

# Genetic control of bud phenology in pole-size trees and seedlings of coastal Douglas-fir<sup>1</sup>

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The extent to which bud phenology is genetically controlled and related to growth traits was examined in seedlings and pole-size trees of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Data on bud burst, bud set, and stem growth were collected from pole-size trees of 60 open-pollinated families growing in four plantations, and from seedlings of 45 of these same families growing in three trials. In both age-classes, bud burst was under moderate to strong genetic control ( $h^2 \geq 0.44$ ) and family breeding values were stable across test environments, indicating that this trait could be readily altered in breeding programs. Bud set was inherited strongly in pole-size trees ( $h^2 = 0.81$ ) but weakly in seedlings ( $h^2 \leq 0.30$ ). Both bud burst and bud set were positively correlated with growth in seedlings and pole-size trees. Thus, selection for greater growth at either age-class is expected to delay bud burst and bud set. We also evaluated the accuracy of two alternatives for assessing bud burst phenology in pole-size trees compared with the traditional method. We show that bud-burst date on lateral branches can be used to accurately rank both individuals and families for bud-burst date on less accessible leader shoots. In addition, we found that families can be ranked for mean bud-burst date by the proportion of trees per family that have flushed on a given scoring day. This method is only effective, however, when between 25 and 75% of all trees in the test have flushed at the time of scoring.

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Le contrôle génétique de la phénologie des bourgeons et les relations entre la phénologie et les caractères de croissance ont été étudiés chez le sapin de Douglas de la côte (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) à partir de semis et d'arbres juvéniles. Des données de débourrement, d'aoûtement et de croissance de la tige ont été prises à partir des arbres juvéniles qui représentaient 60 descendance issues de pollinisation libre et ce, au sein de quatre plantations. Les mêmes données furent prises à partir des semis qui représentaient 45 des 60 descendance mentionnées précédemment et ce, au sein de trois tests. Pour les deux classes d'âge, le débourrement est apparu sous un contrôle génétique variant de modéré à fort ( $h^2 \geq 0,44$ ) alors que les valeurs en croisement des familles étaient stables d'un environnement expérimental à l'autre, indiquant que ce caractère pourrait être facilement modifié dans les programmes d'amélioration. L'aoûtement était très héritable chez les arbres poteaux ( $h^2 = 0,81$ ) mais de façon moindre chez les semis ( $h^2 \leq 0,30$ ). Le débourrement et l'aoûtement étaient tous deux fortement corrélés à la croissance chez les semis et les arbres juvéniles. Il est donc prévisible que la sélection pour une croissance supérieure à l'un ou l'autre âge résultera en un délai de débourrement et d'aoûtement. Nous avons aussi évalué la précision de deux méthodes alternatives visant à estimer la phénologie du débourrement chez les arbres juvéniles, comparativement à la méthode traditionnelle. Nous montrons que la date de débourrement évaluée à partir des branches latérales peut être utilisée afin de classer avec précision à la fois les individus et les descendance quant à la date de débourrement des pousses terminales moins accessibles. De plus, nous avons découvert que les descendance pouvaient être classées selon la date moyenne de débourrement à partir de la proportion d'arbres par descendance qui avaient débouillé pour un jour particulier de mesurage. Toutefois, cette méthode n'est efficace que lorsque 25–75% de l'ensemble des arbres du test ont débouillé à la date de mesurage.

[Traduit par la rédaction]

## Introduction

An important facet of plant adaptation is the synchronization of growth rhythm with the seasonal weather cycle (Dietrichson 1964). Thus, bud phenology (timing of bud burst and bud set) is important in determining both adaptation and growth (Skrøppa 1982; Ford 1984). Provenance tests reveal the adaptive significance of bud phenology by showing that early flushing seed sources are the most susceptible to damage from spring frost (Nienstaedt and King 1969; Steiner and Wright 1974; Christophe and Birot 1979) and that seed sources with late bud set are the most prone to damage from summer drought, fall frost, and winter cold (Campbell and Sorensen 1974; Griffin and Ching 1977; Rehfeldt 1979;

Mikola 1982; White 1987; Loopstra and Adams 1989). Potentially, frost or drought damage to planting stocks can be reduced by manipulating bud phenology in tree improvement programs. To better assess the potential for genetic manipulation, however, the extent of genetic variation and genetic control of bud-phenology traits must be understood.

To date, most studies on bud phenology of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and other conifers have been on seedlings. These studies have shown that seedling bud phenology varies extensively among and within populations and that bud burst and bud set are under strong genetic control (Christophe and Birot 1979; Rehfeldt 1983; Nienstaedt 1985; Campbell et al. 1989; Ekberg et al. 1991). The genetics of bud phenology in older trees is also of interest. The large number of Douglas-fir progeny tests established by tree improvement programs in the Pacific northwest and Europe provide an opportunity to select for bud phenology traits in 10- to 20-year-old field-grown trees, the age range in which decisions are typically made on a tree's economic value

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TABLE 1. Test site characteristics and bud-phenology measurements for pole-size trees and seedlings

Test site	Location		Elevation (m)	Year (sown)	Survival (%)	Measurements
	Latitude	Longitude				
<b>Pole-size trees</b>						
Oxbow	43°51'N	123°34'W	396	1972	85	Bud burst on leader in 1986 and 1987
Coyote Creek	43°55'N	123°18'W	274	1973	85	Bud burst on leader in 1986
Clay Creek	43°55'N	123°35'W	137	1973	89	Bud burst on leader in 1986 and 1987
Smith Creek	43°52'N	123°24'W	305	1975	70	Bud burst on leader and branches in 1987 Bud burst and bud set on branches in 1988
<b>Seedlings</b>						
Bare-root trial						
Washington	46°50'N	123°08'W	46	1986 1987	72 86	First-year bud set and second-year bud burst First-year bud set and second-year bud burst
Greenhouse trial						
Washington	46°50'N	123°57'W	61	1987	94	First-year bud set
Oregon	44°32'N	122°54'W	110	1987	96	First-year bud set
Transplant trial						
Washington <sup>a</sup>	46°50'N	123°08'W	46	— <sup>b</sup>	74	Second-year bud burst and bud set
Oregon	43°38'N	123°34'W	62	— <sup>b</sup>	81	Second-year bud burst and bud set

<sup>a</sup>Same nursery as used for the bare-root seedling trial.

