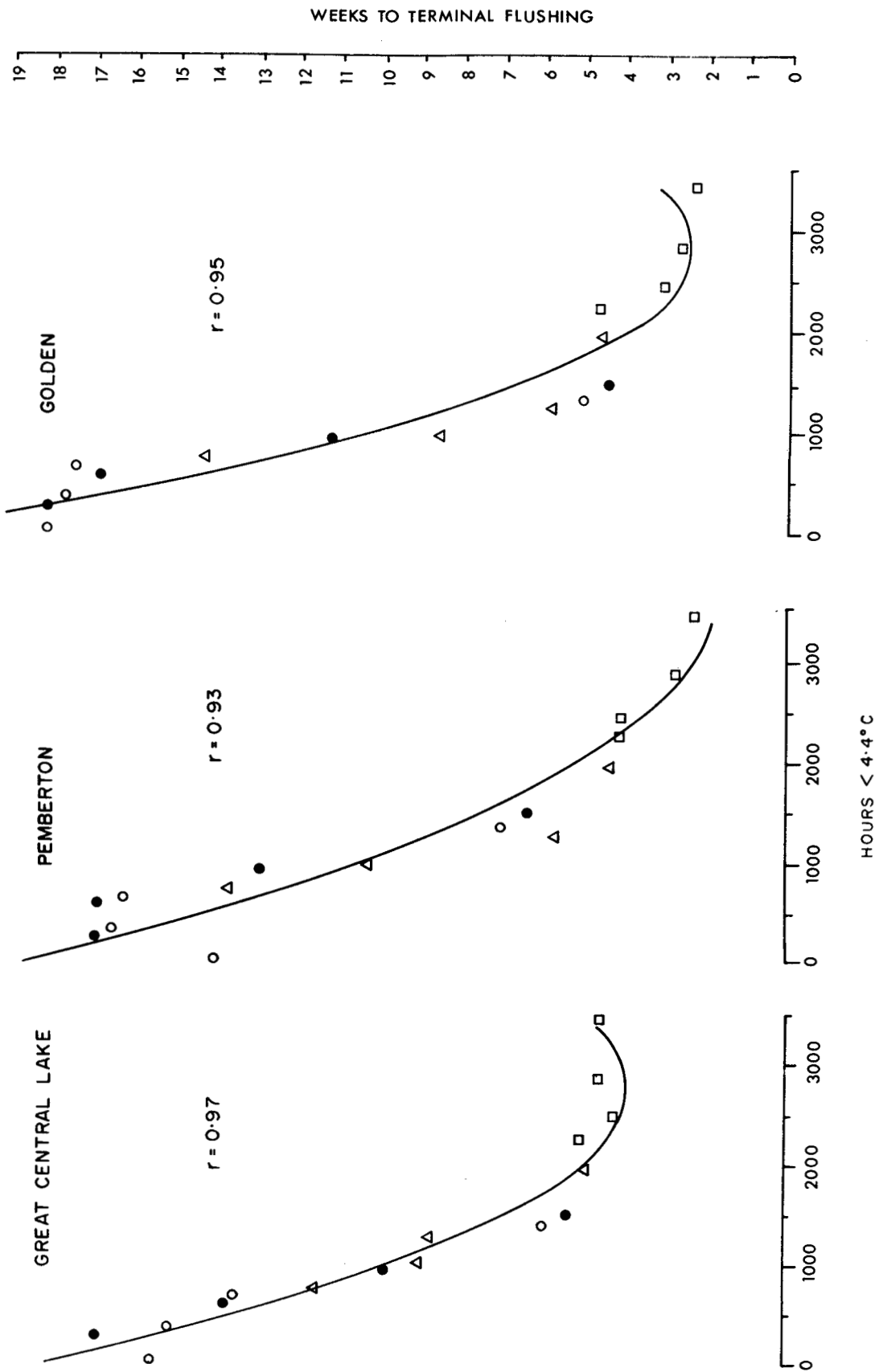


Figure 1. Relationship between weeks required for flushing of terminal buds in the greenhouse and duration of exposure to chilling below 4.4°C. Symbols relate to "lifting" date: open circles October, closed circles November, triangles December, squares February.

