PERSISTENCE AND AGE-AGE GENETIC CORRELATIONS OF STEM DEFECTS IN COASTAL DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* VAR. *MENZIESII* (MIRB.) FRANCO)[1]

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ABSTRACT

Persistence of stem defects, including bole sinuosity, large branch size and the occurrence of steep-angled branches (*i.e.*, forks and ramicorns), and the efficiency of early selection against these traits, were investigated in 90 open-pollinated families of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) from coastal Oregon. Trees originally measured for these traits at age 12 were remeasured at age 24 in three progeny test plantations. The majority of trees scored as having ramicorn branches at age 12 (62%) still had them at age 24, but most forks (53%) had become ramicorns by the second measurement. Thus, there seems little need to score forks and ramicorns separately; simply counting the number of whorls with steep-angled branches seems sufficient for selection purposes. Branch size scores were relatively consistent between the two ages, but not scores for bole sinuosity. Because of low estimated individual and family heritability estimates (≤0.13 and ≤0.41, respectively), predicted genetic responses in DBH and individual stem-defect traits were only modest for this population. Nevertheless, with the exception of sinuosity, genetic correlations between comparable stem-defect traits at the two ages were strong ($r_A \geq 0.82$), and predicted responses in traits at age 24, from selection at age 12, were nearly as great as responses expected if selection was delayed until age 24. Branch size and occurrence of steep-angled branches were unfavorably (positively) correlated with DBH (estimated $r_A = 0.56$ and 0.41, respectively). Thus, it is important to include these stem defect traits as selection criteria in Douglas-fir breeding programs, if stem volume growth is to be improved without sacrificing wood quality.

Key words: *Pseudotsuga menziesii*, forks and ramicorn branches, stem sinuosity, wood quality, early selection, genetic gains.

INTRODUCTION

Although most breeding programs in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) focused primarily on improving bole volume growth in their early years, increasing attention is now given to wood quality (WOODS 1993). Wood density is the most important criterion influencing wood quality, but stem form and branching habit also have considerable impact on the yield and value of wood (KELLOGG & KENNEDY 1986, AUBRY *et al.* 1998). Stem form and branching deficiencies (*i.e.*, stem defects) include bole sinuosity, large diameter branches, and the presence of forks and ramicorns (Figure 1). Stem defects, especially when present in the lower bole, not only lower the magnitude and grade of lumber recovered from trees, but also increase the cost of transportation, and decrease the efficiency of timber processing (SHELBOURNE 1969, 1970). In addition, forked stems and large branches magnify the difficulty and cost of pruning,

increase knottiness and compression wood, and reduce lumber strength and pulp yield (ZOBEL 1971, SCHERMANN *et al.* 1997).

Most selections in first-generation Douglas-fir progeny tests were made by age 15 (SILEN 1978), and recent results indicate that to maximize genetic gains in bole volume over time, selections should be completed even a few years earlier (JOHNSON *et al.* 1997). It is also convenient to assess stem defect traits at this early age when these traits are most easily observed and measured (ADAMS & HOWE 1985, KING *et al.* 1992). In order to maximize genetic response of individual traits and minimize costs, however, it is necessary to restrict selection to as few traits as possible. Thus, it is reasonable to question the need for assessing stem defects at this age, if at all.

There are three arguments for not including stem defect traits as selection criteria. First, stem defects observed in young Douglas-fir trees may diminish as the trees become larger, and therefore, have only a minor impact on overall

wood quality. Although, young, especially fast-growing, plantations of Douglas-fir often exhibit high frequencies of stem defects (CAMPBELL 1965, WALTERS & KOZAK 1967, ADAMS & BASTIEN 1994, SCHERMANN *et al.* 1997), mature stands appear, at least superficially, to be straight stemmed and of good form (SILEN 1978). Thus, the extent to which stem defects persist over time is of interest. Second, the value of including stem defect traits in early selection may be questioned if stem defects scored at young ages are poorly correlated with defects realized in older trees. Finally, if stem defects are weakly associated with rate of stem growth, there may be little need to include these defects as selection criteria, at least in early generations of breeding, because selection for faster stem growth will have limited, if any, practical consequences for stem form and branching habit. If strong, unfavorable genetic correlations between stem growth and stem defects exist, however, inclusion of stem defect traits in breeding programs may be unavoidable (ADAMS & BASTIEN 1994).

