GENECOLOGY OF BUD-BURST PHENOLOGY IN DOUGLAS-FIR: RESPONSE TO FLUSHING TEMPERATURE AND CHILLING

ROBERT K. CAMPBELL AND ALBERT I. SUGANO

U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Corvallis, Oregon 97331

We studied the process by which bud burst of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) is synchronized to seasonal cycles. Seedlings from 23 populations were treated in 12 growth-chamber combinations of chilling periods and flushing temperatures. Bud-burst rates increased approximately logarithmically with temperature. Rates also depended on the duration of chilling, with temperature coefficients (Q_{10}) increasing from 2.7 after 11 days of chilling to 3.5 after 77 days. The annual temperature cycle, moisture relation, latitude, elevation, and distance from the ocean of the site of origin of a population also influenced the rate of bud burst in the population under controlled conditions. The adaptive significance of these responses is discussed in terms of LEVINS's dormancy strategy hypothesis.

Introduction

We have proposed that Douglas-fir uses temperature and photoperiod during dormancy as cues for bud-burst timing (CAMPBELL 1974; CAMPBELL and SUGANO 1975). Our previous work indicated that flushing rate is influenced by the interdependent action of flushing temperature, photoperiod, and chilling; effects are specific to populations. LEVINS (1969) examined dormancy as an adaptive strategy and hypothesized that (1) response of a population to a cue during dormancy may be immediate or delayed, large or small, depending on the probability of adverse growing conditions in the days or weeks following the cue; (2) because the relationship between cues and probabilities is expected to vary geographically, the reaction to cues is also expected to vary geographically among populations; and (3) response of a population to cues will tend to maximize adaptive fitness by optimizing the timing of dormancy release.

We examine herein the variation in bud-burst response of Douglas-fir populations to temperature during dormancy. We describe flushing rate of seedlings from 23 populations as a reaction of population genotypes to factorial combinations of chilling period and flushing temperature in growth chambers, holding photoperiod constant. To test the hypothesis that variation among populations is clinally related to factors at population origin, we use two models. The first relates flushing rate to annual temperature cycles and moisture deficits at population origin; the second, to geographic and topographic features (this model follows from our ultimate goal of providing rules for seed transfer in reforestation). Finally, we discuss results as an adaptive strategy by which bud-burst timing in coastal Douglas-fir populations is optimized in a complex regional climate.

Numerous reports show genetic variation in effects

of chilling on dormancy release of vegetative buds among species (NIENSTAEDT 1967), provenances (WOMMACK 1964), or even genotypes within local populations (WORRALL and MERGEN 1967). Variation is sometimes related to population habitat, e.g., frost-free season (PERRY and WANG 1960), latitude (KRIEBEL and WANG 1962), or elevation (FARMER 1968). Reports rarely treat the influence of chilling on the actual timing of bud burst, either in its individual role (COOPER 1963) or in conjunction with flushing temperature (VAN DEN DRIESSCHE 1975). Even fewer reports treat influences quantitatively (COUVILLON and HENDERSHOTT 1974). None, to our knowledge, considers chilling and flushing temperature as having complementary functions in controlling release of dormancy in the context of dormancy as an adaptive strategy.

Material and methods

Samples from each of 23 populations were prepared by mixing equal numbers of seeds from each of five seed trees. Most populations—ranging from 40° to 49°N latitude, from 6 to 1,460 m elevation, and from the Pacific Coast to mountain passes on the Cascades crest—were sampled within .75 km of a U.S. Weather Bureau Station (table 1). On March 14, 1973, seeds were soaked in water for 24 h, drained, stratified at 2 C for 4 wk, and germinated on moist filter paper in petri dishes at 30 C day and 21 C night, with 12-h photoperiod and 12-h thermoperiod. Germinated seeds were planted in 11.5-cm half-liter pots containing Willamette riverbottom loam mixed with peat and vermiculite (2, 4, 3 by volume). Early losses were replaced by planting to maintain five plants per pot. Seedlings were grown in the greenhouse until May 18, then moved into a lathhouse at Corvallis, Oregon, to grow through the summer under 50% shade.

On October 1, treatments were started which subjected seedlings to consecutive periods of pre-chilling, chilling, and flushing. Some of the factors