WEEKS TO FLUSHING OF LATERAL BUDS COMPLETED

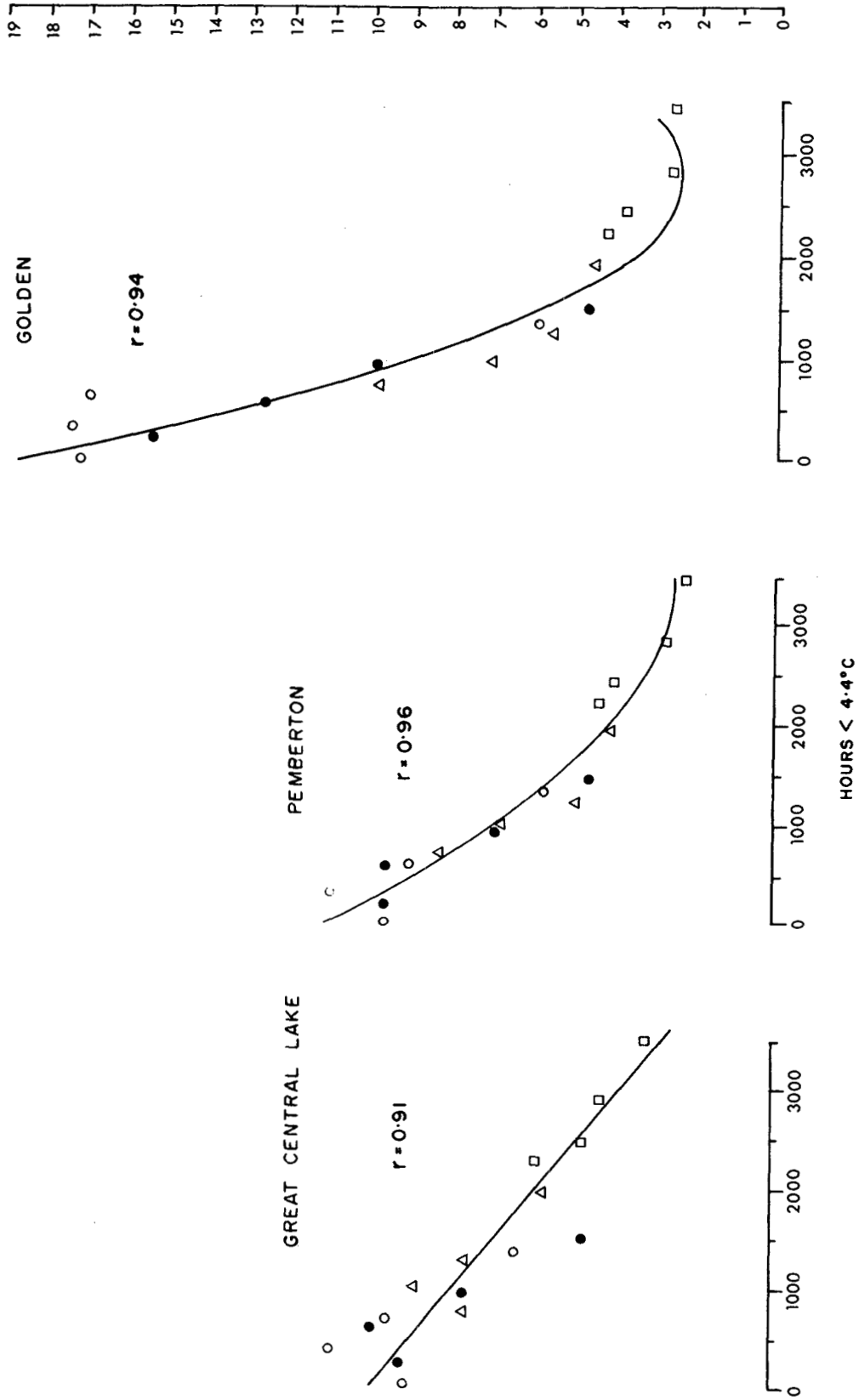


Figure 2. Relationship between weeks required for flushing of lateral buds in the greenhouse and duration of exposure to chilling below 4.4°C. Symbols relate to "lifting" date: open circles October, closed circles November, triangles December, squares February.

Table 2. Correlation coefficients for time required to flush regressed on two measures of low temperature exposure.

Provenance	Hours $< 4.4^{\circ}\text{C}$	$^{\circ}\text{C}$ hours $< 4.4^{\circ}\text{C}$
Terminal buds		
Great Central Lake	0.97*	0.96
Pemberton	0.93	0.92
Golden	0.95	0.94
Lateral buds		
Great Central Lake	0.91	0.84
Pemberton	0.96	0.93
Golden	0.94	0.93

* All coefficients are significant at $p = 0.01$

Lapse of time, between the beginning of the experiment and placing plants into conditions suitable for flushing in the greenhouse, increased in much the same way as exposure to low temperature. It seemed desirable therefore to see if lapse of time, and so perhaps some endogenous process, could account for increased rates of flushing as the experiment ran its course. Plotting weeks required for terminal buds to flush over lapse of time from start of the experiment until placement in the greenhouse (Fig. 3), showed that weeks required for flushing was not related to lapse of time for the first three lifting dates. The steady decrease in weeks required for flushing between lifting dates 3 and 4 could, however, have been partly related to lapse of time. In general, though, this examination of the data did not invalidate duration of exposure below 4.4°C as a means of measuring chilling.

Based on exposure to temperatures below 4.4°C, chilling requirements for terminal bud flushing of the Great Central Lake and Golden provenances were completely satisfied by about 2,500 hours, whereas the Pemberton provenance required about 3,000 hours. Flushing was relatively rapid in all provenances, however, after about 2,000 hours chilling.

The relationship between time required for complete flushing of lateral buds and chilling exposure was clearly different between provenances (Fig. 2). Decrease in time for lateral bud flushing of the Great Central Lake provenance was proportional to increase in chilling, but in the Pemberton provenance time required to flush decreased less rapidly with more chilling. In the Golden provenance the relationship was clearly curvilinear and showed little differences from the relationship for terminal buds.

Experiment 2

A minimum time of two weeks under long photoperiods, at 24°C in the greenhouse, was required for terminal buds of plants, which had received 8 weeks (1,344 hours) chilling, to start flushing (Fig. 4). Rate of flushing decreased as the weeks of exposure to chilling decreased, with the exception that 4 weeks chilling, preceded by 2 weeks in the greenhouse and broken in the middle by two weeks in the greenhouse, resulted in a lower rate of flushing than any other treatment.

This experiment failed to demonstrate significant differences between provenances, although means for the experiment (Fig. 4), indicated the Chehalis provenance flushed faster than the other two provenances. There was no indication of any interaction between provenance and treatment. Not all terminal buds had flushed after 11 weeks in the greenhouse when plants had received 8 weeks chilling. The final flushing values were: Sechelt 72%, Chehalis 100%, and Pemberton 63%, and these values had remained constant for about 3 weeks indicating no more flushing could be expected.