<sup>b</sup>Greenhouse-grown seedlings were transplanted into the two nurseries in late April 1988.

(e.g., bole volume and wood quality). Selection for late flushing in order to avoid damage from late spring frosts is already an important consideration in these tests (Biro and Christophe 1983; Wheeler et al. 1990). Timing of bud set is apparently of less interest in older trees because bud set occurs in midsummer, well before early fall frosts (Walters and Soos 1963; Emmingham 1977), and the relationship between bud-set timing and development of cold or drought hardiness is less obvious. Nevertheless, the extent to which selection for growth alone in older trees affects bud phenology is a significant concern. In Douglas-fir seedlings, for example, height is positively correlated with late bud set, indicating that selection for greater height will result in extension of the growing period (Rehfeldt 1983; Campbell 1986; Kaya et al. 1989).

Apparently, there have been only two reports on the inheritance of bud-burst timing in coastal Douglas-fir (*var. menziesii*) trees 10 years or older (Biro and Christophe 1983; Bastien and Roman-Amat 1986) and no reports on the inheritance of bud-set timing. There is good reason to suspect, however, that bud-set inheritance may not be the same in seedlings and older trees, because conifer shoot-growth patterns differ between the two age classes. Shoot growth results from both predetermined and free growth in seedlings, but mainly from predetermined growth in older trees (Jablanczy 1971; Logan and Pollard 1975; Lanner 1978).

Despite the potential importance of bud-phenology traits, their inclusion in selection programs is hampered by their difficulty of measurement. Accurate scoring of bud burst and bud set with traditional methods is both time-consuming and costly because of the recommended frequency with which test sites must be visited during the flushing and bud-setting periods (twice weekly for bud burst and once weekly for bud set according to Biro and Christophe (1983) and Campbell (1986)). In addition, beginning at the sapling stage, bud-phenology scoring is complicated by the difficulty of observing the terminal bud of the leading shoot from the ground.

In this paper, we report on the genetic control of bud phenology in both seedlings and pole-size (13- to 16-year-old) trees of coastal Douglas-fir families from western Oregon. Specifically, we (i) evaluate, for each age-class, the extent of genetic variation and genetic control of bud-phenology traits in the leader shoot, the phenotypic stability of these traits across test environments, and the genetic relationships between bud-phenology traits; (ii) examine the genetic relationships between growth traits and bud phenology; and (iii) in an attempt to identify alternative methods of measuring bud-burst phenology, evaluate the accuracy of (a) using bud burst on branches as an indirect measure of bud burst on the leader shoots of pole-size trees and (b) using proportion of trees within each family whose buds have flushed on a single scoring date to rank families for mean bud-burst date. Relationships between the same bud-phenology trait at different ages, and the potential for early testing of bud phenology, are the subjects of a second paper (P. Li and W.T. Adams, in preparation).

## Materials and methods

### Pole-size trees

#### Field test design and measurements

The 60 parent trees whose open-pollinated progenies (families) were used in this study were selected in natural stands within the Noti Breeding Unit (52 000 ha, 150- to 549-m elevation) of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979), located in the central portion of the Oregon Coast Range. Between 1973 and 1976, 1-year-old seedlings of these families were planted (3.05 × 3.05 m spacing) at four test plantations within the breeding unit (Table 1). The 60 families were divided into two 30-family sets, the parent trees represented in each set coming from adjacent but not overlapping geographical areas. Each family set comprised a separate randomized complete block experiment, with four blocks in each plantation. Within each block, each family was represented by a four-tree noncontiguous plot.

Bud burst (first appearance of new needles emerged beyond the bud scales) on the terminal buds of leader shoots was scored with

binoculars in three plantations in both 1986 (weekly) and 1987 (once every three days) (Table 1). At Smith Creek in 1987, bud burst was also scored on one branch from each of seven lateral whorls (the first, second, third, fourth, fifth, seventh, and ninth down from the leader) in two of the blocks of each family set. In 1988, on all trees at Smith Creek, both bud burst and bud set (when brown bud scales are first visible) were scored twice a week on terminal buds of two opposite, fifth-whorl branches. The fifth whorl was used because its branches could be reached for direct examination from the ground. (Scoring bud set on the leader shoots of pole-size trees is not possible from the ground because needles at the leader tip block the terminal bud from view.) In all analyses, the observed dates of bud burst (or bud set) were assumed to be the actual bud-burst (or bud-set) dates. For the 1988 data, the averages of bud-set and bud-burst dates for the two fifth-whorl branches were utilized. Duration of shoot growth was calculated as the number of days between bud burst and bud set.

Fifteen-year stem height and diameter at breast height (DBH; measured at 1.37 m) of the test trees in each plantation were supplied by the plantation owners. Bole volume at 15 years was estimated from the stem-height and DBH data by using an equation for young Douglas-fir given in Adams and Joyce (1991).