TABLE 1

WEATHER STATION LOCATIONS AND CLIMATIC DATA FOR POPULATION COLLECTIONS

Name (1)	U.S. Weather Bureau (Index No.) (2)	Elevation (m) (3)	Latitude (°) (4)	Distance from ocean (km) (5)	Mean annual temperature (C) (6)	Temperature amplitude (C) (7)	Days to moisture deficit (from Dec. 22) (8)	Total annual moisture deficit (cm) (9)
Gold Beach	3356	24	42.05	2	11.93	2.90	162	29.17
Cedar Lake	1233	475	47.42	188	8.71	6.45	190	8.50
Cloverdale	1682	6	45.22	5	10.90	4.27	171	12.42
Corvallis	1862	69	44.63	60	11.73	6.83	118	35.88
Cushman Dam	1934	232	47.42	80	10.47	7.03	155	18.47
Glacier	3160	285	48.88	220	8.50	7.82	148	15.24
Detroit	2277	483	44.73	135	10.08	7.12	159	21.37
Elkton	2633	35	43.60	78	12.29	6.34	137	33.60
Centralia	1276	56	46.72	89	11.16	6.56	134	28.66
Forks	2914	107	47.95	19	9.57	5.33	171	10.76
Government Camp	3402	1,213	45.30	167	5.79	6.37	176	12.98
Cave Junction	1448	404	42.17	84	11.67	7.90	131	42.31
Howard Prairie	4060	1,391	42.22	157	6.53	7.62	131	37.20
Lacomb	4603	203	44.88	101	11.10	6.70	142	27.30
Rainier Longmire	6894	841	46.75	167	7.33	7.60	169	13.54
Marion Forks	5221	754	44.60	159	8.03	7.96	159	24.12
Oakridge	6213	388	43.75	133	11.79	7.41	136	33.35
Odell Lake	6251	1,460	43.58	164	4.99	7.68	157	23.97
Port Townsend	6678	20	48.12	138	10.33	5.58	90	33.66
Idleyld	4126	329	43.37	106	11.06	6.88	153	27.56
Sexton Summit	7698	1,169	42.62	120	8.94	6.96	130	30.36
Stampede Pass	8009	1,206	47.28	208	4.22	8.00	180	11.11
Valsetz	8833	346	44.83	31	9.99	5.86	168	14.90
$\bar{x}$		500	45.13	114	9.44	6.66	151	23.76
SD		481	2.08	63	2.34	1.24	23	9.95

SOURCE.—Weather station location from WAKEFIELD (1969), vol. 1, pt. B.

known to influence bud burst, such as temperature fluctuations or variable photoperiods, could not be examined because of limited facilities. It was also necessary to start flushing treatments simultaneously. Consequently, chilling periods were begun at different times, and the duration of prechilling was unavoidably confounded with the duration of chilling.

For prechilling, seedlings were placed into growth chambers held at constant 16 C with 9-h daylength until scheduled chilling treatments began. On October 23, eight pots of each population were placed in a chilling chamber at 4 C, 9-h daylength; other similar sets were added on November 25 and December 28. All pots were removed on January 8, thus providing three chilling periods of 77, 44, and 11 days. After chilling, the eight pots in each combination of population × chilling period were divided into four sets of two each (two replications). One set was placed in each of four flushing chambers operating at constant temperatures of 10 C, 14 C, 18 C, and 22 C with a 14-h photoperiod.

Treatment results were assessed by their effect on length of flushing period, measured in days to bud burst (W) from the time a plant entered the flushing chamber. Bud burst occurred when scales of the terminal bud first opened to expose green needles, as determined by observation every Monday morning and Thursday afternoon.

Data analysis proceeded in several steps. First, the response variable (W) was transformed to $\log_e$

$(100\ W^{-1})$ (CAMPBELL 1974; CAMPBELL and SUGANO 1975). Second, data were analyzed according to two regression models: topographic and climatic. In the former, from previous experience (CAMPBELL and SORENSEN 1978), we related flushing rate, as $\log_e$ $(100\ W^{-1})$, to latitude, elevation, and distance from the ocean of provenance origin. For the latter, it was first necessary to derive predicting variables which would summarize moisture and temperature climates from weather station data.

We settled on four climatic variables, two each for describing annual moisture and temperature cycles. Monthly moisture deficit was calculated as the difference between average monthly precipitation and adjusted potential evapotranspiration (THORNTHWAITE 1954). Most averages used in calculations were based on 30 yr of weather records (WAKEFIELD 1969). By plotting monthly deficits against year-day, we estimated the first day of the season at which a deficit could be expected (table 1, col. 8). The total yearly moisture deficit is the summation of monthly deficits (table 1, col. 9).

In many regions the annual wave of daily mean temperatures can be closely approximated by a sine wave function (LEE and JONES 1968). For each of the 23 weather stations, we fitted monthly average temperatures to the sine wave by the least-squares procedure of NEILD and GREIG (1972). In each case, more than 98% variation ($R^2 > .98$) was associated with mean annual temperature (table 1,

col. 6) and seasonal temperature amplitude (table 1, col. 7).

