

## Genetic variation in cambial phenology of coastal Douglas-fir<sup>1</sup>

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The objectives of this study were to (i) determine the extent of genetic variation and genetic control of cambial phenology in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), (ii) assess the degree to which cambial phenology is genetically related to bud-burst timing, (iii) examine genetic relationships between cambial phenology and growth traits, and (iv) evaluate the potential for indirectly altering cambial phenology in breeding programs when selection is for stem volume. Dates of diameter-growth initiation and cessation, and duration of diameter growth (i.e., cambial phenology traits), as well as diameter increment for a single growing season (1987, at the age of 15 years from seed), were estimated from cumulative diameter growth curves of individual trees of 60 open-pollinated families growing in one plantation. Data on stem height and diameter (DBH), and date of bud burst in 1987 were also collected. Dates of diameter-growth initiation and cessation differed significantly among families, but had lower estimated individual heritabilities ( $\leq 0.23$ ) than date of bud burst (0.87). Weak genetic correlations between date of bud burst and dates of diameter-growth initiation and cessation (range  $-0.09$  to  $0.26$ ) indicate that timing of diameter growth cannot be reliably predicted from observations on the more easily measured bud burst. Cambial phenology traits were weakly correlated with 1987 diameter increment and moderately correlated with 15-year DBH and volume. Selection of parents in this study for stem volume at age 15 and subsequent crosses among them, would be expected to lead to earlier initiation of diameter growth in the offspring, and possibly later cessation as well. The practical implications of these indirect responses in terms of increased risk of frost damage are unclear, since projected changes are small (i.e., a few days).

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Les objectifs de cette étude visaient à (i) déterminer l'amplitude de la variation génétique et du contrôle génétique de la phénologie du cambium chez le sapin de Douglas (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), (ii) apprécier le niveau de relation entre la phénologie du cambium et le débourrement, (iii) étudier les relations génétiques entre la phénologie du cambium et les caractères de croissance et (iv) évaluer la possibilité de modifier indirectement lors de l'amélioration de cette espèce la phénologie du cambium par la sélection au niveau du volume de la tige. Les dates de début et de fin de la croissance saisonnière en diamètre (c.-à-d. les caractères de phénologie du cambium), ainsi que l'augmentation annuelle en diamètre (en 1987, alors que les arbres étaient âgés de 15 ans depuis le stade de graine) ont été estimées au sein d'une plantation à partir des courbes de croissance cumulative en diamètre chez des arbres individuels représentatifs de 60 descendance issues de pollinisation libre. Des données sur la hauteur et le diamètre (DHP) des tiges, ainsi que sur le débourrement en 1987, ont aussi été prises. Les dates de début et de fin de la croissance saisonnière en diamètre variaient significativement parmi les descendance, mais elles affichaient des valeurs d'héritabilité individuelle plus faibles ( $\leq 0,23$ ) que celle pour la date de débourrement (0,87). Des corrélations génétiques faibles entre la date de débourrement et les dates de début et de fin de la croissance saisonnière en diamètre ( $-0,09$  à  $0,26$ ) indiquaient que le début de cette dernière ne pouvait pas être prédit de façon sûre à partir des observations plus facilement mesurables de débourrement. Les caractères de phénologie du cambium étaient faiblement corrélés à la croissance en diamètre de 1987 et modérément corrélés au DHP et au volume de la tige à 15 ans. La sélection de parents pour un volume accru de la tige à 15 ans et les croisements subséquents entre ces derniers devraient résulter en un début plus hâtif de la croissance saisonnière en diamètre chez les descendants et possiblement, une fin plus tardive de cette croissance. Les conséquences pratiques de ces réponses indirectes en terme d'augmentation des risques de dommages dus aux gelées demeurent nébuleuses, puisque les changements anticipés sont de faible amplitude (c.-à-d. quelques jours).

