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Effects of Provenance, Years, and Planting Location on Bud Burst of Douglas-fir

T. L. White
K. K. Ching
J. Walters

Abstract. For 3 years and in two planting locations, date of bud burst was monitored on Douglas-fir saplings from 16 Pacific Northwest provenances. Provenances planted in the Willamette Valley in western Oregon differed genetically in their date of bud burst. Saplings planted in western British Columbia burst bud an average of 16 days later than in Oregon. The significant provenance × year interaction in Oregon seemed due more to a scale effect rather than to a large shifting in provenance rankings in the different years. Correlations showed that provenances originating from areas with low summer rainfall tended to have early bud burst. These field results, coupled with those of recent growth-room studies, indicate that summer drought in some areas of the Pacific Northwest may have resulted in the natural selection of seedlings with early bud burst. Forest Sci. 25:161–167.

Additional key words. Provenance variation, genotype × environment interaction, *Pseudotsuga menziesii*, phenology.

When seedlings with early bud burst are planted on sites with late spring frosts, they are susceptible to frost and other damage. Consequently, the ability to predict a provenance's time to bud burst on any planting site is important in reforestation.

Phenological studies of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] indicate that the time to bud burst is under strong genetic control with large differences between provenances (Morris and others 1957, Irgens-Moller 1957, Ching and Bever 1960, Silen 1962, Walters and Soos 1963, Sweet 1965). In controlled environment studies of Douglas-fir provenances, the date of bud burst correlated with climatic and topographic variables of the provenances (Campbell 1974, Campbell and Sugano 1978). Bud burst time and provenance climatic variables failed to correlate for 30 Douglas-fir provenances grown in a New Zealand nursery, although the lag time between the bursting of the terminal bud and the most advanced lateral bud was related to the climate of the provenances (Sweet 1965).

We outplanted Douglas-fir seedlings to study whether provenance differences in bud burst are stable from year to year and from one planting location to another. We also studied the possibility that the time of bud burst of a provenance is related to the climate at its place of origin.

The first two authors are Research Assistant and Professor, School of Forestry, Oregon State University, Corvallis, Oregon 97331. The third author is Director, Research Forest, University of British Columbia, Maple Ridge, B.C., Canada. Submitted as Publication 1,216 of the Forest Research Laboratory, Oregon State University. The authors thank Robert K. Campbell, Denis P. Lavender, and Paul Hinz for their helpful suggestions and review of this manuscript. Manuscript received 22 January 1977.

TABLE 1. Topographic and climatic data associated with provenances.[a]

Provenance	Latitude	Longitude	Elevation	Mean temperature January[b]	Time to last spring frost[b,c]	Length of FFGS[b,d]	Precipitation		
							May	June	July
	Degrees		*m*	*°C*	*Days*	*Days*		*cm*	
1	49.17	124.00	840	−2.9	165	77	3.7	3.9	2.3
2	49.75	125.00	460	−0.5	151	119	4.9	4.9	3.5
3	48.83	124.25	200	1.0	123	190	5.3	5.0	3.2
4	50.50	126.75	150	2.5	99	220	5.5	5.3	5.2
5	46.75	122.75	590	1.4	140	125	10.0	9.4	3.1
6	47.25	123.33	90	3.6	123	167	4.7	4.7	2.4
7	45.50	123.50	580	0.9	126	173	4.9	3.8	1.1
8	44.83	123.05	60	4.1	125	169	4.7	3.4	0.7
9	45.17	122.10	550	0.9	113	179	9.5	6.5	1.5
10	45.17	121.75	1,070	−0.9	154	95	12.1	9.5	2.2
11	44.50	123.60	580	2.4	154	98	10.0	6.6	2.2
12	43.75	122.17	580	1.1	130	138	6.7	1.9	0.3
13	43.75	122.17	840	−0.3	143	113	6.7	1.9	0.3
14	42.34	123.25	910	1.7	155	132	1.1	1.1	0.4
15	49.17	122.50	180	1.2	110	190	11.1	9.2	6.8
16	47.50	121.33	1,220	−4.4	148	123	9.3	9.4	4.2

[a] Climatic data, based on 20-year normals, were taken from the weather station nearest the collection of the provenance material.