In 1984, the Pacific Northwest Tree Improvement Research Cooperative (PNWTIRC) undertook the "Douglas-fir Measurement Study" as its first project, with the goals of evaluating the potential for genetic improvement of stem quality in young (10 to 15 year-old) coastal Douglas-fir plantations, achieving a better understanding of the inheritance of stem form and branching traits, and developing inexpensive, but efficient measurement methods for these traits (PNWTIRC Annual Reports: 1987, 1988, 1989, Forestry Research Laboratory, Oregon State University, Corvallis). Twelve to 13 year-old trees were measured in 90 open-pollinated families on each of three test sites. These same trees were measured in 1996 when the trees were 24–25 years old, or about one-half rotation age, with the following objectives in mind: (1) To determine the degree of persistence of stem defects with age; (2) To evaluate the efficiency of early selection for these traits; and, (3) To assess the implications of selection for stem growth on stem defect traits. Results of this follow-up to the "Measurement Study" are reported here.

MATERIALS AND METHODS

Materials

Families included in this study are progeny from first-generation (*i.e.*, wild stand) parent-tree selections made in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program, located in the Central Oregon Coast Range (QUAM 1988). At each test site (all at < 500 m elevation), the 90 families were planted as three 30-family sets; each set as a separate randomized complete block experiment with four replications. Families were represented by four-tree non-contiguous plots in each replication, with spacing of 3.05 × 3.05 m at planting (1–0

container stock). The test sites were fenced in order to prevent browsing by deer and elk. Survival of seedlings one year after planting was very high (> 85%), and dead trees were replaced the first 4 years following planting. Replacement trees, however, were not included in any of the analyses.

At the time of the original measurements in 1984, trees were 12 years old from seed at two of the test sites (Coyote Creek and Clay Creek), and one year older at the Oxbow site. Systematic thinning removed 25% of the trees at Coyote Creek and 34% from Oxbow prior to the 1996 measurements, but the Clay Creek plantation was re-measured prior to thinning. In total, over all three sites, 3755 trees were measured at age "12" (*i.e.*, ages 12–13), and 2974 trees at age "24" (*i.e.*, ages 24–25).

Traits and measurement methods

One goal of the original measurement study was to develop quick, but accurate, methods of measuring stem form and branching characteristics, including bole sinuosity, branch size and angle, number of branches, and occurrence of forks and ramicorns. Forks and ramicorns (Figure 1) are steep-angled branches (SABs) diverging less than 30° from the bole; forks being of similar diameter to the main stem, while ramicorns are definitely smaller. In 1984, the frequencies of forks and ramicorns were scored separately as the total number of whorls (not including the uppermost whorl on the tree) with at least one of these defects. Branch angle and size were measured on one side of the tree at the whorl nearest to breast height (1.37 m). The total number of branches at this whorl was also recorded. Branch angle was visually estimated using angles etched on clear plastic as a guide, and branch size by averaging the diameters of the two largest branches at the whorl (3 cm away from the bole). Sinuosity, defined as waviness in the bole between whorls (Figure 1), was scored for the second interwhorl from the top of tree, where it could be easily seen from the ground, using a sinuosity index (ADAMS & HOWE 1985). The sinuosity index is calculated as the product of the number of displacements or crooks in the interwhorl times the maximum distance the bole is displaced from the position it would occupy if the stem had no sinuosity, measured in units of ½ the diameter of the interwhorl.

In 1996, all stem defects were scored visually in the lowest 5 m section of the bole, with height to 5 m visually estimated. Measurements were restricted to the lowest 5 m log because it is the most valuable portion of the tree, and because it roughly corresponds to the portion of the bole measured at age 12. Instead of scoring forks and ramicorns as separate traits in 1996, all whorls with SABs in the lowest 5 m log were recorded, and SABs placed into
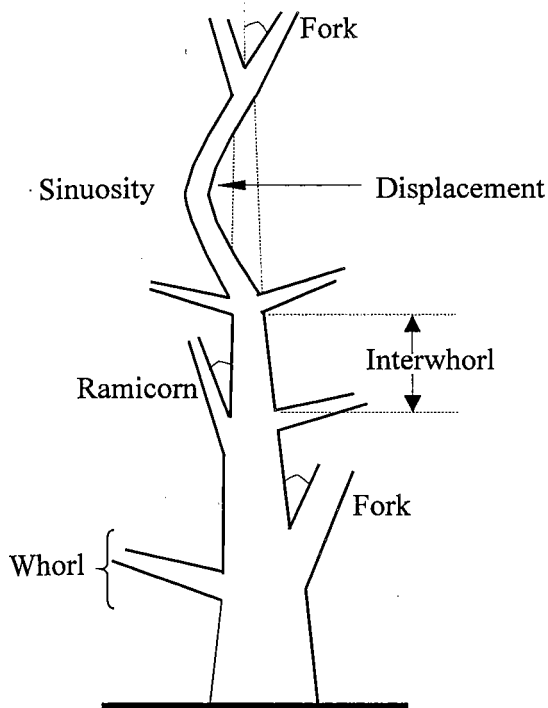
Figure 1. Illustration of terms used in defining stem defects in Douglas-fir (note: all angles are <30°).

