AN ABSTRACT OF THE THESIS OF

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Title: Genetic Variation in Phenology of Bud and Cambial Activity in Coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco)

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Growth phenology (i.e., timing of growth initiation and cessation) is important to adaptation. This study examined the extent of genetic control of bud and cambial phenology and their relationships with stem growth in pole-size Douglas-fir (ages 13 to 16 years) from 60 open-pollinated families. The availability of bud phenology data from two-year-old seedlings of 45 of the 60 families also made it possible to examine the potential of early testing for bud phenology. The difficulty of scoring terminal buds on leaders of large trees and the expense of multiple visits to test plantations to score budburst and budset timing, however, discourage the inclusion of these traits in breeding programs. Thus, the efficiency of two alternative methods of scoring bud phenology was explored.

The strong genetic control ($h^2 \geq 0.73$) and moderate genetic variation in dates of budburst and budset indicate that bud phenology can be readily altered in pole-size trees via selection and breeding. Early testing appears to be effective for both budburst and budset, especially for early culling of families. In both pole-size trees and seedlings, height growth had positive genetic correlations ($0.19 \leq r_A \leq 0.77$) with dates of budburst and budset, indicating that selection for greater height growth at either stage will lead to delayed budburst and

budset. Delayed budburst reduces risk of spring frost damage, whereas delayed budset increases risk due to damage from late summer drought or early fall frost, especially in seedlings which continue growth until early September.

With the exception of the lowest lateral branches, scoring budburst on branches was found to be a very efficient means to rank families and individuals for date of budburst on the leader shoot. Scoring budset on branches may not be as effective since the genetic correlation between dates of budset on branches and the leader appears only to be moderate ($r_A < 0.70$). The proportion of trees in a family which burst (or set) buds on a single scoring date was found to have a strong negative genetic correlation with mean date of family budburst (or budset). Thus, data from a single measurement date is adequate for the purpose of ranking families for bud phenology.

In contrast to bud phenology traits, the cambial phenology traits measured in this study in 1987 (i.e., dates of diameter initiation and cessation in the 15th growing season) were weakly inherited ($h^2 < 0.23$). In addition, only weak relationships were observed between diameter growth increment and diameter growth phenology, with diameter increment being more a function of growth rate rather than growth duration in 1987. The estimated genetic correlation between dates of budburst and diameter growth initiation was unexpectedly low ($r_A = 0.26$). Because cambial phenology traits were weakly correlated with diameter growth and budburst timing, selection for greater growth or delayed budburst is expected to produce little correlated response in cambial phenology.

Genetic Variation in Phenology of Bud and Cambial Activity in Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco)

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CHAPTER I

GENERAL INTRODUCTION

During the last two decades, tree breeding activities around the world have flourished. In the Pacific Northwest, coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) has been the main species under domestication. Common garden studies have revealed clinal patterns of genetic variation in Douglas-fir over geographical gradients, suggesting that this species is closely adapted to the extreme environmental heterogeneity in this mountainous region (Griffin and Ching 1977, Campbell 1979, Sorensen 1983). Thus, to minimize risk of maladaptation, many small breeding units (often less than 40,000 hectares) have been delimited, with a separate breeding program established in each unit (Silen and Wheat 1979). Because of the expense of maintaining a large number of separate breeding programs, consolidation of breeding units and development of broadly adapted genotypes are desirable. Development of broad adaptability, however, requires understanding of the genetics of adaptive traits and their relationships with traits of economic interest.

One major cause of maladaptation is the mismatch of a tree's inherent growth rhythm with the seasonal cycle of local climate (Dietrichson 1961, 1964). Growth rhythm in temperate tree species is

marked by the initiation and cessation of shoot and cambial growth during the growing season. Trees with early growth initiation may be susceptible to spring frost damage (Nienstaedt and King 1969, Christophe and Birot 1979, Rehfeldt 1979) while trees with late growth cessation, on the other hand, may be susceptible to damage from summer drought, fall frost, or winter cold (Dietrichson 1961, 1964, Griffin and Ching 1979, Rehfeldt 1983, Loopstra and Adams 1989). In milder habitats, extended growth periods are often positively associated with total stem growth, showing that stem growth and growth phenology are intimately related. The implications of genetic manipulation of growth phenology on stem growth, and vice versa, therefore, are of considerable interest to tree breeders.

Previous studies in Douglas-fir and other conifers have found that bud phenology (dates of budburst and budset) is genetically variable among populations and among individuals within populations (Dietrichson 1971, Campbell 1979, Rehfeldt 1979, Pollard and Ying 1979, White et al. 1979, Ekberg et al. 1985, Loopstra and Adams 1989), and that dates of budburst and budset are under strong genetic control (Wright 1963, Eriksson et al. 1978, Birot and Christophe 1983, Campbell 1979, Rehfeldt 1983, Mangold 1987, Kaya et al. 1989). This suggests that it is possible to improve adaptability by genetic manipulation of bud phenology via selection and breeding. This prospect may be limited by unfavorable genetic correlations between growth and phenology traits. In Douglas-fir, height growth in seedlings is positively correlated with date of budset (Campbell 1979, Rehfeldt 1983, Kaya et al. 1989, Loopstra and Adams 1989), indicating that selection for earlier budset

to reduce fall frost damage would indirectly lead to reduced height growth, while selection for greater height will result in later budset, which may cause seedlings to be prone to fall frost damage (Rehfeldt 1983). Date of budburst, however, has been found to be only weakly correlated with height growth in this species (Campbell 1986, Rehfeldt 1983, Kaya et al. 1989). Most genetic studies of bud phenology in Douglas-fir, however, have been on seedlings (less than 4 years old). There are apparently only two studies on the inheritance of budburst in trees older than 10 years (Birot and Christophe 1983, Bastien et al. 1986), but none on the genetic control of budset in older trees. Because growth patterns in older trees differ from seedlings (Jablanczy 1971, Lanner 1978), genetic control of bud phenology traits and their relationships with growth traits may not be the same at different ages. It seems particularly relevant to examine the genetics of growth phenology in 15- to 20-year old progeny tests, since it is at this age that final selections are expected to be made in Douglas-fir breeding programs (Silen and wheat 1979).

If bud phenology traits are controlled largely by the same set of genes in seedlings and older trees, early testing for phenology would be possible. Early testing can be used to shorten the testing phase of the breeding cycle and/or to provide information for the early culling of inherently poor families prior to field testing (Lambeth 1983, Talbert and Lambeth 1984). At present, there is a great deal of interest in applying early testing to growth traits (Lambeth 1983, Lowe and van Buijtenen 1989). Early testing could be applied to adaptive traits as well. Several studies in controlled environments, for

example, indicate that early testing is effective for cold hardiness, and disease and drought resistance (Talbert and Lambeth 1984, Nilsson and Eriksson 1986, Nilsson and Anderson 1987).

The inclusion of particular traits in a breeding program depends not only on their importance and degree of genetic control, but also on the ease and cost of their measurement. Scoring bud phenology on the leader shoot is difficult in older trees because of their height (i.e., long distance between the observer on the ground and the terminal bud), and because needles on the shoot tip block the terminal bud from view. To overcome these difficulties, terminal buds on branches might be scored instead, assuming that bud phenology on branches is highly correlated with that on the leader. A strong correlation between dates of budburst on the leader and the highest lateral branch was reported for 8-year-old trees in a Douglas-fir progeny test (Christophe and Birot 1979). As trees grow taller, however, the highest branches become increasingly out of reach for measurement from the ground, thus it is important to determine how well bud phenology on lower branches is correlated with that on the leader.

Determining dates of budburst and budset in individual trees or families requires frequent visits to test sites to score buds, which is tedious and time-consuming. If we are only interested in relative timing of bud phenology among genetic entries (e.g., provenances, families or clones), scoring the proportion of trees in each entry that have burst (set) bud on a single measurement date, may be adequate for selection purposes (Irgens-Moller 1958, Sweet 1965, Falkenhagen 1977, Steiner 1979, Libby et al. 1980). The accuracy of this approach for

assessing timing of bud phenology, however, has not been determined.

The extent of genetic variation and genetic control of cambial phenology has not been extensively studied because cambial phenology is extremely difficult to measure. Different species growing in the same region can differ in the timing of initiation and cessation of cambial growth (Studhalter et al. 1963, Slee 1972, Creber and Chaloner 1984). Genetic variation in cambial phenology has also been demonstrated among populations within a number of tree species (Daubenmire 1950, Klem 1957, Dietrichson 1961, Dodge 1963, Dietrichson 1971, Worrall 1975, Santamour 1982, O'Reilly and Owens 1989), including Douglas-fir (Emmingham 1977). There apparently has been only one previous report in forest trees on family variation in cambial phenology within populations. Dietrichson (1971) found that timing of cambial cessation is under strong genetic control in three conifer species(Picea abies, P. mariana, and Abies lasiocarpa), and that date of cambial growth cessation is positively correlated with diameter growth, indicating that selection for diameter growth may result in greater susceptibility to fall frost, or winter cold damage. Physiological studies (Kozlowski 1971, Little and Savidge 1987) indicate that cambial growth initiation depends on the resumption of shoot growth. Thus, a strong genetic relationship between dates of budburst and cambial initiation might be expected.

The main objectives of this study were: 1) to determine the inheritance of bud phenology traits and the relationships of these traits with stem growth in seedlings and pole-size trees of coastal Douglas-fir, 2) to evaluate alternative methods for measuring bud

phenology in seedling and field genetic tests, and 3) to determine genetic variation and control of cambial phenology, and its relationships with bud phenology and stem growth traits. This thesis is organized into five chapters, with the next three chapters addressing each of the above objectives in turn.

Chapter II examines the extent of genetic variation and control of bud phenology in seedlings and pole-size trees, and the potential for early testing of bud phenology traits. Genetic relationships between bud phenology and stem growth are also investigated, and implications of selection for increased growth on bud phenology traits are assessed.

Chapter III evaluates alternative methods of measuring bud phenology traits in progeny tests. The relative efficiency of scoring bud phenology in lateral branches is compared to scoring phenology in the leader shoot. The efficiency of ranking families for mean date of budburst or budset on the basis of the proportion of family members with budburst or budset on single measurement date, is also examined.

Chapter IV deals with genetic variation and control of cambial phenology, and the relationships between cambial phenology, bud phenology, and growth traits. This is apparently the first report on the inheritance of cambial phenology in Douglas-fir.

Finally, in Chapter V, major conclusions from this study and their implications for breeding are summarized, and the need for further research is discussed.

CHAPTER II

GENETIC CONTROL OF BUD PHENOLOGY TRAITS IN COASTAL DOUGLAS-FIR AND PROSPECTS FOR EARLY TESTING

ABSTRACT

Bud phenology is important to adaptation of forest trees. This study had three objectives: 1) to determine the extent of genetic control of bud phenology (i.e., timing of budburst and budset) in coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) in seedlings (ages 1 and 2) and in pole-size trees (ages 13 to 16 years), 2) to assess the potential for early testing of bud phenology traits, and 3) to determine genetic relationships between phenology and stem growth. We collected data on dates of budburst and budset and stem growth from sixty open-pollinated families growing in four field test plantations, and from 45 of these families growing in six nursery and greenhouse tests. Date of budburst was strongly inherited in both seedlings and pole-size trees ($h^2 \geq 0.44$), and family breeding values were stable across test sites and years, indicating this trait could be readily manipulated in breeding programs. Furthermore, moderate genetic correlations ($0.54 \leq r_A \leq 0.71$) in date of budburst between seedlings and pole-size trees means that budburst timing in older trees can be predicted fairly reliably at the seedling stage. Date of budset was found to be under strong genetic control in pole-size trees ($h^2 = 0.81$), but was weakly inherited in seedlings ($h^2 \leq 0.30$), and the genetic correlation between pole-size trees and

seedlings was weak to moderate ($0.30 \leq r_A \leq 0.55$). Thus, while inherent budset timing can readily be changed in older trees when selection is made at the same age, early testing for this trait is expected to be less effective than for budburst. Early testing, however, would be effective for identifying particularly undesirable families for either budburst or budset timing prior to outplanting field tests, and thus, for reducing the size and cost of field tests. The genetic correlations between growth and dates of budburst and budset were positive in seedlings and pole-size trees. Thus, selection for greater growth at either stage is expected to result in delayed budburst and budset, although the effect on budburst in seedlings is expected to be minimal. Other studies have shown that delayed budburst reduces risk of spring frost damage, whereas delayed budset potentially increases risk of summer drought or fall frost damage, especially in seedlings which were found in this study to continue growth into early September.

INTRODUCTION

An important facet of plant adaptation is the synchronization of growth rhythm with the seasonal weather cycle (Dietrichson 1964). Thus, bud phenology (i.e., timing of budburst and budset) is an important determinant of adaptation and growth (Ford 1984). In conifers, genetic variation in timing of budburst and budset is strongly associated with climate such that inherent growth of each seed source is closely attuned to the growing season available in the source environment (Hermann and Lavender 1968, Campbell and Sorensen 1978, Sorensen 1983, Kuser and Ching 1980, Mikola 1982, Michaud 1985).

The adaptive significance of bud phenology is revealed in provenance tests, which show that seed sources with the earliest budburst are the most susceptible to damage from spring frost (Holzer 1969, Nienstaedt and King 1969, Steiner and Wright 1974, Christophe and Birot 1979), while seed sources that set buds the latest are the most prone to damage from summer drought, fall frost, or winter cold (Campbell and Sorensen 1973, Griffin and Ching 1977, Rehfeldt 1979, White 1987, Loopstra and Adams 1989). Because of the adaptive importance of bud phenology, seed source differences in these traits are often emphasized in developing seed transfer guidelines and defining breeding zones (Campbell 1974). The potential also exists for improving the adaptability of planting stocks by manipulating bud phenology in breeding programs. To better appreciate the potential for genetic manipulation, however, the extent of genetic variation and control of bud phenology must be understood.

In Douglas-fir (Pseudotsuga menziesii) and other conifers, most studies on bud phenology have been conducted with seedlings. These studies indicate that bud phenology varies extensively among populations and especially among individuals within populations, and that dates of budburst and budset are under strong genetic control (Christophe and Birot 1979, Campbell 1986, Rehfeldt 1983, Sorensen 1983, Mangold 1987, Campbell et al. 1989, Kaya et al. 1989). Thus, great potential exists for genetic manipulation of bud phenology to improve adaptability at the seedling stage. Genetics of bud phenology in older trees, however, is poorly understood. In coastal Douglas-fir (var. menziesii), only two reports have dealt with the genetics of budburst timing in trees older than 10 years (Birot and Christophe 1983, Bastien et al. 1986), and none have dealt with the genetics of budset timing. Shoot growth patterns in conifers differ between seedlings and older trees (Jablanczy 1971, Lanner 1978). In seedlings, shoot growth results from both predetermined and free growth, but mainly from predetermined growth in older trees. Therefore, genetic control of bud phenology may be different in seedlings and older trees. Studies on the inheritance of bud phenology at ages 15 to 20 years are particularly important in coastal Douglas-fir because it is at this age that final selections are expected to be made in breeding programs (Silen and Wheat 1979).

If bud phenology is largely controlled by the same genes in seedlings and older trees, early testing for these traits would be possible. Early testing can be defined as the process by which families are selected based on their performance as seedlings grown in

nurseries, greenhouses, or growth chambers. Early testing can be used to shorten the testing phase of the breeding cycle, and thus, to improve the efficiency of tree breeding. Because genetic correlations between juvenile and mature traits are often small, the main use of early testing may be to cull poor-performing families prior to field testing so that smaller field tests can be established (Lambeth 1983, Talbert and Lambeth 1984). Early testing is effective in screening families for cold hardiness, and disease and drought resistance (Talbert and Lambeth 1984, Nilsson and Anderson 1987, Johnson and Apeland 1988), and is being used by the Western Gulf Forest Tree Improvement Program to cull families of southern pines for growth and drought resistance (Lowe and van Buijtenen 1989).

The ability to improve adaptability by altering bud phenology may be limited by the degree to which stem growth and bud phenology are genetically correlated. In Douglas-fir seedlings, for example, height is positively correlated with date of budset (Campbell 1979, Rehfeldt 1983, Loopstra and Adams 1989), indicating that selection for early budset in seedlings to reduce risk from frost damage, would result in decreased height growth. Equally important is the extent to which selection for faster stem growth affects bud phenology. If selection for increased stem growth results in an extended growing season (i.e., earlier budburst and/or delayed budset), tradeoffs between maximizing growth and maintaining adaptability need to be considered.

The objectives of this study were: 1) to determine and compare the extent of genetic variation and genetic control of bud phenology traits in seedlings and pole-size (ages 13-16 years) trees of Douglas-fir; 2)

to evaluate the potential of early testing for bud phenology; and 3) to examine genetic relationships between stem growth and bud phenology. Bud phenology and growth traits were measured on open-pollinated progenies of 60 parent trees growing in four test plantations. The potential of early testing was examined retrospectively (Lambeth 1983) by evaluating seedlings from the same parent trees in nursery and greenhouse tests, and comparing family means for bud phenological traits in seedlings with those of the same families in field test plantations.

MATERIALS AND METHODS

Field Test Designs and Measurements

The 60 parent trees whose open-pollinated progenies (families) were sampled in this study are located in the central Oregon Coast Range, and are part of 270 parent trees of the initial base population in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979, Quam 1988). These parent trees were the result of low intensity road-side selection within the breeding unit, which represents about 36,000 hectares of forest land. Between 1973 and 1976, 1-year-old seedlings from the 60 families were planted (3.05 m by 3.05 m spacing) as two 30-family sets (Sets 2 and 4) at eight test plantations within the breeding unit, four of which were measured in this study (Appendix 1). Each set of families comprises a separate randomized block experiment, with four blocks at each plantation. Within blocks, families were represented at planting by four-tree non-contiguous plots, with trees in each plot assigned to planting spots at random. All trees dying within the first two years of planting were replaced with seedlings from the same family, but replacements were not measured in this study. Excluding replacement trees, survival of originally planted trees from the two family sets at age 15 ranged from 70 to 89 percent (Appendix II.1), with the mean number of live trees per family plot being 3.1 (range 2.8 to 3.4) across the four plantations.

Date of budburst was scored from the ground using binoculars, as the date when new needles emerged beyond bud scales in the terminal bud

of the leading shoot (leader). In 1986, budburst was recorded once a week in three plantations (Clay Creek, Coyote Creek, and Oxbow, ages 14 to 15 years from seed). Because the difference in date of budburst between the earliest and latest flushing trees was only 35 days in 1986, budburst was recorded once every 3 days in 1987. Three plantations (ages 13 to 16 years) were also measured in 1987, Coyote Creek and Oxbow as in 1986, and a third plantation, Smith Creek. Clay Creek was not scored in 1987 because stand closure made scoring very difficult.

Date of budset was scored as the date when brown bud scales were first visible. Scoring budset on the leader of these large trees (about 11 m tall) was not possible from the ground, even using binoculars, because needles at the tip of the leader blocked the terminal bud from view. Furthermore, average date of budset in these plantations occurred within a month of average date of budburst, and some trees were already setting terminal buds while others had not yet flushed. Thus, in order to score budset, all trees must be visited on a regular basis throughout the growing season until budset occurs. This was not done in 1986 and 1987; thus, no data on budset are available for these two years. In 1988, both budburst and budset were scored twice a week at the Smith Creek plantation (age 14 years). Trees at Smith Creek were smaller (average height about 10 meters) than at other plantations, and all branches were still alive. Terminal buds on two opposite branches at the fifth whorl down from the leader were scored, beginning on the day the first tree flushed in this plantation and continuing until all trees had set buds. The fifth whorl was

chosen for scoring because this whorl was the highest whorl at which terminal buds could be reached for examination at eye level from the ground. In Chapter III of this dissertation it is shown that bud phenology in upper branches is strongly correlated with that on the leader. Dates of budburst and budset averaged over the two branches were used in statistical analyses. Duration of shoot growth in days was calculated as the difference between mean dates of budset and budburst.

Data on stem height (to the nearest dm) and breast height (1.37 m) diameter (DBH; to the nearest 0.25 cm) at the end of the 15th growing season were provided by the owners of the test plantations. Bole volume was calculated from height and DBH using the equation for young Douglas-fir given by Adams and Joyce (1990).

Seedling Test Designs and Measurements

The seedling tests used in this study were part of an early testing study conducted by Pacific Northwest Tree Improvement Research Cooperative (PNWTIRC) (Adams et al. 1987). In 1985, seeds were obtained from the cooperators for 45 of the 60 families grown in the field plantations. Open-pollinated seeds were recollected from 21 parent trees in Set 2 and 23 in Set 4. In addition, stored seed was available for one family in Set 4. Seeds could not be obtained from the remaining 15 parent trees because they were either no longer standing or did not produce seed in 1985. Seeds from the 45 families were used to establish three seedling tests, each with two replicates. In the first test (direct sown test), recent germinants were directly

sown into nursery beds and grown for 2 years. In the second (greenhouse test), germinants were sown into containers and grown for one season in greenhouses. In the third (transplant test), one-year-old seedlings from the second test were transplanted into nursery beds and grown for a second season.

The direct sown test was replicated in 1986 and 1987 in a Washington nursery. The experimental design for the two replicates was a split-plot with 9 blocks. Within each block, sets were whole plots, and families within sets, subplots, with each family represented by a four-tree row plot. Rows of seedlings were separated by 15.2 cm and seedlings within rows by 8.9 cm (Adams et al. 1987). Seedlings were fertilized and watered following the operational regime in this nursery, and weeding was done by hand. Due to poor survival in 3 blocks sown in 1986 and 2 blocks in 1987, only 6 and 7 blocks were included in statistical analyses, respectively. Survival across the two family sets in the blocks included in the analyses was 72% for the 1986 replicate, and 86% for the 1987 replicate.

Containerized seedlings were established in 1987 in two greenhouses (the greenhouse test), one in Washington and the other in Oregon. Germinants were sown into Ray-leach Super cell (10^3 in) plastic containers. The experimental design was the same as in the direct sown test, but with 8 blocks. Seedlings were watered and fertilized according to usual greenhouse operations, except that watering was gradually reduced in late spring so that moisture stress would not limit the expression of inherent variation in budset timing. Seedlings, however, were exposed to water stress more abruptly and

earlier in the Washington greenhouse (early July) than in Oregon (late July), resulting in more uniform budset in Washington. Because of poor emergence and survival in the Washington greenhouse, seedlings from the original 8 blocks were consolidated into 6 blocks. Seedling survival in the Oregon greenhouse and the remaining blocks in the Washington greenhouse was high (96% and 94%, respectively).

The 1-year-old seedlings from the greenhouse test were lifted in November of 1987 and stored in cold rooms during the winter. They were transplanted in late April of 1988 into two nurseries (i.e., the transplant test), one in Washington (the same as in the direct sown test) and the other in Oregon. Each nursery received three blocks of seedlings from the Washington greenhouse and 4 blocks of seedlings from the Oregon greenhouse. During winter storage, however, the terminal buds on the leader shoot in about 20% of the Oregon seedlings were eaten by mice. Fortunately, most of this damage was restricted to two blocks, one of which had been transplanted to each of the two nurseries. These two blocks were subsequently discarded in the statistical analyses, resulting in a total of 6 blocks included in each transplant nursery (i.e., 3 blocks of seedlings from each greenhouse). All mouse damaged seedlings in the remaining blocks were also deleted prior to the analyses. The proportion of undamaged, surviving seedlings in the six blocks was 74% in the Washington nursery, and 81% in the Oregon nursery.