[b] Corrected for discrepancies in elevation between weather station and provenance collection site (Sweet 1965).

[c] Number of days from January 1 to average date of last spring frost.

[d] Frost-free growing season (FFGS) = average length of time when temperature is continuously above 0°C.

Materials and Methods

In 1954, Douglas-fir seed was collected from 16 sources between latitudes 42.34°N and 50.50°N (Table 1) on the west side of the Cascade Mountains of Oregon, Washington, and British Columbia. In 1959, 2-0 seedlings from 14 provenances were outplanted at two sites. A year later, provenances 15 and 16 were similarly outplanted. Nursery performance, plus survival and height growth in the field, have been reported (Ching and Bever 1960, Rowe and Ching 1973).

Bud burst was monitored at each site. Plantation I, located in Oregon's Willamette Valley near provenance 8, has relatively mild winters and dry summers. Plantation II, located 300 miles away in Haney, British Columbia, near provenance 15, has slightly cooler winter temperatures and very moist summers (Table 1).

In Plantation I, trees were outplanted in a randomized complete block design with two blocks. In each of the 16 provenance plots within a block, 121 trees of a given provenance were planted, but only the innermost 49 trees (actually 9–49 trees because of mortality) were monitored for bud burst. A total of 1,100 trees were monitored for bud burst in each of 3 years, 1962, 1963, and 1965. On each tree, both the terminal bud and the most advanced lateral bud were observed at least weekly. A bud was considered burst when parting bud scales exposed new needles. All analyses were done on the plot means (n = 9–49 trees per plot) of the number of days after January 1 that bud burst occurred. Because the same

TABLE 2. Analysis of variance: terminal bud burst at Plantation I (Willamette Valley).

Source	d.f.	Mean square
Block	1	91.90**
Provenance	15	42.13**
Error (a)	15	6.31
Years	2	232.33**
Provenance × years	30	5.44**
Slopes	15	6.37**
Concurrence	1	67.60**
Nonconcurrence	14	2.00 n.s.
Remainder	15	4.52**
Error (b)	32	1.62

** Significant at $P = 0.01$.

trees were measured each year, the design was treated as split plot with provenance as the whole-plot factor and years as the subplot factor.

In Plantation II, only terminal bud burst was monitored on one of the two blocks in 1962, 1963, and 1964. We randomly selected 6 of the possible 49 trees within each provenance plot, then used the same trees each year. Because the given design precluded calculation of a legitimate error term, the data from this plantation were not subjected to an analysis of variance.

Results

Relation Between Terminal and Lateral Bud Burst at the Willamette Valley Plantation.—On almost all trees in Plantation I, the most advanced lateral bud flushed before the terminal bud. This lag time did not differ among seed sources, but yearly differences were highly significant ($P = 0.01$). In 1962 and 1963, lateral buds burst an average of 10 days before the terminal bud, compared to only 3 days in 1965.

Provenance means for terminal and lateral bud burst correlated highly ($P = 0.01$) in all 3 years ($r = 0.96$, 0.98, and 0.86 for 1962, 1963, and 1965—all with 14 d.f.). Consequently, only terminal bud burst was used in subsequent analyses.

Terminal Bud Burst.—In Plantation I, the provenance, year, and the provenance × year interaction were all highly significant (Table 2). In all 3 years, provenance differences accounted for a high percentage of the total within-year variation in bud burst ($r^2 = 0.78$, 0.88, and 0.92 for 1962, 1963, and 1965—all highly significant with 14 d.f.). Examination of provenance means for each of the 3 years showed that the provenance × year interaction at Plantation I did not indicate large changes in provenance rankings from year to year (Table 3).

To further examine this interaction, the yearly bud burst mean for a provenance was regressed on the average bud burst date for the year (Mandel 1961), a type of analysis previously used to assess the relative reactions of a set of genotypes to varying environments (Finlay and Wilkinson 1963). The slopes of the regression lines showed how responsive the bud burst of a particular provenance was to yearly changes in bud burst date. For example, whereas provenance 4 was responsive to these yearly differences (Fig. 1), provenance 8 was stable. The highly significant ($P = 0.01$) concurrence and the lack of nonconcurrence (Table 2) indicate that these regression lines tended to have a common intersection, then fan out from there. In 1965 when bud burst was earliest, the dates of bud burst tended

TABLE 3. Provenance means for terminal bud burst date[a] for 3 years at Plantation I (Willamette Valley).