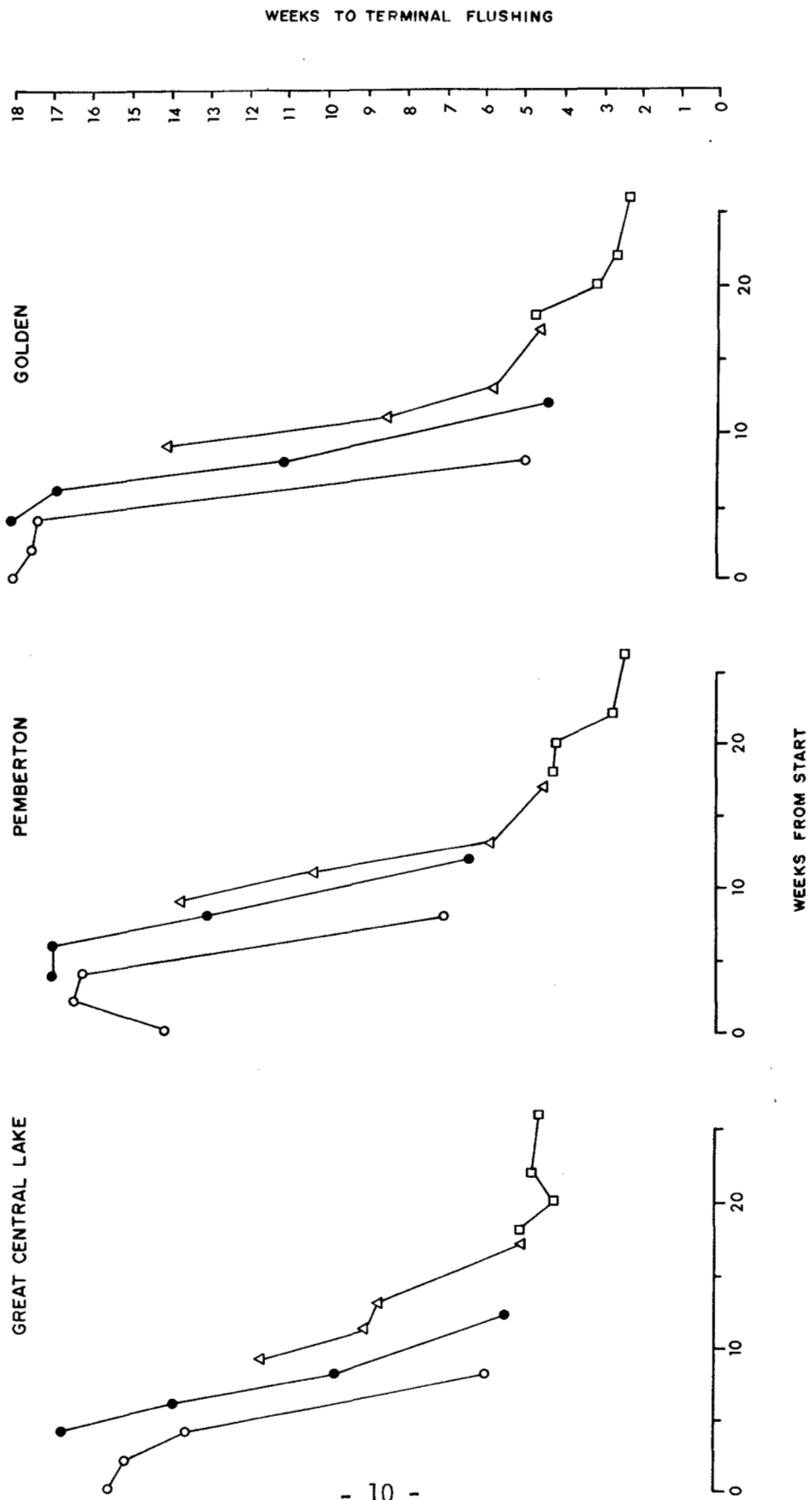


Figure 3. Relationship between weeks required for flushing of terminal buds in the greenhouse and elapse of time from the start of the experiment on 4 October. Symbols as in Figures 1 and 2.