#### Statistical analyses and estimation of genetic parameters

All statistical analyses were conducted using the ANOVA procedure of the SAS software program (SAS Institute Inc. 1985). Because the plantations and time intervals used for bud-burst scoring of pole-size trees differed in 1986 and 1987, the bud-burst data for each year were treated separately in the analyses. Combined analyses of variance (ANOVA) and covariance across plantations were conducted for each year using the bud-burst values for the plantations scored in that year in conjunction with the 15-year growth data (stem height, DBH, and volume) for the same plantations. A random model for plot means was employed:

$$[1] Z_{ijkl} = \mu + P_i + S_j + PS_{ij} + B_{k(i,j)} + F_{l(j)} + FP_{l(j)i} + \gamma_{jk(i)}$$

where  $Z_{ijkl}$  is the plot mean of a trait for the  $l$ th family ( $F$ ) within the  $j$ th set ( $S$ ) in the  $k$ th block ( $B$ ) in the  $i$ th plantation ( $P$ ),  $\mu$  is the experimental mean, and  $\gamma_{jk(i)}$  is the family within set  $\times$  block within plantation interaction (plot error). All effects in this model were assumed to be normally distributed. In analyzing the 1988 bud-burst and bud-set data for Smith Creek, in conjunction with the 15-year growth data for this plantation, model 1 was also employed, but with all terms that included plantation as a factor discarded. Finally, analyses were also conducted on the leader and branch bud-burst data collected at Smith Creek in 1987. Within-plot variances and covariances appropriate to the above analyses were calculated separately by pooling individual plot values (Milliken and Johnson 1984). Missing plot values were estimated separately for each family set in each plantation with methods described by Steel and Torrie (1980) and with degrees of freedom for plot error adjusted accordingly. The proportion of missing plots, however, was small (less than 1% of the total in each plantation).

The extent of genetic variation for bud-phenology traits was quantified by estimating pooled family within set variance components and testing their significance. For the purpose of statistical testing, significance in this paper refers to the 5% probability level. Individual phenotypic variances and additive genetic variances were estimated from the appropriate variance components. Because progenies in open-pollinated families are more closely related than half-sibs, the additive genetic variance was calculated as three times the family variance (Campbell 1979). Individual ( $h^2$ ) and family ( $h^2_f$ ) heritabilities and their approximate standard errors were calculated following Namkoong (1981). Genetic relationships between bud phenology and growth traits were examined by estimating phenotypic and genetic correlations (Becker 1984).

The phenotypic stability of bud-phenology traits across plantations, or across years in the same plantation, was assessed in two ways:

(i) by testing the significance of family within set  $\times$  plantation interaction variance in the same year (model 1), and (ii) by estimating genetic correlations between years or plantations. For bud burst scored in the same plantation over years, genetic correlations ( $r_A$ ) were calculated as in Becker (1984). For bud burst scored in different plantations,  $r_A$  was estimated using the following equation by Burdon (1977):

$$[2] r_A = \frac{\text{Cov}_{F12}}{\sqrt{\sigma_{F1}^2 \sigma_{F2}^2}}$$

where  $\text{Cov}_{F12}$  is the family within set covariance between plantations 1 and 2, and  $\sigma_{F1}^2$  and  $\sigma_{F2}^2$  are the family within set variances at plantations 1 and 2, respectively.  $\text{Cov}_{F12}$  was calculated by adding the sums of the cross products of family means determined separately for each family set and then dividing this total by the sum of the degrees of freedom. The family variances were estimated for each plantation by using model 1, but discarding the terms that included plantation as a factor.

The accuracy of using branch bud-burst date to predict leader bud-burst date was evaluated by estimating the relative efficiency (RE) of indirect selection for leader bud burst on the basis of branch bud burst, for both individuals and families. RE, the ratio of genetic gain expected from indirect selection to that expected from direct selection, was calculated for each of the seven lateral whorl - leader combinations for the 1987 Smith Creek data as follows (Falconer 1981):

$$[3] \text{RE} = r_A (h_X/h_Y)$$

where  $r_A$  is the genetic correlation between branch and leader bud-burst dates, and  $h_X$  and  $h_Y$  are square roots of either the individual or family heritabilities for branch and leader bud-burst dates, respectively.

To examine the efficiency of using bud-burst proportion (the proportion of trees that have flushed on a given scoring date) to rank families for bud-burst date, leader bud-burst data for each of the six plantation-year combinations (three plantations each in 1986 and 1987) were treated separately. First, we computed the proportion of trees in each family plot that had flushed on each of the scoring dates and subjected the proportions to arc-sine transformation (Steel and Torrie 1980). Then, the transformed proportions for each scoring date and the plot means of bud-burst date for each plantation-year combination were subjected to ANOVA so that family differences for these traits could be tested. When bud-burst proportion and bud-burst date both differed significantly among families, the RE of indirect family selection for leader bud-burst date based on bud-burst proportion was estimated (eq. 3). Because bud burst was scored on several dates from the beginning of bud burst until all trees had flushed, it was possible to examine the extent to which RE is a function of the overall proportion of trees in a plantation (plantation proportion, or PP) that had flushed at the time of scoring.

#### Seedling trials

Seeds from 45 of the 60 families in the field tests (21 families in one set and 24 in the other) were used to establish three seedling trials (bare root, greenhouse, and transplant), each with two replicates (Table 1).