Rank	1962		1963		1965	
	Provenance	Mean	Provenance	Mean	Provenance	Mean
		Days		*Days*		*Days*
1	8	118.8	8	119.1	13	119.2
2	12	120.4	12	122.2	11	119.2
3	13	121.0	11	123.8	8	119.4
4	9	122.3	13	124.0	12	119.9
5	5	122.9	5	125.3	1	120.9
6	16	123.0	14	125.5	9	120.9
7	11	123.0	9	125.9	2	121.3
8	10	124.6	3	126.4	14	121.4
9	14	124.8	16	128.4	5	121.6
10	3	125.8	1	128.4	3	121.7
11	15	127.0	10	128.6	4	121.8
12	1	127.4	2	129.8	7	122.3
13	7	127.7	6	129.9	6	122.4
14	4	127.9	7	130.1	16	123.1
15	6	128.0	4	131.0	10	124.5
16	2	128.5	15	133.6	15	126.3
Average		124.6		127.0		121.6
Range		9.7		14.5		7.1
95 percent LSD[b]		4.8		3.7		1.7
99 percent LSD[b]		6.7		5.1		2.4

[a] Days from January 1.

[b] Calculated from within-year ANOVA.

to cluster for the provenances, but they spread out more in years when the bud burst was later (Fig. 1). The smaller range in provenance means in years with early bud burst also exemplified this trend (Table 3). Therefore, provenances that burst bud late in 1 year tended to be late all 3 years; however, later provenances were progressively later, relative to early provenances, in later years.

The slopes of these regression lines failed to account for a significant portion of the provenance × year interaction (the remainder in Table 2), possibly indicating the presence of another kind of genotype × environment interaction. The sum of squares associated with this uninterpretable remainder represented only 4.5 percent of the total variation, compared to 42 and 31 percent represented by the provenance and year sums of squares.

At Plantation II, the average date of bud burst for all provenances was always much later (145, 134, and 143 days after January 1 in 1962, 1963, and 1964). Averaged over all 3 years, Plantation II burst bud an average of 16 days later than the Willamette Valley trees.

Because Plantation II data were not replicated, the provenance × year interaction and the provenance × plantation interaction could not be determined by standard analysis of variance techniques. Correlations of provenance bud burst means between years at Plantation II were quite low: 0.45, 0.46, and 0.65 (with 14 d.f.) between 1962 and 1963, 1962 and 1964, and 1963 and 1964 ($r = 0.50$ and $r = 0.62$ are significant at $P = 0.05$ and $P = 0.01$). When provenance means were averaged for all 3 years, Plantation I correlated poorly with Plantation II ($r = 0.35$ n.s.). These poor correlations—between year and between plantation—