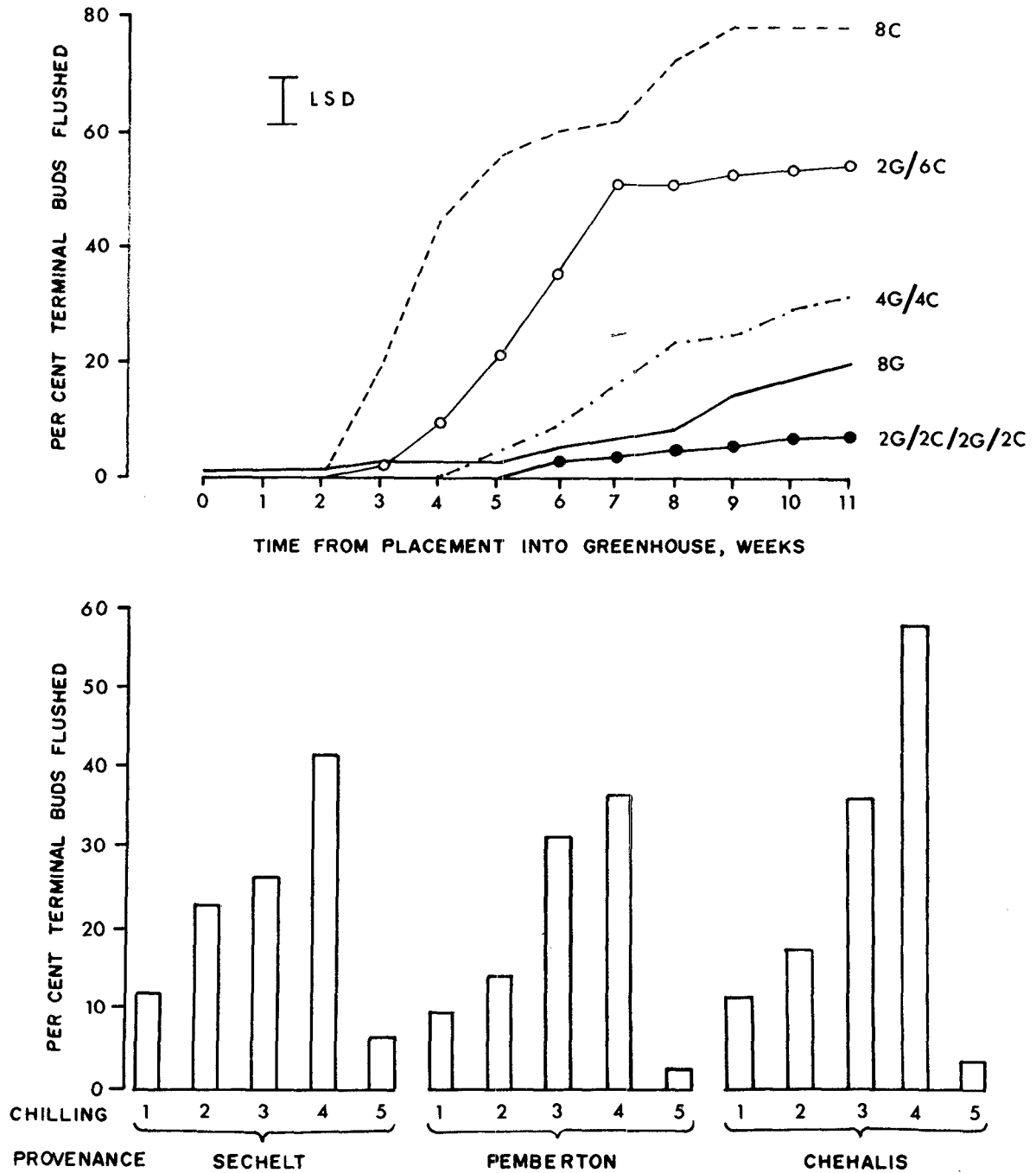


Figure 4. Time taken for terminal buds to flush is shown for all provenances by treatments in upper graph. Labels refer to number of weeks in chilling conditions (C) or in the greenhouse (G).

Below is shown the final percentage of terminal buds flushed by provenance and treatment. Treatment 1 = 8G, 2 = 4G/4C, 3 = 2G/6C, 4 = 8C, 5 = 2G/2C/2G/2C.

Length of new shoot growth in cm, measured after 11 weeks in the greenhouse, was, for treatments 1 to 5 respectively: 0.43 ab, 1.34 bc, 1.58 c, 2.54 d, and 0.13 a. (The same letter following a value indicates lack of difference ($p=0.05$) from other values followed by the letter).

Experiment 3

All plants had received 1,250 hours chilling below 4.4°C on placement into the growth chambers, and flushing of terminal buds commenced after 14 days at 24°C in regime 4 (Fig. 5). In the three treatments with a mean temperature of 13°C flushing of terminal buds did not occur until after 35 days in the growth chamber. The manner in which high and low temperatures were distributed between day and night also affected the rate of flushing in these three treatments. The uniform distribution of 13°C during day and night (regime 2) resulted in the latest start of flushing. A 24°C day temperature combined with a 2°C night temperature resulted in an earlier start to flushing. Plants in the 18.5°C day and 7.5°C night showed the most rapid flushing of those in the three temperature regimes which averaged 13°C .

Flushing of lateral buds started sooner than flushing of terminal buds: after 9 days in regime 4, and after 23 days in the other three regimes (Fig. 5). Lateral buds showed the same general relationship between regimes as did terminal buds, but the difference between regimes 1 and 3 was not so pronounced in the lateral bud data.

The mean length of old main stems did not vary between regimes, as might be expected, and was 30.9 cm. Length growth of main stems during the experiment was related to temperature regimes, however, with greatest length growth occurring in regime 1, and least in regimes 3 and 4 (Table 3). Increase in plant dry weight was not affected by temperature regimes in the same way as main stem length. Greatest shoot and root weight occurred in the $24^{\circ}\text{C}/24^{\circ}\text{C}$ regime. The next largest plants occurred in the $18.5^{\circ}\text{C}/7.5^{\circ}\text{C}$ regime, and growth was least in regimes 2 and 3. New shoot dry weight growth expressed as a percentage of old shoot dry weight was not different between regimes 1 and 4, but this was partly due to a significant increase in old shoot dry weight which occurred in regime 4.