In the bare-root trial, recent germinants were sown directly into the beds of a Washington nursery in each of two replicate years (1986 and 1987) and grown for two seasons. The experimental design was a split plot, with six blocks in 1986 and seven in 1987. Within each block, sets were whole plots and families within sets were subplots, with each family represented by a four-tree row. Spacing of seedlings was 15.2 cm between rows and 8.9 cm between trees within rows.

In the greenhouse trial, germinants were sown in 1987 in two replicate greenhouses, one in Washington and the other in Oregon, and grown for a single season. The same split plot design as in the bare-root trial was used, with six blocks in Washington and eight in Oregon. Mild water stress was utilized to promote bud set, but

TABLE 2. Analyses of variance of bud-phenology traits in pole-size trees (ages 13–16) presented as intraclass correlation coefficients, estimated means, and individual heritabilities

	Bud burst on leader shoot		Bud phenology on fifth-whorl branches (1988)		
	1986	1987	Bud burst	Bud set	Duration of shoot growth
Intraclass correlations <sup>a</sup>					
Plantations	0.114 (2)*	0.044 (2)	—	—	—
Sets	0.000 (1)	0.008 (1)	0.000 (1)	0.072 (1)*	0.064 (1)**
Plantations × sets	0.004 (2)	0.014 (2)	—	—	—
Blocks within sets within plantations	0.006 (18)*	0.011 (18)**	0.013 (6)*	0.005 (6)	0.008 (6)
Families within sets	0.214 (58)**	0.227 (56)**	0.295 (56)**	0.249 (56)**	0.052 (56)*
Plantations × families within sets	0.011 (116)	0.022 (112)*	—	—	—
Plot error	0.003 (518)	0.009 (498)	0.078 (164)	0.061 (164)	0.075 (164)
Within-plot error	0.647 (1601)	0.665 (1450)	0.614 (421)	0.612 (421)	0.800 (421)
Means					
Test	137.7	127.3	140.5	154.3	13.9
Family range	130.6–144.3	122.5–132.7	134.2–149.3	149.7–162.2	10.1–16.2
<i>h</i> <sup>2</sup> (SE)	0.73 (0.11)	0.74 (0.12)	0.90 (0.16)	0.81 (0.16)	0.17 (0.10)

NOTE: Bud burst and bud set are days after January 1 and duration of shoot growth is number of days between bud burst and bud set. See Table 1 for sources of data.

<sup>a</sup>Intraclass correlation coefficients are computed as the ratio of individual variance component estimates to the sum of all components. Degrees of freedom are in parentheses.

\*Significant at 0.05 probability level.

\*\*Significant at 0.01 probability level.

seedlings in the Washington greenhouse were exposed to the water stress more abruptly and earlier (early July) than in Oregon (late July).

The transplant trial was established from seedlings lifted from both greenhouses in November 1987. After overwintering in cold rooms, half the blocks from each greenhouse were transplanted into each of two nurseries, one in Washington (same as used for the bare-root trial) and the other in Oregon, where the seedlings grew for one additional season. One of four Oregon blocks transplanted to each nursery was subsequently deleted from the analyses because of mouse damage during overwintering; thus, each transplant replicate was left with six blocks.

Buds on leader shoots of all seedlings were scored once a week for bud set in the first and second growing seasons and twice a week for bud burst in the second growing season (Table 1). Only the first bud set of each growing season was scored (i.e., second flushing was not recorded). For the bare-root trial, second-year bud-set data was not analyzed because bud-set scoring in the second year began too late in both replicates. First- and second-year height and second-year diameter at the root collar (caliper) were also measured on all seedlings. Second-year height increment was calculated as the difference between second- and first-year heights.

Each seedling trial was analyzed according to a random model for plot means:

$$[4] Z_{ijkl} = \mu + R_i + S_j + RS_{ij} + B_{k(i)} + \alpha_{k(i)j} + F_{l(j)} + FR_{l(j)i} + \gamma_{l(j)k(i)}$$

where  $Z_{ijkl}$  is the plot mean of a trait for the  $l$ th family ( $F$ ) within the  $j$ th set ( $S$ ) in the  $k$ th block ( $B$ ) in the  $i$ th trial replicate ( $R$ ),  $\mu$  is the experimental mean,  $\alpha_{k(i)j}$  is set × block within replicate error, and  $\gamma_{l(j)k(i)}$  is the family within set × block within replicate interaction (plot error).

As with model 1, all effects were assumed to be normally distributed. Because all seedlings from two families died in the 1986 replicate of the bare-root trial, analyses of this trial were based on only 43 families. All 45 families were included in the analyses of the greenhouse and transplant trials. With the exception of the above losses of families, less than 4% of the plots in any trial were missing. All statistical analyses and genetic parameter estimation paralleled the procedures described for the pole-size trees (Li 1990).

## Results

### Genetic variation and inheritance of bud phenology traits Pole-size trees

Bud burst on the leader shoots differed significantly among families in both 1986 and 1987, and estimated heritabilities were high in both years (Table 2). All three phenology traits (bud burst, bud set, and duration of shoot growth) scored on the fifth-whorl branches in 1988 at Smith Creek, differed significantly among families; estimated heritability was high for bud burst and bud set but low for duration of shoot growth (Table 2). The estimated genetic correlation ( $r_A$ ) was strong between bud set and bud burst ( $0.96 \pm 0.02$ ) but weak between duration of shoot growth and bud burst ( $-0.34 \pm 0.24$ ) and between duration of shoot growth and bud set ( $-0.07 \pm 0.28$ ).