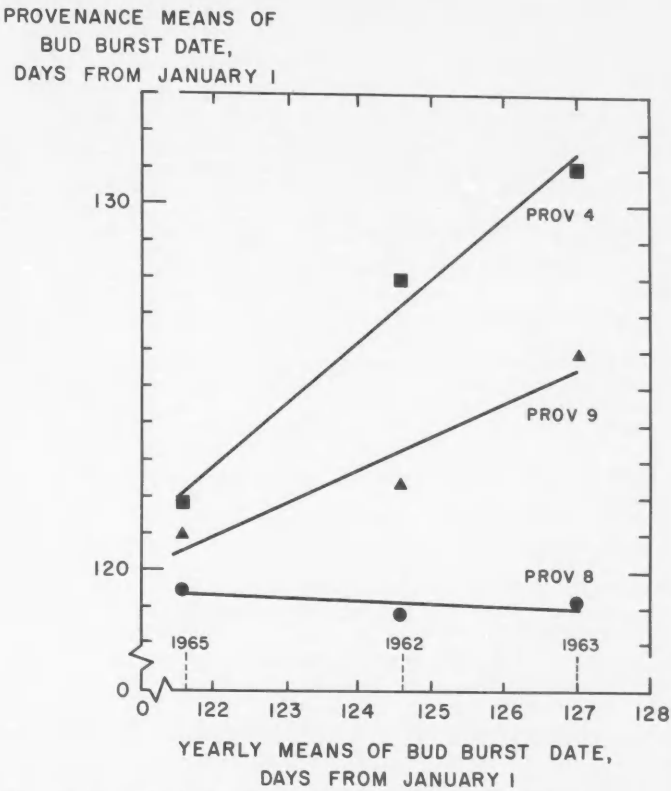

FIGURE 1. Bud burst date for provenances responds differentially to yearly changes in average bud burst date. Each point represents the mean of all trees in both blocks at Plantation I (Willamette Valley).

may indicate provenance × year and provenance × plantation interactions. On the other hand, only six trees represented each provenance at Plantation II, and bud burst was scored only weekly; therefore, the poor correlations may reflect large experimental error.

Relationship of Provenance Climate and Location to Bud Burst.—Correlation analyses were run between bud burst means at both plantations and all climatic and location variables for each provenance (Table 1). At Plantation I, provenance latitude and July precipitation consistently correlated with provenance bud burst date; seed from southern provenances or from provenances with low July precipitation tended to produce saplings with early bud burst when planted in the Willamette Valley (Table 4). Because the July rainfall and latitude correlated highly (r = 0.82, 14 d.f.) for these 16 provenances (i.e., northerly latitudes tended to have more July rainfall), both variables may have accounted for a similar portion of the variation among provenance bud burst means.

At Plantation II, the correlations between provenance bud burst date and provenance climate and topography were not as consistent from year to year

TABLE 4. Correlations of provenance means of bud burst date and provenance climatic variables.[a]

Provenance variables	Plantation I			Plantation II		
	1962	1963	1965	1962	1963	1964
Latitude	0.68	0.67	0.42	0.02	0.15	0.15
Elevation	−0.19	−0.04	0.04	0.09	0.31	−0.16
Longitude	0.60	0.29	−0.15	−0.02	−0.02	0.02
January mean temperature	−0.10	−0.28	−0.28	0.12	0.25	0.27
Date of last spring frost	0.08	−0.21	−0.21	0.13	0.02	−0.37
Length of growing season >0°C	0.19	0.24	0.24	−0.23	−0.11	0.28
Precipitation						
May	−0.24	0.13	0.13	0.53	0.57	0.46
June	0.17	0.41	0.41	0.56	0.51	0.48
July	0.53	0.73	0.73	0.30	0.44	0.50

[a] $r = 0.50$, significant at $P = 0.05$.
$r = 0.62$, significant at $P = 0.01$.

(Table 4). Still, provenances from areas with lower summer precipitation tended to burst bud earlier.

Discussion

Our results confirm other studies showing that Douglas-fir from different provenances can genetically differ in its bud burst date (Campbell 1974, Campbell and Sugano 1975, Irgens-Moller 1957, Morris and others 1957). Morris and others (1957) found some minor shifting in provenance rankings for different years and in different plantations. At Plantation I, we found a significant provenance × year interaction in bud burst date; however, this seemed due to a scale effect, rather than a major shifting in rankings. Provenances tended to maintain their rankings over the years, but clustered more in the years with early bud burst and spread out more in years of later bud burst.

The terminal bud burst date of Douglas-fir seedlings grown in a New Zealand nursery showed no differences attributable to provenances (Sweet 1965); however, the lag time between terminal and lateral bud burst correlated with certain provenance climatic variables. In our study, lag time did not vary by provenance. This discrepancy may be due either to the fact that most of Sweet's provenances came from much farther south in the Douglas-fir range or to the differing influence of the New Zealand nursery.

In Plantation I, provenances from southerly areas or from areas with low July precipitation tended to burst bud early, confirming recent controlled-environment provenance studies of Douglas-fir (Campbell 1974, Campbell and Sugano 1978). Because July precipitation and latitude correlated highly in our study, their effects cannot be differentiated. However, completing height growth before it is limited by drought would seem highly advantageous for plants from areas with dry summers. This could be done by beginning height-growth earlier—that is, bursting bud earlier. When 2-0 Douglas-fir seedlings were subjected to a summer drought, those from xeric provenances burst bud earlier and survived better in the following growing season than did those from a mesic provenance (Heiner and Lavender 1972). Perhaps, high summer moisture deficits have selected for early bud burst in some provenances.