one of five size classes relative to the diameter of the bole (*i.e.*, ≤ 20% of the bole diameter, 21–40%, 41–60%, 61–80%, >80%). SABs in > 80% class are considered forks and all others as ramicorns. We compared three measures of total SABs: total number of SABs, total number of whorls with one or more SABs, and total weighted SABs, where each SAB was weighted by its size class (> 80% was given a weight of 5, 61–80% was given a weight of 4, etc.) before summing. Estimated genetic correlations (see below) between these measures were near unity (TEMEL 1997); thus, we report only on the number of whorls with SABs (forks and ramicorns) because this is the easiest trait to score. Forks and ramicorns reduce usable wood volume in two major ways. First, when SABs are large, the section of the log around the whorl must be cut out. Second, even when an SAB is relatively small, the diameter of the bole below the SAB appears to be reduced relative to what it would have been without the SAB. In an attempt to quantify such loses we scored the impact of SABs (ISAB) on log value into four classes: 1 = no impact; 2 = low impact or slight reduction in harvestable wood volume; 3 = moderate impact; and 4 = severe impact, including loss of a section of the bole or otherwise greatly reduced wood volume.

Branch size in 1996 was measured by visually scoring the largest branch in diameter from 1 (small) to 4 (thick). Branch angle was not measured because branch angle

flattens with age and there appeared to be little variation among trees for this trait in lowest 5 m log. Number of branches was not recorded since it is unlikely to change over time. We do not consider branch angle and number of branches further in this paper, but see KING *et al.* (1992) and ST.CLAIR (1994) for information on the genetics of these traits in Douglas-fir.

Sinuosity was also estimated visually, by scoring the most sinuous interwhorl in the lowest 5 m log on a scale of 1 (perfectly straight) to 4 (very sinuous). Bole diameters at breast height (DBH) were recorded in both measurement years.

Data analysis

Objective 1 – Persistence of stem defects with age. Measurements made in 1996 were compared to those made on the same trees in 1984.

To assess the persistence of forks and ramicorns observed in 1984 in trees measured in 1996, the frequencies of trees with one or more of these defects in the lowest 5 m of the bole were compared at the two ages. Trees ranged in height between 3 m and 11 m (mean = 7.64 m) at age 12, but trees less than 6 m tall at this age (total of 300 trees) were not included in the comparison. This is because only forks and ramicorns found below the top whorl in the tree were counted in 1984, and the uppermost of these whorls may have been below 5 m at this time. Thus, one or more whorls in the first 5 m of these trees at age 24 may not have been scorable at age 12. Likewise, forks and ramicorns counted in whorls above 5 m in 1984, should not be included in the analysis. Fortunately, forks and ramicorns were recorded individually for the second, third, and fourth whorls from the top of the tree in 1984. Using heights taken at ages 5, 10 and 12 (as part of the routine measurement schedule for these plantations), we developed a crude yearly-height increment curve for each tree, and removed forks and ramicorns counted in 1984 that were likely to have been in whorls above 5 m. After these adjustments, trees were subdivided in four classes at the two ages: trees with (1) only ramicorns, (2) only forks, (3) both forks and ramicorns, and (4) neither forks nor ramicorns. The proportion of trees in each of the four classes at age 24 that fall within each class at age 12 was calculated, and vice versa. In this manner, the persistence of SAB types observed at age 12, and the origin of these types observed at age 24, could be evaluated.

All trees available in 1996 could be used for branch size comparisons between the two ages, because branches were measured near breast height in 1984, when all trees were at least 3 m tall. Measurements could not be compared directly, however, because different methods were used to assess branch diameter in the two years. Nevertheless, it is possible to determine whether relative branch

sizes in 1996 are consistent with those in 1984. Trees falling into the thickest 10% (n = 297) and thinnest 10% of branch diameters in 1984 were identified and frequency distributions of the four 1996 branch size scores within each 1984 branch size class compared. We also estimated the correlation between mean family branch sizes (over all three sites) at the two ages.

Because sinuosity was measured only at the second interwhorl from the top of the tree in 1984, all trees whose second interwhorl was likely above 5 m at this time, were removed from the comparison (n = 2494, or 80% of the trees). Analyses similar to those described above for branch size was then carried out with the remaining trees. First, trees having perfectly straight index values (n = 171) and those making up the most sinuous 10% of trees in 1984 (n = 48) were identified, and the frequency distribution of the 1996 sinuosity scores within each of these classes compared. The correlation between mean family scores at ages 12 and 24 was also estimated using data for all measured trees at the two ages.