The plantation × family within set interaction variance for bud burst was significant in 1987 but not in 1986 (Table 2). Family × environment interaction, however, does not appear to be important because in both ANOVAs the interaction component of variance was never greater than 10% of the family component. In addition, all estimated genetic correlations between test environments were very strong for bud burst, regardless of whether the correlations were between years in the same plantation (mean 0.98, range 0.97–0.99), among different plantations in the same year (mean 0.94, range 0.87–1.05), or among different plantations in different years (mean 0.95, range 0.84–1.03) (Li 1990).

### Seedlings

In the bare-root trial, first-year bud set and second-year bud burst differed significantly among families; estimated heritability was weak for first-year bud set and moderate for second-year bud burst (Table 3). Second-year bud burst was uncorrelated with first-year bud set ( $r_A = 0.10 \pm 0.22$ ).

In the greenhouse trial, first-year bud set differed significantly between replicates (Table 3); this timing difference

reflected the earlier and more abruptly imposed water stress in the Washington greenhouse. Because of this timing difference between replicates, the bud-set data for the two greenhouses were analyzed separately as well as in combination. The estimated heritability for the Washington greenhouse was only half that for the Oregon greenhouse, and when the data were combined, heritability was lower than for either greenhouse analyzed individually (Table 3).

In the transplant trial, second-year bud burst and bud set and duration of shoot growth all varied significantly among families (Table 3). Heritability was moderate for bud burst but low for bud set and duration of shoot growth. Estimated genetic correlation between bud burst and bud set was weak ( $0.24 \pm 0.25$ ). Duration of shoot growth was correlated strongly with bud set ( $r_A = 0.87 \pm 0.07$ ) but weakly with bud burst ( $r_A = -0.26 \pm 0.24$ ).

Replicate  $\times$  family within set interaction variance was significant only for first-year bud set in the greenhouse trial and second-year bud burst in the bare-root trial (Table 3). For first-year bud set, estimated genetic correlations between replicates of the bare-root trial (1.02) and between replicates of the bare-root trial and the Oregon greenhouse trial (mean 0.85, range 0.71–1.00) were high, but they were low between the Washington greenhouse trial and all other test replicates (mean 0.46, range 0.29–0.57) (Li 1990). For second-year bud burst, estimated genetic correlations were high between replicates of the same trials and between replicates of the bare-root trial and the replicate of the Washington transplant trial (mean 0.94, range 0.90–0.97) but were lower between replicates of the bare-root trial and the Oregon replicate of the transplant trial (mean 0.78, range 0.68–0.87) (Li 1990). For second-year bud set, genetic correlations between the two replicates of the transplant trial could not be estimated because bud set did not differ significantly among families when each replicate was analyzed separately.

*Genetic relationships between phenology and growth traits Pole-size trees*

Fifteen-year growth traits (height, DBH, and bole volume) were analyzed for the two sets of plantations scored for bud burst in 1986 and 1987 and for Smith Creek alone. In all three analyses, the three growth traits differed significantly among families but were under weak genetic control; estimated  $h^2$  ranged from 0.11 to 0.21 (Li 1990). Estimated genetic correlations between bud burst and all three growth traits were positive regardless of whether bud burst was scored on the leader (1986 and 1987) or on fifth-whorl branches (1988) (Table 4). For the 1988 Smith Creek data, bud set on fifth-whorl branches was also positively correlated with all three growth traits (Table 4). Genetic correlations between duration of shoot growth on the fifth-whorl branches and all three growth traits were negative, but the standard errors were in each case larger than the estimates (Table 4). Except for duration of shoot growth, estimated phenotypic correlations between phenology and growth traits were of the same sign as genetic correlations but usually were smaller in magnitude.

*Seedlings*

First-year height differed significantly among families in bare-root and greenhouse trials but was under weak genetic control ( $h^2 \leq 0.22$ ) (Li 1990). First-year bud set was uncorrelated with first-year height in both trials (bare-root  $r_A = 0.04 \pm 0.21$ , greenhouse  $r_A = -0.03 \pm 0.39$ ). Seedling

TABLE 3. Analyses of variance of first- and second-year bud-phenology traits in seedlings presented as intraclass correlation coefficients, estimated means, and individual heritabilities

Source	Bare-root trial			Greenhouse trial (first year bud set)			Transplant trial		
	First-year bud set	Second-year bud burst	Duration of shoot growth	Individual replicates			Second-year bud burst	Second-year bud set	Duration of shoot growth
				Combined	Washington	Oregon			
Intraclass correlations <sup>a</sup>									
Replicates	0.481 (1)**	0.098 (1)**	0.796 (1)**	—	—	0.832 (1)**	0.618 (1)**	0.441 (1)**	
Blocks within replicates	0.002 (11)	0.003 (11)	0.003 (12)	0.000 (5)	0.015 (7)	0.012 (10)**	0.110 (10)**	0.017 (10)**	
Sets	0.000 (1)	0.000 (1)	0.005 (1)**	0.050 (1)	0.012 (1)	0.002 (1)	0.000 (1)	0.000 (1)	
Sets $\times$ replicates	0.002 (1)	0.000 (1)	0.000 (1)	—	—	0.001 (1)	0.014 (1)	0.015 (1)	
Sets $\times$ blocks within replicates	0.004 (11)	0.022 (11)**	0.003 (12)**	0.005 (5)	0.019 (7)	0.004 (10)**	0.027 (10)**	0.039 (10)**	
Families within sets	0.038 (41)**	0.138 (41)**	0.006 (43)**	0.049 (43)**	0.091 (43)**	0.022 (43)**	0.005 (43)*	0.007 (43)*	
Replicates $\times$ families within sets	0.002 (41)	0.039 (41)*	0.009 (43)**	—	—	0.001 (43)	0.000 (43)	0.000 (43)	
Plot error	0.084 (439)	0.087 (439)	0.014 (512)	0.069 (212)	0.077 (301)	0.002 (410)	0.000 (410)	0.000 (410)	
Within-plot error	0.385 (1192)	0.612 (1192)	0.165 (1758)	0.827 (741)	0.787 (1011)	0.124 (1130)	0.227 (1130)	0.327 (1130)	
Means									
Test	278.5	111.2	236.3	225.1	247.8	137.4	248.9	111.5	
Family range	270.9–284.7	104.3–116.9	233.4–241.6	220.2–229.0	243.5–257.7	133.3–139.8	242.2–256.0	103.3–117.7	
$h^2$ (SE)	0.22 (0.07)	0.47 (0.12)	0.09 (0.05)	0.16 (0.07)	0.30 (0.08)	0.44 (0.10)	0.07 (0.03)	0.07 (0.03)	