Regression equations were fitted to plot means by selecting predicting variables from preliminary models by stepwise multiple regression (DRAPER and SMITH 1966). Provisional variables in preliminary models were made up as an expansion series of polynomial linear, quadratic, and cubic terms of the primary variables, chilling period, flushing temperature, and the appropriate provenance variable set (i.e., depending on whether responses were being described in the topographic or climatic model). Such a series with only two primary predicting variables (e.g., chilling period $[X_1]$ and provenance latitude $[X_2]$) has the form $Y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_{12} x_1 x_2 + \beta_{11} x_1^2 + \beta_{122} x_1 x_2^2 + \beta_{112} x_1^2 x_2 + \beta_{111} x_1^3 + \beta_{222} x_2^3 \ldots$, where $Y = \log_e (100\ W^{-1})$. From the set of provisional variables, the procedure builds an equation variable by variable, by adding in sequence variables that contribute significantly $(P < .05)$ in reducing sums of squares in the response variable. The process is completed when no more variables are admitted to the equation and no more are rejected.

After equations were chosen, residuals (differences between observed and predicted values) were analyzed by analysis of variance appropriate to the classification model of the split-plot growth-chamber design. Error variances were homogeneous across provenance, chilling, and flushing-temperature levels in the analysis, thus obviating the major objection to analyzing nested treatments by regression (DANIEL and WOOD 1971). In other respects, regression models were not entirely satisfactory.

The chosen regression equations were complex and included third- or higher-order terms for interactions. To simplify interpretation and to illustrate results, each equation was solved for W for a factorial set of selected values for chilling period and flushing temperature (chilling: 11, 44, and 77 days; flushing temperature: 10, 14, 18, and 22 C) and for provenance topographic variables (43°, 45.5°, and 48°N latitude; 100, 600, 1,100 m elevation; 60, 120, and 180 km from the ocean) or climatic variables (mean annual temperature: 6 C and 12 C; temperature amplitude: 5 C and 8 C; days to start of moisture deficit: 125 and 160; total moisture deficit: 15 cm and 37 cm). Chilling periods and flushing temperatures correspond to treatments in the experimental design; provenance variables were chosen arbitrarily to sample climates and topographies in western Washington and Oregon evenly.

Solutions of equations provided 324 expected values for the topographic system (3 chilling periods × 4 flushing temperatures × 3 latitudes × 3 elevations × 3 distances) and 192 for the climatic system. For each combination, values were averaged over all provenance points in the respective systems (e.g., topographic = 3 latitudes × 3 eleva-

tions × 3 distances = 27). Expected population responses were plotted graphically as deviations from these averages to provide sets of curves for describing clinally related genetic variation of population samples flushed in each of the chilling-flushing temperature combinations.

Results

Regression equations accounted for 86% and 87% of the variation in bud-flushing rate in climatic and topographic models, respectively (table 2, $R^2 = .86$, .87). Although, on the average, flushing rate increased directly with temperature (table 2, variable F), the rate at any given temperature also depended strongly on duration of chilling (table 2, variable FC or FC^2). These interacting responses were, in turn, modified by provenance, and modifications were related clinally to population location or climate (table 2, variables FCL or FC^2T and F^3C^2M).

The patterns of average population response in chilling period and flushing temperature combinations were similar, although not identical, in the two models. Developmental rates (100 W^{-1}) increased approximately logarithmically with increasing flushing temperature (fig. 1). The rate increased with added chilling. Hence, the approximate Q_{10} of

TABLE 2

GENERAL MAKEUP AND STATISTICS OF REGRESSION EQUATIONS CHOSEN TO PREDICT FLUSHING RESPONSE FROM TOPOGRAPHIC AND CLIMATIC FACTORS OF POPULATION ORIGIN

TOPOGRAPHIC MODEL		CLIMATIC MODEL	
Variables	Coefficients[a]	Variables	Coefficients[a]
Constant.......	$-$**	Constant......	$-$**
F..........	$+$**	F..........	$+$**
E^2..........	$-$**	FC..........	$+$**
L^2..........	$+$**	CA..........	$-$*
FE..........	$-$*	FSM........	$+$**
FL..........	$-$**	F^2AM.......	$+$**
CD..........	$+$**	CTA........	$-$**
F^3..........	$-$**	FC^2T........	$-$**
FC^2..........	$-$**	F^3C^2M.......	$-$*
F^2L..........	$+$**		
E^2L..........	$+$**		
FCL.........	$+$**		
F^2E.........	$+$*		
Regression:			
df..........	12		8
MS........	13.41		19.80
F..........	301**		406**
Residuals:			
df..........	539		543
MS........	.045		.049
R^2............	.87		.86

NOTE.—F = flushing temperature, C = chilling period, E = population elevation, L = population latitude, D = population distance from ocean, T = population mean annual temperature, A = population seasonal temperature amplitude, M = population total annual moisture deficit, S = population moisture deficit starting date.
[a] ± = Sign of regression coefficient.
* Significant at 5%.
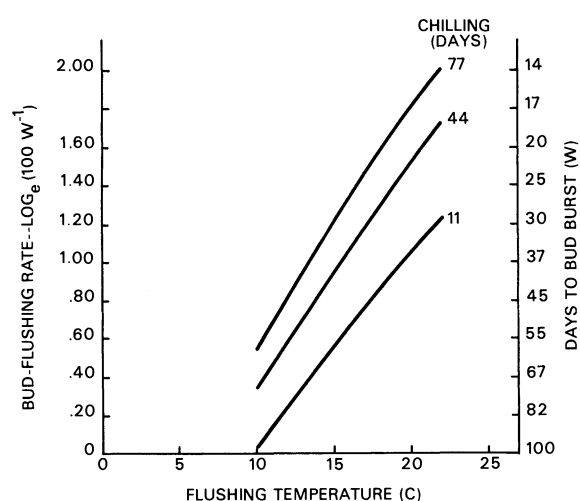** Significant at 1%.