Objective 2 – Efficiency of early selection. The efficiency of early selection depends, to large extent, on the degree to which selection (early age) and response (later age) traits are controlled by the same genes. Inheritance of traits at ages 12 and 24 was compared by estimating individual tree narrow sense heritabilities at the two ages, and genetic correlations between traits at each age and between ages. The efficiency of early selection was also evaluated directly by comparing predicted genetic response in stem-defect traits at age 24 when these traits are selected at the same age (direct response) with responses at age 24 when these traits are selected at age 12 (correlated response).

All traits were subjected to analysis of variance (ANOVA) using the data set combined over three sites and the following linear model to represent values of individual trees:

$$z_{ijklm} = \mu + t_i + s_j + ts_{ij} + b_{ijk} + f_{jl} + ft_{ijl} + e_{ijkl} + w_{ijklm} \qquad [1]$$

where: μ is the overall mean, t_i is the random effect of the ith test site, $E(t_i) = 0$, $Var(t_i) = \sigma_t^2$; s_j is the random effect of the jth set, $E(s_j) = 0$, $Var(s_j) = \sigma_s^2$; ts_{ij} is the random interaction effect of the jth set with i^{th} test site, $E(ts_{ij}) = 0$, $Var(ts_{ij}) = \sigma_{ts}^2$; b_{ijk} is the random effect of the kth block within the jth set and i^{th} test site, $E(b_{ijk}) = 0$, $Var(b_{ijk}) = \sigma_b^2$; f_{jl} is the random effect of the lth family within the jth set, $E(f_{jl}) = 0$, $Var(f_{jl}) = \sigma_f^2$; ft_{ijl} is the random interaction effect of the lth family within the jth set and with the ith test site, $E(ft_{ijl}) = 0$, $Var(ft_{ijl}) = \sigma_{ft}^2$; e_{ijkl} is the random plot error of the lth family within k^{th} block of the jth set of the ith test site (plot error), $E(e_{ijkl}) = 0$, $Var(e_{ijkl}) = \sigma_e^2$, and w_{ijklm} is the random tree error of the mth tree in the $ijkl^{th}$ plot, $E(w_{ijkl}) = 0$, $Var(w_{ijkl})$

$$= \sigma_w^2.$$

ANOVAs were first conducted using the GLM (general linear models) procedure of the SAS statistical software package (SAS Institute Inc. 1990) in order to test significance of the pooled family(set) and site × family(set) variances (using Type III sums of squares). Variance components were then estimated using the REML (restricted maximum likelihood) method of the SAS VARCOMP (variance components) procedure. Because of mortality and thinning, there was considerable imbalance in the data sets by age 24 (TEMEL 1997). REML estimates of variance components are considered more reliable than ANOVA estimates when such imbalance exists (SWALLOW & MONAHAN 1984, SEARLE et al. 1992, WHITE 1996). Preliminary analyses indicated that several traits violated basic assumptions of ANOVA (STEEL & TORRIE 1980). Thus, the total number of whorls with SABs (WSAB) in both years was transformed to $\sqrt{WSAB + 0.5}$ prior to analysis, while sinuosity index (SIN) in 1984 was transformed to LOG (SIN + 1) (ADAMS & HOWE 1985). Means appearing in tables are in the original scales of measurement. All tests of significance were conducted at the 0.05 probability level.

Because the open-pollinated families came from parent trees in wild stands, it was assumed that individuals within open-pollinated families are more closely related than half-sibs (CAMPBELL 1979), and additive genetic variance (σ_A^2) was estimated as $3\sigma_f^2$. Individual-tree heritability was then calculated as

$$h_i^2 = \frac{\sigma_A^2}{\sigma_P^2} \qquad [2]$$

where $\sigma_P^2 = \sigma_w^2 + \sigma_e^2 + \sigma_{ft}^2 + \sigma_f^2$. Genetic correlation was estimated as

$$r_A = \frac{Cov_{f(x,y)}}{\sqrt{\sigma_{f(x)}^2 \sigma_{f(y)}^2}} \qquad [3]$$

where $Cov_{f(x,y)}$ is the family component of covariance between traits x and y, and $\sigma_{f(x)}^2$ and $\sigma_{f(y)}^2$ are the respective family components of variance. $Cov_{f(x,y)}$ was calculated by conducting ANOVA on the sums of traits, and then using the relationship:

$$Cov_{f(x,y)} = (\sigma_{f(x+y)}^2 - \sigma_{f(x)}^2 - \sigma_{f(y)}^2)/2$$

(FREUND 1962).