[Traduit par la rédaction]

### Introduction

Growth in woody plants results primarily from two centers of meristematic activity: the shoot apex and the cambium (Zimmermann and Brown 1971). In trees from temperate zones, periods of meristem activity alternate with periods of dormancy, so that growing seasons of indigenous species

are closely matched to local climatic cycles (Dietrichson 1964; Lanner 1976). When nonnative sources are planted, they may initiate growth too early or become dormant too late, and thus, are susceptible to shoot and cambium damage from late spring or early fall frosts. Frost damage to cambial zones results in frost rings, incomplete lignification of xylem cells, lower wood specific gravity, and increased risk of snow breakage (Kennedy 1961; Dietrichson 1961, 1964, 1969a, 1971). The genetics of shoot phenology and the potential for altering shoot phenology traits via selection and breeding, have been studied in conifers (e.g., Eriksson et al. 1978; Skråppa 1982; Nienstaedt 1985; Rehfeldt 1985), including Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)

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(Birot and Christophe 1983; Rehfeldt 1983; Li and Adams 1993); but little is known about the genetic control of cambial phenology.

Measuring phenology of cambial activity is difficult and time consuming. The most reliable method is to microscopically examine the presence of dividing cells in the cambial zone (reviewed in Kozlowski 1971; also see Wolter 1968). Because the microscopic method is very laborious and involves destructive sampling, indirect methods have been employed to assess cambial phenology when large numbers of trees are measured. These include (i) peelability of bark strips (Priestley et al. 1933) and (ii) measurements of electrical resistance in the cambium (Davis et al. 1979). The most commonly used method, however, is to infer the timing of initiation and cessation of cambial activity from cumulative growth curves derived from periodic diameter measurements with high-precision dendrometers (Kozlowski 1971; Cattelino et al. 1986). Cambial phenology assessments by this method have two main sources of error: diurnal stem shrinkage can exceed net growth, and shrinkage caused by a severe drought can exceed total growth up to that time (Dobbs and Scott 1971; Zaerr 1971; Kozlowski 1982). Thus, the dendrometer method can only be used to approximate the timing of initiation and cessation of cambial activity in trees (Kozlowski 1971).

Studies of genetic variation in cambial phenology are few. Conifers usually have a longer period of cambial activity than deciduous trees in the same region (Reukema 1965; Kozlowski 1971). Cambial phenology varies among populations within species, with trends closely associated with geographical gradients. For example, cambial growth cessation progresses earlier as latitude of seed source increases in alpine fir (*Abies lasiocarpa* (Hook.) Nutt.), red ash (*Fraxinus pennsylvanica* Marsh.), Norway spruce (*Picea abies* (L.) Karst.), black spruce (*Picea mariana* (Mill.) B.S.P.), Scots pine (*Pinus sylvestris* L.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Dietrichson 1961, 1964, 1969a, 1969b, 1971; Worrall 1975; Santamour 1982; O'Reilly and Owens 1989). Provenances of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) from high elevations start diameter growth earlier than those from lower elevations (Daubenmire 1950). Families within populations differ significantly in timing of cambial growth cessation in Norway spruce, black spruce, and alpine fir, although the magnitude of family variation is much smaller than variation among populations (Dietrichson 1967, 1969b, 1971).

The difficulty of assessment precludes the inclusion of cambial phenology traits in typical tree breeding programs. Nevertheless, selection for faster stem growth could unintentionally result in unfavorable, correlated responses in cambial phenology. Understanding the potential for such unfavorable responses requires information on the magnitude of genetic variation and control of cambial phenology traits, as well as their genetic correlation with stem growth. Moreover, because the onset and maintenance of cambial activity depend on plant hormones transported from the actively growing shoot (Wareing 1958; Savidge and Wareing 1984; Little and Savidge 1987), strong genetic relationships between timing of bud burst and cambial growth initiation might be expected. If so, timing of bud burst might prove to be an easily measured surrogate for timing of cambial growth initiation.

