AN ABSTRACT OF THE THESIS OF

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Defects in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco).

Abstract approved: _____

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Wesley Thomas Adams

Stem defects, including sinuosity, large branches, and the occurrence of steep-

angled branches (e.g., forks and ramicorns) can occur with high frequency in young

plantations of Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco).

The importance of including these stem defects as criteria in early selection depends, in

great part, on their persistence over time, and the efficiency of early selection for these

traits. In this study, 90 open-pollinated families of Douglas-fir growing on three test sites

in the Oregon Coast Range, and originally measured in 1984 at age 12, were remeasured

in 1996, at age 24 (approximate mid-rotation age for managed plantations in this region).

While the majority (62%) of trees scored as having ramicorns at age 12 still had them at

age 24, most forks (53%) had become ramicorns by the second measurement. Thus, there

does not seem to be a need to score forks and ramicorns separately. Although branch size

was highly correlated between the two measurement dates, sinuosity scores were poorly

correlated. Estimated heritabilities and genetic correlations between stem defect traits,

and between stem defect traits and bole diameter at breast height (DBH), were similar at

the two ages. Due to low heritabilities, estimated genetic gains for DBH and individual

stem defect traits were low but consistent with earlier studies. Both branch size and the number of whorls with steep-angled branches had positive genetic correlations with DBH, indicating that selection for stem size alone will indirectly increase stem defects. Thus, it may be prudent to include these traits along with DBH as selection criteria. Sinuosity was nearly uncorrelated with DBH. With the exception of sinuosity, genetic correlations between comparable traits at the two ages were very high (>0.75), and predicted correlated responses in these traits at age 24, from selection at age 12, were nearly as great as those expected if selection was delayed until age 24.

Persistence and Age-Age Genetic Correlations of Stem Defects in Douglas-fir
(*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco)

By

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I understand that my thesis will become part of the permanent Collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Fatih Temel, Author

ACKNOWLEDGMENTS

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INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is one of the most important tree species in western North America, where it dominates the most productive forest lands. This species is distributed in the region from 19° to 55° North latitude. On a map of North America its range resembles an inverted V. The shorter arm extends southward from its northern limits in British Columbia to the west along the Pacific slope into California and the longer arm extends south eastward into Mexico (Silen, 1978). It is valuable for timber, pulp, and Christmas trees (Bormann, 1984). Because of its good growth and wood characteristics, it has also been introduced to Europe, Oceania and South America as an exotic (Silen, 1978).

Research on the genetics of Douglas-fir was started in the beginning of this century (Munger and Morris, 1936), with breeding programs initiated in the mid 1950's (Woods, 1993). Over the years the intensity of breeding has increased and has mainly concentrated on adaptive and growth traits. The Pacific Northwest region has been divided into 102 breeding zones by state agencies and private industry, with more than 28384 first generation parent trees selected and tested in more than 1200 progeny test plantations (Woods, 1993). Selection and breeding efforts in Douglas-fir by the United States Forest Service matches this effort (Adams et al., 1990). Progeny and provenance trials have also been established for Douglas-fir in France and New Zealand. Substantial

genetic variation has been documented for growth, stem form, branching, phenology, and adaptability traits in this species, ensuring great potential for improvement through breeding (Silen, 1978).