To compare direct and correlated responses, we assumed that the top 10% of parent trees in each set are selected on the basis of the performance of their open-pollinated offspring and clones of these trees randomly mated in an open-pollinated seed orchard to produce improved progeny. Under this scenario, expected response

of trait at age 24 (*i.e.*, genetic gain) from direct selection (G_y) is calculated as

$$G_y = 2i h^2_{f(y)} \sqrt{\sigma^2_{\bar{P}(y)}} \qquad [4]$$

where, i = 1.755, $h^2_{f(y)}$ is heritability of family means for this trait, and $\sigma^2_{\bar{P}(y)}$ is phenotypic variance of family means (NANSON 1970, NAMKOONG 1979, BECKER 1984). Family heritability was estimated as

$$h^2_f = \frac{\frac{1}{4} \sigma^2_{A(y)}}{\sigma^2_{\bar{P}(y)}} \qquad [5]$$

Correlated response in trait y at age 24 when selection is applied to the same trait at age 12 (*i.e.*, trait x) was calculated as

$$CR_y = 2 i r_A \sqrt{h^2_{f(y)} h^2_{f(x)} \sigma^2_{\bar{P}(y)}} \qquad [6]$$

where $h^2_{f(y)}$ and $h^2_{f(x)}$ are family heritabilities for traits y and x, respectively.

Objective 3 – Implications of selection for stem growth on stem defect traits. To evaluate the potential implications of selecting for stem growth while ignoring stem defect traits, we calculated predicted correlated responses in stem defect traits when DBH is selected. These calculations were carried out using equation [6], where y is the stem defect trait at age 24, and x is DBH at either age 12 or 24.

RESULTS AND DISCUSSION

Persistence of stem defects

Trees more than doubled in DBH, on average, from 1984 to 1996 (Table 1). Although trees at the Oxbow test site were one year older, they had the slowest growth (mean DBH in 1996 = 219.7 mm versus 231.4 mm at Coyote Creek and 228.1 mm at Clay Creek), but only half the number of whorls with SABs (mean WSAB in 1996 = 0.25 versus 0.45 at Coyote Creek and 0.58 at Clay Creek). Site differences, however, were non-significant for all traits.

The proportion of trees across all three sites with at least one steep-angled branch was almost the same in 1996 (32.3%) and 1984 (31.8%), but the relative distribution of ramicorns and forks differed at the two ages. The proportion of trees with only ramicorns increased from 24.5% at age 12 to 30.2% at age 24, while the proportion with only forks decreased from 5% to 1.5%. The proportion with

both ramicorns and forks was small at both ages (2.3% and 0.6%, respectively). The majority of trees with only ramicorns at age 12 still had ramicorns at age 24 (62%, Figure 2a), but only a few trees scored as having only forks at the early age still had them 12 years later (14%, Figure 2b). Interestingly, more than half (53%) of the trees with only forks at age 12, were recorded as having only ramicorns at age 24. The majority (83%) of trees free of SABs at age 12 were also scored as having no SABs at age 24.

The above results show that a high proportion of SABs persist the largest SABs (*i.e.*, forks) at age 12, became ramicorn branches by age 24. A likely explanation for the
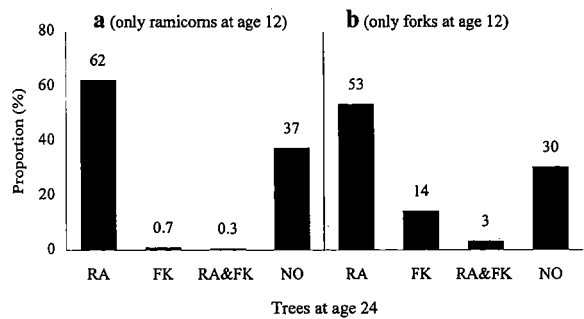

Figure 2. Distribution of trees with only ramicorns (RA), only forks (FK), both ramicorns and forks (RA & FK), and neither forks nor ramicorns (NO), in the lowest 5 m log at age 24, among trees with only ramicorns (a) or with only forks (b) at age 12.

loss of forks is that differential growth between the forked leaders resulted in one stem gaining dominance as trees aged. Of trees that had no SABs at age 12, 17% were recorded with at least one SAB at age 24. Since it is unlikely that trees developed new SABs in this period of time, SABs on these trees were either missed in the earlier assessment, and/or the process of determining 5 m log height at one or both ages resulted in some errors in counting SABs. Because so few forks remained at age 24, and the majority of forks at age 12 developed into ramicorn branches, there does not seem to be a compelling reason to distinguish between these two branching types. Therefore, for the remainder of this paper, forks and ramicorns will be considered together in the single category of SABs.