Budset was scored once a week in the first and second growing seasons, and budburst twice a week in the second growing season by measurement crews supplied by members of the PNWTIRC, using the same

criteria as in field tests. Budset was scored when the first budset occurred (second flushing not recorded). Data for second-year budset, however, is only reported for the transplant test, since scoring of second-year budset in the direct sown test did not begin until more than 60% of the seedlings had set buds. Duration of second-year shoot growth in the transplant test (i.e., number of days) was calculated as the difference between dates of budset and budburst. In addition to the bud phenology information, growth data were available for the seedling tests. These included first-year height, second-year height, height increment and root collar diameter (caliper).

Statistical Analyses and Estimation of Genetic Parameters

Field Tests

Since the plantations and time intervals used in the budburst measurements differed in 1986 and 1987, the data for the two years were analyzed separately. Combined analyses of variance in each year (across 3 plantations) for date of budburst and growth traits were used to calculate variance components according to a random model (Table II.1) (Adams and Joyce 1990). Estimation of covariance components between any two traits followed the same form by substituting covariance components for variance components. Variance and covariance components for bud phenology and growth in the Smith Creek plantation were also calculated from the model in Table II.1, but terms including plantation as a factor were excluded.

Because of the large data sets, statistical analyses were performed on a plot mean basis, with within-plot variances and

covariances estimated by pooling individual-plot values (Milliken and Johnson 1984, p.160). Missing plot values (plots were missing when all 4 trees within a plot had died) were estimated for each set in each plantation as a randomized block design using methods described by Steel and Torrie (1980, pp. 209-213), and degrees of freedom for the error term adjusted accordingly. There were four missing plots in the 1986 data, two each in the Clay Creek and Coyote Creek plantations. One family from each of the two sets was deleted from the 1987 data because all but one tree from both families had died in the Smith Creek. Thus, only 58 families were included in the 1987 analyses. In addition, there were five missing plots in the 1987 data, two at Coyote Creek, and three at Smith Creek. Four missing plots occurred for the 1988 data at Smith Creek. All the statistical analyses were conducted by the SAS computer package (SAS Institute Inc. 1985). For the purpose of statistical testing, significance in this chapter refers to the 0.05 probability level.

The extent of variation among individuals for phenology traits (objective 1) was quantified by calculating phenotypic and genetic coefficients of variation (i.e., phenotypic and genetic standard deviations divided by the mean for each trait). Individual tree phenotypic variances and genetic (additive component) variances were estimated from the appropriate variance components (Table II.1). Because progenies in wind-pollinated families are expected to be related to a greater extent than half-sibs, the additive genetic variance was calculated as three times the family variance component (Campbell 1979). To determine the extent of genetic control of bud

phenology and stem growth traits (objective 1), individual tree heritabilities (h^2) and their approximate standard errors were calculated following Namkoong (1981). Relationships between bud phenology and growth traits (objective 3) were examined by estimating phenotypic and genetic correlations and their approximate standard errors (Becker 1984).

To further evaluate the strength of inheritance of budburst, the stability of the expression of this trait over years within the same plantation and across plantations within the same or different years was assessed. The stability over years in the same plantation was quantified by estimating genetic correlations (Becker 1984). The stability across plantations within the same year was first evaluated by testing significance of the family-by-plantation interaction variance in analyses of variance (Table II.1). Stability across plantations within the same or different years was also calculated by estimating genetic correlations for budburst between pairs of plantations (Burdon 1977). A high genetic correlation (near 1) indicates that the expression of budburst in different plantations and years represents nearly the same character determined by the same set of genes (Falconer 1981), and that family breeding values are stable over different environments (years and plantations). The genetic correlation (r_A) between plantations was estimated as,

$$r_A = \frac{Cov_{Fxy}}{/\sigma^2_{Fx}\ \sigma^2_{Fy}} \qquad (1)$$

where Cov_{Fxy} is the family covariance in date of budburst between plantations, σ^2_{Fx} is the family variance at plantation x and σ^2_{Fy} is the

family variance at plantation y (Burdon 1977). Because families were divided into two sets, a pooled estimate of covariance (Cov_{Fxy}) over the two sets was calculated by adding the sums of cross products from each of the two sets and dividing by the sum of degrees of freedom from the two sets. The family variance component (pooled over sets) was calculated for each plantation separately by using the same model as in Table II.1, but with exclusion of terms containing plantation as a factor. Standard errors of genetic correlation estimates between plantations could not be calculated since formulae for computing them are not available (Burdon 1977).

Seedling Tests

For each trait (or combination of two traits), variance (or covariance) components were calculated from a random model (Table II.2) for each of the three tests (the direct sown, greenhouse, and transplant test). Because all seedlings from two families died in the 1986 replicate of the direct sown test, analyses of this test were based on only 43 families. All 45 families were included in the analyses for the greenhouse and transplant tests. Missing plots were handled the same way as described for field tests. The direct sown test had 13 missing plots out of the total 559 plots in the two replicates, the greenhouse test had 3 missing plots out of 630, and 20 plots out of 540 plots were missing in the transplant test.

In the same fashion as in field plantations, phenotypic and genetic coefficients of variation were calculated to assess the extent of variation in seedling phenology traits, and individual tree

heritabilities and their standard errors were estimated to examine the extent of genetic control for each growth and phenology trait (objective 1). Likewise, stability of timing of budburst and budset across replicates was evaluated by testing the significance of the family-by-replicate interaction variance within the same test (Table II.2), and by calculating genetic correlations between replicates of the same or different tests according to equation 1 (objective 1). The family variance component for each replicate was calculated separately by using the same model as in Table II.2, but with the exclusion of terms containing replicate as a factor. Relationships between growth and bud phenology traits (objective 3) were determined by calculating genetic and phenotypic correlations and their standard errors.

Early Testing

The potential of early testing for dates of budburst and budset (objective 2) was first evaluated by calculating the relative efficiency (RE) of indirect selection of families for bud phenology traits expressed at the pole-size stage based on measurements made in seedlings (Falconer 1981),

$$RE = r_A \, (h_X/h_Y) \qquad (2)$$

where r_A is the genetic correlation between dates of budburst (or budset) measured in seedlings and pole-size trees, and h_X and h_Y are the square roots of family heritabilities for date of budburst (or budset) in seedlings and pole-size trees, respectively. Since only 45 families were common to seedling and field tests, combined analyses of variance for date of budburst (over 3 plantations) in 1986 and 1987, and analyses of variance for dates of budburst and budset at Smith Creek in

1988 had to be redone with only 45 families. Variance components derived from the above analyses were used to estimate family heritabilities for dates of budburst and budset (Namkoong 1981). For the purpose of early testing, each replicate of the seedling tests was intended to be adequate by itself (Adams et al. 1987). Thus, appropriate family heritability estimates had to be calculated from analyses of variance applied to each replicate, using the model in Table II, but with the exclusion of terms containing replicate as a factor. Based on the same 45 families (43 in the direct sown test), genetic correlations (equation 1) in date of budburst were calculated between each replicate of the seedling tests and field data in 1986, 1987 and 1988, and for date of budset between each seedling test replicate and the 1988 field data. The phenotypic correlations in dates of budburst and budset between each pair of seedling and field data sets were also calculated in a similar fashion, but by substituting the family variances in equation 1 by phenotypic variances among family means (Burdon 1977). In this manner, it was possible not only to test the reliability of replicates from the same or different seedling tests for early testing of budburst and budset, but also to evaluate the repeatability of early testing results for budburst when field measurements were made in different years.

The above estimate of relative efficiency (equation 2) assumes that selection of families for bud phenology traits in seedlings replaces selection at the pole-size stage. Another approach to early testing is two-stage selection: an early culling of poor-performing families at the seedling stage, followed by selection among the

remaining families in long-term field tests. Predicted genetic gains from the two-stage selection can be evaluated by assuming that two-stage selection is equivalent to simultaneous truncation selection on each of two correlated traits (Namkoong 1970). Gains expected after two stages of selection can then be compared to genetic gains expected from one-stage selection in field trials (Falconer 1981). At a fixed overall selection intensity, a tradeoff exists between the amount of culling at the seedling stage (stage 1) and the subsequent size of the field test, and the magnitude of genetic gains attained after two stages of selection. The more families culled at stage 1, the smaller the field test, but the greater the chance a good family will inadvertently be culled at stage 1, so that final genetic gains (after stage 2) will be compromised. The efficiency of two-stage family selection for bud phenology traits was investigated by evaluating final expected gains in dates of budburst and budset after two stages of selection under different levels of culling for these traits at the seedling stage, assuming a fixed final overall selection intensity.

RESULTS

Genetic Variation in Bud Phenology - Field Tests

The average date of budburst across three plantations was May 18 in 1986 (i.e., 137.7 days from January 1), and May 8 in 1987; thus, budburst, on average, occurred 10 days earlier in 1987 than in 1986 (Table II.3). In 1986, date of budburst differed significantly among plantations (Appendix 2), with trees flushing at Clay Creek (May 16) 3 days earlier than at Coyote Creek, and 4 days earlier than at Oxbow. There was no significant difference in date of budburst among plantations in 1987 (Appendix 2), but trees at Coyote Creek burst buds first (May 7), 1 day earlier than at Smith Creek, and 2 days earlier than at Oxbow. Families differed significantly in date of budburst in both years (Appendix 2), with the mean date ranging 14 days among families in 1986, and 10 days in 1987 (Table II.3). Date of budburst was under strong genetic control, with estimated individual tree heritability being 0.73 in 1986, and 0.74 in 1987.

At Smith creek in 1988, families differed significantly in mean dates of budburst and budset and growth duration on fifth whorl branches (Appendix 3). The mean date of budburst was May 21, and for budset was June 4; thus, the mean duration of shoot growth at the fifth whorl was only 14 days (Table II.3). Families ranged in mean budburst and budset date by about 2 weeks, but by only 6 days for duration of shoot growth. Estimated heritability was high for date of budburst (0.90), and date of budset (0.81), but was low for duration of shoot growth (0.17). The estimated genetic correlation (r_A) between dates of

budset and budburst was very high (r_A = 0.96±0.02). Although the estimated genetic correlation between growth duration and date of budburst was weakly negative (r_A = -0.34±0.24), it was essentially zero between growth duration and date of budset (r_A = -0.07±0.28).

The family (within set) by plantation interaction variance for date of budburst was significant in 1987, but not in 1986 (Appendix 2). Estimated genetic correlations (r_A) for date of budburst between plantations measured in the same or different years, however, were all very high (Appendix 4), regardless of whether they were between years in the same plantations (mean r_A = 0.98, range 0.97-0.99), between different plantations in the same year (mean r_A = 0.94, range 0.87-1.05), or between different plantations in different years (mean r_A = 0.95, range 0.84-1.03). These results indicate that at the pole-size stage, estimated family breeding values for date of budburst are very stable across different plantations and years.

Genetic Variation in Bud Phenology - Seedlings

In the direct sown test, mean dates of first-year budset and second-year budburst were significantly different between the two replicates (Appendix 5), with first-year budset 16 days earlier and second-year budburst 3 days earlier in the 1986 replicate than in the 1987 replicate. Families also differed significantly for the two traits (Appendix 5), with the range among family means being 14 days for first-year budset and 12 days for second-year budburst (Table II.4). Estimated individual tree heritability was relatively high

(0.47) for date of second-year budburst, but weak (0.22) for date of first-year budset. Date of second-year budburst was uncorrelated with date of first-year budset ($r_A = 0.10 \pm 0.22$).

In the greenhouse test, date of first-year budset differed significantly between the two greenhouses (Appendix 6), with the mean date of budset being 22 days earlier in the Washington greenhouse (Table II.4), reflecting the impact of the earlier and more abrupt withholding of water in the Washington greenhouse. The range among family means was 5 days less in the Washington greenhouse (9 days) than in the Oregon greenhouse (14 days). Thus, estimated heritability of first-year budset in Washington (0.16) was only one-half that found in the Oregon greenhouse (0.30). Heritability of first-year budset estimated from the combined analysis of variance across the two greenhouses was considerably lower (0.09) than that for either greenhouse analyzed individually.

In the transplant test, dates of second-year budburst and budset and shoot growth duration were significantly different between the two nurseries (Appendix 7), with second-year budburst being 10 days later, budset 37 days later, and duration of shoot growth 27 days longer in the Washington nursery than in the Oregon nursery. All three traits differed significantly among families (Appendix 7). Although the range in family means for date of budburst was less than one-half (6 days) that observed in the direct sown test, estimated individual tree heritability for this trait was nearly the same (0.44) (Table II.4). Estimated heritabilities were low (0.07) for both date of second-year budset and duration of shoot growth, with family means ranging over 14

days for both traits. The genetic correlation between dates of second-year budburst and budset was weak ($r_A = 0.24 \pm 0.25$). Duration of shoot growth was strongly correlated with date of budset ($r_A = 0.87 \pm 0.07$), but weakly correlated with date of budburst ($r_A = -0.26 \pm 0.24$).

Combined analyses of variance showed a significant family-by-greenhouse interaction variance for date of first-year budset in the greenhouse test (Appendix 6). Only second-year budburst showed a significant family-by-year interaction in the direct sown test (Appendix 5), and no traits had significant family-by-nursery interaction in the transplant test (Appendix 7).

For date of first-year budset, estimated genetic correlations between the two replicates of the direct sown test ($r_A = 1.02$) and between the direct sown test and the Oregon greenhouse (mean $r_A = 0.85$, range 0.71-1.00) were high, but were low between the Washington greenhouse and all other test replicates (mean $r_A = 0.46$, range 0.29-0.57) (Appendix 8). For date of second-year budburst, genetic correlations between replicates within the same test (i.e., between years in the direct sown test and between nurseries in the transplant test) were greater than 0.90 (mean $r_A = 0.94$, range 0.90 to 0.97) (Appendix 9). The genetic correlations were also high between the replicates of the direct sown test and replicates of the transplant test (mean $r_A = 0.86$, range 0.68-0.95). The genetic correlations between the two replicates of the direct sown test (at the Washington nursery) and the replicate of the transplant test at the Washington nursery, however, were greater (mean $r_A = 0.94$, range 0.93-0.95) than between replicates of the direct sown test and the Oregon transplant

test (mean r_A = 0.78, range 0.68-0.87) (Appendix 9). Thus, family breeding values for second-year budburst appear to be stable over different nursery test conditions. The genetic correlation in date of second-year budset between the two replicates of the transplant test could not be estimated because date of second-year budset was not significantly different among families when each replicate was analyzed separately.

Early Testing for Bud Phenology Traits

Because of moderate genetic variation and strong genetic control of bud phenology in pole-size trees, selection is expected to be quite effective in manipulating bud phenology traits. For example, if the parent trees with the latest flushing progenies are selected, and the top 20% of these parents in each set are intermated at random, the resulting progeny would be expected to flush, on average, 6.2 days later than in the previous generation, when based on the 1986 data, 4.6 days later when based on the 1987 data, and 4.5 days later when based on the 1988 data. Assuming again that the top 20% of the parents in each set are selected, genetic gains from selection for earlier budset in fifth whorl branches at Smith Creek, would be expected to be 4.3 days.

Early testing for bud phenology also appears to be promising, especially for date of budburst. Estimated genetic correlations in date of budburst between seedlings and pole-size trees (1986 and 1987 data) were moderately strong for all pairs of seedling test replicates and 1986 and 1987 field tests (mean r_A = 0.66, range across field tests

and replicates 0.61 to 0.71) (Table II.5). Estimated phenotypic correlations in date of budburst between seedlings and pole-size trees were moderate (mean = 0.55, range 0.51 to 0.61). Because estimated family heritabilities for date of budburst were comparable in seedlings and pole-size trees, estimated relative efficiencies of early selection for date of budburst were moderately high (mean RE = 0.60, range 0.55-0.66). These results indicate that selection of families for date of budburst at the seedling stage (age 2) will result in about 60 percent of genetic gain in delayed budburst expected from direct selection of families at the pole-size stage.

For the 1988 field data, genetic correlations in date of budburst between the two stages was moderately strong (mean r_A = 0.63, range 0.54-0.70), whereas the mean relative efficiency of early selection for 14-year budburst on the fifth whorl branches based on date of second-year budburst was 0.60 (range 0.54-0.65) (Table II.6). These results support the findings above. Early selection for date of budset, however, was less effective. The estimated family heritability for date of fifth whorl budset was strong (h_F^2 = 0.60), but was lower for date of first-year budset (mean h_F^2 = 0.38, range over replicates 0.27-0.54) (Table II.6). Also, estimated genetic correlations between dates of budset in seedlings and pole-size trees were only moderate (mean r_A = 0.43, range 0.30-0.55), and the estimated phenotypic correlations were even weaker (mean r_P = 0.28, range 0.22 to 0.34). Thus, the estimated relative efficiency of early selection for date of budset was only about one-half (mean RE = 0.34, range 0.20-0.43) that for date of budburst at Smith Creek in 1988. Relative efficiency of selection for

budset in pole-size trees on the basis of second-year budset could not be estimated because second-year budset was recorded too late in the direct sown test, and because families did not differ significantly in the replicates of the transplant test.

The effectiveness of two-stage selection for delayed budburst is illustrated in Figure II.1. This example is based on genetic parameters for date of second-year budburst in the Oregon transplant test and 1987 budburst in pole-size trees (all other pair-wise comparisons between seedling and field tests gave similar results). The final culling level was assumed to be 0.80 (i.e., 20% of parents selected). The figure shows the final gains expected after two stages of selection, given different levels of culling (from 0.0 to 0.8) at the seedling stage (stage 1). If all culling is done at the pole-size stage (i.e., culling level 0.0 at the seedling stage), expected genetic gain in delayed budburst is 4.6 days. If all culling is done at the seedling stage (i.e., culling level 0.80 at the seedling stage), the expected genetic gain is 3.0 days. From Figure II.1, it is apparent that 40% to 60% of the parents (families) could be culled at stage 1 with little or no loss of genetic gains in delayed budburst in all selections were delayed to age 15.

Although early selection for date of budset was not as efficient as that for date of budburst, two-stage selection may still be viable for improving timing of budset. Based on genetic parameters in the 1986 direct sown test and 1988 budset data at Smith creek, up to 50 percent of families could be culled at the seedling stage, while still obtaining 90% of the gains expected if all selections had been based on

pole-size trees (Figure II.2). All other pair-wise comparisons between the 1988 budset data at Smith Creek and first-year budset data in seedling tests produced similar results.

Genetic Relationships Between Phenology and Growth Traits

In field tests, 15-year height, DBH and volume showed significant family differences, but were under weak genetic control ($h^2 \leq 0.21$) (Table II.7). Estimated genetic correlations were positive between date of budburst and all three growth traits, but were strongest with 15-year height ($0.37 \leq r_A \leq 0.64$). Date of budset in fifth whorl branches was also positively correlated with all three growth traits ($0.22 \leq r_A \leq 0.49$). Phenotypic correlations between phenology and growth traits were smaller in magnitude than genetic correlations. These results indicate that selection for increased 15-year volume will lead to delayed budburst and budset. The genetic correlations between growth duration at the fifth whorl and all growth traits were negative, but the standard errors in each case were larger than the estimates.

First-year height differed significantly among families in the direct sown and greenhouse tests, but was under weak genetic control ($h^2 \leq 0.22$). Date of first-year budset was uncorrelated with first-year height in both the direct sown ($r_A = 0.04 \pm 0.21$) and greenhouse tests ($r_A = -0.03 \pm 0.39$). Total seedling height, height increment and caliper at age 2 differed significantly among families in the direct-sown and transplant tests, and were under weak to moderate genetic control ($h^2 \leq 0.36$) (Table II.8). Date of second-year budburst was weakly correlated with total height and height increment ($r_A \leq 0.26$).

In the transplant test, second-year budset and growth duration were strongly correlated with total height and height increment ($0.64 \leq r_A \leq 0.77$), but were uncorrelated with caliper (Table II.8). Phenotypic correlations between phenology and growth traits were generally smaller in magnitude. These results indicate that selection for total height at age 2 would have little, if any, effect on second-year budburst, but would lead to prolonged growth duration through delayed budset.

DISCUSSION AND CONCLUSIONS

Genetic Variation and Inheritance of Bud Phenology Traits

This study found that date of budburst varies among families, is under strong genetic control, and is stable across test environments in both seedlings and pole-size trees of Douglas-fir. There is also a moderately strong genetic correlation in date of budburst between seedlings and pole-size trees (mean over all pairwise combinations = 0.66) (Table II.5), indicating that this trait is in large part controlled by the same set of genes in the two age classes. Strong genetic control and high stability of budburst timing were also found in earlier seedling studies of Douglas-fir (Christophe and Birot 1979, Campbell 1986, Kaya et al. 1989), and in older trees of Douglas-fir and other conifers (Wilkinson 1977, White et al. 1979, Birot and Christophe 1983, Bastien and Roman-Amat 1986, Bongarten and Hanover 1986).

The strong genetic control of budburst timing in both seedlings and older trees reflects a common physiological control. If the chilling requirement is satisfied, budburst is mainly a response to heat accumulation in the spring (Campbell 1978, Lavender 1981). In this study, the chilling requirement was presumably met in seedlings and in pole-size trees, thus, differences in timing of budburst among families reflect differences in their heat sum required for budburst. Apparently, the genetic control of the heat sum requirement is strong (Nienstaedt and King 1969, Ekberg et al. 1985), so while mean temperatures varied and mean date of budburst changed between years, relative order of budburst timing among families was consistent among

tests and from one year to another.

Compared to the results for date of budburst, budset timing in pole-sized trees was only weakly correlated with date of first-year budset in seedlings (mean $r_A = 0.43$) (Table II.6). Furthermore, while date of budset was strongly inherited in pole-size trees ($h^2 = 0.81$), it was weakly inherited in seedlings (h_2 ranged from 0.07 to 0.30). The weaker genetic control of budset in seedlings and the lack of a strong relationship in budset timing between the two stages, is probably due to differences in the physiological control of budset at the two stages. In seedlings, much of shoot growth is due to free growth, which occurs in Douglas-fir with or without second flushing (Kaya et al. 1989). Shoot growth in older trees is primarily predetermined (Jablanczy 1971, Lanner 1978). No second flushing was observed at Smith Creek, suggesting that little or no free growth occurred in these 14-year-old trees.