Most breeding programs in Douglas-fir have focused mainly on improving bole volume growth, with less attention given to wood quality (Woods, 1993). Although wood density is the single most important criterion determining wood quality, stem form and branching habit also have considerable impact on wood quality (PNWTIRC Annual Report, 1987-88). Part of the lack of emphasis on stem form and branching habit is that mature Douglas-fir stands are characterized by straight stems and good form (Schermann et al., 1997). Young plantations of Douglas-fir, however, often exhibit high frequencies of stem defects (Campbell, 1965; Walters and Kozak, 1967; DeChamps, 1978; King, 1986; Adams and Bastien, 1994). Stem form deficiencies include bole sinuosity, large diameter branches, and the presence of forks and ramicorns (Figure 1). Sinuosity is stem crookedness or 'waviness' which takes place totally within interwhorl segments. Forks and ramicorns are steep-angled branches diverging less than 30° from the main stem, with forks having diameters similar in size to the main stem, while ramicorns are significantly smaller. Stem form deficiencies, especially when present in the lower bole, not only lower the magnitude and value of timber recovered from trees, but also increase the cost of transportation, and decrease the efficiency of timber processing (Shelbourne, 1969 and 1970). In addition, forked stems and large branches increase the difficulty and
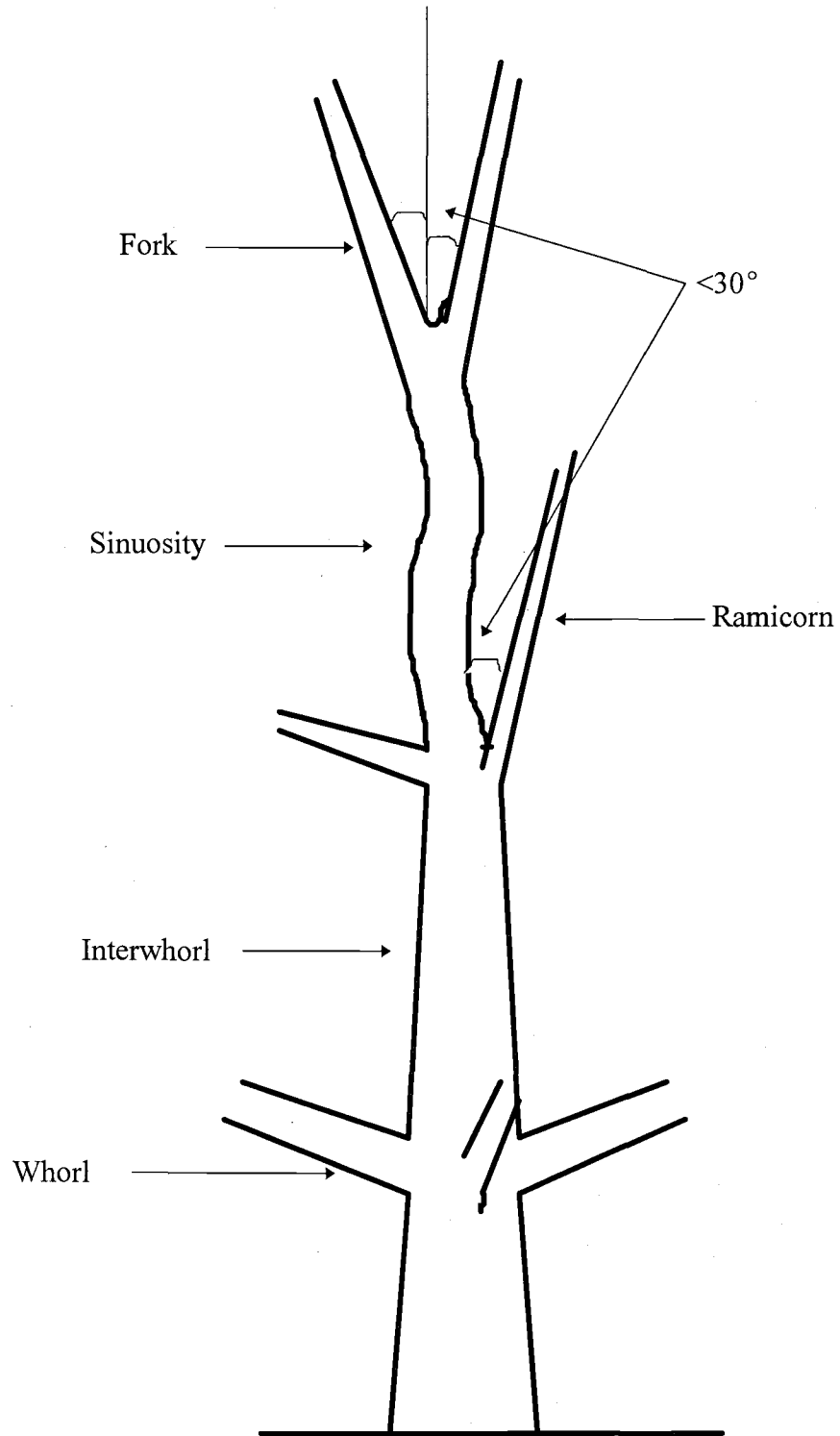
Figure 1. Illustration of terms used in defining branching habit and stem form in Douglas-fir (See also Table 2).

cost of pruning, increase knottiness and compression wood, and reduced lumber strength, value, and pulp yield (Schermann et al., 1997; Zobel, 1971).