In this paper, we report on the genetics of cambial phenology in young coastal Douglas-fir (*Pseudotsuga menziesii*

var. *menziesii* (Mirb.) Franco). Dates of initiation and cessation of diameter growth were estimated from cumulative diameter growth curves constructed from weekly measurements of diameter increment for 60 open-pollinated families growing in one plantation. The specific objectives were to (i) determine the extent of genetic variation and genetic control of cambial phenology traits, (ii) assess the extent to which cambial phenology traits are genetically related to bud-burst timing, (iii) examine genetic relationships between cambial phenology and stem growth, and (iv) evaluate the potential for indirectly altering cambial phenology in Douglas-fir breeding programs, when selection for stem volume is emphasized.

## Materials and methods

### Materials

The progeny test plantation measured in this study is near Eugene, Ore. (45°58'N, 123°18'W, elevation 274 m). The open-pollinated families came from individual mother trees located in nearby stands (150–450 m elevation) in the central Oregon Coast Range, and constitute part of first-generation selections in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979). The families were planted as two 30-family sets, each set comprising a separate randomized complete block experiment having four blocks, with each family represented by a four-tree noncontiguous plot in a block (spacing 3.05 × 3.05 m). The only criterion used in choosing these sets of families for sampling was that they showed good precision for revealing family differences in height at age 5. At the end of the 1987 growing season, trees were 15 years old from seed, averaging about 11 m in height and 14 cm in diameter at breast height (DBH), and the survival was 85%. Crown closure had begun, with lower branches experiencing mortality up to 3.16 m.

### Measurements

Weekly measurements of DBH were made on all trees of the 60 families in 1987, beginning March 26, before measurable diameter growth began, and ending October 16, when no further diameter growth was detected. Two tacks were inserted and glued to the bark on directly opposite sides of the main stem, with the tacks shortened so that they did not penetrate into the cambium. The distance between tacks was measured (to the nearest 0.025 mm) using a dial caliper (model M.N. 84, Mitutoyo Co., Japan) with arms extended to 15 cm so that the biggest tree could be measured. To minimize the influence of diurnal fluctuations in stem diameter owing to water loss during the day and replenishment at night, all measurements were begun at dawn and completed by 10:00. During this measurement period, no stem shrinkage was detected in individual trees. Because only two or three blocks could be measured on the same morning, it took 3 days to measure all the trees, with blocks measured in the same order each week. Because position of the live crown may influence timing of cambial growth phenology (Kozlowski 1971), the distance between the tacks and lowest live branches on each tree was recorded. The intent was to use this distance, if necessary, in covariance analyses to adjust for the effect of live crown position on cambial phenology traits.

Bud burst (first appearance of new needles emerged beyond bud scales) of the terminal bud on the leader shoot was scored once every 3 days in the spring of 1987 with the aid of binoculars (Li and Adams 1993). The observed dates of bud burst were assumed to be the actual bud-burst dates. Bud burst on the leader shoot is strongly correlated with bud burst on lateral branches (Li and Adams 1993). Stem height and DBH were also measured at the end of 1987 growing season. Bole volume was calculated from height and DBH with an equation for young Douglas-fir (Adams and Joyce 1991).

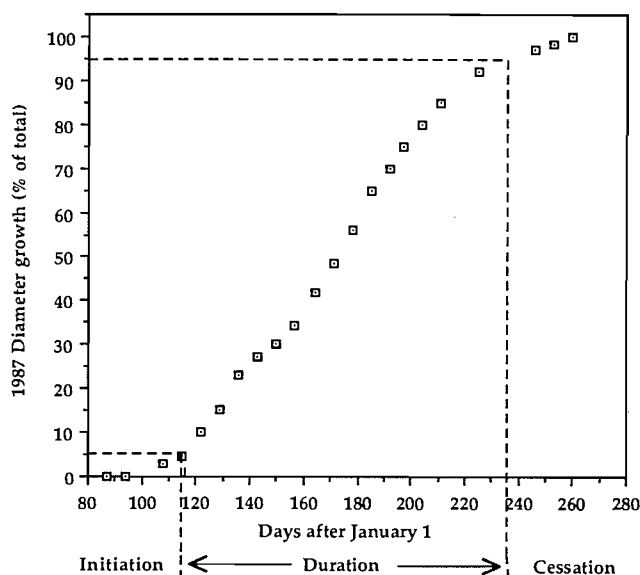


FIG. 1. An example of a cumulative diameter growth curve for an individual tree in 1987. Dates of diameter-growth initiation and cessation were defined as the dates when 5 and 95% of the cumulative growth, respectively, occurred. Duration of diameter growth was estimated as the difference between the dates of diameter-growth cessation and initiation. Data points were measured weekly.