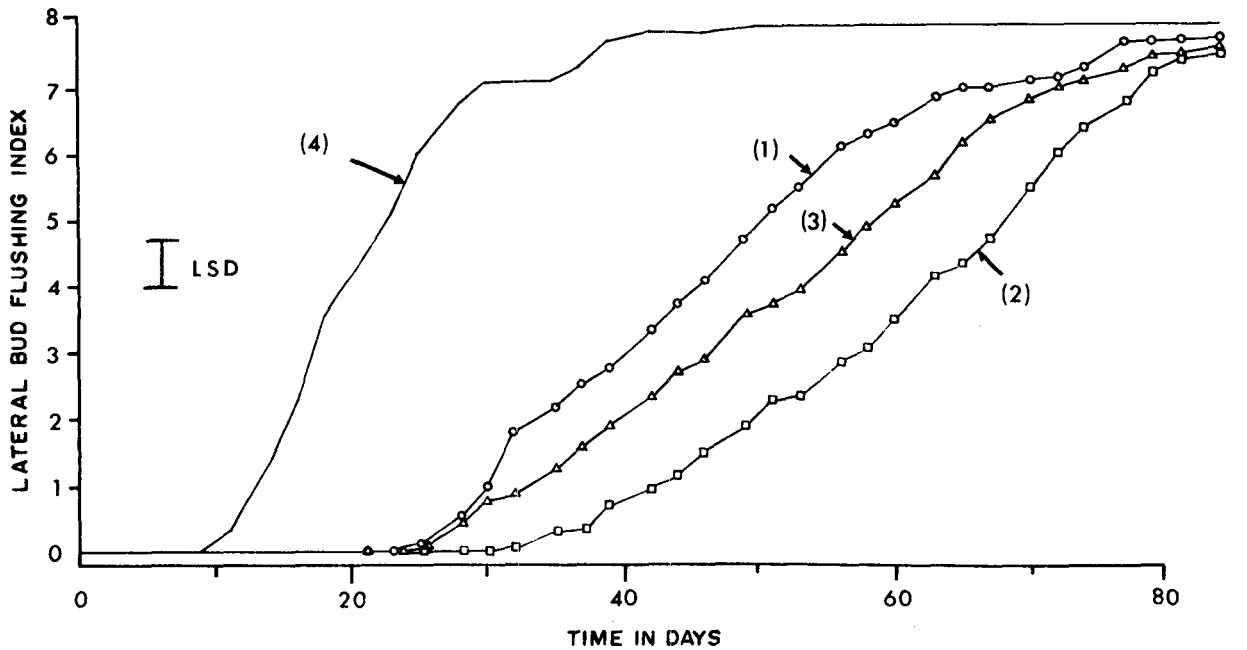
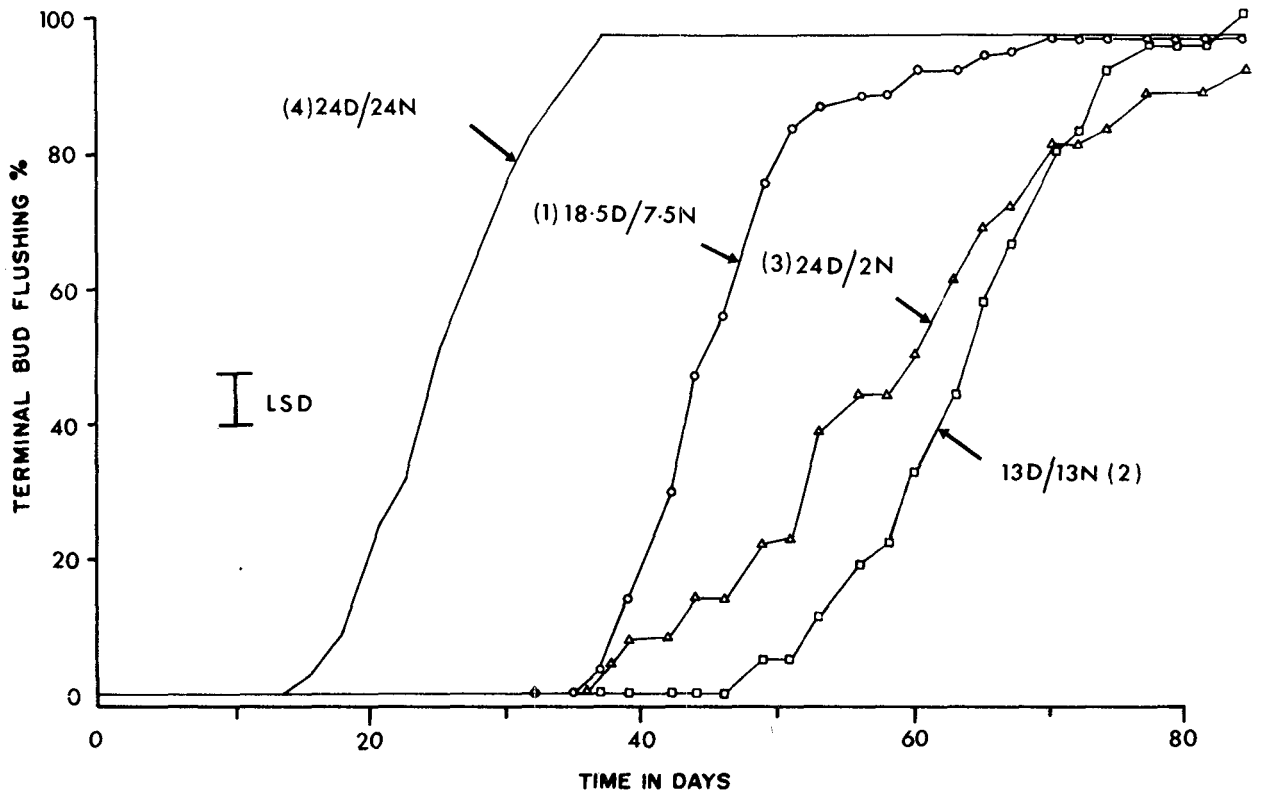


Figure 5. Rates of flushing of terminal and lateral buds in experiment 3. Numbers in brackets are treatment numbers, and labels on terminal bud curves show day (D) and night (N) temperatures in $^{\circ}\text{C}$.

Table 3. Length and dry weight measurements of stems and roots at the ends of experiments 3 and 4.