NOTE: Bud burst and bud set are days after January 1 and duration of shoot growth is number of days between bud burst and bud set. See Table 1 for sources of data.  
<sup>a</sup>Intraclass correlation coefficients are computed as the ratio of individual variance component estimates to the sum of all components. Degrees of freedom are in parentheses.  
 \*Significant at 0.05 probability level.  
 \*\*Significant at 0.01 probability level.

TABLE 4. Estimated genetic ( $r_A$ ) and phenotypic ( $r_P$ ) correlations between bud-phenology traits and 15-year growth traits for pole-size trees

Bud-phenology trait		Growth trait at 15 years			
		Height	DBH	Volume	
Bud-burst date					
	1986	$r_A$	0.37 (0.16)	0.01 (0.20)	0.12 (0.19)
		$r_P$	0.18 (0.03)	0.09 (0.03)	0.12 (0.03)
1987		$r_A$	0.64 (0.12)	0.46 (0.18)	0.50 (0.15)
		$r_P$	0.23 (0.03)	0.18 (0.03)	0.20 (0.03)
1988		$r_A$	0.53 (0.26)	0.34 (0.29)	0.49 (0.30)
		$r_P$	0.35 (0.04)	0.33 (0.04)	0.34 (0.04)
Bud-set date					
	1988	$r_A$	0.49 (0.27)	0.22 (0.30)	0.40 (0.27)
		$r_P$	0.34 (0.04)	0.35 (0.04)	0.37 (0.04)
Duration of shoot growth					
	1988	$r_A$	-0.25 (0.51)	-0.51 (0.54)	-0.43 (0.53)
		$r_P$	-0.02 (0.04)	0.03 (0.04)	0.03 (0.04)

NOTE: Standard errors of estimates are in parentheses. Calculations for 1986 and 1987 are based on data from three plantations, and calculations for 1988 are based on data from a single plantation (see Table 1).

growth traits at age 2 (height, height increment, and caliper) differed significantly among families in both the bare-root and transplant trials but also exhibited low heritabilities (Table 5). Genetic correlations between bud burst and growth traits in 2-year-old seedlings were weak for both the bare-root and transplant trials (Table 5). In the transplant trial, second-year bud set and duration of shoot growth were uncorrelated with caliper, but both of these phenology traits had moderate and positive genetic correlations with total height and height increment. Estimated phenotypic correlations between seedling phenology and growth traits were generally of the same sign as genetic correlations but were smaller in magnitude.

#### Alternatives for measuring bud-burst phenology

At Smith Creek in 1987, families differed significantly in bud-burst timing on both the leader and all branches. Estimated heritabilities for bud-burst date on branches were generally as high as or higher than those for bud-burst date on the leader (Table 6). For branches above the seventh whorl, genetic correlations between leader and branch bud-burst dates were very strong ( $\geq 0.91$ ), resulting in REs of indirect selection for leader bud burst based on branch bud burst greater than 1.00 for individual selection and greater than 0.98 for family selection (Table 6). RE values less than 0.90 were found only for branches on the seventh and ninth whorls, where genetic correlations between leader and branch bud burst were weaker.

In all six plantation-year data sets derived from the 1986 and 1987 measurements, bud-burst date differed significantly among families, and estimated family heritabilities were moderate (mean 0.58, range 0.54–0.62) (Li 1990). Among the six data sets, there were 24 of 28 scoring date – plantation combinations where family differences in bud-burst proportion in the plantation (PP) were significant. (In the remaining four combinations the  $PP > 0.95$  or  $PP < 0.07$ .) For these 24 combinations, REs of family selection for bud-burst date on the basis of bud-burst proportion were calculated. REs were highest (mean 0.91, range 0.84–1.00) on scoring dates with intermediate (0.25–0.75) PP values (Fig. 1). On these scoring dates, family heritabilities for bud-burst proportion were greater than 0.44, and genetic correlations between bud-burst

proportion and date were strong ( $r_A \leq -0.93$ ) (Fig. 1). RE values were generally lower at more extreme PP values, most markedly at the lower end ( $PP < 0.25$ ) and less so at the high end ( $RE > 0.80$  even when  $PP > 0.90$ ).