CHILLING
(DAYS)

FIG. 1.—Bud-burst response to flushing temperature and chilling period based on population averages calculated from the regression equation for the climatic model. W = days to bud burst from the time plants entered the flushing chamber.

the bud flushing process was 2.7, 3.3, and 3.5 for plants chilled 11, 44, and 77 days, respectively. Deviations from this average response of individual populations were associated with the factors describing population origin. In the model based on climatic factors, deviations were mainly associated with moisture deficit and secondarily with the annual temperature cycle. The relationship with moisture deficit is described first for populations from the more continental climates, i.e., with relatively low mean annual temperatures (6 C) and high seasonal amplitudes (8 C).

Populations from areas with the largest total moisture deficit tended to burst buds earlier than the average in the lowest flushing temperature (10 C). The tendency was magnified as moisture deficit started later in the season. For example, populations from regions with moisture deficits of 37 cm starting 160 days after December 22 were calculated to burst buds 13 days before the average (96 days) of all provenances (fig. 2, 11 days chilling, 10 C flushing temperature). The tendency toward earlier bud burst in this type of population was even stronger after 77 days of chilling. If chilling remained short, bud burst tended to occur later, in relation to the average for all provenances, as flushing temperature increased (fig. 2, 11 days chilling, 22 C).

For sources from maritime climates (mean annual temperature, 12 C; temperature amplitude, 5 C), patterns were similar to those in figure 2 and consequently are not illustrated. Differences between populations from maritime and continental climates resulted because, with added chilling, flushing rates in maritime sources tended to fall behind those in continental sources. With increasing flushing tem-

peratures, they moved steadily ahead. At 10 C after 77 days of chilling, maritime populations burst buds about 10 days later than continental populations with corresponding moisture deficits. They were about 5 days earlier at 22 C and 11 days chilling.

When the topographic model was used to describe genetic variability among populations, variability was much larger in some environmental combinations than in others. Variability among populations was generally smaller, the longer the chilling period or the higher the flushing temperature (figs. 3, 4). The exception occurred in variability related to population distance from the ocean; variability was smallest in the combination involving the shortest chilling duration and the highest flushing temperature (fig. 4).

The extremes in elevation-related variability among populations occurred in the treatment with lowest flushing temperature (10 C) and shortest chilling period (11 days). In this treatment, samples from 600 m, 48°N latitude burst buds 9 days later than the system average, whereas high elevation samples (1,100 m) were 2 days earlier (fig. 3). In the same treatment, southern samples (43°N latitude) at 100 m and 1,100 m burst buds 10 and 1 day earlier than average, respectively. Comparable variation with elevation was not found in any other treatment.

Latitude-related genetic variability was greatest when seedlings were flushed at 14 C, compared with higher and lower temperatures, and was most evident after shortest chilling (11 days). For populations 120 km from the ocean at 600 m, those from 48°N latitude flushed 15 days later than the average, or 24 days later than comparable sources from 43°N latitude (fig. 3). In comparison, if flushed at 10 C, a minimally chilled northern population burst buds about 14 days later than the southern population.

Population variability related to distance from the ocean increased with longer chilling, in contrast to patterns with elevation and latitude. The trend was consistent over all flushing temperatures (fig. 4) and persisted regardless of population elevation; interactions of elevation with distance from the ocean were nonsignificant (table 2).

Discussion

Even though effects were measured in growth chambers, responses of populations to temperature during dormancy are considered to be adaptive. All populations had generally similar reactions to chilling duration and flushing temperature; hence, reactions could be described by an "average" response curve. The curves of individual populations differed quantitatively from this average, and these differences were clinally related to factors of climate or topography at population origin. It is difficult to account for such an ordered patterning of variation