Measurement	Regime			
	1	2	3	4
Day/night temperatures in °C for experiment 3				
	18.5/7.5	13/14	24/2	24/24
New stem length as % old	35.2 a*	29.5 b	20.6 c	23.6 c
New shoot weight as % old	66.7 a	36.6 b	43.1 b	66.8 a
Old shoot weight, g	4.01 a	3.54 a	3.61 a	5.41 b
Total shoot weight (old & new), g	6.67 a	4.86 b	5.18 b	9.01 c
Root weight, g	3.26 a	2.61 ab	2.47 b	5.98 c
Hours x day/night temperatures in °C for experiment 4				
	6x18.3 /18x10.9	14x18.3 /10x5.0	6x18.3 /18x14.6	14x18.3 /10x11.7
New stem length as % old	29.0 ab	25.0 b	36.2 a	29.2 ab
New shoot weight as % old	43.7 a	48.5 a	72.2 b	78.6 b
Total shoot weight (old & new), g	5.23 a	5.40 a	6.71 ab	7.62 b

* values followed by the same letter not significantly different at p=0.05

Experiment 4

Plants had received 2,070 hours exposure to temperatures below 4.4°C at the time of placement under the four different temperature regimes and flushing was rapid. Flushing of terminal buds commenced after 5 to 10 days, depending on temperature regime, and flushing of lateral buds commenced after 3 to 5 days (Fig. 6). Regimes 3 and 4, with the higher mean daily temperature of 15.5°C, resulted in more rapid flushing of terminal buds than the other two regimes where the mean daily temperature was 12.8°C. Within each pair of regimes with the same mean daily temperature, however, the longer period of high temperature, followed by a shorter period of relatively low temperature, promoted flushing more than the other treatment. The only clear difference between rates of flushing of lateral buds was that plants in regime 1 flushed more slowly than plants in the other regimes.

Temperature regimes affected main stem length and shoot dry weight growth during the experiment (Table 3). Shoot length growth in regime 3 was significantly greater than in regime 2, and new shoot dry weight growth was greater in regimes 3 and 4 than in regimes 1 and 2.

DISCUSSION

Chilling requirements of Douglas fir plants are said to be satisfied by 8 to 12 weeks (1,344 to 3,016 hours) at a temperature between 3 and 6°C (Lavender and Hermann 1970). This is largely confirmed by the results of the present experiments. In experiment 1 increase in chilling beyond 2,000 hours resulted in very little reduction in time necessary for terminal buds to flush, except perhaps in the Pemberton provenance. On the other hand, the regressions suggested that lateral buds of the Great Central Lake and Pemberton provenances responded to chilling of up to 3,000 hours. In experiment 2, plants which had received 1,344 hours of chilling flushed after two weeks, although not all terminal buds had flushed after 9 weeks, showing that chilling requirements for some of the plants were not fully satisfied.

Terminal buds of plants, which had received 1,250 hours chilling in experiment 3, commenced flushing after 14 days at an average daily temperature of 24°C, but there was a further delay of 21 days before flushing commenced in the regimes with an average daily temperature of 13°C. On the other hand, in experiment 4, terminal buds of plants which had received 2,070 hours chilling flushed after 10

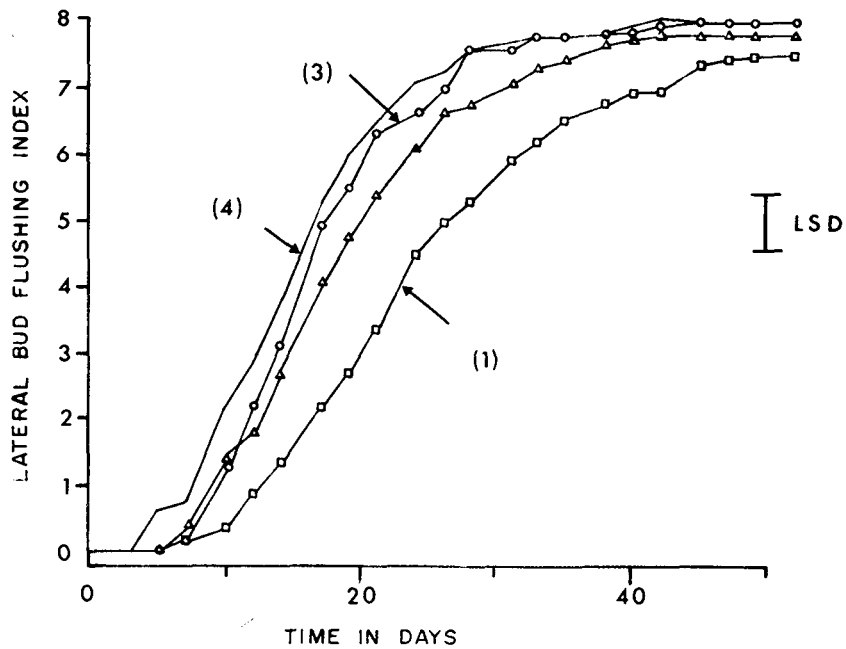
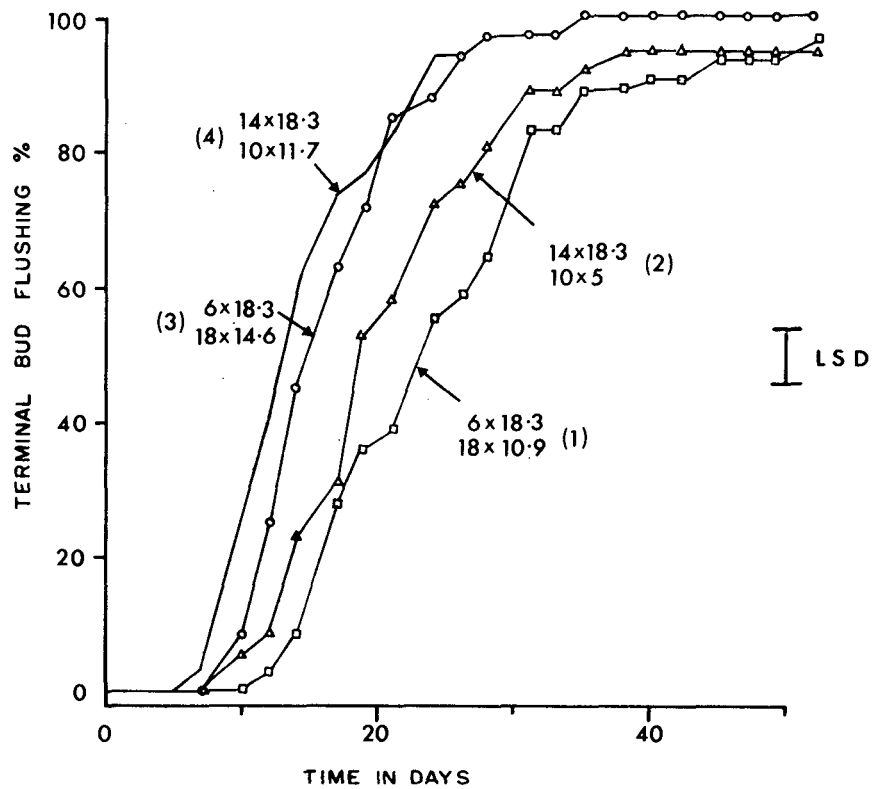