Heritability estimates for date of budset in seedlings were lower than previously reported for Douglas-fir (Campbell 1986, Rehfeldt 1983, Mangold 1987, Kaya et al. 1989, Loopstra 1984). Date of budset in this study was recorded as the date when the first terminal buds appeared, but in previous studies was recorded as the date of final budset, after all multiple flushing. Although not recorded, multiple flushing was observed in the direct sown and transplant tests, but not in the greenhouse test. Since the propensity for multiple flushing differs among families and is highly correlated with final budset (Rehfeldt 1983, Campbell 1986), heritability estimates for budset timing recorded after multiple flushing are expected to be higher than for budset as

recorded in this study. The estimated heritability for date of first-year budset was particularly low in the Washington greenhouse. This is most likely due to the early and abrupt withholding of water in the Washington greenhouse, which suppressed free growth, and thus, genetic differences in date of budset among families (Table II.4). The suppressed free growth in the Washington greenhouse could also explain why genetic correlations in date of first-year budset between this greenhouse and other nursery tests are low.

Duration of shoot growth was under weak genetic control in both 2-year-old seedlings and pole-size trees ($h_2 \leq 0.17$), but mean growth duration was much longer in the seedlings (112 days) than in pole-size trees (14 days for fifth whorl branches, and 30 days for the leader shoot based on a subsample of 53 trees at Smith Creek in 1988). In seedlings, the propensity for free growth under favorable conditions leads to extended shoot growth periods. Thus, seedlings are presumably more susceptible to potential damage due to fall frost than pole-size trees. Because date of budset in fifth whorl branches had a strong positive genetic correlation with date of budburst ($r_A = 0.96$), and essentially no correlation with shoot growth duration ($r_A = -0.07$), selection for later budburst will indirectly delay budset, with little effect on the growth duration in pole-size trees. For example, progenies resulting from intermating of the top 20% of parents selected for later budburst would be expected to set buds 4 days later, with growth duration reduced by only 0.4 day.

Early Testing for Bud Phenology

The ability to delay budburst timing is particularly important in areas where late spring frosts are a frequent occurrence (Birot 1974, Wheeler et al. 1990), whereas the ability to advance date of budset is important in areas where fall frosts occur early. The strong genetic control and moderate genetic variation for both dates of budburst and budset in both seedlings and pole-size trees indicate that both traits could be readily altered at either stage via selection and breeding in Douglas-fir. In addition, breeding for bud phenology in pole-size trees can be further aided by early testing. Early testing may be used in two ways: 1) to reduce the generation interval through early selection, and 2) to serve as an early culling device to reduce size of long-term field tests (two-stage selection). Based on the results of this study, early testing for both purposes would be more effective for budburst timing than for timing of budset. This is especially true for early selection, where the estimated relative efficiency of early testing for delayed budburst (RE = 0.60) was nearly twice that for advancing budset. Nevertheless, two stage-selection appears quite promising for both traits. The results showed that 40% to 50% of families could be culled for either trait at the seedling stage with little loss in the genetic gains expected if all selections were delayed to age 15. The ability to cull families at the seedling stage means that smaller and more efficient field tests can be carried out, resulting in considerable savings in cost associated with establishing, maintaining and measuring these tests.

Genetic Relationships Between Phenology and Growth Traits

The genetic correlation between date of budburst and height was found to be positive, but weak in seedlings (mean r_A = 0.21) and moderate in pole-size trees (mean r_A = 0.51) (Tables II.7 and II.8). Similar results were observed in earlier studies of seedlings and older trees in Douglas-fir and other conifers (Wilkinson 1977, Christophe and Birot 1979, Birot and Christophe 1983, Rehfeldt 1983, Ekberg et al. 1985, Bongarten and Hanover 1986, Campbell 1986). This generalization could not extended to all populations. For example, in two-year-old Douglas-fir seedlings in southwest Oregon, Mangold (1987) found that date of budburst was negatively correlated with height in low-elevation (r_A = -0.17±0.27) and high-elevation (r_A = -0.50±0.23) populations. In southwest Oregon, where the growing season is restricted by summer drought at low elevations, and by cold at high elevations, trees with early budburst will presumably better utilize the growing season and grow more than trees with late budburst (Campbell and Sugano 1979). For breeding purposes, the positive relationship between date of budburst and growth is favorable because selection for greater growth is expected to result in the correlated response of delayed budburst, and presumably, reduced risk to spring frost damage. For example, based on data in this study, offspring from intermating the top 20% of the parents selected for greater height growth would be expected to flush 0.68 day later in two-year-old seedlings (when based on the direct sown test; 0.45 day later when based on the transplant test), and 1.8 days later in pole-size trees (when the 1986 data is utilized; 2.2 days later when the 1987 data is used).

Date of budset in this study was also positively correlated with growth traits in seedlings (second-year) and pole-size trees. This supports the results from an 8-year Picea sitchensis provenance-progeny test (Birot and Christophe 1983). Other seedling studies in Douglas-fir have reported similar relationships between date of second-year budset and growth traits (Rehfeldt 1983, Campbell 1986, Campbell et al. 1989, Kaya et al. 1989). In 2-year-old Douglas-fir seedlings in southwest Oregon, however, Mangold (1987) found positive genetic correlations between height and budset timing only in populations originating from middle elevations (915 m, $r_A = 0.59 \pm 0.28$), not in populations from low (610 m, $r_A = -0.01 \pm 0.37$) or high elevations (1220 m, $r_A = 0.01 \pm 0.27$). The weak genetic correlations between budset timing and growth in the low and high elevation populations are probably due to strong selection pressures to set buds prior to damage from summer drought at low elevations, and prior to frost damage at high elevations (Mangold 1987). At middle elevations where most parent trees used in this study originate, selection pressure for budset timing is presumably low, so that greater height growth is associated with later budset.

The positive genetic correlation between budset timing and growth is unfavorable for breeding since selection for greater growth will result in delayed budset in seedlings and pole-size trees. For example, if the tallest 20% of the families in the two measured in this study were randomly mated, their progeny would be expected to set bud 2.7 days later, on average, at age 2, and 0.5 day later in pole-size trees. A small delay in budset is likely to have little or no impact

on adaptability of pole-size trees, since mean date of budset seems to occur quite early at this stage (mid-June in 1988 at Smith Creek), far before low killing temperatures occur in the fall. Extension of budset timing in seedlings, however, may have more serious implications for adaptability because under favorable growing conditions, two-year-old seedlings do not set buds until late summer (early September) or early fall (Kaya et al. 1989). Because the particularly favorable growing conditions in nurseries encourage free growth in seedling tests and extended growing periods, it is of interest to determine whether seedlings continue to grow as long after field planting, where growing conditions are not as favorable. If budset occurs late in the growing season and is positively correlated with growth in field-grown seedlings, budset timing will need to be carefully considered in breeding programs. Presumably, as the propensity for free growth decreases with age, potential for fall frost damage decreases.

Table II.1. Form of analyses of variance of bud phenology and growth traits in pole-size trees in 1986 and 1987.[a]

Source of Variation	Degrees[b] of Freedom	Expected Mean Squares[c]
Plantations	p-1	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(s)P} + f\sigma^2_{B(SP)} + fb\sigma^2_{SP} + fbs\sigma^2_P$
Sets	s-1	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(s)p} + bp\sigma^2_{F(S)} + f\sigma^2_{B(SP)} + fb\sigma^2_{SP} + fbp\sigma^2_S$
Sets x Plantations	(s-1)(p-1)	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(s)P} + f\sigma^2_{B(SP)} + fb\sigma^2_{SP}$
Blocks (Sets X Plantations)	(b-1)sp	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{B(SP)}$
Families(Sets)	(f-1)s	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(s)p} + bp\sigma^2_{F(S)}$
Families(Sets) x Plantations	(f-1)(p-1)s	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(s)P}$
Plot error	(f-1)(b-1)sp	$\sigma^2_W/k + \sigma^2_E$
Within-plot error	$\sum_{i=1}^{t}(n_i-1)$	σ^2_W

[a] Replace expected mean squares with expected mean cross-products for estimating covariance components.

[b] p = number of plantations,
s = number of sets,
b = number of blocks within each set,
f = number of families within each set,
n_i = number of individuals within the i^{th} plot, and
t = number of plots.

Table II.1. (Continued)

[c] k = harmonic mean number of individuals per plot,

σ^2_W - Within-plot variance,

σ^2_E - plot variance,

$\sigma^2_{F(s)p}$ - family (within sets) by plantations interaction variance,

$\sigma^2_{F(S)}$ - family (within sets) variance,

$\sigma^2_{B(SP)}$ - block (within sets by plantations) variance,

σ^2_{SP} - set by plantation interaction variance,

σ^2_S - set variance, and

σ^2_P - plantation variance.

Table II.2. Form of analyses of variance of bud phenology and growth traits in replicate[a] seedling tests.[b]

Source of Variation	Degrees[c] of freedom	Expected Mean Squares[d]
Replicates	r-1	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)R} + f\sigma^2_{SB(R)} + bf\sigma^2_{SR} + fs\sigma^2_{B(R)} + bfs\sigma^2_R$
Blocks(Replicates)	$\sum_{i=1}^{2}(b_i-1)r$	$\sigma^2_W/k + \sigma^2_E + f\sigma^2_{SB(R)} + fs\sigma^2_{B(R)}$
Sets	s-1	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)R} + br\sigma^2_{F(S)} + f\sigma^2_{SB(R)} + bf\sigma^2_{SR} + brf\sigma^2_S$
Sets x Replicates	(s-1)(r-1)	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)R} + f\sigma^2_{SB(R)} + bf\sigma^2_{SR}$
Sets x Blocks(Replicates)	$\sum_{i=1}^{2}(s-1)(b_i-1)r$	$\sigma^2_W/k + \sigma^2_E + f\sigma^2_{SB(R)}$
Families(Sets)	$\sum_{j=1}^{2}(f_j-1)$	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)R} + br\sigma^2_{F(S)}$
Families(Sets) x Replicates	$\sum_{j=1}^{2}(f_j-1)(r-1)s$	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)R}$
Plot error	$\sum_{i=1}^{2}\sum_{j=1}^{2}(f_j-1)(b_i-1)sr$	$\sigma^2_W/k + \sigma^2_E$
Within plot error	$\sum_{k=1}^{t}(n_k-1)$	σ^2_W

[a] Replicates were different years in the direct sown test, different greenhouses in the greenhouse test and different nurseries in the transplant test.

Table II.2. (continued)

[b] The expected values of mean squares were derived according to Searle (1971, pp. 393-394). Replace expected mean squares by expected mean cross-products for estimating covariance components.

[c] r = number of replicates,

b_i = number of blocks within the i^{th} replicate,

s = number of sets,

f_j = number of families within the j^{th} set,

n_k = number of individuals within the k^{th} plot, and t = number of plots.

[d] k = harmonic mean number of seedlings per plot,

b = harmonic mean number of blocks per replicate,

f = harmonic mean number of families per set,

σ^2_W - within-plot variance,

σ^2_E - plot variance,

$\sigma^2_{F(S)R}$ - family (within sets) by replicate variance,

$\sigma^2_{F(S)}$ - family (within sets) variance,

$\sigma^2_{SB(R)}$ - set by block (within replicates) variance,

σ^2_{SR} - set by replicate variance,

σ^2_S - set variance,

$\sigma^2_{B(R)}$ - block (within replicates) variance, and σ^2_R - replicate variance.

Table II.3. Estimated test means, individual tree heritabilities (h^2) and coefficients of variation for bud phenology traits in pole-size trees (age 14 to 16 years).

Traits	Mean[a]	h^2 [b]	Coefficient of variation	
			Phenotypic	Genetic
Date of budburst on leader shoot[c]				
1986	137.7 (130.6-144.3)	0.73(0.11)	4.34	3.72
1987	127.3 (122.5-132.7)	0.74(0.12)	3.24	2.78
Bud phenology on 5th whorl branch[d]				
Date of budburst	140.5 (134.2-149.3)	0.90(0.16)	3.30	3.12
Date of budset	154.3 (149.7-162.2)	0.81(0.16)	2.98	2.68
Duration in[e] shoot growth	13.9 (10.1-16.2)	0.17(0.10)	20.83	8.58

[a] Range over 60 families in parentheses.

[b] Standard error in parentheses.

[c] Budburst in days from January 1 for terminal bud on leader shoot, measured in each of three plantations in both 1986 and 1987.

[d] Mean dates of budburst and budset in days from January 1 for the terminal bud of two branches on the fifth whorl down from the leader.

[e] Date of budset minus date of budburst (in days).

Table II.4. Estimated test means, individual tree heritabilities (h^2) and coefficients of variation for bud phenology traits[a] in seedlings.

Test Type	Mean[b]	h^2 [c]	Coefficient of variation	
			Phenotypic	Genetic
Direct sown test[d]				
First-year budset	278.5 (270.9-284.7)	0.22(0.07)	4.14	1.96
Second-year budburst	111.2 (104.3-116.9)	0.47(0.12)	5.72	3.93
Greenhouse test - First-year Budset				
Washington	225.1 (220.2-229.0)	0.16(0.07)	2.16	0.85
Oregon	247.8 (243.5-257.7)	0.30(0.08)	3.82	2.09
Combined[d]	236.3 (233.4-241.6)	0.09(0.05)	3.32	0.98
Transplant test[d]				
Second-year budburst	137.4 (133.3-139.8)	0.44(0.10)	2.27	1.50
Second-year budset	248.9 (242.2-256.0)	0.07(0.03)	6.28	1.63
Duration in shoot growth	111.5 (103.3-117.7)	0.07(0.03)	14.22	3.69

[a] Dates (days from January 1) of budset (first and second year) and budburst (second year) for the terminal bud of leader shoot, and duration of growth in the second year (date of budset minus date of budburst, in days).

[b] Range over family means in parentheses.

[c] Standard error in parentheses.

[d] Based on pooled data from two replicates.

Table II.5. Estimated family heritabilities (h_F^2)[a] for date of budburst measured in field and seedling tests, genetic (r_A) and phenotypic (r_P) correlations in date of budburst between seedlings and pole-size trees, and relative efficiency (RE) of selecting families for budburst in pole-size trees based on measurements made in seedlings.

		Field Tests							
Seedling tests		1986				1987			
Test/Replicate	h_F^2	h_F^2	r_A	r_P[b]	RE	h_F^2	r_A	r_P[b]	RE
Direct sown									
1986	0.60(0.04)	0.69(0.02)	0.66	0.56	0.62	0.68(0.02)	0.66	0.57	0.62
1987	0.60(0.04)	0.69(0.02)	0.71	0.61	0.66	0.68(0.02)	0.61	0.52	0.57
Transplant									
Oregon	0.51(0.04)	0.69(0.02)	0.64	0.50	0.55	0.68(0.02)	0.66	0.51	0.57
Washington	0.58(0.04)	0.69(0.02)	0.66	0.55	0.60	0.68(0.02)	0.66	0.55	0.61

[a] Standard errors in parentheses.

[b] Correlations between family means in seedlings and pole-size trees.

Table II.6. Estimated family heritabilities (h_F^2)[a] for dates of first-year budset and second-year budburst in seedling tests, genetic (r_A) and phenotypic (r_P) correlations between dates of budset and budburst in fifth whorl branches of pole-size trees at Smith Creek and in seedlings, and relative efficiency (RE) of selecting families for bud phenology traits in pole-size trees based on measurements made in seedlings.

Test/Replicate	h_F^2	r_A	r_P[b]	RE
	Date of first-year budset[c]			
Direct sown test				
1986	0.37(0.09)	0.55	0.34	0.43
1987	0.27(0.11)	0.30	0.22	0.20
Greenhouse test				
Oregon	0.54(0.05)	0.38	0.28	0.36
Washington	0.37(0.09)	0.48	0.29	0.38
	Date of second-year budburst[d]			
Direct sown test				
1986	0.61(0.03)	0.64	0.52	0.64
1987	0.61(0.03)	0.54	0.43	0.54
Transplant test				
Washington	0.51(0.06)	0.70	0.50	0.65
Oregon	0.58(0.04)	0.63	0.49	0.62

[a] Standard errors in parentheses.

[b] Correlations between family means in seedlings and pole-size trees.

[c] Estimated family heritability for date of budset at Smith Creek in 1988 was 0.58 ± 0.04 based on 43 families common to the direct sown seedling test, and 0.57 ± 0.05 based on 45 families common to the greenhouse test.

[d] Estimated family heritability for date of budburst at Smith Creek in 1988 was 0.61 ± 0.03 based on 43 families common to the direct sown seedling test, and 0.60 ± 0.03 based on 45 families common to the transplant test.

Table II.7. Estimated individual tree heritabilities (h^2) for 15-year height, DBH and bole volume, and genetic (r_A) and phenotypic (r_P) correlations between bud phenology and growth traits in field tests.[a]

Bud phenology traits		15-year[b] Height	DBH	Volume
		1986 data[c]		
	h^2	0.17(0.05)	0.12(0.05)	0.13(0.05)
Date of budburst	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 data[d]		
	h^2	0.21(0.06)	0.11(0.04)	0.14(0.05)
Date of budburst	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 data[e]		
	h^2	0.14(0.11)	0.12(0.10)	0.13(0.10)
Date of budburst	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)
Date of budset	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)
Growth duration	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)

[a] Standard errors of estimated genetic parameters in parentheses.

[b] Families differed significantly in 15-year height, DBH, and bole volume in all test sites.

[c] Sixty families in three plantations: Clay Creek, Coyote Creek and Oxbow.

[d] Fifty-eight families in three plantations: Smith Creek, Coyote Creek and Oxbow.

[e] Fifty-eight families at a single plantation (Smith Creek).

Table II.8. Estimated individual tree heritabilities (h^2) for 2-year growth traits, and genetic (r_A) and phenotypic (r_P) correlations between 2-year bud phenology and growth traits in seedling tests[a]

Bud phenology traits		Second-year[b] Height	Height increment	Caliper
		Direct sown test		
	h^2	0.36(0.10)	0.32(0.09)	0.29(0.08)
Second-year budburst	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 test		
	h^2	0.27(0.07)	0.19(0.05)	0.10(0.05)
Second-year budburst	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)
Second-year budset	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)
Growth duration	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)

[a] Standard errors of estimated genetic parameters in parentheses.

[b] Families differed significantly for 2-year height, height increment, and caliper.

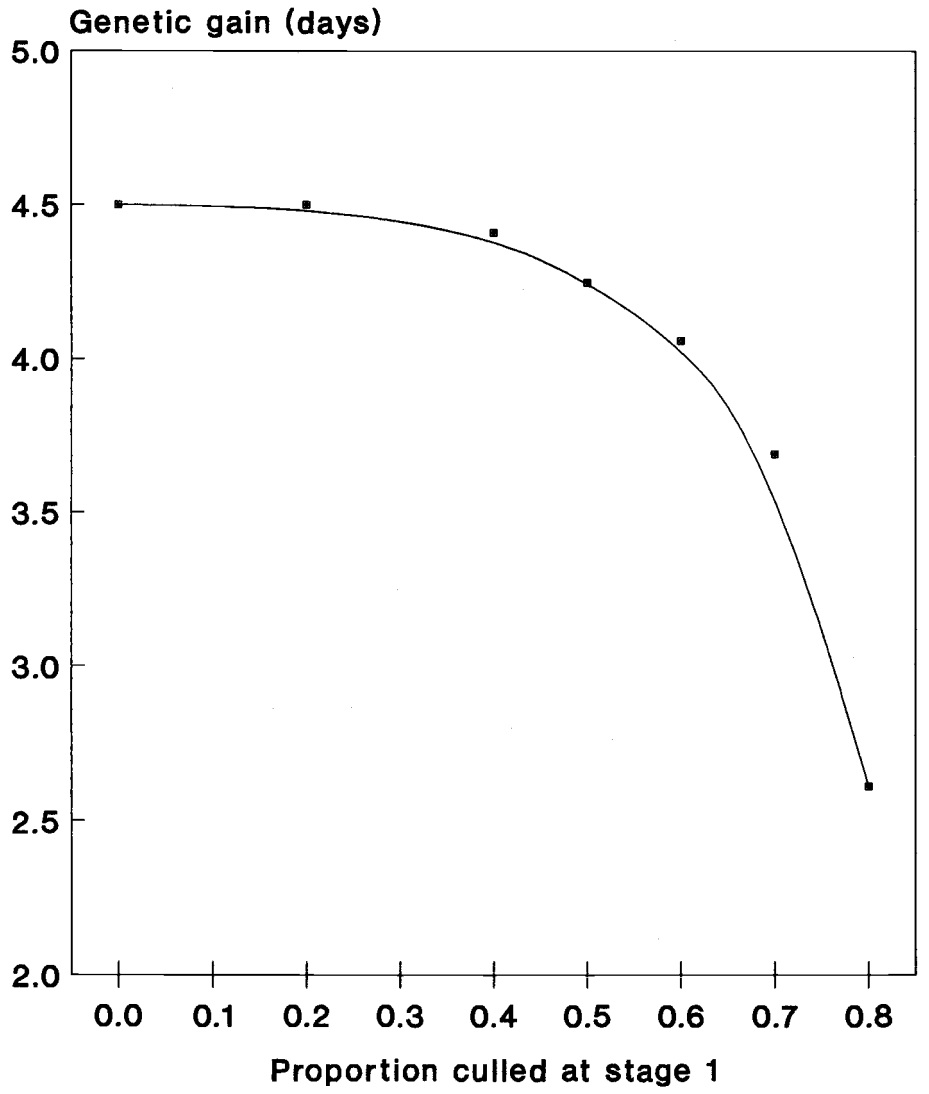

Figure II.1. Example of expected genetic gains in date of budburst of pole-size (age 14-16 years) trees after two stages of family selection. Selection in the first stage is based on budburst in nursery tests (age 2). The estimated phenotypic correlation between family means for budburst date in seedlings and pole-size trees in this example is 0.52.