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Percent Bias and Standard Error in Logarithmic Regression

Harry V. Wiant, Jr., and E. James Harner

ABSTRACT. An approximation of the percent bias of the mean predicted values for models of the form $Y = \alpha X^{\beta}\epsilon$ is $[(e^{\hat{\sigma}^2/2} - 1)/e^{\hat{\sigma}^2/2}] \times 100$, where $\hat{\sigma}^2$ is the estimated variance of $\ln \epsilon$. The standard error as a percent of the unbiased predicted values is estimated as $(e^{\hat{\sigma}^2} - 1)^{1/2} \times 100$. Both of these expressions are constant over the range of X values. FOREST SCI. 25:167–168.

ADDITIONAL KEY WORDS. Biomass, weight equations.

NUMEROUS BIOMASS STUDIES have used statistical models of the form

$$Y = \alpha X^{\beta}\epsilon$$

where ϵ is the random error term. This equation is linearized by taking logarithms into

$$\ln Y = \ln \alpha + \beta \ln X + \ln \epsilon. \tag{1}$$

The authors are, respectively, professor of forestry and associate professor of statistics, West Virginia University, Morgantown. West Virginia University Agricultural and Forestry Experiment Station Scientific Paper 1542. Manuscript received 17 April 1978.

The ordinary least squares estimates of the parameters in equation (1) are given by $\widehat{\ln \alpha}$ and $\hat{\beta}$. Thus the prediction model in terms of the arithmetic units is given by

$$\hat{Y} = e^{(\widehat{\ln \alpha} + \hat{\beta} \ln X)} \tag{2}$$

where "e" is the base of the Napierian logarithms. However, the mean predicted values for given values of X are biased.

Baskerville (1972) gave an approximation of the estimate corrected for this bias:

$$\hat{Y}_c \doteq e^{[\widehat{\ln \alpha} + \hat{\beta} \ln X + (\hat{\sigma}^2/2)]} \tag{3}$$

where $\hat{\sigma}^2 = \Sigma(\ln Y - \widehat{\ln Y})^2/(n - 2)$ is the estimated variance of $\ln \epsilon$ and n is the sample size. The bias, $(\hat{Y}_c - \hat{Y})$, as a percent of the unbiased estimate (Brown 1976), is

$$B \doteq [(\hat{Y}_c - \hat{Y})/\hat{Y}_c] \times 100. \tag{4}$$

Apparently, it has not been noted before that B reduces to

$$[(e^{\hat{\sigma}^2/2} - 1)/e^{\hat{\sigma}^2/2}] \times 100.$$

Interestingly, for this multiplicative model, percent bias is constant over the range of X values.

Baskerville indicated the estimated variance of $\hat{Y}_c$ for a given value of X is approximated by

$$\hat{\sigma}_{\hat{Y}_c}{}^2 \doteq e^{[2\hat{\sigma}^2 + 2(\widehat{\ln \alpha} + \hat{\beta} \ln X)]} - e^{[\hat{\sigma}^2 + 2(\widehat{\ln \alpha} + \hat{\beta} \ln X)]}. \tag{5}$$

It is informative to express the standard error given X as a percent of $\hat{Y}_c$. This becomes

$$\hat{\sigma}_{\hat{Y}_c}/\hat{Y}_c \times 100 \doteq (e^{\hat{\sigma}^2} - 1)^{1/2} \times 100.$$

Thus, the percent standard errors are also constant over the range of X values.

As an example, for a biomass weight equation with a logarithmic variance estimate ($\hat{\sigma}^2$) of 0.03575, we find

$$\text{Percent bias} \doteq [(e^{(0.03575)/2} - 1)/e^{(0.03575)/2}] \times 100$$
$$= 1.77.$$
$$\text{Percent standard error} \doteq (e^{0.03575} - 1)^{1/2} \times 100$$
$$= 19.08.$$

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