Most selections in Douglas-fir progeny tests are made by age 15 (Silen, 1978). There are three arguments for not including stem form defects as selection criteria at this age. In breeding programs, selection should be restricted to as few traits as possible to maximize response to selection for those traits and to minimize measurement cost (Campbell, 1965). Secondly, stem form defects observed in young Douglas-fir trees may disappear as the trees become larger, and therefore may have only a minor impact on overall wood quality. Third, stem form defects scored at young ages may be poorly correlated with defects realized in older trees. Thus, the value of these traits as selection criteria in young trees and the efficiency of early selection may be questioned. In order to clarify this point, the degree to which these traits persist and remain under genetic control needs to be determined. If the traits persist, it is important to evaluate how well family performance for stem form defects in older trees can be predicted in young trees. It is also important to understand the genetic relationships between stem form and growth traits. If strong, unfavorable correlations exist, inclusion of stem form traits in breeding programs may be unavoidable (Adams and Bastien, 1994).

The goal of an advanced-generation tree breeding program is to maximize gain achieved per unit of time (van Buijtenen, 1981). Thus, determining the youngest age at which selection can be reliably done is crucial for determining the length of the breeding cycle and the amount of gain per unit of time (Vargas-Hernandez and Adams, 1992). In other words, it is highly desirable to have strong genetic correlations between traits at the

time of selection and at the end of the rotation period. These correlations are called juvenile-mature correlations and their magnitude is the most important factor determining efficiency of early selection (Zobel and Talbert, 1984).

In 1984, the Pacific Northwest Tree Improvement Research Cooperative (PNWTIRC) undertook the Coastal 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 (var. *menziesii*) plantations, achieving a better understanding of the inheritance of stem form and branching traits, and developing inexpensive but efficient measurement methods for those traits (PNWTIRC Annual Reports, 1986-87, 1987-88, and 1988-89). In 1996, this follow-up to the Measurement Study was undertaken with the following objectives:

1) To determine the degree of persistence of stem defects with age.

2) To investigate the genetics of stem form defects and genetic interrelationships among these traits.

3) To examine breeding implications of 2) and the efficiency of early selection for stem form defects.

To accomplish the above objectives, the same 90 open-pollinated families and three Coastal Douglas-fir progeny test plantations used in the original Measurement Study were remeasured for a number of stem form and growth traits, and comparisons were made between the two sets of measurements.

MATERIALS and METHODS

Plant Materials

Families measured 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 location (Table 1), the 90 families were planted as three 30-family sets, each set as a separate randomized complete block experiment with four replications. Each family was represented by a four-tree non-contiguous plot in each replication, with a spacing of seedlings (1-0 container grown) at planting 3.05m x 3.05m. The test sites were fenced in order to prevent browsing by deer and elk. Survival of seedlings one year after planting was very high (> 0.85, Table 1), 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 (Clay Creek and Coyote Creek), and one year older at the Oxbow site. Trees were 24 - 25 years-old at the time of the second measurements in 1996, about one-half the rotation age of trees in this breeding zone. Systematic thinning in 1995 removed 25% of the trees at Coyote Creek and 34% from Oxbow; the Clay Creek plantation was measured prior to the thinning. In total, over all three sites, 3755 trees were measured at age-12, and 2974 trees at age-24.

Table 1. Information on progeny test plantations included in this study.

	Site		
	Clay Creek	Coyote Creek	Oxbow
Elevation (m)	137	274	396
Latitude	43°55'N	43°55'N	43°51'N
Longitude	123°35'W	123°18'W	123°34'W
Survival[a] (%)	89	85	85
Year Planted	1973	1973	1972
Ownership	Roseburg Forest Resources	Roseburg Forest Resources	Bureau of Land Management
Thinning	No	Yes	Yes
Number of Trees Measured in 1996	1205	955	814

[a] Survival of seedlings one year after planting.

Traits and Measurement Methods

Three criteria were recommended in determining whether or not to include a trait

in a breeding program: 1) cost of measurement, 2) inheritance of the trait, and 3) its

impact on the product value of the tree (Adams and Howe, 1985). Campbell (1964)

suggested that selection be restricted to a few traits in which improvement will give the