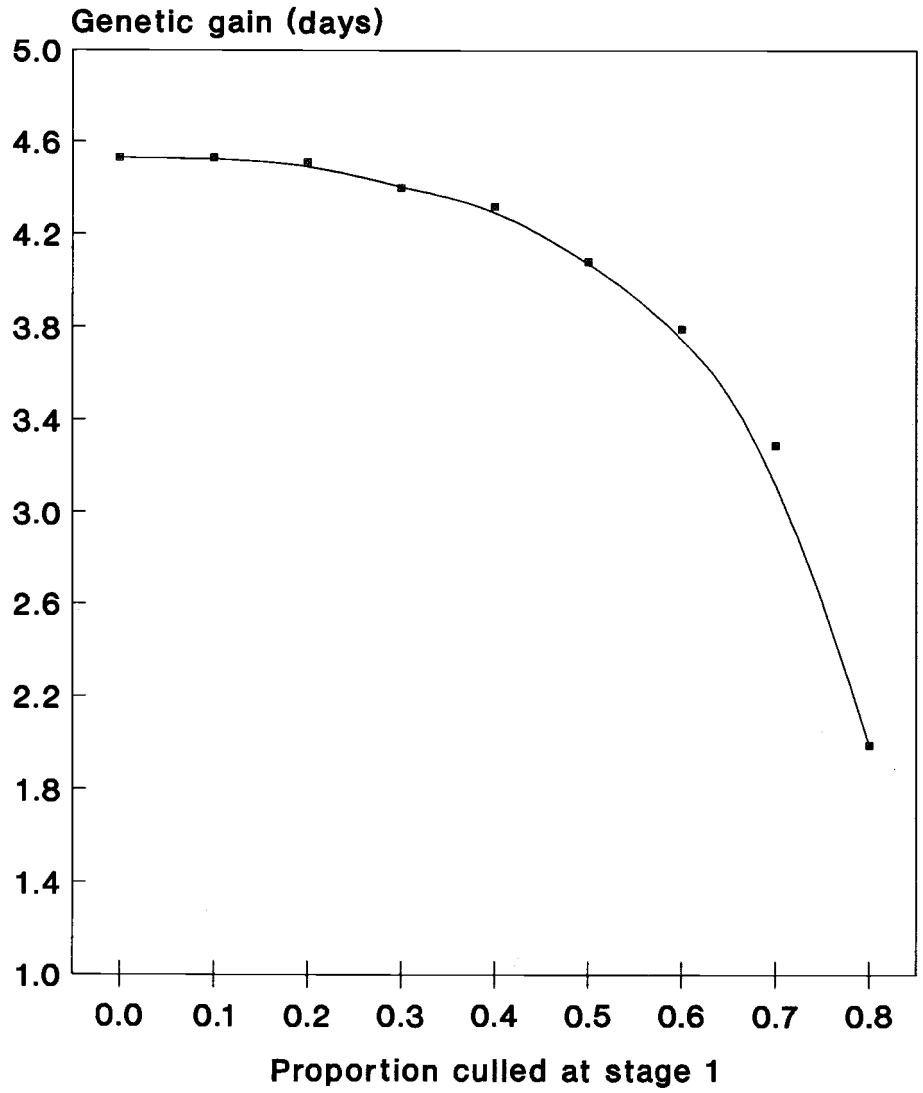

Figure II.2. Example of expected genetic gains in date of budset of pole-size (age 14 years) trees after two stages of family selection. Selection in the first stage is based on budset in nursery tests (age 1). The estimated phenotypic correlation between family means for budset date in seedlings and pole-size trees in this example is 0.34.

CHAPTER III

ALTERNATIVE METHODS OF MEASURING BUD PHENOLOGY IN GENETIC TESTS OF COASTAL DOUGLAS-FIR

ABSTRACT

Bud phenology (i.e., timing of budburst and budset) is important to the adaptation of genetically improved stocks, but difficulty in scoring leader phenology in larger trees and the expense of many periodic visits to genetic tests in order to determine dates of budburst and budset, discourage the inclusion of bud phenology traits in breeding programs. The objective of this study was to evaluate alternative methods of measuring bud phenology in coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) at both pole-size (ages 12-16) and seedling (ages 1-2) stages. First, the extent to which leader bud phenology in pole-size trees could be predicted from bud phenology measured on more easily scored lateral branches, was explored using data from 60 open-pollinated families. In all but the lowest branches, strong genetic correlations were found between dates of budburst in laterals and the leader ($r_A \geq 0.91$), and estimates of relative efficiency (RE) of indirect selection of budburst timing in the leader based on lateral branch measurements were high ($RE \geq 0.95$). Although genetic correlations between dates of budset in laterals and the leader could not be calculated, an estimate of the phenotypic correlation between budset timing in fifth whorl branches and the leader was only moderate, suggesting that indirect selection of leader

budset timing based on lateral branch measurements would be less reliable. Second, the extent to which family mean date of budburst (or budset) could be predicted from the proportion of trees within a family which had flushed (or set) buds on a single measurement date, was explored in both pole-size trees and seedlings (45 families). Despite the fact that plots contained, on average, less than 4 surviving trees, the results of the analyses indicate that if scoring is done when the proportion of trees in a test having flushed (or set) buds is at an intermediate level (e.g., between 0.30 and 0.70), the relative efficiency of indirect selection will be high ($RE \geq 0.80$) in both seedlings and pole-size trees. Thus, bud phenology scored on a single measurement date is an efficient means of ranking families for timing of budburst and budset.

INTRODUCTION

Bud phenology (i.e., dates of budburst and budset) determines the synchronization of shoot growth with the seasonal weather cycle. Thus, bud phenology is important to both growth and adaptation of trees (Ford 1984). Trees whose shoot growth periods are out of phase with the seasonal weather cycle are in danger of damage from early or late frost and/or water stress (Holzer 1969, Campbell and Sorensen 1973, Griffin and Ching 1977, White 1987, Loopstra and Adams 1989). Studies on bud phenology in conifers indicate that timing of both budburst and budset is under strong genetic control (Dietrichson 1971, Campbell 1979, Birot and Christophe 1983, Rehfeldt 1983, Ekberg et al. 1985, Kaya et al. 1989, Chapter II of this dissertation). Therefore, great potential exists to improve adaptability through genetic manipulation of bud phenology in breeding programs.

The inclusion of traits in breeding programs depends not only on their importance and degree of genetic control, but also on their ease and cost of measurement. Scoring bud phenology in genetic tests is very time-consuming, since it normally involves frequent visits to test sites in coastal Douglas-fir (Pseudotsuga menziesii var. menziesii) (e.g., twice weekly for budburst or once weekly for budset, Campbell 1986, Christophe and Birot 1983), until all trees have been scored for date of budburst or budset. In older trees (e.g., sapling and older), scoring bud phenology in the leader shoot is further complicated by the difficulty of observing the tip of the leader from the ground. This is especially true for budset, where needles block terminal buds from

view. Scoring bud phenology in older trees, however, may be necessary because it is the performance of these trees upon which final selections are based for the next generation breeding.

Assuming that bud phenology on lateral branches is highly correlated with that on the leader, scoring terminal buds on laterals may be a reliable substitute for assessing bud phenology on the leader shoot (Wilkinson 1977, Birot and Christophe 1983). In an 8-year-old coastal Douglas-fir genetic test, Christophe and Birot (1979) mentioned that date of budburst on the highest branch was highly correlated with the leader, but did not give the magnitude of the correlation. If branches are to be used in scoring bud phenology, it is important to determine the extent to which the correlation in bud phenology between branches and the leader is a function of the position of branches in the crown. The correlation may decrease with lower branches because as stands begin to close, lower branches become increasingly susceptible to differential shading from neighboring trees. Thus, lower branches may be less reliable in assessing bud phenology on the leader.

In situations where ranking of families (or other groups of genotypes, such as clones or provenances) is of interest, scoring budburst or budset on a single date and calculating proportions of trees which have burst or set buds (referred here as budburst proportion or budset proportion), may be an effective means of assessing bud phenology, with considerable savings in effort (Irgens-Moller 1958, Sweet 1965). For this method to be useful, budburst or budset proportions must be under strong genetic control, and strongly correlated with family mean dates of budburst or budset.

The timing of scoring date must be also carefully considered, since this method will presumably be most effective when the variance among families in budburst or budset proportion is maximum.

The objective of this study was to evaluate alternative methods of measuring bud phenology in genetic tests of coastal Douglas-fir. In particular, it was of interest to determine: i) the reliability of scoring bud phenology on branches as an indirect measure of terminal bud phenology on the leader of pole-size trees (ages 12-16 years), and ii) the effectiveness of budburst or budset proportions scored on a single date as a substitute for mean dates of family budburst or budset when assessing bud phenology in both seedlings and pole-size trees. Both methods proved to be effective means of assessing bud phenology in this species.

MATERIALS AND METHODS

Field tests and measurements

Materials used in this study were wind-pollinated progenies (families) of 60 Douglas-fir parent trees. The parent trees, located in the central Coast Range of Oregon, were selected as part of the initial base population in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979). Between 1972 and 1975, 1-year-old seedlings from these families were used to establish eight test plantations within the breeding unit, four of which were measured in this study (Appendix 1). The 60 families were divided into two 30-family sets (Sets 2 and 4), with each set comprising a separate randomized block experiment with four blocks in each plantation. Within a block each family was represented by a four-tree non-contiguous plot, with the trees in each plot assigned to planting spots at random. At the time of the measurements, trees in the four plantations were 12- to 16-years-old and 6 to 11 meters in average height. All trees dying within the first two years of planting were replaced with seedlings from the same family, but replacements were not measured in this study. Excluding replacement trees, survival of originally planted trees in the two family sets ranged from 70 to 89 percent, with the mean number of live trees per family plot being 3.1 (range 2.8 to 3.4) across the four plantations.

To investigate the influence of the position of lateral branches on the relationship in date of budburst between the leader and branches, two blocks within each of the two family sets in one

plantation (Smith Creek) were measured in 1986 and 1987. This plantation was the youngest of the four (12 years from seed in 1986) with smallest trees (about 6 m on average). Competition was just beginning in this plantation, so that branches were alive even at ground level. Phenology was scored on the terminal bud of the leader shoot and the tip of lateral branches, with date of budburst defined as the date when new needles emerged beyond bud scales. Budburst on the leader and upper branches was observed using binoculars while budburst on lower branches was examined at eye level. Scoring was begun when the first tree was observed to flush and continued periodically until all study trees had flushed. In 1986, date of budburst was recorded once a week on the leader and on two branches in each of five whorls; i.e., the first, third, fifth, seventh, and ninth whorl down from the leader. The two branches were usually opposite to each other, one facing north and the other south. Because the latest flushing tree had burst buds only 35 days after the earliest in 1986, budburst was measured once every three days in 1987 on the leader and on one branch in each of seven whorls; i.e., the first, second, third, fourth, fifth, seventh, and ninth down. Only one branch was measured per whorl in 1987 because the estimated genetic correlation in date of budburst between the two branches on the same whorl in 1986 was 1.0 (estimates ranged 0.996-1.016 over the five different whorls).

To determine repeatability of the relationships between timing of branch and leader budburst across plantations and years, budburst was scored on the leader and fifth whorl branches of all trees from the 60 families in three test plantations in each of two years (i.e., Clay

Creek, Coyote Creek and Oxbow in 1986; and Smith Creek, Coyote Creek and Oxbow in 1987, Chapter II of this dissertation). The fifth whorl was scored because it was the highest whorl that could be reached from the ground for examination at eye level, and because the fifth whorl was free of shade from surrounding trees in all plantations.

Date of budset was scored when brown bud scales were first observed on the terminal buds. Scoring budset on the leader from the ground was impossible because needles hid terminal buds from view. Thus, budset can only be reliably scored at eye level. Dates of budburst and budset on two opposite branches on the fifth whorl were scored from the ground twice weekly in all trees of the 60 families at Smith Creek in 1988. In addition, to examine the relationship between timing of leader and branch budset, dates of budburst and budset were also scored in the leaders of a subset of 53 smaller (about 6 m high) trees whose terminal buds could be inspected at eye level from a portable leader. These trees were located within a small area to minimize environmental differences between trees, and included individuals from 28 families in two blocks of set 4.

Seedling tests and measurements

Terminal bud phenology of 45 of the 60 families (21 in Set 2 and 24 in Set 4) was investigated in seedling tests established for an early testing study conducted by the Pacific Northwest Tree Improvement Research Cooperative (Adams et al. 1987). Details on experimental designs and seedling culture are given elsewhere (Chapter II of this dissertation). For 45 of the 60 parent trees whose progeny were

growing in the field plantations, open-pollinated seed either from stored seedlots or recollected in 1985, was used to establish three types of seedling tests, each having 2 replicates. 1) Direct sown test: germinants were sown directly into a bareroot nursery in Washington and replicated in two years (1986 and 1987) in adjacent nursery beds (with 6 and 7 blocks, respectively). For this test, data were available on dates of first-year budset and second-year budburst. 2) Greenhouse test: germinants were sown directly into containers and replicated in 2 greenhouses in 1987 (with 6 and 8 blocks, respectively), and were measured for date of first-year budset. 3) Transplant test: seedlings from 2) were transplanted in the spring of 1988 into a bareroot nursery in Oregon and another in Washington (same nursery used for 1), and were measured for dates of second-year budburst and budset. The same criteria as in the field measurements were used for defining budburst and budset in seedlings. Budburst was scored twice weekly, and budset once weekly. Average number of seedlings per plot ranged from 2.9 to 3.8 (mean = 3.4) across the 6 replicates of the three seedling tests.

Statistical Analyses

Relationships between the leader and branches in bud phenology

The first step in data analyses of budburst data was to determine the significance of family differences in dates of budburst on the leader and branches through analyses of variance. The analyses were performed on eight data sets: budburst data in the leader and multiple laterals at Smith Creek in each of 1986 and 1987 (2 data sets), and

budburst data in the leader and fifth whorl branches in three plantations measured in each of 1986 and 1987 (6 data sets). For each trait (or each lateral whorl-leader combination), variance (or covariance) components were estimated from a plot mean model,

$$Y_{ijk} = u + S_i + B_{j(i)} + F_{k(i)} + e_{ijk} \qquad (1)$$

where Y_{ijk} = plot mean date of budburst for the k^{th} family of the i^{th} set in the j^{th} block, u = grand mean, S_i = i^{th} set effect, $B_{j(i)}$ = j^{th} block effect within set i, $F_{k(i)}$ = k^{th} family effect within set i, and e_{ijk} = plot error. Within-plot variances and covariances were estimated by pooling individual-plot values (Miliken and Johnson 1984). In the model, family and error effects were considered random, while sets and blocks were considered fixed effects. Values for missing plots (i.e., plots where all trees had died), totaling 7 for the four plantations, were estimated for each set as in a randomized block design according to the methods described in Steel and Torrie (1980, pp. 209-213), and degrees of freedom for error adjusted accordingly. All the statistical analyses were conducted by the SAS computer package (SAS Institute Inc. 1985). For the purpose of statistical testing, significance refers to the 0.05 probability level.

The effectiveness of using budburst measurements on branches to assess budburst on the leader was evaluated by calculating relative efficiencies of indirect selection for leader budburst on the basis of branch budburst, under both individual and family selection. This was done for each lateral whorl-leader combination in the eight data sets. Relative efficiency (RE), the ratio of the genetic gain from indirect selection to that expected from direct selection, under the assumption

that the intensity of selection applied to both direct and indirect traits is equal (Falconer 1981), can be calculated as,

$$RE = r_A \ (h_X/h_Y) \qquad (2)$$

where r_A is the genetic correlation between the direct (date of leader budburst in this case) and indirect traits (date of branch budburst), h_X is the square root of individual (under individual tree selection) or family (under family selection) heritability for the indirect trait, and h_Y is the square root of individual or family heritability for the direct trait. Individual tree and family heritabilities for date of budburst in the leader and in branches, genetic correlations between these traits, and standard errors for genetic parameter estimates were calculated from appropriate variance and covariance component estimates (Namkoong 1981, Becker 1984). Because progenies within open-pollinated families are expected to be related to a greater extent than half-sibs, additive genetic variance was estimated as three times the family variance component (Campbell 1979).

The relative efficiency of measuring date of budset on branches could not be calculated because only a subsample of trees (53) were scored for both leader and branch (fifth whorl) budset at Smith Creek. The degree of relationship between date of budset in branches and the leader was assessed by calculating their phenotypic correlation. Since two fifth whorl branches were scored in the 53 tree subsample, the average date of budset on the two branches was used in this calculation.

Relationships between mean date of budburst (or budset) and budburst (or budset) proportion

The first step in these analyses was to compute the proportion of trees in each plot which flushed (or set) buds on each scoring date (i.e., budburst or budset proportion). Budburst or budset proportions were then compared to date of budburst or budset on a plot mean basis. Since trees were scored periodically from the beginning of budburst or budset in each test, until all individuals had burst or set buds, it was possible not only to correlate the two measures of bud phenology, but also to determine the influence of measurement date (i.e., overall test proportion of budburst or budset) on the degree of their association. Because budburst was scored on both the leader shoot and fifth whorl branches in three plantations in each of 1986 and 1987, the opportunity also existed to examine how well budburst proportions measured on branches could substitute for date of budburst on the leader.

The remaining steps in the data analyses were similar to those described in the previous section. For the field tests, analyses of variance (equation 1) were conducted on plot mean dates of leader budburst and budburst proportions for the leader and fifth whorl branches in the three plantations measured in 1986 and 1987 (6 data sets), and plot mean dates and proportions for both budburst and budset scored on the fifth whorl branches at Smith Creek in 1988. Budburst and budset proportions were subjected to arcsin transformation prior to the analyses in order to meet the assumption that treatment effects are additive (Gilbert 1989).

For plot mean dates of budburst (or budset) and budburst (or budset) proportions, variance (or covariance) components were computed separately for each replicate of the three seedling tests, according to the following model,

$$Y_{ijk} = u + S_i + B_j + BS_{ij} + F_{k(i)} + e_{ijk} \qquad (3)$$

where Y_{ijk} = plot mean for date of budburst (or budset), or budburst (or budset) proportion for the k^{th} family within the j^{th} block and i^{th} set, S_i = i^{th} set effect, B_j = j^{th} block effect, BS_{ij} = interaction effect between block i and set j, $F_{k(i)}$ = k^{th} family effect within set i, and e_{ijk} = plot error. Family and error effects were assumed to be random while all other effects were assumed to be fixed. Again, budburst and budset proportions were subjected to arcsin transformation prior to statistical analyses.

As in the previous section, the effectiveness of budburst (or budset) proportions for assessing timing of budburst (or budset) in each test was evaluated by calculating relative efficiencies of indirect selection for date of leader budburst (or budset) on the basis of budburst (or budset) proportion (equation 2). Since proportions were calculated on a plot mean basis, only relative efficiencies for family selection could be estimated. Family heritabilities for date of budburst (or budset) and budburst (or budset) proportions, genetic correlations between the two traits, and standard errors for these genetic parameters, were estimated from the appropriate variance and covariance components, as described above. Relative efficiencies were calculated only when both mean dates of budburst (or budset) and budburst (or budset) proportions differed significantly among families

within a test. Because family differences in date of second-year budset were non-significant (P-value > 0.05) in the two replicates of the transplant test (Chapter II of this dissertation), relative efficiencies of using budset proportions to evaluate budset timing in the second-year seedlings could not be calculated.

RESULTS

Relationships between the leader and branches in bud phenology

On average, leader shoots in the two blocks at Smith Creek in which multiple whorls of branches were measured, burst bud on May 17 in 1986 (i.e., 137 days from January 1), and on May 7 in 1987 (Tables III.1 and III.2). The terminal buds on the lowest whorl of branches were the earliest to flush in both years; 8 days earlier than the leader in 1986 and 4 days earlier in 1987 (Tables III.1 and III.2). The leader shoots flushed at about the same time as laterals above the 5th whorl in 1986, and laterals above the 7th whorl in 1987. The relative timing of budburst on the leader and branches within a tree, however, varied a great deal among trees. In some trees, the leader flushed earlier, and in others later than laterals, and still in others all buds on the tree flushed at the same time.

Families differed significantly for date of budburst on the leader and on all branches regardless of the whorl position. Mean date of budburst on the leader differed among families by about 15 days in both years, while in branches family differences ranged from 12 to 22 days over the two years (Tables III.1 and III.2). With the exception of the 9th whorl in 1987, the family range in mean date of budburst was greater on branches than on the leader shoot. With a couple exceptions, estimated heritabilities for date of budburst in branches were as high as or higher than in the leader, and genetic correlations between dates of budburst in the leader and branches were high ($r_A \geq 0.91$) (Tables III.1 and III.2). Thus, in most cases, relative

efficiencies of selection for leader budburst based on branch budburst were very high, with RE expected to be greater than 0.99 when individual tree selection is applied, and greater than 0.95 under family selection. The only exceptions were branches on the lowest two whorls (7th and 9th) in 1987, which had lower genetic correlations with leader budburst (0.83 and 0.66, respectively), and thus, lower RE (0.86 and 0.62, respectively) (Table III.2).

Consistent with the above results from the two blocks at Smith Creek, genetic correlations between dates of budburst in the leader and fifth whorl branches were very strong ($r_A \geq 0.97$) when the data from each of the three plantations in each of two years were analyzed (Appendix 10). The relative efficiencies under both family and individual selections were nearly 1 over plantations in both years. These results indicate that branch budburst is a reliable indicator of leader budburst across different plantations and years.

For the 53 trees at Smith creek measured for dates of budburst and budset on the leader and fifth whorl branches in 1988, the mean date of budburst on the leader and fifth whorl branches was May 17 and May 18, respectively, while the mean dates of budset were June 18 and June 2, respectively. Date of budburst differed among trees by 17 days on the leader and by 16 days on the branches, while date of budset differed by 18 days on the leader and 16 days on the branches. The phenotypic correlation in date of budset between the leader and the fifth whorl branches was 0.54, considerably smaller than observed for date of budburst in the 53 trees (0.81). Estimated individual tree heritabilities for both date of budburst (0.90) and date of budset

(0.81) in fifth whorl branches were both high (Chapter II of this dissertation).

Relationships between mean date of budburst (or budset) and budburst (or budset) proportion

In each of the three plantations measured in 1986 and 1987, date of budburst differed significantly among families and was under strong genetic control (mean h_F^2 = 0.78, range 0.72-0.83) (Appendix 11). With the exclusion of the last scoring date when all trees have burst buds (i.e., the budburst proportion is 1.0), there were 28 scoring date-plantation combinations where budburst proportions ranged from 0.01 to 0.99. With only one exception (when budburst proportion was 0.07), family differences in budburst proportions on the leader were significant in 25 scoring date-plantation combinations when mean budburst proportions over the entire test were between 0.01 to 0.96. Family differences were not significant in the three remaining cases when budburst proportions were equal to 0.96, 0.98 and 0.99. Relative efficiency of selection for budburst timing on the basis of budburst proportion varied depending on the plantation mean for budburst proportion (RE range 0.46-1.00). Pooling results across the six plantation data sets, RE was found to be high (Mean RE = 0.88, range 0.81-1.00) on scoring dates when mean budburst proportions were between 0.29 and 0.91 (Figure III.1). These high RE's were due to high family heritabilities for budburst proportion ($h_F^2 \geq 0.59$) and strong genetic correlations between budburst proportion and budburst date ($-1.00 \leq r_A \leq -0.87$). When plantation mean budburst proportion was less than 0.29 or greater than 0.91, low RE's resulted from lower h_F^2 for budburst

proportion and/or low r_A between budburst proportion and date of budburst (Figure III.1, Appendix 11). Estimated relative efficiencies of selection for budburst timing on the leader based on budburst proportion scored on fifth whorl branches were high (mean RE = 0.87, range 0.77-0.98) when mean budburst proportions on fifth whorl branches were between 0.13 and 0.88 (Appendix 12).

At Smith Creek in 1988, families differed significantly for dates of budburst and budset on fifth whorl branches, with h_F^2 being 0.76 and 0.77, respectively (Appendix 13). On the five scoring dates for budburst, the mean proportion of budburst per plot varied from 0.08 to 0.95 (Appendix 13). Family differences in budburst proportions were statistically significant on all five dates. Relative efficiencies of selection for budburst timing based on budburst proportion were high when the mean proportions of budburst per plot were between 0.22 and 0.87 (mean RE = 0.87, range 0.83-0.94). Mean budset proportion ranged between 0.26 to 0.996 over the seven dates when this trait was scored (Appendix 13). Families differed significantly in budset proportions on the 4 dates when mean budset proportion was $\leq$ 0.92, whereas family differences were not significant on the 3 scoring dates when budset proportions were greater than 0.92. Relative efficiencies of selection for date of budset timing based on budset proportion were high (0.85 and 0.88) for two of the scoring dates, when mean budset proportions were 0.59 and 0.81, respectively (Figure III.2, Appendix 13).