11 DAYS CHILLING

44 DAYS CHILLING

77 DAYS CHILLING
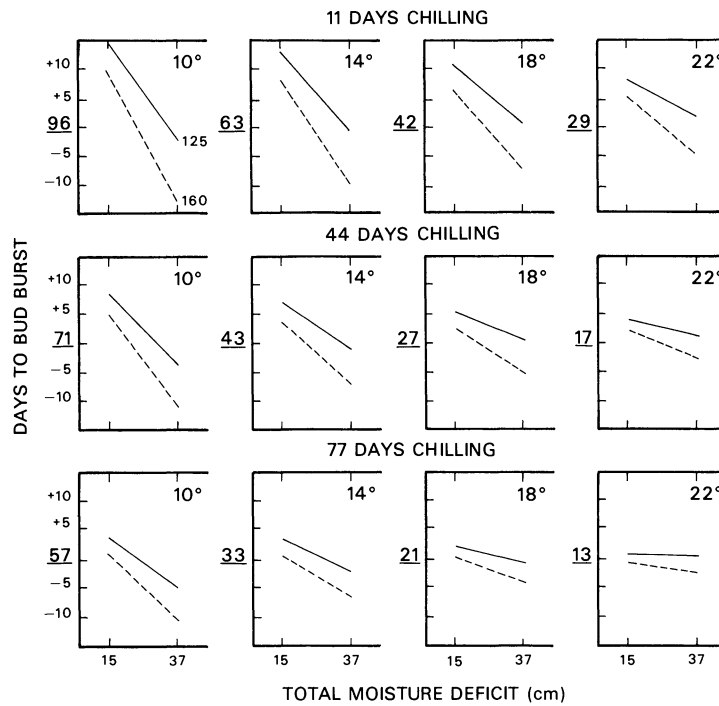
TOTAL MOISTURE DEFICIT (cm)

FIG. 2.—In each flushing temperature (C)–chilling period combination, response is given in terms of an expected treatment average (underlined) and plus or minus deviations in days to bud burst. Lines are for provenances from areas with total moisture deficits ranging from 15 to 37 cm starting 125 (———) and 160 (- - - -) days after December 22. Expected values apply to populations from areas with mean annual temperature of 6 C and amplitude of 8 C, i.e., the continental-like areas.

11 DAYS CHILLING

44 DAYS CHILLING
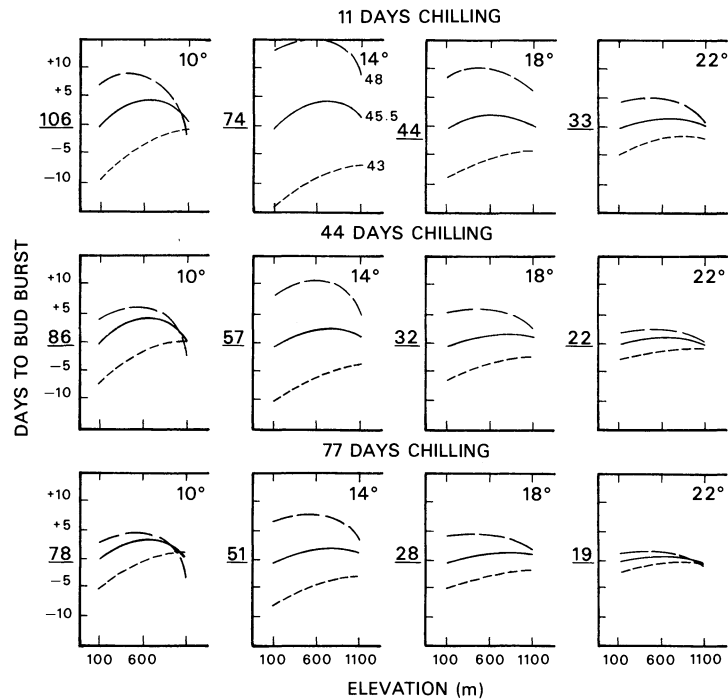
77 DAYS CHILLING

ELEVATION (m)

FIG. 3.—In each flushing temperature (C)–chilling period combination, population response is given as an expected treatment average (underlined) and deviations in days to bud burst. Lines are for provenances from 100 to 1,100 m elevation at 43° (- - - -), 45.5° (———), and 48° (—— ——) N latitude. Expected values apply to populations located 120 km from the Pacific Ocean.
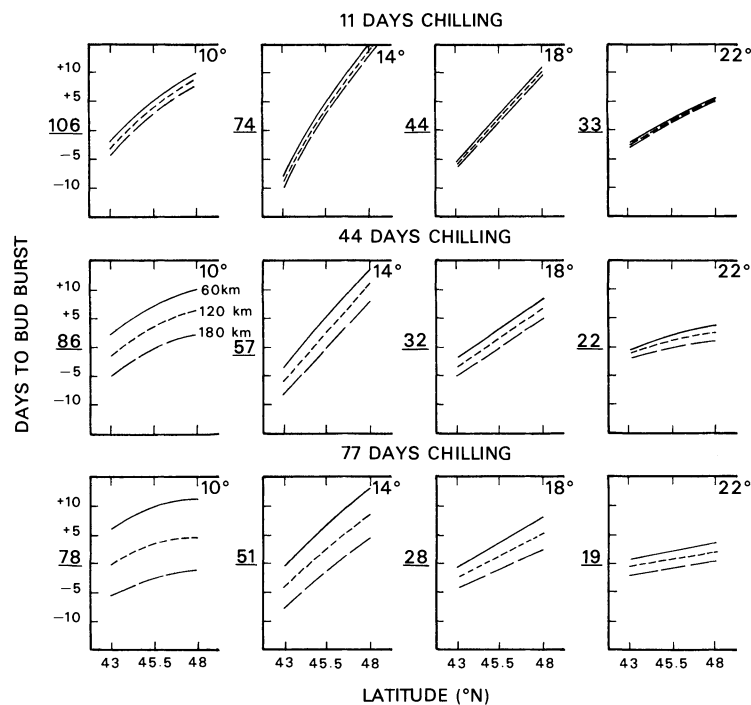
FIG. 4.—In each flushing temperature (C)–chilling period combination, population response is given as an expected treatment average (underlined) and deviations in days to bud burst. Lines are for populations from 43° to 48°N latitude at 60 (———), 120 (– – – –), and 180 (—— ——) km from the Pacific Ocean. Expected values apply to populations from 600 m elevation.