#### Data analyses

From the weekly diameter measurements, a cumulative diameter growth curve for the 1987 growing season was plotted for each tree (Fig. 1). Dates of diameter-growth initiation and cessation were estimated by interpolation as dates when 5% and 95%, respectively, of annual growth were completed (Worrall 1970), and duration of diameter growth (in days) as the difference between dates of cessation and initiation (Fig. 1). Diameter increment was calculated as the difference between diameters when 95% and 5% of annual growth were completed. Families did not differ significantly in the distance between live crown and breast height (statistical significance refers to the 0.05 probability level in this paper). Furthermore, phenotypic correlations of this distance with dates of diameter-growth initiation and cessation were essentially zero (absolute values less than 0.1). Therefore, adjustments of cambial phenology traits for the position of live crown were not warranted.

Data on dates of diameter-growth initiation and cessation, duration of diameter growth, date of bud burst, and diameter increment in the 1987 growing season, as well as 15-year DBH and volume were analyzed with a random model:

$$[1] Z_{ijkl} = \mu + S_i + B_{j(i)} + F_{k(i)} + \gamma_{jk(i)} + \epsilon_{ijkl}$$

where  $Z_{ijkl}$  is the performance of the  $l$ th individual of the  $k$ th family ( $F$ ) in the  $j$ th block ( $B$ ) within the  $i$ th set ( $S$ ),  $\mu$  is the experimental mean,  $\gamma_{jk(i)}$  is the plot error, and  $\epsilon_{ijkl}$  is the within-plot error. The statistical analyses were based on plot means, with within-plot variances and covariances estimated by pooling individual-plot values (Milliken and Johnson 1984). Only three of a total of 240 plots were missing (i.e., a plot where all four trees had died). Values for missing plots were calculated for each family set as a randomized complete block experiment following Steel and Torrie (1980), and degrees of freedom for plot error were adjusted accordingly. The analyses were conducted by using the ANOVA procedure of the SAS statistical package (SAS Institute Inc. 1985).

The extent of genetic variation in phenology and growth traits was examined by testing the significance of the family-within-set variance. Individual phenotypic variances and additive genetic

variances were estimated from appropriate variance components. Because open-pollinated families came from mother trees in wild stands, additive genetic variance was estimated as three times the family variance component (Campbell 1979). Individual heritabilities and their standard errors were estimated following Namkoong (1981), with set and block variances not included when estimating the individual phenotypic variance (see [1]). To determine relationships between cambial phenology traits, between cambial phenology and bud-burst timing, and between cambial phenology and growth traits, phenotypic and genetic correlations and their approximate standard errors were calculated from appropriate variance components and covariance components (Becker 1984). If a trait did not differ significantly among families, genetic correlations involving this trait were not estimated. To evaluate the potential of indirectly altering cambial phenology in Douglas-fir breeding programs, expected correlated responses in cambial phenology traits due to selection of parents for 15-year volume were calculated (Falconer 1981).

## Results

### Genetic variation and inheritance of phenology traits

Mean date of diameter-growth initiation (5% criterion) was April 14 (i.e., 104 days after January 1), 23 days earlier than bud burst (Table 1). Diameter-growth cessation (95% criterion), on average, occurred on August 10, resulting in a mean duration of diameter growth of 118.5 days. Families differed significantly in dates of bud burst (range 11.6 days), diameter-growth initiation (8.6 days) and cessation (12.9 days), but not in duration of diameter growth (9.8 days; Table 1). Estimated individual heritabilities for dates of diameter-growth initiation and cessation were considerably lower than for date of bud burst (Table 1). Heritability was not estimated for duration of diameter growth because family differences were not significant (Table 1). Family differences were significant for 15-year DBH, height, and volume, but not for diameter increment (Table 1). Estimated heritabilities were low for 15-year DBH and volume.