## Discussion

### Genetic variation and inheritance of bud phenology traits

In this study, bud-burst phenology for both pole-size trees and seedlings of coastal Douglas-fir varied significantly among families, was under moderate to strong genetic control, and showed high phenotypic stability across test environments. Strong genetic control and high stability of bud-burst timing have also been found in earlier studies both of Douglas-fir seedlings (Christophe and Birot 1979; Kaya et al. 1989) and of older trees (White et al. 1979; Birot and Christophe 1983; Bastien and Roman-Amat 1986). Thus, great potential exists in this species to genetically alter bud-burst phenology in breeding programs and thereby improve adaptability of both seedlings and pole-size trees. Particularly useful would be selection for late bud burst to reduce the risk of frost damage in areas with frequent late spring frosts (Birot 1974).

The strong genetic control of bud-burst timing in both seedlings and pole-size trees, and the moderate genetic correlation for this trait between the two growth stages (Li 1990), suggest common physiological controls. If chilling requirements are satisfied, bud burst is mainly a response to heat accumulation in the spring (Campbell 1978; Lavender 1981). In this study, chilling requirements presumably were met for both seedlings and pole-size trees; thus, bud-burst timing differences among families reflected different heat sums required for bud burst. As other studies have shown, genetic control of response to heat accumulation is strong (Nienstaedt and King 1969; Ekberg et al. 1985), so although mean temperatures and bud-burst timing varied among years for this study, the relative order of bud-burst timing among families was consistent over tests and years.

Bud set was strongly inherited in pole-size trees but only weakly inherited in seedlings (Tables 2 and 3). In addition, bud-set timing in pole-size trees appears to be only weakly

TABLE 5. Estimated individual heritabilities ( $h^2$ ) for growth traits, and genetic ( $r_A$ ) and phenotypic ( $r_P$ ) correlations between growth and bud phenology traits in 2-year-old seedlings

Bud-phenology trait		Growth trait		
		Height	Height increment	Caliper
Bare-root trial				
Bud-burst date	$h^2$	0.36 (0.10)	0.32 (0.09)	0.29 (0.08)
	$r_A$	0.19 (0.21)	0.26 (0.21)	-0.06 (0.21)
	$r_P$	0.22 (0.03)	0.16 (0.03)	0.13 (0.03)
Transplant trial				
Bud-burst date	$h^2$	0.27 (0.07)	0.19 (0.05)	0.10 (0.05)
	$r_A$	0.22 (0.19)	0.15 (0.26)	0.12 (0.20)
	$r_P$	0.14 (0.03)	0.16 (0.03)	-0.01 (0.03)
Bud-set date	$r_A$	0.77 (0.24)	0.70 (0.23)	-0.03 (0.38)
	$r_P$	0.17 (0.03)	0.21 (0.02)	0.01 (0.03)
Duration of shoot growth	$r_A$	0.64 (0.25)	0.63 (0.23)	-0.12 (0.39)
	$r_P$	0.14 (0.03)	0.21 (0.02)	-0.02 (0.03)

NOTE: Standard errors of estimates are in parentheses. Calculations are based on combined data for two replicates in each of the trials (see Table 1).

TABLE 6. Estimated mean bud-burst dates on the leader shoot and lateral branches of trees at Smith Creek in 1987; estimated individual ( $h^2$ ) and family ( $h_F^2$ ) heritabilities for these traits; genetic correlations ( $r_A$ ) between branch and leader bud burst; and relative efficiencies of individual ( $RE_I$ ) and family ( $RE_F$ ) selection for leader bud burst based on branch bud-burst dates

Position of terminal bud	Mean <sup>a</sup>	$h^2$	$h_F^2$	$r_A$	$RE_I$	$RE_F$
Leader	127.1	0.86 (0.21)	0.49 (0.07)	—	—	—
Lateral branches <sup>b</sup>						
1st whorl	127.1	1.01 (0.20)	0.54 (0.06)	0.97 (0.03)	1.05	1.02
2nd whorl	127.7	1.16 (0.20)	0.57 (0.05)	0.91 (0.04)	1.06	0.98
3rd whorl	127.5	1.15 (0.20)	0.58 (0.05)	0.93 (0.04)	1.08	1.01
4th whorl	127.9	1.07 (0.20)	0.57 (0.05)	0.94 (0.04)	1.05	1.01
5th whorl	128.0	1.02 (0.20)	0.54 (0.05)	0.93 (0.05)	1.01	0.98
7th whorl	127.0	0.97 (0.20)	0.53 (0.06)	0.83 (0.08)	0.88	0.86
9th whorl	123.1	0.70 (0.21)	0.43 (0.08)	0.66 (0.14)	0.60	0.62

NOTE: Standard errors of estimates are in parentheses.

<sup>a</sup>Days from January 1.

<sup>b</sup>Whorls numbered down from the leader shoot.

correlated with bud-set timing in seedlings (Li 1990). These results suggest that bud-set phenology at the two growth stages may in large part be controlled by different physiological mechanisms. In seedlings, much of shoot growth results from free growth (Pollard and Logan 1974; Cannell and Johnstone 1978; von Wuehlisch and Muhs 1991), which occurs in Douglas-fir with or without second flushing (Kaya et al. 1989). The extent to which free growth contributes to height increment in pole-size coastal Douglas-fir is not known although no second flushing was observed in the 14-year-old trees in Smith Creek, where bud set was scored. However, free growth contributed substantially to height increment in 15-year-old trees of some interior Douglas-fir (var. *glauca*) provenances (Bongarten 1978) and in sapling-size trees of western larch (*Larix occidentalis* Nutt.) (Joyce 1987).