Date of second-year budburst differed significantly among families, with estimated family heritabilities ranging from 0.68 to 0.80 across the four replicates of the direct sown and transplant

seedling tests (Appendix 14). In 6 of the 10 scoring date-replicate combinations when mean budburst proportions for the tests were less than 0.31 or greater than 0.90, family differences in budburst proportions were non-significant. In all of the remaining 14 scoring date-replicate combinations (i.e., where mean budburst proportions were between 0.31 to 0.90), family differences were always significant. Pooling results from the four replicates, relative efficiencies of selection for budburst timing on the basis of budburst proportion were high (Mean RE = 0.87, range 0.80-0.94) when mean test budburst proportions were between 0.38 and 0.81 (Figure III.3).

Date of first-year budset differed significantly among families, with estimated family heritabilities ranging from 0.49 to 0.72 across the four replicates of the direct sown and greenhouse tests (Appendix 15). In only 2 of the 8 scoring date-replicate combinations where budset proportions were less than 0.38 or greater than 0.91, were family differences significant. Family differences were significant for all remaining 9 cases, when budset proportions were between 0.38 to 0.91. Pooling results across the four replicates, relative efficiencies of selection for first-year budset timing on the basis of budset proportion were high (mean RE = 0.84, range 0.71-1.01) when mean budset proportions were between 0.41 and 0.85 (Figure III.4).

DISCUSSION AND CONCLUSIONS

Relationships between the leader and branches in bud phenology

The results of this study indicate that scoring terminal buds on mid- to upper branches is a reliable substitute for the leader in assessing date of budburst for both individuals and families in pole-size Douglas-fir. Although earlier studies in Douglas-fir and other species (Christophe and Birot 1979, O'Reilly and Parker 1982, Worrall 1983) reported high correlations in budburst timing between the leader and the highest branch, this study showed that budburst on the leader is strongly correlated with all branches ($r_A \geq 0.91$) on open-grown trees, except those near the ground.

Budburst is mainly a response to spring heat accumulation (Campbell 1978, Lavender 1981, Thompson and Moncrieff 1981, Worrall 1983). On average, budburst occurred 10 days earlier in 1987 than in 1986 (Table III.1. and III.2), which is due to a warmer spring in 1987 than in 1986 (mean daily temperature from April 1 to May 7 was 9.2°C in 1986, but 12.1°C in 1987; May 7 was the average date of budburst in 1987). Previous studies have showed that upper branches burst buds earlier than the leader in seedlings or trees less than 10 years old (Sweet 1965, White et al. 1979, Worrall 1983). In this study, while branches near the ground did burst bud, on average, earlier than buds on the leader (i.e., 8 days earlier in 1986 and 4 days earlier in 1987), buds on branches as low as the seventh whorl flushed at about the same time as the leader. Because air temperatures are higher near the ground in open stands (Jones 1983), branches near the ground would

reach their required heat sum for budburst earlier than branches above. The lower estimated heritability for budburst timing on the ninth whorl branches in 1987 may be due to more temperature variation near the ground caused by differential shading from the surrounding trees.

Date of budset on the leader may not be predicted as reliably by scoring buds on branches as date of budburst. The phenotypic correlation in date of budset between fifth whorl branches and the leader (0.54) was smaller than for date of budburst (0.81) in the subset of 53 trees at Smith Creek scored for both dates of budburst and budset on the leader and fifth whorl branches in 1987. Phenotypic correlations, however, usually underestimate genetic correlations (Cheverud 1988). For example, the phenotypic correlation in date of budburst between the leader and fifth whorl branches based on all trees measured at Smith Creek in 1987 was 0.77, as compared to a genetic correlation of 0.99. If the same relationship observed between the phenotypic and genetic correlations for budburst holds true for budset, the genetic correlation between leader and branch budset would be about 0.70. If it is assumed that the heritability of leader budset is as high as fifth whorl branch budset ($h^2 = 0.81$, Chapter II of this dissertation), relative efficiency of using branch budset as an indirect measure of leader budset would be moderate (about 0.7).

Relationships between mean date of budburst (or budset) and budburst (or budset) proportions

Results from this study showed that relative timing of budburst or budset among families can be accurately assessed in seedlings and pole-

size trees of Douglas-fir, by calculating the proportions of trees per plot that have flushed or sets buds on a single measurement date. Earlier studies found significant differences among provenances in budburst and budset proportions (Falkenhagen 1977, Steiner 1979, Libby et al. 1980), but the genetic control of these proportions, and their relationships with mean dates of budburst and budset have apparently not been previously reported. On scoring dates when mean budburst or budset proportions were at intermediate levels (e.g., between 0.3 to 0.7), budburst and budset proportions were found to be under strong genetic control and have strong negative correlations with mean dates of budburst and budset. As a result, relative efficiency of selecting budburst or budset timing on the basis of budburst or budset proportion is expected to be high. It is surprising that budburst or budset proportions were found to be so efficient for ranking families for mean dates of budburst or budset in the materials in this study, where plot sizes were no more than 4 individuals.

The application of this method in progeny tests is simple, as long as the tests can be visited regularly to determine when the proportion of trees that have burst (or set) buds is at an intermediate level. Ideally, scoring should be done when about 50 percent of the trees in a test have burst (or set) buds. The ability to accurately rank families for timing of budburst or budset on the basis of proportions determined on a single measurement date, represents a considerable saving of effort relative to that needed to estimate mean dates of budburst or budset. This approach is especially useful for roguing seed orchards or in early testing where family selection is of main interest.

Table III.1. Estimated test means for date of budburst on the leader shoot and lateral branches of trees at Smith Creek in 1986, estimated individual tree (h^2) and family (h_F^2) heritabilities for these traits, genetic correlations (r_A) between dates of lateral and leader budburst, and relative efficiencies of individual (RE_I) and family (RE_F) selection for date of leader budburst based on lateral budburst measurements.[a]

Position of terminal bud	Mean[b]	h^2 [c]	h_F^2 [c]	r_A [c]	RE_I	RE_F
Leader	136.9 (128.0-142.6)	0.69(0.09)	0.46(0.08)	____	____	____
Lateral branches[d]						
1st whorl	136.5 (125.1-143.5)	0.77(0.20)	0.47(0.07)	1.07(0.04)	1.06	1.01
3rd whorl	136.6 (125.1-143.5)	0.74(0.21)	0.45(0.08)	0.98(0.22)	1.01	0.97
5th whorl	136.5 (125.1-144.7)	0.70(0.21)	0.43(0.08)	0.98(0.03)	0.99	0.95
7th whorl	134.4 (123.2-144.7)	1.05(0.21)	0.54(0.06)	1.04(0.04)	1.23	1.08
9th whorl	128.9 (119.0-141.2)	0.84(0.20)	0.50(0.07)	1.07(0.07)	1.10	1.04

[a] Families differed significantly ($p < 0.01$) for date of budburst on the leader shoot and all laterals.

[b] Days from January 1, 1986; range among family means in parentheses.

[c] Standard errors in parentheses.

[d] Whorls are numbered from the top of the crown.

Table III.2. Estimated test means for date of budburst on the leader shoot and lateral branches of trees at Smith Creek in 1987, estimated individual tree (h^2) and family (h_F^2) heritabilities for these traits, genetic correlations (r_A) between dates of lateral and leader budburst, and relative efficiencies of individual (RE_I) and family (RE_F) selection for date of leader budburst based on lateral budburst measurements.[a]

Position of terminal bud	Mean[b]	h^2 [c]	h_F^2 [c]	r_A [c]	RE_I	RE_F
Leader	127.1 (119.0-133.0)	0.86(0.21)	0.49(0.07)	____	____	____
Lateral Branches[d]						
1st whorl	127.1 (119.4-134.5)	1.01(0.20)	0.54(0.06)	0.97(0.03)	1.05	1.02
2nd whorl	127.7 (119.0-135.0)	1.16(0.20)	0.57(0.05)	0.91(0.04)	1.06	0.98
3rd whorl	127.5 (119.4-135.5)	1.15(0.20)	0.58(0.05)	0.93(0.04)	1.08	1.01
4th whorl	127.9 (119.4-136.0)	1.07(0.20)	0.57(0.05)	0.94(0.04)	1.05	1.01
5th whorl	128.0 (119.7-136.5)	1.02(0.20)	0.54(0.05)	0.93(0.05)	1.01	0.98
7th whorl	127.0 (118.2-134.5)	0.97(0.20)	0.53(0.06)	0.83(0.08)	0.88	0.86
9th whorl	123.1 (116.4-128.5)	0.70(0.21)	0.43(0.08)	0.66(0.14)	0.60	0.62

[a] Families differed significantly ($p < 0.01$) for date of budburst on the leader shoot and all laterals.

[b] Days from January 1, 1986; range among family means in parentheses.

[c] Standard errors in parentheses.

[d]. Whorls are numbered from the top of the crown.

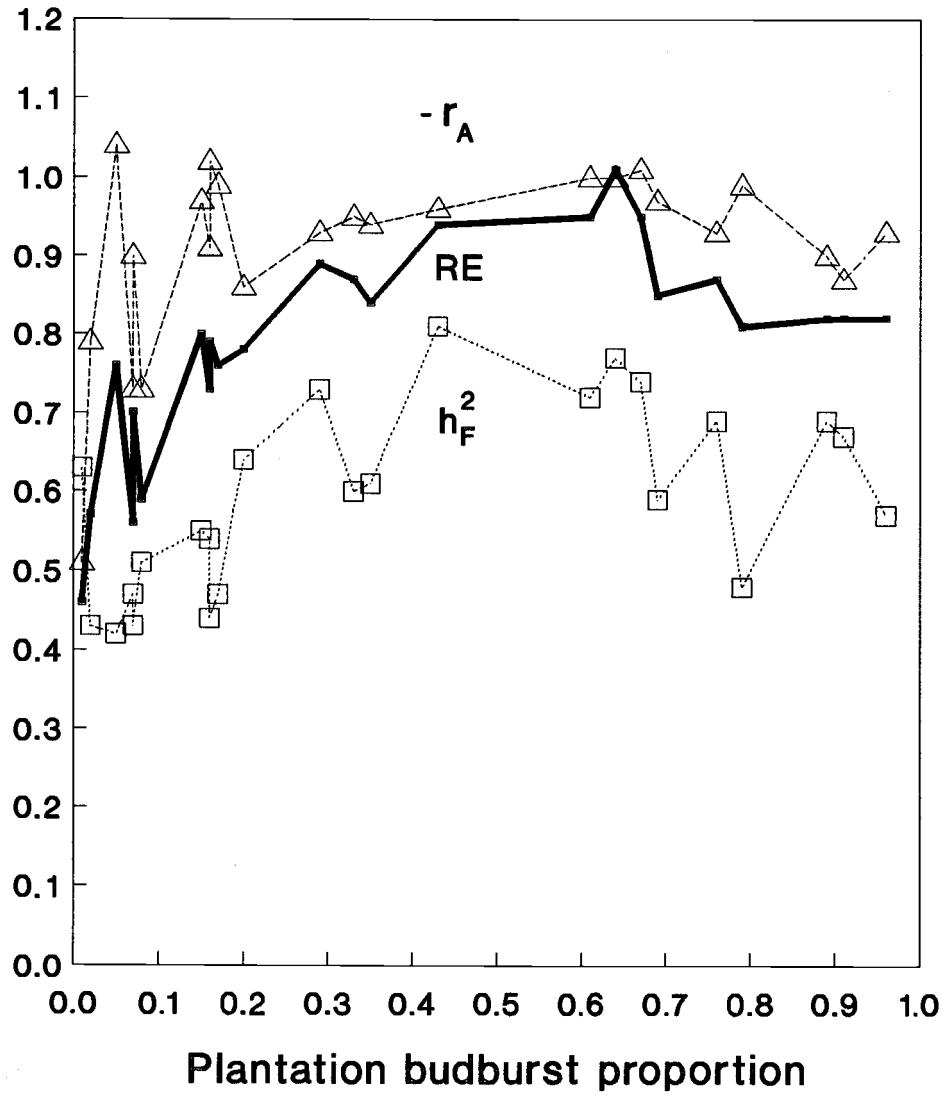

Figure III.1. Relationships between plantation mean budburst proportion and family heritability (h_F^2) for budburst proportion, genetic correlation between budburst proportion and budburst date (r_A), and relative efficiency (RE) of selecting budburst date based on budburst proportion. Pooled results from analyses of data from 3 plantations in each of two years.

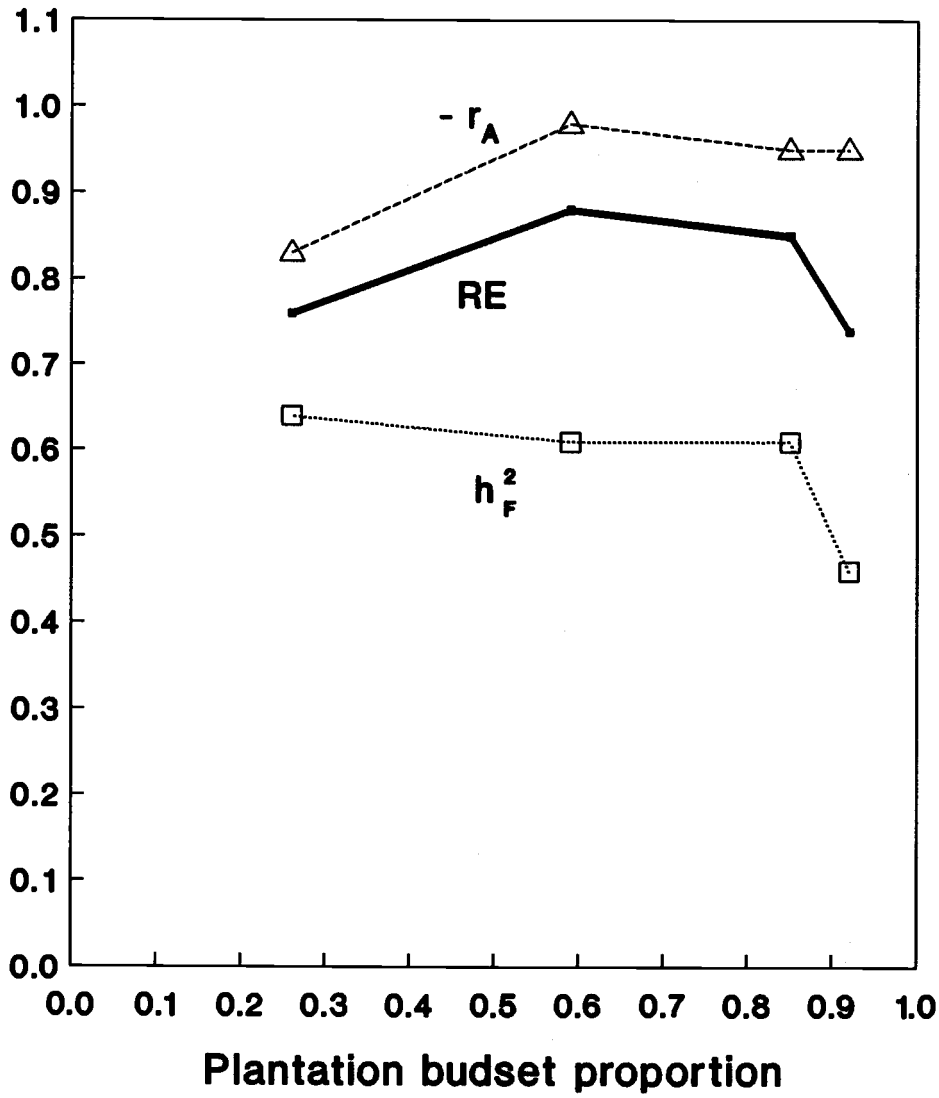

Figure III.2. Relationships between plantation budset proportion and family heritability (h^2_F) for budset proportion, genetic correlation between budset proportion and budset date (r_A), and relative efficiency (RE) of selecting budset date based on budset proportion. Results from measurements on fifth whorl branches at the Smith Creek plantation in 1988.

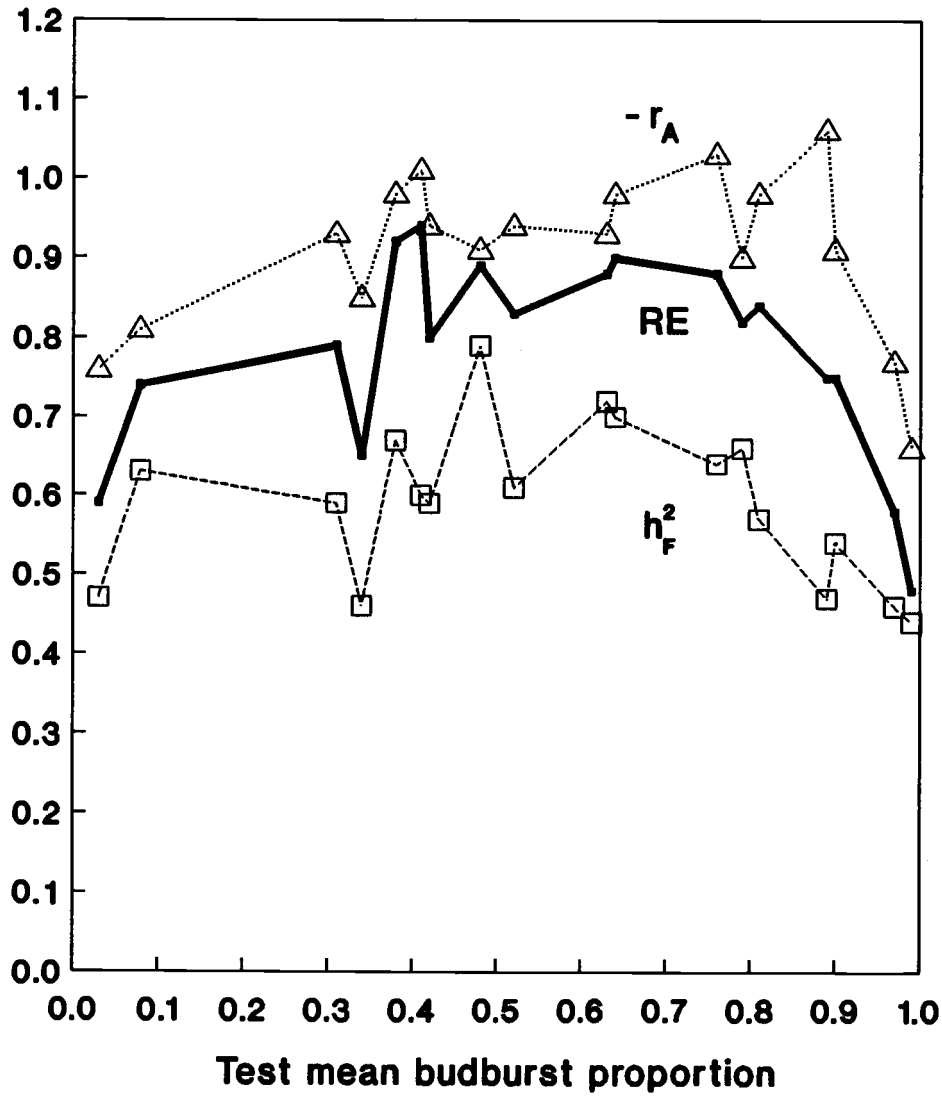

Figure III.3. Relationships between nursery budburst proportion and family heritability (h^2_F) for budburst proportion, genetic correlation between budburst proportion and budburst date (r_A), and relative efficiency (RE) of selecting budburst date based on budburst proportion for two-year-old seedlings. Pooled results from four seedling test replicates.

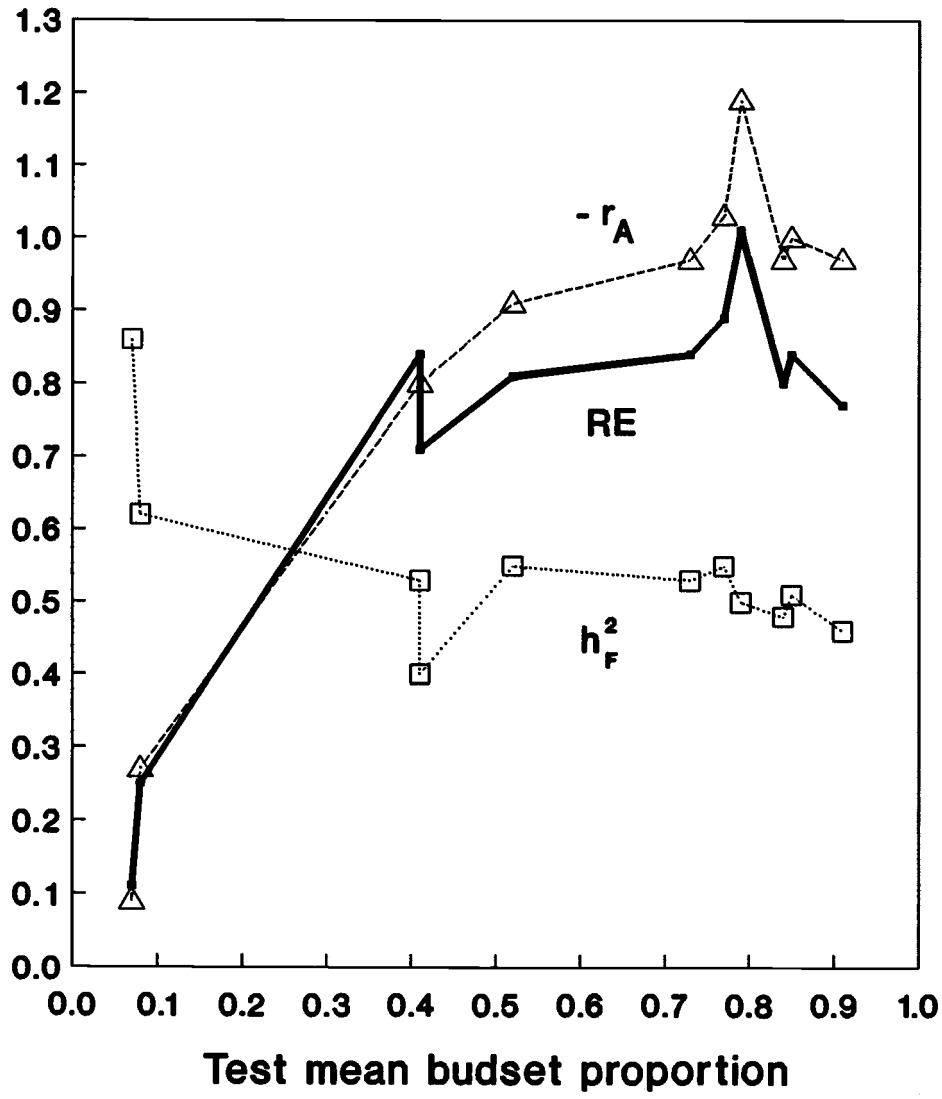

Figure III.4. Relationships between seedling test budset proportion and family heritability (h^2_F) for budset proportion, genetic correlation between budset proportion and budset date (r_A), and relative efficiency (RE) of selecting budset date based on budset proportion in one-year-old seedlings. Pooled results from four seedling test replicates.