### Relationships between phenology traits

The estimated genetic correlation between dates of diameter-growth initiation and cessation was positive (Table 2), which indicates that genotypes with early growth initiation also have a tendency to cease growth early. Duration of diameter growth did not differ significantly among families, so genetic correlations between this trait and other traits were not estimated. Growth duration had a strong phenotypic correlation with date of diameter-growth cessation, but was uncorrelated with date of diameter-growth initiation (Table 2). These results suggest that variation in growth duration among individuals is primarily a function of variation in date of growth cessation. Date of bud burst was positively, but weakly, correlated with date of diameter-growth initiation, and uncorrelated with date of growth cessation (Table 2).

### Relationships between phenology traits and stem growth

Phenotypic correlations between 1987 diameter increment and dates of growth initiation and cessation were weak, but positive (Table 3), as was found for correlations between shoot phenology traits (dates of bud burst and bud set) and total stem size in the same families (Table 3; Li and Adams 1993). However, 15-year stem growth traits had weak negative phenotypic correlations with date of diameter-growth initiation and were uncorrelated with date of cessation (Table 3). Estimated genetic correlations of 15-year growth traits with both dates of initiation and cessation were negative

and moderate in magnitude, meaning that larger trees began and ceased growth earlier in the 1987 growing season; but, the correlation estimates were accompanied by large standard errors (Table 3).

### Discussion

#### *Genetic variation in phenology of diameter growth*

The timing of diameter-growth initiation observed in this study (April 14) was at the early end of previous reports for coastal Douglas-fir (mid-April to mid-May), whereas the timing of diameter-growth cessation (August 10) was several weeks earlier than reported previously (Reukema 1965; Griffith 1968; Emmingham 1977). Lack of agreement in the timing of diameter-growth cessation could be due to differences in the populations sampled, the test locations, or the years of measurement (Emmingham 1977). The early cessation of diameter growth found in this study, however, is most likely due to the low precipitation observed during the latter part of the 1987 growing season (June to October). Compared with the 14-year average of 210 mm during this period since establishment of the test in 1974, only 96 mm fell in 1987. Although precipitation in July (76 mm) was well above average, it was only 2 mm in June (5% of average) and totaled only 18 mm from August to October (12% of average). It has been shown that cessation of cambial growth occurs earlier in dry summers (Zahner 1963; Reukema 1965). Stem shrinkage due to drought may also have contributed to the estimation of the earlier cessation dates.

Timing of diameter-growth initiation and cessation appears to be under weak genetic control in Douglas-fir (Table 1). In addition, genetic control of cambial phenology is much weaker than bud-burst timing measured in the same year (Table 1; also see Li and Adams 1993). In the only other study on genetic control of cambial phenology, timing of cambial growth cessation (as defined by relative lignification) had family heritabilities of 0.65 and 0.71 in 4-year-old seedlings of Norway spruce and black spruce, respectively (Dietrichson 1967, 1969b; individual tree heritabilities not reported). The estimated family heritabilities in our study were 0.49 for growth initiation, and 0.34 for growth cessation. Because complete lignification of the outermost xylem cells occurs only after termination of cambial cell divisions (Wardrop 1957), relative lignification may be a more precise measure of cessation of cambial activity than date of cambial growth cessation as estimated from dendrometer measurements. The extent to which an unusually dry summer may influence the expression of genetic variation in cambial phenology is unclear. Presumably, date of initiation in our study was unaffected because diameter growth began before the drought occurred. The range among families in date of diameter-growth cessation, however, may be less in dry conditions so that the estimated heritability of this trait may be somewhat less than what would be obtained in a normal (moister) growing season. Summer drought had little effect on variation in cambial growth initiation, but reduced variation in cambial growth cessation among coastal Douglas-fir provenances (Emmingham 1977).