The distributions of branch diameter scores at age 24 among trees with the 10% smallest (Figure 3a) and 10% largest (Figure 3b) branches at age 12, indicate that branch size measurement remain consistent across the two ages. This is confirmed by the relatively strong family mean correlation (r_f) estimated between branch measurements at ages 12 and 24 ($r_f = 0.70, p < 0.01$).

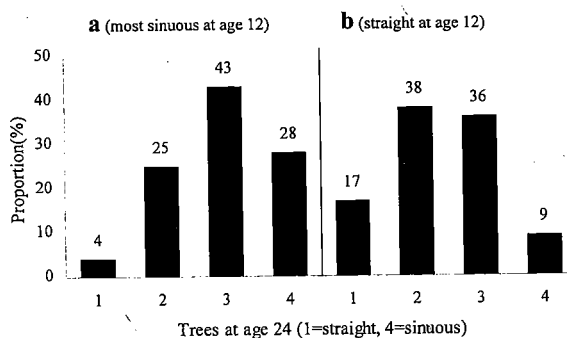Sinuosity scores, on the other hand, appear to lack consistency between ages 12 and 24. While there is a

a (most sinuous at age 12) **b** (straight at age 12)

Trees at age 24 (1=straight, 4=sinuous)

Figure 3. Distribution of branch size scores at age 24 among the 10 % of trees with the smallest branches at age 12 (a), and the 10 % with the largest branches at age 12 (b).

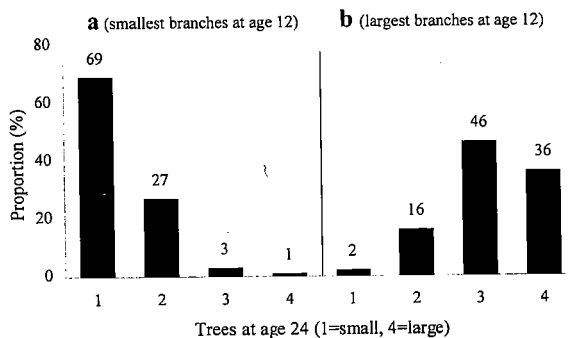tendency for high sinuosity scores at age 24 among the

a (smallest branches at age 12) **b** (largest branches at age 12)

Trees at age 24 (1=small, 4=large)

Figure 4. Distribution of sinuosity scores at age 24 among the 10 % of trees with the highest sinuosity index scores at age 12 (a), and perfectly straight trees at age 12 (b).

10% most sinuous trees at age 12, almost 30 % of these trees were scored in the lowest two sinuosity classes at the older age (Figure 4a). In addition, among trees scored as perfectly straight at age 12, more than 40 % were scored in the two most sinuous classes at age 24 (Figure 4b). Thus, while the most sinuous stems may persist over time, stem sinuosity at age 12 appears to be only poorly related to sinuosity seen in older trees. This is confirmed by the weak family mean correlation between sinuosity scores at the two ages ($r_f = 0.22$, $p > 0.05$).

Two reasons for lack of consistency in sinuosity scores can be offered. First, because mean DBH more than doubled in the 12-year period between measurements, much of the sinuosity observed at age 12 was probably covered up by radial growth (SPICER *et al.* 2000). Second, the measurement methods were quite different at the two ages. At age 12, only the second interwhorl from the top of the tree was scored for sinuosity, while at age 24, the most sinuous interwhorl in the lowest 5 m log was scored.

Efficiency of early selection

Means and frequency distributions of traits measured in

1984, based on only trees remaining in 1996, were very similar to those based on all trees present in 1984 (TEMEL 1997). It is concluded, therefore, that tree losses from 1984 to 1996 (mostly due to the systematic thinning in 1995) resulted in little or no bias in estimating population means, variances, and genetic parameters of traits measured in 1996.

Considerable genetic variation was observed for all traits at both ages, with pooled family-within-set variances statistically significant in all cases. The 90 families ranged by about 25% in mean DBH at both ages (Table 1). Families also ranged widely in stem defect traits. In both years, for example, the mean number of whorls with SABs ranged from as few as one in every 10 trees in some families, to more than one for every tree in other families.