CHAPTER IV

GENETIC VARIATION IN CAMBIAL PHENOLOGY OF COASTAL DOUGLAS-FIR

ABSTRACT

This study had three objectives: 1) to determine the extent of genetic variation and control of cambial phenology (i.e., timing of diameter growth initiation and cessation) in coastal Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco), 2) to assess the degree to which cambial phenology is genetically related to timing of budburst, and 3) to assess the genetic relationships between cambial phenology and growth traits. Diameter growth was measured weekly from late March to mid-October in 1987 on 15-year-old trees of 60 wind-pollinated families growing at a single plantation site. From the cumulative growth curve of each tree, dates of initiation and cessation, and duration of diameter growth (i.e., cambial phenology traits) in 1987 were estimated, as well as the diameter increment and rate of diameter growth. In addition, data on total stem height and diameter (DBH), and date of budburst were collected. Dates of diameter growth initiation and cessation differed significantly among families, but were found to be under weaker genetic control ($h^2 \leq 0.23$) than date of budburst ($h^2 = 0.89$). Estimated genetic correlations between budburst timing and dates of diameter growth initiation and cessation were weak ($0.09 \leq r_A \leq 0.26$), suggesting that timing of bud flushing and diameter growth are under nearly independent genetic control. Growth rate in 1987 was found to be strongly correlated with growth

increment in the same year, and with 15-year DBH ($r_P \geq 0.41$ and $r_A \geq 0.93$), but duration of diameter growth was weakly correlated with growth traits ($0.09 \leq r_P \leq 0.33$). This indicates that diameter growth in these families is mainly determined by growth rate rather than by growth duration. Although diameter increment in 1987 was weakly and positively correlated with dates of growth initiation and cessation in the same year ($0.17 \leq r_P \leq 0.38$), 15-year DBH and stem volume were negatively correlated with dates of initiation and cessation in 1987 ($-0.29 \leq r_P \leq -0.03$ and $-0.59 \leq r_A \leq -0.35$). Genetic correlations for cambial phenology with budburst timing and growth traits, however, were always small, suggesting that selection for delayed budburst or greater growth will have little adverse effect on adaptability of improved stocks through altering cambial phenology traits.

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 climatic zones, periods of meristem activity alternate with periods of dormancy, which closely match the growing season of the local climate (Lanner 1976, Liphschitz and Lev-Yadun 1986, Ajmal and Iqbal 1987). When seed sources with early growth initiation are moved to areas with frequent occurrence of spring frost, they are susceptible to shoot and cambial damage from spring frost. When seed sources with late growth cessation are moved to severe climates, they are prone to shoot and cambial damage from early fall frost, or winter cold. Symptoms of cambial damage include occurrence of frost rings, incomplete lignification of xylem cells, lower wood specific gravity, and increased snowbreak in seedlings and mature trees (Dietrichson 1961, Klem 1957, Kennedy 1961, Dietrichson 1964, 1969a). The extent of genetic control of shoot phenology traits and the potential for altering these traits via selection and breeding have been studied extensively in Douglas-fir, especially at the seedling stage (Birot and Christophe 1983, Rehfeldt 1983, Mangold 1987, Kaya et al. 1989, Chapter II of this dissertation), but little is known about the genetic control of cambial phenology.

Measuring timing of initiation and cessation of cambial activity in stems is difficult and time-consuming (Kozlowski 1971). The most reliable method is to microscopically examine the presence of dividing cells in the cambial core at different times of the year (Johansen

1940). By using markers such as the uptake of radioactively labeled CO_2 (Waisel and Fahn 1965), presence of reaction wood by tilting seedlings (Kennedy and Farrar 1965), and presence of injuries caused by piercing micro-needles into the cambium zone (i.e., "pin-pricking method", Wolter 1968), the annual growth ring can be marked periodically during the growing season, and examined microscopically later for the timing of cambial activity. Because microscopic methods are very laborious and involve destructive sampling, indirect methods are often used to assess cambial phenology when large numbers of trees are measured. These methods include the ease of peeling off bark (Priestley et al. 1933, Wilcox et al. 1956), and measurement of electrical resistance in cambial regions (Davis et al. 1979, van Daalen 1988); but, the most common method is to infer relative timing of initiation and cessation of cambial activity from cumulative growth curves constructed from weekly diameter measurements with dendrometers (Kozlowski 1971, Cattelino et al. 1986). Two main factors contribute to inaccuracy of cambial phenology estimates based on dendrometer measurements: diurnal shrinkage can often exceed net growth in any single day, and the amount of seasonal shrinkage during a severe drought can exceed total growth up to that time (Dobbs and Scott 1971, Zaerr 1971, Kozlowski 1982). Thus, dendrometers can only be used to approximate the timing of initiation and cessation of cambial activity in trees (Kozlowski 1971).

Cambial activity is a complicated physiological process and is not well understood. In temperate conifers, the resumption of cambial activity is preceded by the swelling of cambial cells associated with

rising temperatures in early spring. The initiation of new cambial growth is correlated with the renewed activity of bud meristems. The cambium becomes active first near the base of swelling buds prior to shoot extension, with activity progressing through the branches toward the base of the trunk (Zimmermann and Brown 1971, Savidge and Wareing 1984). Continued cambial cell-divisions depend on the presence of extending buds because hormones, particularly indole-3-acetic acid (IAA) produced in the growing shoots, regulate cambial activity (Wareing 1958, Savidge and Wareing 1984, Little and Savidge 1987). The cessation of cambial activity has no apparent association with cessation of shoot growth, but there is evidence suggesting that cessation of active shoot growth marks the beginning of latewood production (Kozlowski 1971).

Variation in timing of cambial initiation and cessation is largely caused by environmental factors. For example, within a tree, diameter growth begins and ceases later in the lower stem than in the upper stem. In addition, duration of cambial growth is shorter for suppressed trees than for dominant trees (Kozlowski 1971, Riding and Little 1986); and, the duration of cambial growth decreases with increasing elevation and latitude (Studhalter et al. 1963, Tranquillini 1979). Variation in cambial phenology is also genetically controlled. In a given region, the duration of cambial activity is often longer in conifers than in deciduous trees (Reukema 1965, Kozlowski 1971). Cambial phenology also varies among populations within species. Using the pin-pricking method, Emmingham (1977) found that an Idaho seed source of Douglas-fir (Pseudotsuga menziesii) had a shorter cambial

growth duration than coastal seed sources. Provenances of Pinus ponderosa from high elevations start diameter growth earlier than those from lower elevations (Daubenmire 1950), while northern sources of Picea abies, Fraxinus pennsylvanica and Pinus contorta start and cease growth earlier than southern sources (Worrall 1975, Santamour 1982, O'Reilly and Owens 1989). Using increased amounts of lignification in the annual ring as an indication of cambial growth cessation, Dietrichson (1961, 1964, 1969a, 1969b, 1971) found provenance variation in relative timing of growth cessation in Abies lasiocarpa, Picea abies, P. mariana, and Pinus sylvestris.

Genetic studies of cambial phenology variation at the family level are few. In apparently the only report on the inheritance of cambial phenology in conifers, family heritability for timing of cambial growth cessation was estimated to be high in Picea abies, P. mariana, and Abies lasiocarpa (Dietrichson 1967, 1969b, 1971). Because of the importance of cambial phenology traits to adaptation in conifers, information on the magnitude of their genetic variation and genetic control is needed to assess the potential for altering cambial phenology in breeding programs to improve adaptability. It is also imperative to know how cambial phenology is correlated with stem growth traits so that indirect effects of selection for greater growth on cambial phenology can be evaluated. Because of the physiological relationships between bud and cambial activity, it is also of interest to examine genetic relationships between cambial and bud phenology traits.

This study had three objectives: 1) to determine the extent of

genetic variation and genetic control of cambial phenology in 15-year-old coastal Douglas-fir (Pseudotsuga menziesii var. menziesii), 2) to determine the extent to which cambial phenology traits are genetically related to bud phenology traits, and 3) to examine genetic relationships between cambial phenology and stem growth traits. Dates of initiation and cessation of diameter growth were estimated from cumulative diameter growth curves constructed from weekly measurements of diameter increment in 60 wind-pollinated families growing at a single plantation site. Cambial phenology was found to vary significantly among families, but was under weak genetic control. In addition, timing of cambial phenology was found to have weak to moderate genetic correlations with budburst timing and stem growth traits, suggesting that selection for greater growth and delayed budburst would have little effect on adaptability of improved stocks through altering cambial phenology.

MATERIALS AND METHODS

Materials

The 60 wind-pollinated families used in this study comprise two 30-family sets (Sets 2 and 4), growing in the Coyote Creek plantation near Eugene, Oregon (45°58'N, 123°18'E, elevation 274 m). The 60 parent trees, located in nearby stands in the central Oregon Coast Range, are a portion of the original wild-stand selections included in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979, Quam 1988). Each set of families was planted as a separate randomized block experiment, with four blocks. Within a block each family was originally represented by a four-tree non-contiguous plot, with trees in each plot assigned to planting spots at random. Original spacing was 3.05 m x 3.05 m. At the time of measurement, trees were 15 years old from seed, averaged about 11 meters in height and 14 centimeters in diameter at breast height (1.37 m) (DBH). Crown closure had begun in this plantation, with lower branches experiencing mortality up to 3.16 meters. All trees dying within the first two years of planting were replaced with seedlings from the same family, but replacements were not measured in this study. Excluding replacement trees, survival of originally planted trees was 85 percent.

Measurements

Weekly measurements of DBH (diameter at breast height, 1.37 m) were made in this plantation during the 1987 growing season. All trees

from the 60 families were measured from March 26, before measurable diameter growth began, until October 16, when no further diameter growth was detected. Points on directly opposite sides of the bole were marked with tacks glued on the bark so that measurements could be made at the same place each time. These points of measurement were as near as possible to breast height, while avoiding branches, unusual bole swelling, and other abnormalities. The nails of the tacks were shortened so that tacks did not penetrate into the cambium and interfere with growth. The distance between the two tacks was measured using a dial caliper (model M.N. 84, MITUTOYO CO., Japan) with arms extended to 15 cm so that biggest trees in the study could be measured. Diameters were measured to the nearest 0.0025 cm. To minimize the influence of diurnal fluctuations in stem diameter due to cycles of water loss during the day and replenishment at night, all measurements were begun at dawn and were completed before 10 am. No stem shrinkage could be detected in trees originally measured at dawn and remeasured by 10 am. Because of the time constraint, only 2 to 3 blocks of one set of families could be measured on the same morning. Thus, it took 3 days to measure all the study trees, with blocks measured in the same order each week. The position of the live crown may influence the timing of cambial growth phenology on the tree stem (Kozlowski 1971). Thus, 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.

The original objective was to measure dates of budburst and budset

in the leader shoot and to determine how they are correlated with cambial phenology traits, but the large size of the trees precluded scoring budset (Chapter II of this dissertation). Budburst on the leader shoot, however, was scored once every three days in the spring of 1987 using binoculars (Chapter II of this dissertation). Stem height and DBH were also measured on each tree at the end of the 1987 growing season (age 15) in accordance with the measurement schedule for genetic test plantations in the breeding unit. Data on 15-year height and DBH were supplied by the landowner. Bole volume was calculated from height and DBH using an equation for young Douglas-fir described in Adams and Joyce (1990).

Data Analyses

From the weekly diameter measurements, a cumulative diameter growth curve for the 1987 growing season was constructed for each tree (Figure IV.1). The date of cambial growth initiation (days after January 1) was estimated by interpolation as the date when 5% of the annual growth was completed, and the date of cambial growth cessation as the date when 95% of annual growth was completed (Worrall 1970). Duration of cambial growth in days was calculated as the difference between the estimated dates of cessation and initiation (Figure IV.1). Since families did not differ significantly (P-value > 0.05) in the distance between live crown and the point where diameter measurements were taken, adjustment of dates of diameter growth initiation and cessation for the position of live crown were not warranted. The 1987 diameter increment was calculated as the difference between the

diameters when 5% and 95% of annual growth was completed. Diameter growth rate in 1987 was computed by dividing the diameter increment by diameter growth duration.

Variance components were calculated form a random model (Table IV.1) for dates of diameter growth initiation and cessation, duration of diameter growth, date of budburst, diameter increment, and growth rate in the 1987 growing season, and 15-year DBH and volume. Covariance components between any two traits were estimated using the same model, with substituting covariance components for variance components. The analyses were performed on a plot mean basis, with within-plot variances and covariances estimated by pooling individual-plot values (Milliken and Johnson 1984). Only 3 plots out of a total of 240 plots were missing (i.e., plots where all four trees had died). Values for missing plots were calculated for each set as a randomized block experiment according to Steel and Torrie (1980, pp. 209-213), and degrees of freedom for error were adjusted accordingly. The statistical analyses were conducted by using the SAS computer package (SAS Institute Inc. 1985). For the purpose of statistical testing, significance refers to the 0.05 probability level.

To determine the extent of genetic control of cambial phenology traits (objective 1), individual tree heritabilities and their standard errors were estimated following the methods in Namkoong (1981). To assess the degree of association between the cambial phenology traits, between cambial phenology and budburst timing, and between cambial phenology and growth traits (objectives 2 and 3), phenotypic and genetic correlations and their approximate standard errors were

calculated from appropriate variance components and covariance components (Table IV.1) according to Becker (1984). Because progenies in wind-pollinated families are related to a greater extent than half-sibs, the additive genetic variance was estimated as three times the family variance component (Campbell 1979). If a trait was not significantly different among families (P-value > 0.05), however, its heritability was not estimated. Likewise, genetic correlations involving these traits were not determined, only phenotypic correlations were calculated. To evaluate the potential of altering diameter growth phenology traits via selection and breeding, expected genetic gains from selection of parents were determined (Namkoong 1981). To assess the potential influence of selection of parents for greater growth or delayed budburst on diameter growth phenology, correlated responses in cambial phenology due to selection for 15-year bole volume were estimated (Falconer 1981).

RESULTS

Genetic variation and inheritance of phenology and growth traits

Mean date of budburst in 1987 was May 7 (i.e., 126 days from January 1), while mean date of diameter growth initiation was April 14 (Table IV.2). Diameter growth cessation, on average, occurred on August 11, resulting in a mean duration of diameter growth of 118.5 days. Families differed significantly for dates of budburst, and for dates of initiation and cessation of diameter growth, but not for duration of diameter growth (Appendix 16). On average, families ranged by 12 days in mean date of budburst, 8 days in date of diameter growth initiation, 13 days in date of diameter growth cessation, and 10 days in duration of diameter growth. Estimated individual tree heritabilities for dates of diameter growth initiation and cessation were considerably lower ($h^2 \leq 0.23$) than for date of budburst ($h^2 = 0.89$). Heritability could not be estimated for duration of diameter growth because family differences were not significant.

During the 1987 growing season, mean diameter increment was 1.42 cm, with a mean growth rate of 0.012 cm per day, while at the end of growing season, trees had a mean DBH of 15.78 cm and a mean stem volume of 93.0 dm^3 (Table IV.2). Although 15-year DBH and volume differed significantly among families, family differences were not significant for the 1987 diameter increment (Appendix 16). Because diameter increment and growth duration were both marginally different among families ($0.07 \leq$ P-value ≤ 0.10), significant differences in diameter growth rate were detected among families, but the range among family

means was not large. Estimated heritabilities were low for 1987 growth rate and for 15-year DBH and stem volume ($0.12 \leq h^2 \leq 0.22$).

Relationships between growth phenology traits

The estimated genetic correlation (r_A) between dates of diameter growth initiation and cessation was positive ($r_A = 0.60$) (Table IV.3), indicating that genotypes with early growth initiation also have tendency to cease growth early. Since family differences were not significant for duration of diameter growth, genetic correlations between this trait and other traits were not calculated. The estimated phenotypic correlation (r_P) between date of diameter growth initiation and growth duration, however, was nearly zero ($r_P = -0.08$), while the r_P between date of diameter growth cessation and growth duration was strong and positive (0.89). These results indicate that variation in growth duration among individual trees in 1987 was primarily a function of the variation in date of growth cessation. The estimated genetic correlation was weakly positive between dates of budburst and initiation of diameter growth ($r_A = 0.26$), and nearly zero between dates of budburst and growth cessation ($r_A = 0.09$) (Table IV.3). When phenotypic and genetic correlations could be calculated between the same two traits, the estimated correlations were always the same in sign, but phenotypic correlations were weaker in magnitude (Table IV.3).

Relationships between growth phenology and stem growth traits

Duration of diameter growth in 1987 was found to have a weak but

positive phenotypic correlation with 1987 diameter increment, 15-year DBH and 15-year stem volume, but the correlation was three times greater with 1987 increment (r_P = 0.33) than with DBH (r_P = 0.11) (Table IV.4). In contrast, the estimated phenotypic correlation of growth rate in 1987 was high with diameter increment ($r_P = 0.93 \pm 0.20$) and moderate with 15-year DBH ($r_P = 0.41 \pm 0.04$, $r_A = 0.96 \pm 0.26$). This indicates that individual tree variation in diameter increment in 1987 was primarily determined by growth rate rather than by duration of diameter growth, and that growth rate also explains variation in 15-year DBH better than growth duration. Given that diameter increment had a strong phenotypic correlation with growth rate, it was not surprising that diameter increment was also moderately correlated with 15-year DBH ($r_P = 0.43 \pm 0.05$).

Relationships of dates of cambial initiation and cessation with diameter increment in 1987 differed from those with 15-year DBH and volume. Trees with later initiation and cessation of diameter growth had larger diameter increment in 1988, but had smaller 15-year DBH and volume (Table IV.4). Estimated genetic correlations between phenology of diameter growth and 15-year DBH and volume were stronger than their corresponding phenotypic correlations. Later budburst, on the other hand, was associated with both larger diameter growth increment in 1987 and larger 15-year DBH and volume (Table IV.4).

DISCUSSION AND CONCLUSIONS

Genetic variation in phenology of diameter growth

Mean dates of initiation and cessation of diameter growth in 1987 were April 14 and August 11, respectively, resulting in a mean growth duration of about 4 months. The timing of growth initiation is comparable to that in three reports of coastal Douglas-fir, in which the initiation of diameter growth (5% completion of annual diameter growth), or cambial cell division was from Mid-April to Mid-May (Reukema 1965, Griffith 1968, Emmingham 1977). The timing of diameter growth cessation in this study, however, is several weeks earlier than observed in previous studies, where the time of 95% (or 90%) completion of annual growth occurred between the end of August and mid-September (Reukema 1965, Griffith 1968, Emmingham 1977). This discrepancy could be due to differences in populations sampled, differences in test locations, or to different years of observation. For example, Emmingham (1977) found that 4 sources of coastal Douglas-fir completed diameter growth at about the same time at one site, while on another site, one of the sources finished growth about one month later than others. The early cessation of diameter growth found in this study, however, is most likely due to low precipitation in 1987, especially during the later part of the growing season (from July to October) in 1987, in which precipitation was 54% of the average observed in these months in the 14 years that the trees had been growing at the test site (94 mm in 1987, vs an average of 256 mm from 1974 to 1987). Earlier studies have shown that cessation of cambial growth occurs early in dry

summers (Zahner 1963, Reukema 1965).

Dates of both initiation and cessation of diameter growth in 1987 appear to be under weak genetic control ($h^2 \leq 0.23$). The only other estimate of genetic control of cessation (as defined by relative lignification) was given by Dietrichson (1971), whose estimates of family heritabilities ranged from 0.65 to 0.71 in 4-year-old Picea mariana and P. abies. The comparable family heritability estimate in this study was somewhat smaller (0.43). Because the complete lignification of the outermost xylem cells occurs only after termination of cambial cessation (Wardrop 1957), the relative lignification may be a more precise measure of cessation of cambial activity than cessation of diameter growth estimated from dendrometer measurements. Genetic control of cambial phenology in this study was found to be much weaker than budburst timing in the same year (h^2 = 0.89), and budset timing estimated for the same families measured in a different site and year (h^2 = 0.81) (Chapter II of this dissertation).

Relationships between bud and cambial phenology traits

Essentially no relationship was found between date of budburst and diameter growth initiation in this study, as indicated by low phenotypic and genetic correlations (Table IV.3). These two phenology traits were only weakly correlated in Picea abies (r_P = 0.33, Worrall 1970). In addition, Griffith (1968) could not detect differences in dates of diameter growth initiation and cessation between early flushing and late flushing trees of coastal Douglas-fir in British Columbia. The weak correlation between dates of budburst and diameter

growth initiation is unexpected because initiation of cambial growth depends on hormones (particularly auxin) produced in growing shoots (Little and Savidge 1987). Apparently, hormone synthesis and transport occur earlier than budburst timing since initiation of diameter growth preceded budburst by 2-3 weeks in this and earlier studies (Griffith 1968, Worrall 1970). Since bud meristematic activity occurs 4 to 6 weeks before budburst in Douglas-fir (Owens 1968, Fiedler and Owens 1989), earlier phenological events might be better associated with initiation of cambial activity. For example, Emmingham (1977) found that bud swelling occurs about 1 month prior to budburst, but only a few days before cambial cell division in Douglas-fir, suggesting that bud swelling may be a good indicator of initiation of cambial activity. Nevertheless, the weak genetic relationship between dates of budburst and diameter growth initiation means that timing of diameter growth initiation cannot be reliably predicted from observations on the more easily measured budburst.

Relationships between phenology and growth traits

Results from this study suggest that diameter growth in pole-size Douglas-fir is primarily determined by growth rate rather than by duration of the growing season, as indicated by the strong genetic correlation between growth rate and diameter increment in 1987, and the weak phenotypic correlations between growth duration and growth traits. Similar findings for diameter growth in Douglas-fir were reported by Emmingham (1977). Some recent studies also suggest that shoot growth is largely determined by growth rate and not by growth duration in

Douglas-fir (Chapter II of this dissertation) and in Picea abies (Skroppa 1982, Ununger et al. 1988).

Results from this study also indicate that the magnitude of diameter growth is not strongly influenced by timing of diameter growth initiation or cessation. Only phenotypic correlations could be computed between the 1987 diameter increment and dates of growth initiation and cessation. These correlations were weak, but they were both positive as found between shoot phenology and shoot growth in the same families (Chapter II of this dissertation). Dietrichson (1969b) also found that the correlation between 4-year height and cessation of cambial activity was positive among provenances of Picea mariana, but stronger in magnitude than that found in this study ($r_p = 0.84$). Interestingly, phenotypic and genetic correlations between DBH (and volume) at age 15 and both cambial growth phenology traits were negative, albeit not strong.