greatest earnings relative to the cost of improvement. When these criteria are examined, freedom from stem defects, stem straightness and growth rate are often given high priority in tree breeding programs (Shelbourne, 1970). Stem straightness is especially recommended for selection because it is frequently under strong genetic control (Mangussen, 1990). Although the frequency of forks and ramicorns have been shown to have low individual-tree heritabilities in previous Douglas-fir studies (King et al., 1992; Adams and Bastien, 1994; Schermann et al., 1997), these defects can have great negative impact on tree value. Forking may be caused by a variety of factors including loss of apical dominance in the terminal bud or leader shoot due to damage by insect attack, bird perching, early season frost, or because of second flushing in young trees (Walters and Soos, 1961; King, 1986; and Adams and Bastien, 1994). Ramicorns on the other hand, seem to be largely due to second flushing. Uncertainty of the cause of these two branch types have resulted in different approaches to scoring these traits. Schermann et al. (1997), who scored these trait separately, reported that forks and ramicorns are only partially controlled by the same genes; however, in previous studies these traits were combined into single scores (Jarret, 1978; Birot and Cristophe, 1983; Adams and Bastien, 1994). Because of its weak inheritance, control of branch diameter by breeding is very difficult (Shelbourne, 1970). Additionally, Wardle (1967) showed that branch size may be more a function of tree spacing than genotype.

Because of the great difficulty and expense of physical measurement of stem form and branching traits, less precise subjective scoring systems are usually employed (Orr-Ewing, 1967; Shelbourne, 1969; Stonecyper and Arbez, 1976; Wilcox et al., 1975;

Cooper and Ferguson, 1981; and Birot and Cristophe, 1983). The range of scores used for each trait needs to be large enough that variation among trees can be accurately reflected, but not so large as to be confusing. It has been suggested that a scale of 4 to 6 classes is adequate for most purposes (Raymond and Cotterill, 1990).

In 1984, much effort was expended in the original Measurement Study to develop quick, but accurate, methods of measuring different stem form characteristics, including sinuosity, branch size and angle, and occurrence of forks and ramicorns (PNWTIRC Annul Report, 1987). Sinuosity was scored only in the top of the tree (second interwhorl from the top) where it was most pronounced and could be seen easily from the ground (Table 2). Branch size and angle were measured on whorls near breast height (1.37m). Frequency of ramicorns and forks were scored separately as the total number of whorls with at least one of these defects. At age 24, all stem form traits were scored visually in the lowest 5m log of the tree; with height to 5m visually estimated (Table 2). The lower 5m of the bole was selected for measurement in 1996 because it is the most valuable portion of the tree, and because it roughly corresponds to the portion of bole measured at age 12. Although branch diameter was scored at age 24, branch angle was not measured because branch angle flattens with age and variation among trees branch angle was limited in the lowest 5m log. Instead of scoring forks and ramicorns as separate traits in 1996, all branches diverging less than 30° from the main stem (steep-angled branches, or SABs) were noted and recorded in five size classes relative to the diameter of the bole (Table 2). With size class information, SABs could be separated into forks and ramicorns after scoring. The number of whorls with SABs was also recorded. Diameter at breast

height (DBH) measurements in 1996 were made by owners of the test sites. Thus it was also possible to compare DBH in 1996 with DBH measured in 1984. All scoring in 1996 was done by two-person crews with the consensus score of crew members recorded.

Table 2. Description of traits and measurement techniques[a].

Age-12:

Number of whorls with steep-angled branches: Total number of whorls on the tree with forks and with ramicorns below the upper-most whorl were recorded separately. In addition, presence or absence of forks and ramicorns on the 2nd, 3rd and 4th whorl from the top of the tree were noted.

Sinuosity: Frequency (the maximum number of sinuosity "crooks" in an interwhorl) and displacement (largest distance the stem is offset from the position it would occupy if the stem had no sinuosity, in 1/2 stem diameter units) was estimated visually from the ground for the second interwhorl from the top of the tree. Sinuosity was then calculated as frequency x displacement.

Branch size (mm): Mean diameter (3 cm away from the bole) of the two thickest branches in the whorl closest to breast height (1.37m).

Diameter (mm): Stem diameter measured at breast height.

Age-24:

Only the first 5m of the bole was considered in these measurements.

Steep-angled branches (SABs)

Trees were scored for three SAB traits:

1) The number of SABs in each of 5 diameter classes relative to the main bole (i.e., ≤20%, 21-40%, 41-60%, 61-80%, > 80%).

2) Total number of whorls with one or more SABs (WSAB).

Table 2. (continued).

3) Impact of SABs on the value of the log in 4 classes: 1 = no impact or no loss in wood volume or value; 2 = low impact, or slight reduction in wood volume; 3 = moderate impact, or moderate reduction in wood volume; 4 = severe impact, or loss of a section of the bole or otherwise greatly reduced wood volume (ISAB).