Despite wide family variation, estimated individual-tree narrow-sense heritabilities were low ($h_i^2 \leq 0.13$) for all traits in both years (Table 1). Significant family by site interaction was observed for three of four traits at age 12 (not including WSAB) and one trait at age 24 (DBH), but this interaction contributed little to the heritability estimates, because within plot error was responsible for nearly 95% of the total variation among individual trees (after adjusting for block effects) (TEMEL 1997). Thus, h_i^2 estimates based on the data pooled across sites were nearly equivalent to the means of the h_i^2's estimated for individual sites. Although low, estimates of h_i^2 in this study do not appear to be particularly unusual or inconsistent with other reports in Douglas-fir. For example, JOHNSON *et al.* (1997) reported h_i^2 estimates for DBH in western Oregon breeding populations tested on a total of 26 sites. Nineteen percent of the individual-site estimates for ages 15 and 20 were less than or equal to the estimates in this study (*i.e.*, ≤ 0.11). Family heritabilities for stem defects were somewhat greater, on average, in two previous investigations (mean = 0.44) than in our study (mean = 0.31), but both of the previous studies included only a single test site (ADAMS & BASTIEN 1994, SCHERMANN *et al.* 1997). Our results support earlier observations that stem defects in Douglas-fir have heritabilities similar in magnitude to tree height and DBH (BIROT & CHRISTOPHE 1983, BASTIEN & ROMAN-AMAT 1990, KING *et al.* 1988, KING *et al.* 1992, ADAMS & BASTIEN 1994, ST.CLAIR 1994, SCHERMANN *et al.* 1997).

The estimated genetic correlation between WSAB and ISAB in 1996 was 1.03 suggesting these traits are under identical genetic control. Thus, only one of these traits needs to be measured when assessing SAB defects. Because WSAB is based on counts, and ISAB on subjective scoring, we believe WSAB is more reliable, even though heritabilities for the two traits were the same in this study (Table 1).

Genetic relationships between traits were similar at the two ages (Table 2). While sinuosity (SIN) was weakly

Table 1. Estimated overall means and family ranges (90 families), and individual-tree and family heritabilities, for stem-defect traits and bole diameter at two ages.

Trait[a]	Mean		Heritabilities[c]	
	Overall	Family range[b]	Individual	Family
Age 12				
WSAB[d]	0.50	0.10–1.16	0.08	0.33
SIN[e]	1.47	0.37–3.57	0.13	0.41
BRS (mm)	21.90	19.9–24.7	0.08	0.30
DBH (mm)	108.70	96.3–120.2	0.08	0.28
Age 24				
WSAB[d]	0.43	0.06–1.08	0.05	0.23
ISAB	0.48	0.31–2.32	0.05	0.23
SIN[e]	2.22	0.20–2.86	0.11	0.36
BRS (mm)	2.28	0.15–2.86	0.10	0.33
DBH (mm)	226.40	204.7–259.1	0.11	0.34

[a] WSAB = Number of whorls with steep-angled branches, ISAB = impact of steep-angled branches, SIN = bole sinuosity, BRS = branch diameter, DBH = diameter at breast height (1.37 m) (see text for details).
[b] Over 90 open-pollinated families.
[c] Standard errors of heritability estimates (DICKERSON 1969) ranged 0.02 to 0.04 for individual tree heritabilities and 0.10 to 0.12 for family heritabilities.
[d] Heritability estimates based on transformed variates ($\sqrt{WSAB + 0.5}$). Means are given in original scale.
[e] Heritability estimates based on transformed variates (LOG(SIN + 1)). Means are given in original scale.

Table 2. Estimated genetic correlations between stem-defect and size (DBH) traits at age 12 (below diagonal) and at age 24 (above diagonal), and between corresponding traits at the two ages (bold on diagonal).

		Age 24			
		WSAB	SIN	BRS	DBH
	WSAB	**0.82**	0.21	0.65	0.41
Age	SIN	0.20	**0.36**	0.12	0.12
12	BRS	0.20	–0.11	**0.89**	0.56
	DBH	0.61	0.01	0.33	**0.84**

correlated with all other traits (mean $r_A = 0.09$), WSAB, branch diameter (BRS) and DBH were positively correlated to varying degrees (mean $r_A = 0.46$). The results are consistent with earlier findings in Douglas-fir (BIROT & CHRISTOPHE 1983, KING et al. 1992, ADAMS & BASTIEN 1994, SCHERMANN et al. 1997). Strong, positive, genetic correlations between ages 12 and 24, for WSAB, BRS and DBH indicate these traits are largely controlled by the same genes at the two ages (Table 2). SIN at age 24, however, appears to have only a weak genetic correlation with SIN at age 12. Recall, however, that the score for SIN at age 24 was based on the most sinuous interwhorl in

the lowest 5 m log, while at age 12 it was based on the second interwhorl from the top of the tree.