#### *Relationships between bud and cambial phenology traits*

Timing of diameter-growth initiation and bud burst were weakly correlated in this study (Table 2), as found earlier in coastal Douglas-fir (Griffith 1968) and Norway spruce (Worrall 1970). Weak correlations between dates of bud burst and diameter-growth initiation might be unexpected

TABLE 1. Analyses of variance of growth and phenology traits presented as intraclass correlation coefficients and estimated means and individual heritabilities

	1987 Diameter growth				15-year		
	1987 bud burst <sup>d</sup>	Initiation <sup>a</sup>	Cessation <sup>a</sup>	Duration (days)	Increment (cm)	DBH (cm)	Volume (dm <sup>3</sup> )
Intraclass correlations <sup>b</sup>							
Sets (1)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0062	0.0070
Blocks within sets (6)	0.0016	0.1798**	0.2288**	0.2085**	0.0804**	0.0009	0.0138
Families within sets (58)	0.2906**	0.0620**	0.0276*	0.0212	0.0208	0.0616**	0.0704**
Plot error (171)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0753*	0.0205
Within-plot error (559)	0.7078	0.7581	0.7436	0.7703	0.8988	0.8560	0.8884
Means							
Test	126.5	104.0	222.5	118.5	1.42	5.8	93.0
Family range	121.1-132.7	101.1-109.7	217.5-230.4	114.4-124.2	1.23-1.63	12.4-18.0	58.8-120.8
$h^{2c}$	0.87 (0.04)	0.23 (0.09)	0.11 (0.07)	— <sup>d</sup>	— <sup>d</sup>	0.19 (0.09)	0.22 (0.09)

<sup>a</sup>Bud burst and diameter-growth initiation and cessation are days after January 1.

<sup>b</sup>Intraclass correlation coefficients are computed as the ratio of individual variance component estimates to the sum of all components; zero indicates a negative variance estimate. Degrees of freedom are given in parentheses.

<sup>c</sup>Standard errors are given in parentheses.

<sup>d</sup>Heritability was not estimated because families did not differ significantly ( $P > 0.05$ ) for this trait.

\*Significant at 0.05 probability level.

\*\*Significant at 0.01 probability level.

TABLE 2. Estimated genetic (above the diagonal) and phenotypic (below the diagonal) correlations among growth phenology traits

	Bud burst	Diameter growth		
		Initiation	Cessation	Duration
Bud burst	—	0.26 (0.19)	-0.09 (0.25)	-0.32 (0.28)
Diameter growth				
Initiation	0.08 (0.04)	—	0.60 (0.26)	-0.05 (0.38)
Cessation	0.02 (0.04)	0.37 (0.04)	—	0.77 (0.17)
Duration	-0.02 (0.04)	-0.08 (0.04)	0.89 (0.02)	—

NOTE: Standard errors of the estimates are given in parentheses.

TABLE 3. Estimated genetic ( $r_A$ ) and phenotypic ( $r_P$ ) correlations between phenology and growth traits

		1987 diameter-growth			1987 bud burst
		Initiation	Cessation	Duration <sup>a</sup>	
1987 growth increment <sup>a</sup>	$r_P$	0.17 (0.04)	0.38 (0.12)	0.33 (0.09)	0.10 (0.04)
15-year DBH	$r_A$	-0.35 (0.27)	-0.59 (0.37)	—	0.31 (0.22)
	$r_P$	-0.29 (0.03)	-0.03 (0.04)	0.11 (0.04)	0.12 (0.04)
Volume	$r_A$	-0.44 (0.24)	-0.54 (0.33)	—	0.42 (0.19)
	$r_P$	-0.25 (0.04)	-0.03 (0.04)	0.09 (0.04)	0.17 (0.04)

NOTE: Standard errors of the estimates in parentheses.