Figure 6. Rates of flushing of terminal and lateral buds in experiment 4. Numbers in brackets are treatment numbers, and labels on terminal bud curves show day (D) and night (N) temperatures in °C.

days even when the average daily temperature was only 12.8°C. Allowance should, perhaps, be made for the difference in high and low temperature combinations between the regimes, but it seemed that chilling for 2,070 hours allowed plants to flush at least as rapidly at a daily average of 12.8°C as those chilled for 1,250 hours could flush at a daily average of 24°C. In other words, more chilling allowed flushing to occur rapidly at a lower daily average temperature.

Bearing in mind that coastal, "transition", and interior provenances were used in experiment 1, flushing of many provenances of dormant Douglas fir can be expected over a range of temperature conditions after exposure to temperatures below 4.4°C for about 2,000 hours. With less chilling, say 8 weeks, the range of temperature, and perhaps other conditions, over which rapid flushing occurs would be less. This is in accordance with the generally accepted view on dormancy (Romberger 1963, Vegis 1963) in which it is considered that as breaking of dormancy becomes more complete, due to continued chilling, growth becomes possible over a wider range of temperature conditions.

It has been suggested that long days can "substitute fully for the cold requirement in breaking bud dormancy" in Douglas fir (Roberts *et al.* 1974). The data supporting this claim are not convincing, since some of the plants did not achieve more than 25% bud break under long day conditions. Results obtained in experiments 1 and 2, in the present work, also conflict with this claim in that bud flushing of plants placed under long photoperiods, in the greenhouse, showed a clear effect of previous chilling treatment. Flushing would have occurred on all plants after an equal delay if long days really substituted fully for chilling requirement. On the other hand, long photoperiods may eventually permit flushing, particularly of partially chilled Douglas fir plants, as they do in some other woody species (e.g. Worrall and Mergen 1967).

Comparison of the two methods of estimating chilling showed duration of exposure to temperatures below 4.4°C was most satisfactory. Chilling measured in degree hours below 4.4°C was not an improvement, and it must be assumed that the level of temperature below the threshold is relatively unimportant. It is likely that temperatures below at least 7°C are effective for chilling (Nienstaedt 1967, Samish 1954), but presumably under natural conditions, in experiment 1, exposure to effective chilling temperatures was proportional to duration of exposure below 4.4°C.

Duration of exposure to chilling was calculated from 1 October, since little chilling is likely to occur before this date; perhaps 50 hours, or less, below 4.4°C at Victoria. After this date chilling in the open seems to have been cumulative since it was comparable with chilling under artificial conditions, as judged from the good fit obtained in the correlations of experiment 1. On the other hand, whether short periods of chilling, during cool nights, are really cumulative, has been questioned (Romberger 1963, p. 159). High temperatures between chilling periods may reverse the effect of chilling. This seems to have occurred in treatment 5 of experiment 2 when plants were exposed to a temperature of about 24°C between two periods of chilling. It must be assumed, however, that day time temperatures experienced by plants of experiment 1 during the fall were not high enough, or of sufficient duration, to offset the cumulative effect of previous chilling. Possibly the reason why cold spells occurring before the 1 October can be ignored in terms of chilling, is because they are usually followed by sufficiently high temperatures to cancel their effect.

Over 11 weeks mean shoot height growth appeared related to chilling treatment through rate of terminal bud flushing in experiment 2. Normal, rapid shoot growth would presumably be dependent on a plant having received adequate chilling during the previous period of dormancy.

Higher mean daily temperature increased the rate of flushing in experiments 3 and 4. Furthermore, differences in rates of flushing occurred among regimes with the same mean daily temperature, depending on how temperature levels were apportioned during the 24 hour period. It must be concluded that flushing of Douglas fir buds showed a thermoperiodic response as well as a dependence on mean daily temperature. These temperatures were measured in ambient air of the growth chambers, and the soil in which the plants were rooted would have had similar temperatures. Different results might have been obtained, however, if soil temperatures had been dissimilar to air temperatures because there is evidence that flushing of Douglas fir is partly dependent on a sufficiently high soil temperature (Lavender *et al.* 1973).

As background information, to assist interpretation of the previous experiments, an indication of chilling exposure attained at five nurseries in various parts of British Columbia is included (Appendix II). The data are limited, but it seems less than 2,000 hours chilling is often received at Surrey and Green Timbers during a winter. At Campbell River 2,000 hours chilling is received by the end of February. At both Skimikin and Red Rock nurseries this amount of chilling is accumulated some time in mid-January.