Despite low heritabilities, modest gains are predicted for all traits at age 24 when the top 10% of parent trees are selected based on the performance of their offspring for these traits (direct selection) (Table 3-A). Thus, when parent trees are selected for DBH, tree diameters at age 24 are expected to increase by 15.05 mm in the next generation, or by 6.7% of the current generation mean. Similarly, selecting the 10% of parent trees with the lowest number of whorls with SABs in their offspring, is expected to reduce the number of whorls with SABs by 21% in the next generation. Given the strong genetic correlations between ages 12 and 24 for DBH, WSAB and BRS, and the similarities of their heritabilities at the two ages, it is not surprising that early selection (age 12) for these traits is predicted to be nearly as effective in improving age 24 performance, as waiting until age 24 to make selections (Table 3-A). Thus, it is clear that selection against SABs and large diameter branches can be effectively done prior to age 15, when selection for stem growth is most efficient (JOHNSON et al. 1997).

Selection against sinuosity at age 12, however, is expected to only be about 40% as effective in reducing stem sinuosity at age 24, as waiting until the later age to make selections. It is unlikely, however, that selections

Table 3. Estimated responses in diameter at breast height (DBH), number of whorls with steep angled branches (WSAB), branch diameter (BRS), and bole sinuosity (SIN) at age 24 A) when the same trait is selected at age 24 or at age 12, and B0 when DBH is selected at age 24 or at age 12 [a,b]. Numbers in parentheses indicate expected responses as percent of experimental population means.

Response trait	(A) Response trait selected at age:		(B) DBH selected at age:	
	24	12	24	12
DBH (mm)	+15.05 (6.7)	+11.44 (5.0)	–	–
WSAB	–0.09 (21.1)	–0.08 (18.6)	+0.03 (6.8)	+0.04 (9.3)
BRS	–0.27 (11.7)	–0.23 (10.1)	+0.15 (6.6)	+0.16 (7.0)
SIN	0.28 (12.6)	–0.11 (5.0)	+0.03 (1.4)	+0.05 (2.3)

a) Assumes top 10% of parent trees are selected within each 30-family set based on the mean values of their offspring.
b) For traits transformed prior to analysis (*i.e.* SIN at age 12 and WSAB at ages 12 and 24), expected responses are given in the original units of the traits (*i.e.*, calculated from back transformed means expected after selection).

would be delayed beyond age 15 for this single trait. An investigation of split stems from 32, 25-year-old trees sampled in the Coyote Creek plantation revealed that sinuosity observed at age 12 only impacted the wood quality of stems within 5–7 cm of the pith in most trees (SPICER *et al.* 2000). Thus, only in extreme cases, is sinuosity in young trees expected to have more than a minor influence on overall wood quality at harvest age. The need, therefore, to measure sinuosity in all young trees being considered for selection is questionable. It would be wise, however, to cull trees with highly sinuous stems when making final selections among trees showing promise for other traits.

Implications of selection for stem growth on stem defect traits

Moderately positive genetic correlations between DBH and both WSAB and BRS (Table 2), indicate that selection for DBH alone will increase the severity of both these stem defects. Indeed, selection of the top 10% of parent trees in this study for DBH at age 12 is predicted to increase WSAB at age 24 by 9.3%, and BRS by 7%, in the next generation (Table 3–B). SIN is also expected to increase

when DBH is selected, but only slightly (2.3%). Although these indirect responses in WSAB and BRS appear small, their economic impact may not be trivial. For example, a 9.3% increase in WSAB is an increase of 0.04 whorls with SABs, or about one additional tree out of 25 with a steep angled branch in the next generation. Because the occurrence of SABs is primarily due to second flushing in young Douglas-fir, and faster-growing trees produce more second-flushes, the frequency of SABs is greatest when stem growth is rapid (ADAMS & BASTIEN 1994, SCHERMANN *et al.* 1997). Thus, the negative impact of ignoring SABs in breeding programs will be most evident on higher quality sites.

This study supports the earlier conclusions that it is impossible to maximize genetic improvement of stem growth in Douglas-fir without also increasing the frequency of stem defects (KING *et al.* 1992, ADAMS & BASTIEN 1994, SCHERMANN *et al.* 1997). Some of the defects can readily be handled, at least partially, by silvicultural means (e.g., spacing, thinning and branch pruning). Nevertheless, the lack of strong genetic correlations between stem growth and stem defect traits means that the frequency of stem defects can be held in check, or even reduced, while improving stem volume growth rates, if stem defect traits are measured and included as selection criteria (KING *et al.* 1992, ADAMS & BASTIEN 1994, SCHERMANN *et al.* 1997). Thus, the increasing attention given to stem defect traits in Douglas-fir breeding programs appears both necessary and prudent.

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