<sup>a</sup>The genetic correlation between this and other traits could not be estimated because families did not differ significantly ( $P > 0.05$ ) for this trait.

because initiation of cambial growth depends on hormones produced in expanding buds (Little and Savidge 1987). Apparently, hormone synthesis and transport occur much earlier than bud burst because initiation of diameter growth precedes bud burst by 2–3 weeks in this and other studies (Griffith 1968; Worrall 1970). Because bud meristematic activity occurs 4–6 weeks before bud burst in Douglas-fir (Owens 1968; Fielder and Owens 1989), earlier phenological events may be closely associated with initiation of cambial growth. For example, Emmingham (1977) found that bud swelling occurs about 1 month prior to bud burst, only a few days before cambial cell division, suggesting that bud swelling may be a good indicator of initiation of cambial activity. Nevertheless, the weak genetic relationship between date of bud burst and diameter-growth initiation indicates that timing of diameter-growth initiation cannot be reliably predicted from observations on the more easily measured bud burst.

#### Relationships between phenology and growth traits

The differences in correlations of cambial phenology traits with 1987 diameter increment versus 15-year stem growth (i.e., DBH and volume) are difficult to explain, but are likely due to the unusually low summer precipitation in 1987. Individuals with greater diameter growth in the dry summer of 1987 had a tendency to initiate diameter growth later, but were able to continue growth longer in the summer (Table 3). Cumulative stem growth over 15 years presumably is mostly a reflection of growth potential in more normal, moister growing seasons. Thus, because diameter-growth initiation occurred too early to be influenced by summer drought in 1987, the moderate negative correlations between 15-year growth traits and date of diameter-growth initiation

in 1987 indicates that individuals growing the fastest in normal years are generally those that initiate diameter growth the earliest. From this study it is not possible to determine the relationships between stem growth and timing of diameter-growth cessation in normal years, because of the presumed effect of drought on growth cessation, but it is likely positive, as was observed for height growth and date of bud set for the same families (Li and Adams 1993). Cambial growth cessation and total height were observed to have positive phenotypic correlations in black spruce and in coastal Norway spruce populations, although in other more continental Norway spruce populations, this correlation was zero and sometimes negative (Dietrichson 1967, 1969b). The negative correlation between stem size at 15 years and date of cambial cessation in 1987 suggests that families that grow best in moister years are the most sensitive to drought. Thus, a negative correlation between 15-year DBH and 1987 diameter increment might be expected. In fact, the estimated phenotypic correlation between these traits (0.48) was positive, but only moderate. Because cambial phenology was recorded in only one, apparently atypical, growing season, it is not possible to form a complete picture of the genetic and phenotypic relationships between cambial phenology and diameter-growth traits in this population of Douglas-fir.

#### Implications for breeding

Because cambial phenology traits appear to be weakly inherited and to have only weak to moderate genetic correlations with diameter growth (Tables 1 and 3), indirect responses in cambial phenology from selection of bole diameter or volume are expected to be small. For example, intermating the top 20% of parents in our study selected for greater stem volume at age 15 is predicted to produce

progenies that will commence diameter growth 0.7 days earlier, on average, than progenies of the unselected parent population. Furthermore, such selection is expected to produce progenies that will cease growth 1.3 days earlier in low-rainfall summers. Earlier growth cessation in dry years would presumably reduce the risk of damage from summer drought and early fall frost, while earlier growth initiation increases the risk of spring frost damage. If 15-year volume is positively correlated with timing of diameter-growth cessation in moist summers, selection for greater volume will extend the cambial growth period. Lengthening the growth period in moist years is of particular concern, since diameter growth may already extend to mid-September when conditions are favorable (Emmingham 1977). The adaptive and economic significance of a few days extension in growth cessation is not clear. Dietrichson (1961, 1964, 1969a, 1971) showed that late cambial cessation in conifers correlated with lower wood density, reduced stem straightness, and greater frequency of frost rings, stem snowbreakage, and winter damage on the shoot. However, this was for cases where provenances were moved from mild to severe climates, and growth cessation of moved provenances was up to more than 1 month later than more local provenances. Extensions of only 1 or 2 days when trees are grown in generally mild environments may have little or no negative impact, but this needs to be tested. In addition, because correlations between stem growth traits and cambial phenology appear weak, it should be relatively easy to select both rapid growth and the absence of damage resulting from extension of cambial growth period, as long as damage is manifested prior to the age of selection.

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