In addition to WSAB and ISAB, the total number of SABs (TSAB, derived from 1 above) and a total steep-angled branch score (SABSC), were included as SAB traits in the analyses. SABSC was calculated using the following formula:
SABSC = (number of SABs in the ≤20% size class x 1) + (number of SABs in the 21-40% size class x 2) + (number of SABs in the 41-60% size class x 3) + (number of SABs in the 61-80% size class x 4) + (number of SABs in the > 80% size class x 5).

Sinuosity (SIN): Deviation from straightness, or crookedness, of the main stem within an interwhorl segment. Visually scored from the ground using a scale from 1 (perfectly straight) to 4 (very sinuous).

Branch Size (BRS): Size of the thickest branch on the bole. Visually scored from the ground on a scale from 1 (smallest) to 4 (thickest).

Diameter (mm) (DBH): Stem diameter measured at breast height.

[a] See Figure 1 for illustration of terms.

Statistical Methods

Objective 1. Persistence of stem form and branching defects:

Measurements made in 1984 were compared to equivalent measurements made in 1996 on an individual tree basis. Only trees still standing (and measurable) in 1996 were included.

Forks and Ramicorns - To assess the persistence of forks and ramicorns observed in 1984 in trees remeasured in 1996, the frequencies of trees with one or more of these

defects in the lowest 5m log were compared at the two ages. Because trees ranged in height between 3m and 11m (mean = 7.64m) at age 12, and because forks and ramicorns were recorded starting with the second whorl from the top of the tree, all trees which did not have a 5m log below the first whorl at age 12 needed to be removed from the analysis. Using the height data available for three different years (1975, 1981, and 1984), annual height increments for each tree were estimated. All trees less than 6m at age 12 (n = 300) were judged not to be tall enough to include a 5m log below the first whorl and were removed. Some trees had measured whorls above 5m at age 12. Fortunately, forks and ramicorns were recorded individually for whorls 2, 3, and 4 in 1984 (Table 2), so by using the estimated height increments it was possible to identify and delete whorls likely to have been above 5m. SABs with percent size class of 80 or greater were defined as forks at age-24; all others were classified as ramicorns. Trees were then subdivided into 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 within each of the four classes at age 24, within each of the four classes at age 12, and vice versa, were calculated. In this manner, the persistence of SAB types observed at age 12, and the origin of these types at age 24, could be determined.

Sinuosity - Because sinuosity was only measured at the second interwhorl from the top of the tree in 1984, all trees whose second interwhorl was likely above 5m at age 12 were removed from this analysis (n = 2494, or 80% of all trees). Sinuosity scoring methods in 1984 and 1996 were too different to make absolute comparisons of scores, but it was possible to determine whether the trees given the straightest scores at age 12 were

still the straightest at age 24, and whether trees observed to be the most sinuous at age 12 were still the most sinuous at age 24. This was done in two ways. First, trees having perfectly straight scores (n = 171), and those falling in the most sinuous 10% of all trees (n = 48) were identified, and the frequency distribution of the 1996 sinuosity scores within each of these classes compared. Secondly, the family mean correlation in sinuosity scores between the two ages over all three sites was calculated.

Branch Size - A similar approach to that used in the sinuosity analysis was employed to examine persistence of branch size. Because branch size was measured near DBH at age 12, and all trees standing at age 24 were taller than 1.37m at age 12, all trees available in 1996 were used in the analysis. Trees falling into the top 10% (thickest, n = 297) and bottom 10% (thinnest, n = 297) branch diameters at age-12 were identified and the frequency distributions of the four 1996 branch size scores within each class compared. The family mean correlation between the two ages for this trait over all three sites was also calculated.

Objective 2. Genetics of stem form and branching defects and genetic interrelationships among the traits:

All 11 individual traits (Table 2) were subjected to analysis of variance (ANOVA) using the data set combined over the three sites (Table 3). Since the error variances were consistent for each trait over the three sites, there was no adjustment necessary to combine the data over the three sites. In addition, analyses of covariance (ANCOVA) were conducted for all pairs of traits measured in each year (1984: 4 traits, 6 pairs; 1996: 7 traits, 21 pairs). The form of ANCOVA was the same as ANOVA (Table 3), but with

expected mean squares replaced by expected cross products. Prior to the analyses, all trees whose main stem forked below breast height (n = 289) were removed. ANOVA was first conducted using the GLM procedure of the SAS statistical software package (SAS Institute Inc., 1990), in order to test the significance of the family/sets and sites x families/sets variances (using type III sums of squares). Variance components were then estimated using the REML method of the SAS VARCOMP procedure. Because of mortality and thinning there was considerable imbalance in the data sets by age 24 (e.g., as many as 11 families were missing in an individual site. In the complete data set, however, all families were represented by at least one plot). REML estimates of variance components are considered the most reliable when such imbalance exists (White, 1996). All tests of significance in this study were conducted at the 0.05 probability level.