ACKNOWLEDGEMENTS

The author gratefully acknowledges statistical advice and data processing assistance from Mr. A. R. Fraser and Mr. M. Kovats, and technical assistance from Mr. M. B. Balderston, who are all members of the British Columbia Forest Service Research Division. Data of Appendix II were prepared by Dr. M. C. Coligado of the British Columbia ELUC Secretariat.

LITERATURE CITED

- Hermann, R. K., D. P. Lavender, and J. B. Zaerr. 1972. Lifting and storing western conifer seedlings. Oregon State University Forest Res. Lab. Res. Pap. 17. pp. 8.
- Lavender, D.P., and R. K. Hermann. 1970. Regulation of the growth potential of Douglas fir seedlings during dormancy. *New Phytol.*, 69:675-694.
- Lavender, D.P., G.B. Sweet, J.B. Zaerr, and R. K. Hermann. 1973. Spring shoot growth in Douglas fir may be initiated by gibberellins exported from the roots. *Science* 182 (4114): 838.
- Lavender, D.P., and P.F. Wareing. 1972. Effects of daylength and chilling on the responses of Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco) seedlings to root damage and storage. *New Phytol.* 71:1055-1067.
- Nagata, H. 1967. Studies on the photoperiodism in the dormant bud of *Pinus densiflora* Sieb. et Zucc. II Effects of temperature and photoperiod on the breaking of winter dormancy of first year seedlings. *J. Jap. For. Soc.*, 49 (12): 415-420.
- Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. *For. Sci.*, 12 (3):374-384.
- Nienstaedt, H. 1967. Chilling requirements in seven *Picea* species. *Silv. Gen.*, 16 (2):65-68.
- Oldenkamp, L., H. Blok, and B. C. M. van Elk. 1969. Opslagperiode en bewaarmethode van zaailingen van bosplantsoen. *Ned. Bosb. Tijdschr.*, 41: 23-29.
- Roberts, A.N., B.J. Tomasovic, and L.H. Fuchigami. 1974. Intensity of bud dormancy in Douglas fir and its relation to scale removal and rooting ability. *Physiol. Plant.* 31: 211-216.

- Romberger, J.A. 1963. Meristems, growth and development in woody plants, U.S. Dept. Agric., Forest Serv. Bull. 1293 pp. 214.
- Samish, R.M. 1954. Dormancy in woody plants. Ann. Rev. Plant Physiol. 5:183-204.
- Vegis, A. 1963. Climatic control of germination, bud break, and dormancy pp. 265-287. In Environmental control of plant growth. Ed. Evans. L.T. Academic Press. New York and London.
- Vegis, A. 1964. Dormancy in higher plants. Ann. Rev. Plant Physiol. 15:185-224.
- Worrall, J., and F. Mergen. 1967. Environmental and genetic control of dormancy in *Picea abies*. Physiol. Plant. 20 : 733-745.

Appendix I Equations for regressions of time required to flush at 24°C on duration of exposure to temperatures of less than 4.4°C, and F ratios for linear and quadratic components of each regression.

Provenance	Equation	F	
		Linear	Quadratic
Terminal buds			
Great Central Lake	$y^* = 17.98 - (1.0368 \times 10^{-2})x + (1.9075 \times 10^{-6})x^2$	85.94 [†]	34.28
Pemberton	$y = 18.67 - (9.4888 \times 10^{-3})x + (1.3312 \times 10^{-6})x^2$	21.07	4.89
Golden	$y = 21.21 - (1.3493 \times 10^{-2})x + (2.3775 \times 10^{-6})x^2$	46.48	17.00
Lateral buds			
Great Central Lake	$y = 9.87 - (2.1095 \times 10^{-3})x$	64.55 (a)	
Pemberton	$y = 11.03 - (4.8045 \times 10^{-3})x + (6.7030 \times 10^{-7})x^2$	39.24	9.00
Golden	$y = 18.59 - (1.1854 \times 10^{-2})x + (2.1428 \times 10^{-6})x^2$	42.21	16.25

* y = time required to flush in weeks

x = duration of exposure to temperatures below 4.4°C in hours

† degrees of freedom appropriate for the F ratios were 2 and 13 with the exception of (a), where 1 and 14 were appropriate.

Appendix II. Accumulation of chilling (hours $<4.4^{\circ}\text{C}$) by month for five nurseries in British Columbia †

Winter	Month						
	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Whalley (for Green Timbers)							
1971-72	2	100	195	842	1,422	1,730	1,879
1972-73	11	53	207	595	984	1,202	1,344
Surrey							
1973-74	-	8*	420	695	1,151	1,422	-
Campbell River							
1971-72	7	134	340	1,060	1,804	2,462	2,940
1972-73	27	545	781	1,326	1,934	2,362	2,705
Skimikin							
1972-73	100	576	1,255	1,963	2,702	3,350	3,934
1973-74	32	322	1,035	1,777	2,472	3,135	3,761
1974-75	35	318	855	1,675	-	-	-
Red Rock							
1969-70	49	423	891	1,585	2,308	2,876	3,349
1970-71	81	366	1,058	1,802	2,524	3,188	3,906
1971-72	132	564	1,205	1,948	2,692	3,386	3,835
1972-73	184	535	1,225	1,941	2,593	3,164	3,723

† Data prepared from maximum and minimum temperature, measured at 1.22 m (4 ft) above ground, by the technique of R.E. Neild (Monthly Weather Review, Vol 95 (8):583-584, 1967).

* from 18 Oct. only.