in a complex response except as a refined adjustment of populations to natural selection.

We suggest that genetic variation in temperature response has evolved as a mechanism for optimizing timing of bud burst. Seasonal changes in response to temperature (and light [see CAMPBELL and SUGANO 1975]) serve as cues to regulate processes in breaking dormancy. The rate at which a bud progresses toward flushing at a given winter or early spring temperature reflects expected future growing conditions, given that particular temperature (after LEVINS 1969).

This hypothesis agrees with two major features of our results: (1) with the responses of seedlings to chilling duration and temperature as described by the "average" curve, and (2) with the relationship of population deviations from the average curve to climatic factors which restrict length of the growing season.

The general response curve (fig. 1) indicates higher flushing rates (earlier flushing dates) with higher temperatures and longer chilling. Although higher rates are expected as the normal metabolic reaction to increased temperature, they are also expected in response to temperature as information. For example, the probability of an additional spring frost within a few weeks after an average daytime spring temperature of 15 C is smaller than the probability of spring frost after an average daytime temperature of 10 C. Reflecting this lower

probability of damage, flushing rates were generally higher at 15 C. Exceptions occur because probabilities at 10 C in February may be lower than the same probabilities at 15 C in December, just by the nature of the annual temperature curve and the longer interval between December and the last spring frost. Thus we expect, and find, that flushing rates increase with added chilling and that flushing rates can be as fast at 10 C after 77 days of chilling as at 15 C after 11 days of chilling (fig. 1). Once high average temperatures are reached in late spring, frost probabilities are minimal at all population locations. Consequently, we also expect, and find, that flushing rates of buds flushed at high temperatures will be similar among all populations, especially after long chilling (figs. 2–4).

For plants to have a longer growing season, some populations deviate from the average responses to flushing temperatures and chilling durations. Deviations are strongly patterned according to population location and can be interpreted as resulting from natural selection by frost and drought. Evidence is provided by both the climatic and topographic models.

CLIMATIC MODEL.—At higher elevations, summer is commonly short; at Government Camp in the Cascade Range of northern Oregon, 1,213 m, the growing season, based on a 20-yr record, is 81 days. In southern Oregon, at lower elevations, seasons are severely restricted by summer drought. At

Cave Junction, 404 m, the average date at which the moisture deficit starts to accumulate (table 1, May 2) precedes the average date of the last spring minimum of -2.2 C by 3 days. In these cases the greater risks associated with early bud burst may be exchanged for gains accruing from longer average effective growing seasons (CLARY 1975). If so, flushing rates of populations from high-moisture-deficit areas should be faster than average, reflecting the probabilities of spring frost followed shortly by drought. Since water deficits that start later in the season tend to occur at higher elevations ($r_{SE} = .29$; descriptive subscripts of this and other simple and partial correlation coefficients are defined in table 2; data from table 1) and higher latitudes ($r_{SL} = .27$), populations growing under these conditions tend to have shorter growing seasons that are restricted by cold. So flushing rates are faster for populations growing under water deficits starting later in the season. These combined effects are indeed the results emphasized in the climatic model (fig. 2).

TOPOGRAPHIC MODEL.—Results related to elevation and latitude may be interpreted on the same basis as those for the climatic model. At any given elevation, effective growing season lengths are more severely restricted by temperature in the north ($r_{TL \cdot E} = -.84$) and by drought in the south ($r_{ML \cdot E} = -.69$). The fastest flushing rates can therefore be expected from either high- or low-elevation populations, depending on whether cold or moisture deficit is most limiting. In regions where both factors provide more or less equal selection pressures, middle elevation populations might be comparatively less influenced by either. Rates would be correspondingly slower for these sources. The elevational patterns (fig. 3) may result from such balanced selection pressures in Washington and northwestern Oregon, south to 45.5°N. In southwestern Oregon (43°N), selection by summer drought has exerted comparatively more pressure at both middle and low elevations.