Bud set had a strong and positive genetic correlation with bud burst at Smith Creek in 1988, indicating that selection for later bud burst would lead to delayed bud set in the next generation. The amount of delay can be estimated by calculating the correlated response on one trait (bud set) when

selection is applied to a correlated trait (bud burst) (Falconer 1981, Ch. 19). If 20% of the parents with the latest flushing progenies in each family set were selected and subsequently intermated in a seed orchard, bud set in their pole-size offspring would be expected to occur an average of 4 days later than in the offspring of all parents. Selection of families for later flushing in the transplant seedlings, on the other hand, is expected to have little or no impact on bud-set timing because the genetic correlation between bud burst and bud set was quite low. Other seedling studies in Douglas-fir have also found low genetic correlations between bud burst and bud set (Rehfeldt 1983; Mangold 1987), although Campbell (1986) found these traits to be moderately correlated ( $r_A = 0.52-0.60$ ) in seed sources from southwest Oregon.

#### Genetic relationships between phenology and growth traits

Although the estimated genetic correlations between bud burst and height were positive in this study, they were weak in seedlings and only moderate in pole-size trees (Tables 4 and 5). In terms of breeding, a positive relationship between

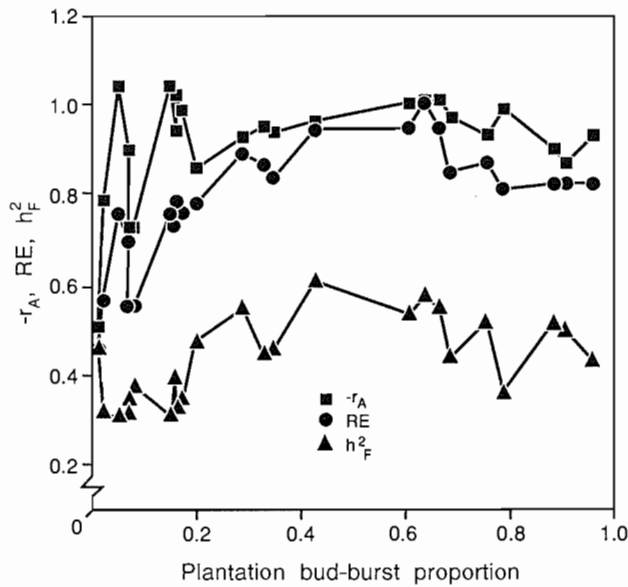


FIG. 1. Relationships of plantation bud-burst proportion (PP) to family heritability for bud-burst proportion ( $h_F^2$ ); genetic correlation between bud-burst proportion and bud-burst date ( $-r_A$ ); and relative efficiency of selecting families for bud-burst date based on bud-burst proportion (RE). Data pooled from six data sets (three plantations each in 1986 and 1987).

bud burst and growth is favorable because selection for greater growth is expected to result in a correlated response of delayed bud burst, and presumably, a reduced risk of spring frost damage. Alternatively, delaying bud burst to reduce risk of spring frost damage is not expected to reduce height growth, but, as discussed in the previous section, it may result in unfavorable bud-set delays. While most earlier studies in Douglas-fir have also found low to moderate positive genetic correlations between bud burst and height (Christophe and Birot 1979; Birot and Christophe 1983; Rehfeldt 1983; Campbell 1986; Kaya et al. 1989), some negative correlations have also been reported (Bastien and Roman-Amat 1986; Mangold 1987). Thus, it may be prudent to examine the relationship between bud burst and height growth in each breeding population separately.

Bud set was moderately and positively correlated with growth traits, in both 2-year-old seedlings and pole-size trees, especially with height (Tables 4 and 5). A positive correlation between bud set and growth in trees of either age is unfavorable because it means that selection for greater growth will result in delayed bud set. This would have greater consequences for seedlings than for pole-size trees, however. For example, selecting the top 20% of parents in each of the family sets tested in this study on the basis of total height of their progeny at age 2 (transplant seedlings) would delay bud set of the next-generation second-year seedlings by an average of 2.7 days. Selecting the top 20% of parents on 15-year height at Smith Creek, however, would delay bud set in next-generation pole-size trees by only 0.5 days. For pole-size trees, a small delay in bud set likely will have little or no impact on adaptability, because, on average, bud set occurs quite early at this age (mid-June in 1988 at Smith Creek, Table 2), well before killing frosts in the fall. Extending bud-set timing in seedlings, however, may be more serious because under favorable growing conditions, 2-year-old seedlings do

not set buds until late summer or early fall (Table 3 and Kaya et al. 1989).

In earlier seedling studies in Douglas-fir, height and bud-set timing were found to be either positively correlated, as in this study (Rehfeldt 1983; Campbell 1986; Mangold 1987; Kaya et al. 1989) or essentially uncorrelated (Mangold 1987; Kaya et al. 1989). Lack of correlation between these traits has been observed in seed sources from stressful (dry or high elevation) sites in southwest Oregon. Presumably, in stressful sites where genotypes with extended growing periods are particularly susceptible to damage from summer drought or fall frost, the height growth advantages that come with delayed bud set are cancelled out by growth losses due to damage.

#### Alternatives for measuring bud-phenology traits

Our evidence indicates that scoring bud burst on lateral branches free from shading by neighboring trees is an accurate means of ranking either individual trees or families for bud burst on the leader shoot. Furthermore, our results show that bud-burst proportion is effective for ranking families of pole-size trees for mean bud-burst date, when the proportion of trees that have flushed in a plantation is between 0.25 and 0.75. Similar analysis of the limited bud-set data for fifth-whorl branches at Smith Creek showed that bud-set proportion is effective for ranking families for bud-set timing (Li 1990). As expected, bud-burst and bud-set proportions also appear to be accurate means of ranking families for bud phenology at the seedling stage (Li 1990).

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