The conflicting relationships of cambial phenology traits with diameter increment in 1987 and with 15-year DBH (and volume) are difficult to explain. The low precipitation in the 1987 growing season may have led to results that are not representative of those in growing seasons with average (or above) precipitation. The amount of variation in diameter growth increment may be suppressed and genetic relationships between diameter growth phenology and growth may be only indicative of those in dry growing seasons. Perhaps, families with the best overall growth continue to grow in growing seasons with average (or above) precipitation, but they are the most susceptible to drought and cease growth the earliest in a dry season like 1987. Testing this

hypothesis would require studies to determine genetic relationships between growth and cambial phenology in different years and test sites using the same materials used in this study. Furthermore, the genetic relationships need to be determined in different populations because the strength of the correlations may vary among populations.

Implications for breeding

The presence of genetic variation in cambial phenology traits indicates that adaptability could be altered through selection of these traits in breeding programs. Weak genetic control of cambial phenology, however, indicates that genetic progress would be small. For example, if the top 20% of the parents in each set were selected on the basis of early growth cessation, seed orchard offspring of these parents would be expected to cease diameter growth only 1.6 days sooner than progeny of all parent trees prior to selection. Similarly, genetic gains in delayed initiation of diameter growth would be only 2.0 days. Because of the extreme difficulty of measuring cambial phenology traits and the weak potential for genetic gains, it is very doubtful that breeders would be interested in manipulating these traits as a means of improving adaptability in coastal Douglas-fir.

Concerns might be expressed, however, over the potential of detrimentally altering cambial phenology indirectly when selection is applied to other adaptive and/or economic traits. Fortunately, timing of diameter growth was not found to be strongly correlated with either budburst timing or diameter growth in Douglas-fir, thus, correlated response in cambial phenology due to selection for delayed budburst or

greater 15-year volume is not expected to be large. Based on the materials in this study, mating of the top 20% of the parents selected for delayed budburst would produce a correlated response of 0.7 day and 0.3 day in delayed initiation and cessation of cambial growth, respectively. These changes are too small to cause any adverse effects on adaptability.

Interpretation of indirect effects on cambial phenology from selection for growth traits is complicated by the conflicting relationships of cambial phenology with the 1987 diameter increment and with 15-year DBH and volume. If genetic correlations between diameter increment and cambial growth phenology in 1987 are similar to, or somewhat larger than the observed phenotypic correlations, selection of individuals with the largest diameter increment would result in trees with slightly longer growing seasons, and with delayed diameter growth initiation and cessation. Because family differences were not significant for diameter increment and the estimated heritabilities for timing of diameter growth were low, the magnitude of change is not expected to be large. On the other hand, selection for larger 15-year volume would indirectly select for trees with earlier diameter growth initiation and earlier growth cessation in dry years. For example, intermating of the top 20% of parents selected for greater bole volume would be expected to produce progenies with earlier diameter growth initiation (0.7 day) and earlier cambial growth cessation (1.3 days). Earlier growth cessation in dry years would presumably reduce risks of summer drought and fall frost, while earlier diameter-growth initiation would pose greater risk due to spring frost. At any rate, the

magnitude of the expected change in cambial phenology from selection for budburst or growth seems small, which would have minimal effect on adaptability of improved stocks.

Table IV.1. Form of analyses of variance of phenology and growth traits measured in the Coyote Creek test plantation.

Source of Variation	Degrees of Freedom	Expected Mean Squares[a, b]
Sets	1	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)} + f\sigma^2_{B(S)} + bf\sigma^2_S$
Blocks(Set)	6	$\sigma^2_W/k + \sigma^2_E + f\sigma^2_{B(S)}$
Families(Set)	58	$\sigma^2_W/k + \sigma^2_E + b\sigma^2_{F(S)}$
Plot error	171	$\sigma^2_W/k + \sigma^2_E$
Within-plot error	559	σ^2_W

[a] Replace expected mean squares by expected mean cross products for estimating covariance components.

[b] k = 2.91, harmonic mean number of trees per plot,

b = 4, number of blocks within sets, and

f = 30, number of families per set.

σ^2_W - Within-plot variance,

σ^2_E - plot variance,

$\sigma^2_{F(S)}$ - family within set variance,

$\sigma^2_{B(S)}$ - block within set variance, and

σ^2_S - set variance.

Table IV.2. Estimated test means, levels of significance among families (P-value), individual tree heritabilities (h^2), and coefficients of variation for growth and phenology traits measured in the 1987 growing season.

Traits	Mean[a]	P-value	h^2 [b]	Coefficient of variation[c] Phenotypic	Genetic
Date of budburst[d]	126.5 (121.1-132.7)	<0.01	0.89(0.04)	3.37	3.19
Diameter growth					
Initiation[d]	104.0 (101.1-109.7)	<0.01	0.23(0.09)	3.88	1.86
Cessation[d]	222.5 (217.5-230.4)	0.02	0.11(0.07)	4.01	1.35
Duration (days)	118.5 (114.4-124.2)	0.07	____[e]	7.00	____[e]
Increment(cm)	1.42 (1.23-1.63)	0.10	____[e]	18.31	____[e]
Rate(cm/day)	0.012 (0.011-0.014)	0.03	0.12(0.07)	17.34	5.95
15-year bole					
DBH(cm)	15.78 (12.39-17.96)	0.01	0.19(0.09)	18.08	7.84
Volume(dm^3)	93.0 (58.8-120.8)	<0.01	0.22(0.09)	33.58	15.66

[a] Range among family means in parentheses.

[b] Standard errors in parentheses.

[c] Square roots of phenotypic and additive genetic variances, respectively, divided by the mean.

[d] Days from January 1, 1987.

[e] It was not estimated because families did not differ significantly (P-value > 0.05) for this trait.

Table IV.3. Estimated genetic (above the diagonal) and phenotypic (below the diagonal) correlations among growth phenology traits.[a]

	Date of Budburst	Date of Diameter growth	
		Initiation	Cessation
Date of Budburst	____	0.26(0.19)	0.09(0.25)
Date of Diameter growth			
Initiation	0.08(0.04)	____	0.60(0.26)
Cessation	0.02(0.04)	0.37(0.04)	____
Diameter growth[b] Duration (Days)	-0.02(0.04)	-0.08(0.04)	0.89(0.02)

[a] Standard errors of the estimates in parentheses.

[b] Genetic correlations of this trait with other traits were not estimated because this trait was non-significant among families.

Table IV.4. Estimated genetic (r_A) and phenotypic (r_P) correlations between phenology and growth traits.[a]

		Date of Diameter Growth Initiation	Date of Diameter Growth Cessation	Diameter Growth[b] Duration	Date of Budburst
1987 diameter growth					
Increment[b]	r_A				
	r_P	0.17(0.04)	0.38(0.12)	0.33(0.09)	0.10(0.04)
Bole volume at age 15					
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)

[a] Standard errors of these estimates in parentheses.

[b] Genetic correlations of this trait with other traits were not estimated because families did not differ significantly (P-value < 0.05) for this trait.

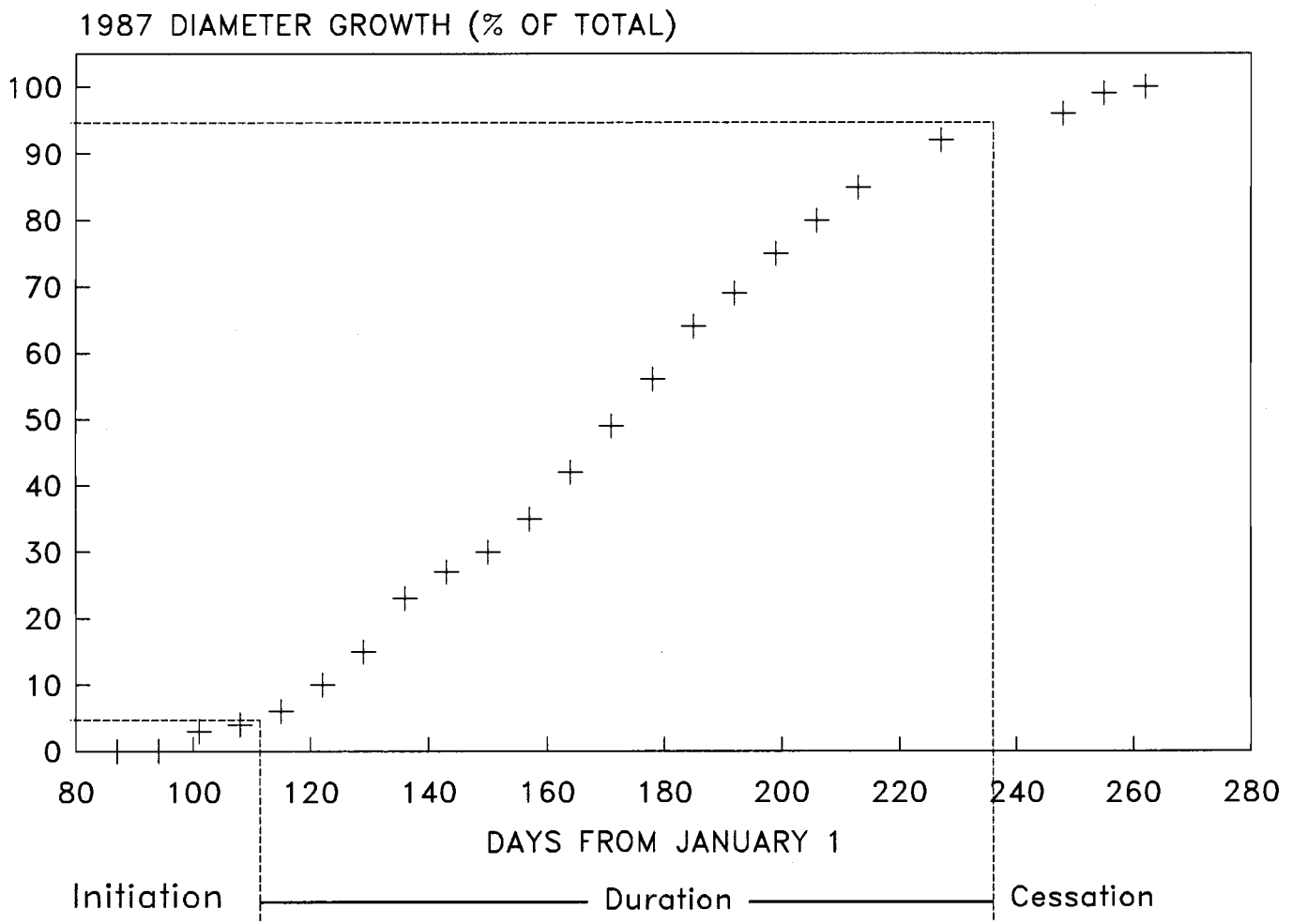

Figure IV.1. A typical cumulative diameter growth curve for an individual tree in 1987. Weekly cumulative increments are shown by +. Dates of cambial growth initiation and cessation are defined as the dates when 5% and 95% of the cumulative growth, respectively, have occurred.

CHAPTER V

GENERAL CONCLUSIONS

Both dates of budburst and budset were genetically variable and strongly inherited in 13- to 16-year-old trees, indicating that bud phenology in coastal Douglas-fir can be readily modified via selection and breeding. Because of a strong genetic correlation between dates of budburst and budset in pole-size trees, selection for delayed budburst timing will result in delayed budset timing, and vice versa. As found in previous studies, bud phenology was also genetically variable and amendable to genetic manipulation in seedlings. Furthermore, because budset timing was weakly correlated with budburst timing in seedlings, selection for one trait will have little influence on the other. The ability to genetically manipulate bud phenology has important implications for breeding because bud phenology is related to adaptability. For example, the risk of spring frost damage can be reduced by selecting trees with delayed budburst, while selection of trees for earlier budset will reduce risk of damage from summer drought and fall frost.

Although genetic gains in bud phenology of pole-size trees from selection applied at this stage are expected to be great, the efficiency of breeding these traits could be substantially improved if early testing is utilized. Early selection, for example, might be employed to shorten the breeding cycle. Based on data in this study, selection for budburst timing at age 2 would result in 60% of the genetic gain expected if selection was delayed to age 15. Adding time

for breeding, breeding cycle could be accomplished less than half the time if selections are made at age 2. Thus, genetic gain per generation for budburst timing would be considerably better with early selection. Early selection for budset timing was less promising since relative efficiency for this trait was only about half that for budburst. Early selection to reduce breeding cycle is only possible if other economic and adaptive traits could be selected at early age. Since this is not likely to be possible in Douglas-fir, the primary role of early testing is as an early culling device, i.e., to identify families with low genetic potential, so they can be culled prior to field testing. In this aspect, early testing is the first stage of two or multiple stages of selection. Two-stage selection (i.e., initial culling at age 1 or 2 followed by final selection at age 15) appears promising for both dates of budburst and budset. Results of this study indicate that 40% to 60% of families could be culled for either trait at the seedling stage with little loss in the genetic gain expected if all selections were delayed to age 15. This would result in considerable savings in cost associated with establishing, maintaining and measuring these tests.

Dates of budburst and budset were positively correlated with growth in both seedlings and pole-size trees in this study. This implies that selection for increased growth will delay budburst and budset in the next generation. Presumably, delayed budburst does not reduce adaptability because it will decrease susceptibility to spring frost damage. Delayed budset, however, will reduce adaptability by increasing the probability of damage from summer drought or fall frost.

This may be especially true in seedlings because under favorable conditions, seedlings continue shoot growth much later (until late summer or early fall) than pole-size trees (early summer).

Genetic relationships between growth and bud phenology need to be examined in additional populations because the strength and direction of these relationships may vary among populations. In addition, seedlings and older trees have different growth patterns. Seedlings have the habit of free growth which leads to delayed budset, whereas in older trees height growth is mainly predetermined. Because growing conditions in nurseries are favorable for free growth, results of nursery seedling studies may not be applicable to the phenology of seedlings outplanted in the field, where the growing conditions are not as favorable. Further research is needed to determine at what age free growth stops and the extent to which free growth is under genetic control in field-grown seedlings. If shoot growth of seedlings continues as late into the year after planting, as observed in the nursery tests of this study, budset timing will need to be given serious considerations in Douglas-fir breeding programs.

This study showed that bud phenology could be effectively measured for selection purposes using less laborious methods than commonly employed. For example, it is not necessary to score bud phenology on the leader, even though phenology of the leader is of primary interest. Scoring buds on branches in pole-size trees was found to be very reliable for ranking both individual trees and families for budburst timing, as long as the branches are not near the ground or shaded by surrounding trees. Scoring buds on branches was not as effective for

evaluating budset on the leader as for budburst. If family ranking for bud phenology is of main interest, scoring budburst or budset on a single day and calculating the proportion of trees which have burst or set buds would be effective for assessing the relative timing of these traits. This method is efficient if scoring occurs when the proportion of trees having burst or set buds in a test is at intermediate levels (i.e., between 30% and 70%). This approach is especially useful in roguing seed orchards or in early testing where family selection is the primary objective.

Because cambial phenology is difficult to measure, it is unlikely to be used in improving adaptability unless it can be readily manipulated in breeding programs or unless selection for increased growth or other traits alters cambial phenology greatly. The limited genetic variation and weak inheritance of cambial phenology traits found in this study indicate that genetic gains in cambial phenology from selection and breeding will be small. Furthermore, because cambial phenology has weak genetic correlations with growth traits and budburst timing, selection for greater growth or delayed budburst will produce little correlated response in cambial phenology, thus, have little influence on the adaptability of improved stocks.

At this point, however, it is not possible to draw firm conclusions about the impact of Douglas-fir breeding programs on cambial phenology since this study was based on only one population. Further research is necessary to determine whether cambial phenology is inherited in a similar fashion in other populations. Furthermore, this study was limited to cambial measurements made in only a single

plantation and growing season in a particularly dry year; which may not be representative of the expression of cambial phenology in more normal years. Thus, additional study is needed to better understand the influence of environment (i.e., weather and test sites) on the genetic expression of cambial phenology. If further studies are to be conducted, more efficient methods of measuring cambial phenology will be needed. For example, Savidge (1989) found that the presence of coniferin (a lignin precursor) is a good indicator of cambial growth activity. But a quick assay method for the coniferin will be required before it can be used in genetic studies of cambial phenology.

In addition to growth phenology, other traits such as drought and cold hardiness are vital to adaptation. The ability to genetically manipulate these traits is important, especially for improving adaptation to sites where drought and winter cold are the main constraints to tree growth. Because hardiness traits are difficult and expensive to measure, their genetics are poorly understood. Results from a few studies suggest that bud phenology traits are correlated with cold and drought hardiness in seedlings and young trees of Douglas-fir. Further research is needed to determine the genetic relationships between hardiness traits and phenology in different populations. Furthermore, genetic relationships between growth and hardiness traits need to be determined in order to evaluate implications of selection for greater growth on hardiness. With better understanding of genetic control of these adaptive traits, and their relationships with growth, more efficient strategies of breeding and deploying genetically improved material can be devised.

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APPENDICES

Appendix 1. Locations of field and seedling tests measured in this study and survival at the time of phenology measurements.

Site	Latitude	Longitude	Elevation (m)	Year sown	Survival (%)
Field Tests					
Oxbow	43°51'29"	123°33'36"	396	1972	85
Coyote Creek	43°55'31"	123°17'46"	274	1973	85
Clay Creek	43°54'36"	123°34'52"	137	1973	89
Smith Creek	43°51'49"	123°23'34"	305	1975	70
Seedling Tests					
<u>Direct-sown</u>					
Washington	46°50'	123°08'	46	1986[a]	72
				1987[a]	86
<u>Greenhouse</u>					
Washington	46°55'	123°57'	61	1987[b]	94
Oregon	44°32'	122°54'	110	1987[b]	96
<u>Transplant</u>					
Washington	46°50'	123°08'	46	1988[c]	74
Oregon	43°38'	123°34'	62	1988[c]	81

[a] Germinant seed sown directly into nursery beds. Corresponding survival is at the end of the second growing season.

[b] Germinant seed sown directly into containers in the greenhouse. Corresponding survival is at the end of the first growing season.

[c] Transplants of 1-0 plug seedlings from greenhouses. Corresponding survival is at the end of the second growing season.

Appendix 2. Analyses of variance for date of budburst[a] in field tests.[b]

Source of variation	1986 Degree of freedom	1986 MS	1986 F-value	1986 P-value	1987 Degree of freedom	1987 MS	1987 F-value	1987 P-value
Plantations	2	1157.3	29.57	0.03	2	230.4	5.54	0.15
Sets	1	140.5	0.98	0.35	1	148.0	1.45	0.26
Plantations x Sets	2	38.9	1.72	0.17	2	41.6	2.67	0.07
Blocks (Plantations Sets)	18	16.8	1.77	0.03	18	10.9	2.27	<0.01
Families(Sets)	58	116.0	12.21	<0.01	56	64.8	9.89	<0.01
Families(Sets) x Plantations	116	11.3	1.19	0.09	112	6.5	1.35	0.02
Plot error	518	9.5			498	4.8		
Within-plot error	1601	26.4			1450	12.2		

[a] Measured as days from January 1.

[b] Based on measurements of individuals from 60 families (30 in each set) in three plantations (Clay Creek, Coyote Creek and Oxbow) in 1986, and 58 families (29 in each set) in three plantations (Coyote Creek, Oxbow and Smith Creek) in 1987.

Appendix 3. Analyses of variance for bud phenology traits measured on the fifth whorl branches in 1988 at the Smith Creek plantation.[a]

Source of variation	Degree of freedom	Date of Budburst[b]			Date of Budset[b]			Growth Duration (days)		
		MS	F-value	P-value	MS	F-value	P-value	MS	F-value	P-value
Sets	1	40.2	0.97	0.36	224.9	5.64	0.02	74.9	6.84	0.01
Blocks(Sets	6	15.9	2.12	0.05	10.9	1.45	0.20	5.8	1.53	0.17
Families(Sets)	56	33.2	4.45	<0.01	30.3	4.06	<0.01	5.7	1.50	0.03
Plot error	164	7.5			7.5			3.8		
Within plot error	421	13.3			14.0			7.2		

[a] Based on 58 families (29 in each set).

[b] Measured as days from January 1.

Appendix 4. Estimated genetic correlations in date of budburst[a] between different measurement years in the same plantations, and between plantations in the same and different years.[b]

	1986			1987			1988
	Clay Cr.	Coyote Cr.	Oxbow	Coyote Cr.	Oxbow	Smith Cr.	Smith Cr.
1986							
Clay Creek	____						
Coyote Creek	1.05	____					
Oxbow	0.93	0.90	____				
1987							
Coyote Creek	0.98	0.99	0.84	____			
Oxbow	0.90	0.92	0.97	0.87	____		
Smith Creek	1.03	0.98	0.99	0.95	0.98	____	
1988							
Smith Creek	1.01	0.94	0.94	0.93	0.94	0.98	____

[a] Measured as days from January 1.

[b] Date of budburst measured on the leader shoot in 1986 and 1987, but on fifth whorl branches in 1988.

Appendix 5. Analyses of variance for bud phenology traits in the direct sown seedling test.[a]

Source of variation	Degree of Freedom	1-year budset[b] MS	1-year budset[b] P-value	2-year budburst[b] MS	2-year budburst[b] P-value
Years	1	34771.8	<0.01	1289.2	0.01
Blocks(Year)	11	109.0	0.34	43.0	0.40
Sets	1	214.4	0.50	32.0	0.75
Sets x Years	1	174.0	0.23	28.3	0.54
Sets x Blocks(Years)	11	85.3	0.17	36.9	<0.01
Families(Sets)	41	192.6	<0.01	108.8	<0.01
Families(Sets) x Years	41	64.1	0.38	26.5	0.03
Plot error	439	60.3		14.8	
Within-plot error	1192	100.3		28.2	

[a] Based on 43 families tested in 1986 and 1987 at the Washington nursery.

[b] Measured as days from January 1.

Appendix 6. Analysis of variance for date of first-year budset[a] in the greenhouse seedling test.[b]

Source of variation	Degree of Freedom	MS	F-value	P-value
Greenhouses	1	79194.2	918.17	<0.01
Blocks(Greenhouses)	12	82.7	1.87	0.15
Sets	1	505.4	81.26	<0.01
Sets x Greenhouses	1	3.6	0.27	1.00
Sets x Blocks(greenhouses)	12	44.2	2.33	0.01
Families(Sets)	43	63.3	1.66	0.05
Families(Sets) x Greenhouses	43	38.2	2.01	<0.01
Plot error	512	19.0		
Within-plot error	1758	53.3		

[a] Measured as days from January 1.

[b] Based on 45 families tested in two greenhouses, one in Washington and the other in Oregon.

Appendix 7. Analyses of variance for bud phenology traits in the transplant seedling test.[a]

Source of variation	Degree of Freedom	2-year budburst[b] MS	2-year budburst[b] P-value	2-year budset[b] MS	2-year budset[b] P-value	Growth Duration (Days) MS	Growth Duration (Days) P-value
Nurseries	1	14661.3	<0.01	189045.8	<0.01	98591.5	<0.01
Blocks(Nurseries)	10	44.5	<0.01	6109.4	<0.01	6591.2	<0.01
Sets	1	68.7	0.26	131.4	0.95	382.3	0.80
Sets x Nurseries	1	20.7	0.17	2733.2	0.09	2251.6	0.12
Sets x Blocks(Nurseries)	10	8.4	<0.01	751.5	<0.01	771.2	<0.01
Families(Sets)	43	20.7	<0.01	141.0	0.02	146.5	0.02
Families(Sets) x Nurseries	43	3.7	0.29	74.9	0.79	78.9	0.80
Plot error	410	3.3		91.7		97.1	
Within-plot error	1130	47.8		247.0		250.0	

[a] Based on 45 families tested in two nurseries, one in Washington and the other in Oregon.