Results related to distance from the ocean primarily reflect the selection pressures afforded by temperature rather than drought. As one moves from the Cascades toward the Pacific Coast at any given elevation, the mean annual temperature increases ($r_{TD \cdot E} = .36$), and the seasonal temperature amplitude decreases ($r_{AD \cdot E} = -.59$). Consequently, near the coast, days warm enough to encourage growth are interspersed with freezing days throughout the winter. At lower elevations in the Coast Ranges, mean minimum and maximum daily temperatures in December and January are about 0 C and 8 C, respectively, with standard deviations of approximately 3.5 C (WAKEFIELD 1969). Farther inland, temperatures fluctuating between growing and freezing conditions occur in comparatively shorter periods in autumn and spring. For coastal

populations, chilling requirements apparently protect against warm-day bud development throughout the winter. Such protection may not be so important in the more inland populations (NIENSTAEDT 1967). This difference produces an increasing disparity in flushing rates and the resultant bud-burst dates between coastal and inland sources as chilling period increases (fig. 4).

One feature of the results in the topographic model which apparently does not agree with our hypothesis is the decreased population variability with latitude and elevation at 10 C compared with 14 C (fig. 3). At the same time, in the same treatments, population variability associated with distance from the ocean appears to be slightly exaggerated at 10 C compared with 14 C, particularly after 77 days of chilling. These irregularities can be explained by our finding (CAMPBELL and SUGANO 1975) that 10 C acts both in a chilling and a flushing capacity. Thus, flushing treatments at 10 C included more chilling than the assigned 11, 44, and 77 days. Accordingly, 10 C flushing accentuated the pattern that otherwise prevailed with added chilling, i.e., a decrease in population variation associated with latitude and elevation and an increase in variation with distance from the ocean.

Clinal trends are more complex in Douglas-fir than in other North American coniferous species. In other species, southern and low-elevation sources have responded more slowly to warming spring temperatures than northern or high-elevation sources (Sitka spruce, Picea sitchensis [Bong.] Carr., BURLEY 1966; black spruce, Picea mariana [Mill.] B.S.P., DIETRICHSON 1969, MORGENSTERN 1969; white spruce, Picea glauca [Moench] Voss, DIETRICHSON 1971; lodgepole pine, Pinus contorta Dougl., HAGNER 1970; red spruce, Picea rubens Sarg., KHALIL 1974). Coastal Douglas-fir differs from this pattern: (1) fastest bursting provenances are found at both high and low elevation depending on latitude, and (2) northern sources generally respond more slowly than southern sources.

We infer that the distinctive north-south pattern in coastal Douglas-fir reflects stronger season-limiting selection pressures of drought compared with cold, especially in Oregon (IRGENS-MOLLER 1967). Excepting Sitka spruce and Douglas-fir, all of the above species come from northern continental areas. These commonly have more summer rainfall than Washington and Oregon, and cooler annual temperatures than even at relatively high elevations in the Pacific Northwest (ANONYMOUS 1941). In northern continental areas, growing season lengths are mainly cold limited; hence, faster-bursting provenances are from the north. The elevational range of Sitka spruce is small, and it inhabits the coastal fog belt, which tends to protect it from the severe moisture deficits ex-

perienced by Douglas-fir. It conforms to the continental pattern by having faster-flushing northern provenances; in all other respects, its bud-bursting genecological trends resemble those in Douglas-fir (BURLEY 1966). Farther north, in British Columbia or in the northern Rocky Mountains, the pattern in Douglas-fir may shift to the cold-limiting mode. Such a pattern, in which the slopes of the north-south gradients of bud-burst phenology are opposite in southern and northern parts of the species range, has been observed in *Populus deltoides* (NIENSTAEDT 1974).

We believe LEVINS's (1969) dormancy strategy hypothesis has provided a worthwhile conceptual framework for interpreting our results. But more factors probably regulate the timing of bud burst in Douglas-fir than this experiment indicates. Neither climatic nor topographic models were entirely satisfactory; 13% or 14% of the variation

among populations remained unexplained. Part of the unexplained variability results from sampling variation, but part undoubtedly results because several factors known to influence flushing rate could not be incorporated as design variables. We kept photoperiod and temperature constant during chilling and flushing treatments. The timing of chilling was also constrained. Flushing rates are influenced differentially among populations by fluctuating temperatures and by interacting effects of photoperiod and chilling (CAMPBELL and SUGANO 1975). Flushing rates are also influenced by temperature and timing of chilling and prechilling (DORMLING, GUSTAFSSON, and VON WETTSTEIN 1968; SUGANO 1971). From our previous experience, we believe that these effects may modify some aspects of results in this experiment, but they would not substantially alter the major features.

LITERATURE CITED

ANONYMOUS. 1941. Climate and man: yearbook of agriculture. Government Printing Office, Washington, D.C. 1248 pp.

BURLEY, J. 1966. Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr. Forestry 39: 69–94.

CAMPBELL, R. K. 1974. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. J. Appl. Ecol. 11:1069–1080.

CAMPBELL, R. K., and F. C. SORENSEN. 1978. Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. Theoret. Appl. Genet. 51:233–246.

CAMPBELL, R. K., and A. I. SUGANO. 1975. Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. BOT. GAZ. 136:290–298.

CLARY, W. P. 1975. Ecotypic adaptation in *Sitanion hystrix*. Ecology 56:1407–1415.

COOPER, J. P. 1963. Species and populational differences in climatic response. Pages 381–400 *in* L. T. EVANS, ed. Environmental control of plant growth. Academic Press, New York. 449 pp.

COUVILLON, G. A., and C. H. HENDERSHOTT. 1974. A characterization of the "after-rest" period of flower buds of two peach cultivars of different chilling requirements. J. Amer. Soc. Hort. Sci. 99:23–26.

DANIEL, C., and F. S. WOOD. 1971. Fitting equations to data. Wiley-Interscience, New York. 342 pp.

DIETRICHSON, J. 1969. Genetic variation of cold damage, growth rhythm and height growth in 4-year-old black spruce (*Picea mariana* [Mill.] B.S.P.). Meddelelser Norske Skogforsöksvesen 27:109–129.

———. 1971. A summary of studies on genetic variation in forest trees grown in Scandinavia with special reference to the adaptation problem. Meddeleser Norske Skogforsöksvesen 29:25–59.

DORMLING, I., Å. GUSTAFSSON, and D. VON WETTSTEIN. 1968. The experimental control of life cycle in *Picea abies* (L.) Karst. I. Some basic experiments on the vegetative cycle. Silvae Genet. 17:44–64.

DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. Wiley, New York. 407 pp.

FARMER, R. E., JR. 1968. Sweetgum dormancy release: effects of chilling, photoperiod and genotype. Physiol. Plantarum 21:1241–1248.

HAGNER, M. 1970. A genecological investigation of the annual

rhythm of *Pinus contorta* Dougl. and a comparison with *Pinus silvestris* L. Stud. Forest. Suecica 81:1–26.

IRGENS-MOLLER, H. 1967. Patterns of height growth initiation and cessation in Douglas-fir. Silvae Genet. 16:56–58.

KHALIL, M. A. K. 1974. Preliminary results of a red spruce (*Picea rubens* Sarg.) provenance experiment in Newfoundland. Can. Forest Service Information Rep. N-X-117. 45 pp.

KRIEBEL, H. G., and C. W. WANG. 1962. The interaction between provenance and degree of chilling in bud-break of sugar maple. Silvae Genet. 11:125–130.

LEE, R., and E. B. JONES. 1968. Chemical measurement of mean temperature. Water Resource Bull. 4:39–45.

LEVINS, R. 1969. Dormancy as an adaptive strategy. Symp. Soc. Exp. Biol. 23:1–10.

MORGENSTERN, E. K. 1969. Genetic variation in seedlings of *Picea mariana* (Mill.) B.S.P. I. Correlation with ecological factors. Silvae Genet. 18:151–161.

NEILD, R. E., and J. K. GREIG. 1972. An agroclimatic procedure to determine growing seasons for vegetables. Agr. Meteorol. 9:225–240.

NIENSTAEDT, H. 1967. Chilling requirements in seven *Picea* species. Silvae Genet. 16:65–68.

———. 1974. Genetic variations in some phenological characteristics of forest trees. Pages 389–400 *in* H. LIETH, ed. Phenology and seasonality modeling. Springer-Verlag, New York. 444 pp.

PERRY, T. O., and C. W. WANG. 1960. Genetic variation in the winter chilling requirements for date of dormancy break for *Acer rubrum*. Ecology 41:790–794.

SUGANO, A. I. 1971. The effects of low temperatures on dormancy release in Douglas-fir from western Oregon, Washington, and California. M.S. diss. Oregon State University, Corvallis.

THORNTHWAITE, C. W. 1954. The determination of potential evapotranspiration. Pages 218–225 *in* J. R. MATHER, ed. The measurement of potential evapotranspiration. Publications in Climatology. Vol. 7. Johns Hopkins University Laboratory of Climatology, Baltimore. 225 pp.

VAN DEN DRIESSCHE, R. 1975. Flushing response of Douglas-fir buds to chilling and to different air temperatures after

chilling. Brit. Columbia Forest Service Res. Note no. 71. 22 pp.

WAKEFIELD, J. D., ed. 1969. Climatological handbook, Columbia Basin States temperature. Vol. 1, pts. A, B. Pacific Northwest River Basins Commission, Vancouver, Wash.

WOMMACK, D. E. 1964. Temperature effects on the growth of Douglas-fir. Ph.D. diss. Oregon State University, Corvallis.

WORRALL, J., and F. MERGEN. 1967. Environmental and genetic control of dormancy in *Picea abies*. Physiol. Plantarum 20:733–745.