[b] Measured as days from January 1.

Appendix II.8. Estimated genetic correlations for date of first-year budset[a] between replicates of seedling tests.

	Direct sown test		Greenhouse test	
	1986	1987	Washington	Oregon
Direct sown test				
1986	____			
1987	1.02	____		
Greenhouse test				
Washington	0.53	0.29	____	
Oregon	1.13	0.71	0.57	____

[a] Measured as days from January 1.

Appendix II.9. Estimated genetic correlations for date of second-year budburst[a] between replicates of seedling tests.

	Direct sown test		Transplant test	
	1986	1987	Washington	Oregon
Direct sown test				
1986	____			
1987	0.90	____		
Transplant test				
Washington	0.93	0.95	____	
Oregon	0.68	0.87	0.97	____

[a] Measured as days from January 1.

Appendix 10. Estimated individual tree (h^2) and family (h_F^2) heritabilities for date of budburst[a] on the fifth whorl branch, genetic correlations (r_A) between dates of budburst on the fifth whorl and leader shoot, and relative efficiencies of individual (RE_I) and family (RE_F) selection for date of leader budburst based on branch budburst measurements.[b, c]

Test plantations	h^2	h_F^2	r_A	RE_I	RE_F
1986					
Clay Creek	0.88(0.14)	0.62(0.03)	0.99(0.01)	1.07	1.01
Coyote Creek	0.83(0.14)	0.60(0.03)	0.99(0.01)	1.06	0.99
Oxbow	0.90(0.15)	0.61(0.03)	0.98(0.02)	1.03	0.99
1987					
Coyote Creek	1.00(0.15)	0.64(0.02)	0.98(0.01)	1.04	0.99
Oxbow	0.83(0.14)	0.60(0.03)	0.97(0.03)	1.14	1.02
Smith Creek	0.84(0.16)	0.58(0.04)	0.99(0.02)	0.99	0.99

[a] Measured as days from January 1.

[b] Families differed significantly ($P < 0.01$) for date of budburst on leader shoot and branches.

[c] Standard errors of estimated genetic parameters in parentheses.

Appendix 11. Relative efficiencies of using proportions of trees that have burst buds on the leader shoot in assessing family ranking in plantations for date of budburst on the leader.

Trait	Mean[a]	P-value[b]	h_F^2 [c]	r_A [d]	RE[e]
Plantation/Year: Clay Creek/1986					
Date of budburst[f]	135.2 (126.4-143.6)	<0.01	0.79(0.04)	____	____
Budburst proportion on scoring date[g]:					
122	0.07 (0.00-0.50)	<0.01	0.47(0.11)	-0.73(0.12)	0.56
129	0.29 (0.00-0.87)	<0.01	0.73(0.06)	-0.93(0.03)	0.89
136	0.76 (0.06-1.00)	<0.01	0.69(0.07)	-0.93(0.04)	0.87
143	0.98 (0.79-1.00)	0.07	____	____	____
Plantation/Year: Coyote Creek/1986					
Date of budburst	138.3 (131.3-144.1)	<0.01	0.79(0.04)	____	____
Budburst proportion on scoring date:					
123	0.02 (0.00-0.29)	<0.01	0.43(0.12)	-0.79(0.14)	0.57
130	0.17 (0.00-0.56)	<0.01	0.47(0.11)	-0.99(0.06)	0.76
137	0.64 (0.08-1.00)	<0.01	0.77(0.05)	-1.01(0.02)	1.00
144	0.99 (0.85-1.00)	0.47	____	____	____
Plantation/Year: Oxbow/1986					
Date of budburst	139.5 (130.0-145.9)	<0.01	0.78(0.14)	____	____

Appendix 11. (continued)

Budburst proportion on scoring date:					
121	0.01 (0.00-0.21)	<0.01	0.63(0.08)	-0.51(0.14)	0.46
128	0.05 (0.00-0.40)	<0.01	0.42(0.10)	-1.04(0.10)	0.76
135	0.15 (0.00-0.62)	<0.01	0.55(0.09)	-0.97(0.05)	0.80
142	0.61 (0.06-1.00)	<0.01	0.72(0.06)	-1.00(0.02)	0.95
149	0.96 (0.75-1.00)	0.11	____	____	____
Plantation/Year: Coyote Creek/1987					
Date of budburst	126.5 (121.1-132.7)	<0.01	0.83(0.04)	____	____
Budburst proportion on scoring date:					
120	0.07 (0.00-0.29)	0.16	____	____	____
123	0.16 (0.00-0.58)	<0.01	0.54(0.10)	-0.91(0.07)	0.73
126	0.43 (0.00-1.00)	<0.01	0.81(0.04)	-0.96(0.02)	0.94
129	0.67 (0.12-1.00)	<0.01	0.74(0.06)	-1.01(0.07)	0.95
132	0.89 (0.40-1.00)	<0.01	0.69(0.07)	-0.90(0.05)	0.82
Plantation/Year: Oxbow/1987					
Date of budburst	128.1 (123.4-132.9)	<0.01	0.72(0.06)	____	____
Budburst proportion on scoring date:					
121	0.07 (0.00-0.42)	<0.01	0.43(0.12)	-0.90(0.10)	0.70
124	0.16 (0.00-0.56)	<0.01	0.44(0.12)	-1.02(0.04)	0.79
127	0.33 (0.00-0.81)	<0.01	0.60(0.08)	-0.95(0.04)	0.87
130	0.79 (0.33-1.00)	<0.01	0.48(0.11)	-0.99(0.07)	0.81
133	0.96 (0.65-1.00)	<0.01	0.57(0.09)	-0.93(0.11)	0.82

Appendix 11. (Continued)

Plantation/Year: Smith Creek/1987

Date of budburst	127.3 (120.7-135.1)	<0.01	0.77(0.05)	____	____
Budburst proportion on scoring date:					
122	0.08 (0.00-0.69)	<0.01	0.51(0.11)	-0.73(0.11)	0.59
125	0.20 (0.00-0.81)	<0.01	0.64(0.08)	-0.86(0.06)	0.78
128	0.35 (0.00-0.87)	<0.01	0.61(0.08)	-0.94(0.04)	0.84
131	0.69 (0.06-1.00)	<0.01	0.59(0.09)	-0.97(0.05)	0.85
134	0.91 (0.27-1.00)	<0.01	0.67(0.07)	-0.87(0.07)	0.82

[a] Plantation mean, with the range among family means in the parentheses.

[b] Level of statistical significance among families.

[c] Family heritability, with standard errors in parentheses.

[d] Genetic correlations between date of budburst and budburst proportion, with standard errors in parentheses.

[e] Relative efficiency of selecting date of budburst based on budburst proportion on the leader shoot.

[f] Measured as days from January 1.

[g] Proportion of trees that have burst buds on a given scoring date (days from January 1).

Appendix 12. Relative efficiencies of using proportions of trees that have burst buds on the fifth whorl branches in assessing family ranking in plantations for date of budburst on the leader.

Trait	Mean[a]	P-value[b]	h_F^2 [c]	r_A [d]	RE[e]
Plantation/Year: Clay Creek/1986					
Date of budburst[f]	135.2 (126.4-143.6)	<0.01	0.79(0.04)	____	____
Budburst proportion on scoring date[g]:					
122	0.12 (0.00-0.54)	<0.01	0.66(0.07)	-0.78(0.12)	0.71
129	0.36 (0.00-0.94)	<0.01	0.75(0.05)	-0.96(0.03)	0.94
136	0.76 (0.12-1.00)	<0.01	0.74(0.06)	-0.80(0.06)	0.77
143	0.98 (0.69-1.00)	<0.01	0.67(0.07)	-0.72(0.09)	0.66
Plantation/Year: Coyote Creek/1986					
Date of budburst	138.3 (131.3-144.1)	<0.01	0.79(0.04)	____	____
Budburst proportion on scoring date:					
123	0.05 (0.00-0.40)	<0.01	0.42(0.12)	-0.73(0.14)	0.53
130	0.21 (0.00-0.75)	<0.01	0.62(0.08)	-0.94(0.04)	0.83
137	0.70 (0.06-1.00)	<0.01	0.81(0.04)	-0.97(0.03)	0.98
144	0.98 (0.79-1.00)	0.04	0.29(0.15)	-1.00(0.24)	0.61
Plantation/Year: Oxbow/1986					
Date of budburst	139.5 (130.0-145.9)	<0.01	0.78(0.14)	____	____

Appendix 12. (continued)

Budburst proportion on scoring date:					
121	0.02 (0.00-0.35)	<0.01	0.37(0.13)	-0.97(0.16)	0.66
128	0.06 (0.00-0.46)	<0.01	0.53(0.10)	-0.92(0.08)	0.75
135	0.15 (0.00-0.69)	<0.01	0.67(0.07)	-0.98(0.05)	0.89
142	0.69 (0.06-1.00)	<0.01	0.73(0.06)	-0.95(0.04)	0.91
149	0.98 (0.79-1.00)	0.30	____	____	____
Plantation/Year: Coyote Creek/1987					
Date of budburst	126.5 (121.1-132.7)	<0.01	0.83(0.04)	____	____
Budburst proportion on scoring date:					
120	0.11 (0.00-0.52)	<0.01	0.51(0.10)	-0.89(0.08)	0.70
123	0.26 (0.00-0.81)	<0.01	0.73(0.06)	-0.89(0.05)	0.83
126	0.44 (0.00-1.00)	<0.01	0.82(0.04)	-0.93(0.03)	0.92
129	0.67 (0.12-1.00)	<0.01	0.80(0.04)	-0.94(0.04)	0.91
132	0.94 (0.54-1.00)	<0.01	0.68(0.07)	-0.78(0.09)	0.70
Plantation/Year: Oxbow/1987					
Date of budburst	128.1 (123.4-132.9)	<0.01	0.72(0.06)	____	____
Budburst proportion on scoring date:					
121	0.13 (0.00-0.67)	<0.01	0.65(0.07)	-0.87(0.08)	0.83
124	0.17 (0.00-0.85)	<0.01	0.73(0.06)	-0.87(0.06)	0.87
127	0.50 (0.00-1.00)	<0.01	0.65(0.07)	-1.00(0.05)	0.95
130	0.88 (0.33-1.00)	<0.01	0.67(0.07)	-0.88(0.08)	0.84
133	0.97 (0.85-1.00)	0.36	____	____	____

Appendix 12. (Continued)

Plantation/Year: Smith Creek/1987					
Date of budburst	127.3 (120.7-135.1)	<0.01	0.77(0.05)	____	____
Budburst proportion on scoring date:					
122	0.09 (0.00-0.69)	<0.01	0.57(0.09)	-0.77(0.11)	0.66
125	0.20 (0.00-0.81)	<0.01	0.61(0.08)	-0.89(0.08)	0.79
128	0.34 (0.00-0.94)	<0.01	0.68(0.07)	-0.96(0.05)	0.90
131	0.70 (0.15-1.00)	<0.01	0.60(0.09)	-0.93(0.07)	0.82
134	0.90 (0.42-1.00)	<0.01	0.60(0.09)	-0.85(0.10)	0.75

[a] Plantation mean, with the range among family means in the parentheses.

[b] Level of statistical significance among families.

[c] Family heritability, with standard errors in parentheses.

[d] Genetic correlations between date of budburst on the leader and budburst proportion on fifth whorl brunches, with standard errors in parentheses.

[e] Relative efficiency of selecting date of budburst based on budburst proportion on fifth whorl branches.

[f] Measured as days from January 1.

[g] Proportion of trees that have burst buds on a given scoring date (days from January 1).

Appendix 13. Relative efficiencies of using proportions of trees that have burst or set buds on the fifth whorl branches in assessing family ranking for date of budburst or budset on the fifth whorl branches at Smith Creek in 1988.

Trait	Mean[a]	P-value[b]	h_F^2 [c]	r_A [d]	RE[e]
Date of budburst[f]	140.4 (133.7-150.0)	<0.01	0.76(0.05)	____	____
Budburst proportion on scoring date[g]:					
132	0.08 (0.00-0.42)	0.02	0.30(0.15)	-1.07(0.19)	0.67
135	0.22 (0.00-0.69)	<0.01	0.65(0.08)	-0.92(0.05)	0.85
139	0.51 (0.00-1.00)	<0.01	0.58(0.09)	-1.07(0.04)	0.94
143	0.87 (0.12-1.00)	<0.01	0.53(0.10)	-1.00(0.07)	0.83
146	0.95 (0.48-1.00)	0.02	0.39(0.13)	-0.97(0.13)	0.69
Date of budset[f]	154.3 (149.9-163.5)	<0.01	0.77(0.05)	____	____
Budset proportion on scoring date[h]:					
149	0.26 (0.00-0.87)	<0.01	0.64(0.08)	-0.83(0.08)	0.76
153	0.59 (0.00-1.00)	<0.01	0.61(0.08)	-0.98(0.04)	0.88
156	0.85 (0.29-1.00)	<0.01	0.61(0.08)	-0.95(0.04)	0.85
160	0.92 (0.35-1.00)	<0.01	0.46(0.12)	-0.95(0.07)	0.74
163	0.97 (0.62-1.00)	0.14	____	____	____
167	0.97 (0.62-1.00)	0.14	____	____	____
170	0.996 (0.87-1.00)	0.59	____	____	____

[a]. Plantation mean, with the range among family means in the parentheses.

[b]. Level of statistical significance among families.

Appendix 13. (continued)

[c] Family heritability, with standard errors in parentheses.

[d] Genetic correlations between date of budburst (or budset) and budburst (or budset) proportion on fifth whorl brunches, with standard errors in parentheses.

[e] Relative efficiency of selecting date of budburst (or budset) based on budburst (or budset) proportion on the fifth whorl branches.

[f] Measured as days from January 1.

[g] Proportion of trees that have burst buds on a given scoring date (days from January 1).

[h] Proportion of trees that have set buds on a given scoring date (days from January 1).

Appendix 14. Relative efficiencies of using proportions of seedlings that have burst buds on the leader shoot in assessing family ranking in seedling tests for date of second-year budburst on the leader.

Trait	Mean[a]	P-value[b]	h_F^2 [c]	r_A [d]	RE[e]
Test/Replicate: Direct sown/1986					
Date of budburst[f]	109.8 (103.1-117.0)	<0.10	0.80(0.05)	____	____
Budburst proportion on scoring date[g]:					
90	0.27 (0.07-0.58)	0.06	____	____	____
93	0.30 (0.07-0.58)	0.16	____	____	____
97	0.34 (0.07-0.65)	<0.01	0.46(0.13)	-0.85(0.15)	0.65
101	0.42 (0.14-0.79)	<0.01	0.59(0.10)	-0.94(0.07)	0.80
105	0.52 (0.18-0.89)	<0.01	0.61(0.09)	-0.94(0.05)	0.83
109	0.63 (0.25-1.00)	<0.01	0.72(0.07)	-0.93(0.04)	0.88
113	0.79 (0.54-1.00)	<0.01	0.66(0.08)	-0.90(0.06)	0.82
117	0.90 (0.68-1.00)	<0.01	0.54(0.11)	-0.91(0.09)	0.75
Test/Replicate: Direct sown/1987					
Date of budburst	112.8 (108.9-116.7)	<0.01	0.82(0.04)	____	____
Budburst proportion on scoring date:					
104	0.15 (0.00-0.42)	0.11	____	____	____
108	0.31 (0.08-0.67)	<0.01	0.59(0.10)	-0.93(0.09)	0.79
110	0.48 (0.21-0.92)	<0.01	0.79(0.05)	-0.91(0.05)	0.89
112	0.64 (0.37-0.96)	<0.01	0.70(0.07)	-0.98(0.02)	0.90
115	0.76 (0.46-1.00)	<0.01	0.64(0.08)	-1.03(0.03)	0.88

Appendix 14. (continued)

117	0.89 (0.62-1.00)	<0.01	0.47(0.13)	-1.06(0.10)	0.75
119	0.97 (0.83-1.00)	<0.01	0.46(0.13)	-0.77(0.16)	0.58
122	0.99 (0.87-1.00)	0.01	0.44(0.13)	-0.66(0.20)	0.48
Test/Replicate: Transplant/Washington Nursery					
Date of budburst	142.6 (139.7-145.1)	<0.01	0.68(0.08)	____	____
Budburst proportion on scoring date:					
137	0.12 (0.00-0.46)	0.12	____	____	____
140	0.41 (0.07-0.83)	<0.01	0.60(0.09)	-1.01(0.02)	0.94
145	0.96 (0.75-1.00)	0.16	____	____	____
Test/Replicate: Transplant/Oregon Nursery					
Date of budburst	132.2 (127.0-135.5)	<0.01	0.77(0.05)	____	____
Budburst proportion on scoring date:					
123	0.03 (0.00-0.33)	<0.01	0.47(0.12)	-0.76(0.15)	0.59
126	0.08 (0.00-0.58)	<0.01	0.63(0.09)	-0.81(0.09)	0.74
130	0.38 (0.06-0.83)	<0.01	0.67(0.08)	-0.98(0.03)	0.92
133	0.81 (0.44-1.00)	<0.01	0.57(0.10)	-0.98(0.06)	0.84
137	0.98 (0.79-1.00)	0.09	____	____	____

[a] Test mean, with the range among family means in the parentheses.

[b] Level of statistical significance among families.

[c] Family heritability, with standard errors in parentheses.

Appendix 14. (continued)

[d] Genetic correlations between date of budburst and budburst proportion, with standard errors in parentheses.

[e] Relative efficiency of selecting date of budburst based on budburst proportion.

[f] Measured as days from January 1.

[g] Proportion of trees that have burst buds on a given scoring date (days from January 1).

Appendix 15. Relative efficiencies of using proportions of seedlings that have set buds on the leader shoot in assessing family ranking in seedling tests for date of first-year budset on the leader.

Trait	Mean[a]	P-value[b]	h_F^2 [c]	r_A [d]	RE[e]
Test/Replicate: Direct sown/1986					
Date of budset[f]	271.4 (258.8-279.7)	<0.01	0.49(0.12)	____	____
Budset proportion on scoring date[g]:					
236	0.26 (0.00-0.51)	0.08	____	____	____
243	0.34 (0.07-0.59)	0.19	____	____	____
252	0.38 (0.11-0.59)	0.27	____	____	____
265	0.41 (0.11-0.68)	0.01	0.40(0.14)	-0.80(0.11)	0.71
276	0.79 (0.43-0.96)	<0.01	0.50(0.12)	-1.19(0.15)	1.01
Test/Replicate: Direct sown/1987					
Date of budset	287.1 (280.5-296.0)	<0.01	0.70(0.07)	____	____
Budset proportion on scoring date:					
273	0.18 (0.00-0.46)	0.07	____	____	____
281	0.52 (0.12-0.87)	<0.01	0.55(0.11)	-0.91(0.06)	0.81
287	0.73 (0.42-0.98)	<0.01	0.53(0.11)	-0.97(0.04)	0.84
294	0.84 (0.46-1.00)	<0.01	0.48(0.12)	-0.97(0.06)	0.80
Test/Replicate: Greenhouse/Oregon					
Date of budset	247.8 (243.5-257.7)	<0.01	0.72(0.06)	____	____

Appendix 15. (continued)

Budset proportion on scoring date:					
233	0.08 (0.00-0.35)	<0.01	0.62(0.08)	0.27(0.22)	0.25
240	0.33 (0.16-0.53)	0.07	____	____	____
247	0.77 (0.44-0.94)	<0.01	0.55(0.10)	-1.03(0.04)	0.89
254	0.85 (0.56-0.97)	<0.01	0.51(0.11)	-1.00(0.05)	0.84
262	0.91 (0.62-1.00)	<0.01	0.46(0.12)	-0.97(0.07)	0.77
Test/Replicate: Greenhouse/Washington					
Date of budset	225.1 (220.2-229.0)	<0.01	0.50(0.12)	____	____
Budset proportion on scoring date:					
213	0.07 (0.00-0.42)	<0.01	0.86(0.03)	0.09(0.23)	0.11
220	0.41 (0.04-0.75)	<0.01	0.53(0.10)	-0.80(0.11)	0.84
227	0.91 (0.75-1.00)	0.12	____	____	____
234	0.99 (0.96-1.00)	0.93	____	____	____

[a] Test mean, with the range among family means in the parentheses.

[b] Level of statistical significance among families.

[c] Family heritability, with standard errors in parentheses.

[d] Genetic correlations between date of budset and budset proportion, with standard errors in parentheses.

[e] Relative efficiency of selecting date of budset based on budset proportion.

[f] Measured as days from January 1.

[g] Proportion of trees that have set buds on a given scoring date (days from January 1).

Appendix 16. Analyses of variance for phenology and growth traits measured at the Coyote Creek plantation.

Source of variation	Degree of freedom	Date of Budburst[a]			Date of Diameter[a] Growth Initiation			Date of Diameter[a] Growth Cessation		
		MS	F-value	P-value	MS	F-value	P-value	MS	F-value	P-value
Sets	1	0.84	0.15	1.00	17.72	0.18	0.82	0.63	0.03	0.98
Blocks(Sets)	6	5.11	1.20	0.31	113.33	22.11	<0.01	775.57	32.81	<0.01
Families(Sets)	58	29.90	7.04	<0.01	10.13	1.97	<0.01	35.73	1.51	0.02
Plot error	171	4.25			5.14			23.64		
Within-plot error	559	13.19			15.25			81.47		

[a] Measured as days from January 1.

Appendix 16. (continued)

Source of variation	Degree of freedom	Diameter Growth								
		Duration(days)			Increment(cm)			Ratex10 (cm/day)		
		MS	F-value	P-value	MS	F-value	P-value	MS	F-value	P-value
Sets	1	25.08	0.07	0.98	0.0032	0.10	0.99	0.000003	0.15	1.00
Blocks(Sets)	6	598.02	27.72	<0.01	0.2066	9.73	<0.01	0.000766	5.18	<0.01
Families(Sets)	58	29.27	1.36	0.07	0.0277	1.30	0.10	0.000218	1.47	0.03
Plot error	171	21.57			0.0212			0.000148		
Within-plot error	559	69.89			0.0693			0.000410		

Appendix 16. (continued)

Source of variation	Degree of freedom	15-year DBH(cm) MS	F-value	P-value	15-year Volume(dm^3) MS	F-value	P-value
Sets	1	14.34	1.70	0.21	1873.54	1.63	0.22
Blocks(Sets)	6	5.16	1.69	0.13	742.47	2.27	0.04
Families(Sets)	58	5.09	1.66	0.01	610.04	1.86	0.01
Plot error	171	3.06			327.30		
Within plot error	559	7.08			892.64		