Although REML is a univariate procedure, ANCOVA and covariance components were computed indirectly using the following relationship:

$$Cov(x, y) = \frac{Var(x + y) - Var(x) - Var(y)}{2},$$

where $Cov(x, y)$ is the covariance component for traits x and y, $Var(x)$ and $Var(y)$ are the corresponding variance components for each trait separately, and $Var(x + y)$ is the corresponding variance component for the sum of the two traits (Freund, 1962).

Preliminary analyses and residual plots indicated that several traits violated the basic assumptions of ANOVA (i.e., independent errors, normal distribution of data points, and variance) (Steel and Torrie, 1980). Therefore, the following traits were

Table 3. Form of the analysis of variance on multiple sites.[a]

Source	Degrees of freedom	Expected Mean Squares
Sites	p-1	$\sigma^2_w + k\sigma^2_e + kr\sigma^2_{pf(s)} + kf\sigma^2_{r(ps)} + krf\sigma^2_{ps} + krsf\sigma^2_p$
Sets	s-1	$\sigma^2_w + k\sigma^2_e + kr\sigma^2_{pf(s)} + krp\sigma^2_{f(s)} + kf\sigma^2_{r(ps)} + krf\sigma^2_{ps} + krpf\sigma^2_s$
Sites x Sets	(p-1) (s-1)	$\sigma^2_w + k\sigma^2_e + kr\sigma^2_{pf(s)} + kf\sigma^2_{r(ps)} + krf\sigma^2_{ps}$
Replications/Sets/ Sites	(r-1) s p	$\sigma^2_w + k\sigma^2_e + kf\sigma^2_{r(ps)}$
Families/Sets	(f-1) s	$\sigma^2_w + k\sigma^2_e + kr\sigma^2_{pf(s)} + krp\sigma^2_{f(s)}$
Sites x Families /Sets	(p-1) (f-1) s	$\sigma^2_w + k\sigma^2_e + kr\sigma^2_{pf(s)}$
Plot Error	(f-1) (r-1) s p	$\sigma^2_w + k\sigma^2_e$
Within plot error	t (k-1)	σ^2_w

[a] Assumes no missing cells in the original design. For analysis of covariance, variances are substituted with covariances. p = number of sites, s = number of sets, r = number of replications per set per site, f = number of families per set, t = total number of plots in the experiment, k = number of trees per plot, σ^2_w = within plot variance, σ^2_e = plot to plot variance, $\sigma^2_{pf(s)}$ = variance due to families-in-sets by site interaction, $\sigma^2_{f(s)}$ = variance due to differences among families in sets, $\sigma^2_{r(ps)}$ = variance due to differences among replications in sets and sites, σ^2_{ps} = variance due to plantation by set interaction, σ^2_s = variance due to differences among sets, σ^2_p = variance due to differences among plantations.

subject to transformation before analyses. Total number of SABs in 1996 and total number of whorls with SABs in 1984 were transformed to SQRT(Trait + 0.5). Total number of whorls with SABs and total SAB score in 1996, and sinuosity in 1984, were transformed to LOG(Trait + 1). Unless otherwise indicated, all means appearing in tables are un-transformed (i.e., were calculated prior to the transformation).

Genetics of the traits and interrelationships among them were investigated by estimating additive genetic variances, individual and family narrow-sense heritabilities, and genetic and phenotypic correlations among traits. Because open-pollinated families in the progeny test came from parent trees in wild stands, additive genetic variance (σ^2_A) was estimated as three times the family component of variance ($\sigma^2_{f(s)}$), which assumes individuals in these families are more closely related than half-sibs (Campbell, 1979). Total phenotypic variation on an individual tree basis was estimated as,

$$\sigma^2_{PI} = \sigma^2_w + \sigma^2_e + \sigma^2_{pf(s)} + \sigma^2_{f(s)},$$

and total phenotypic variation on a family basis as,

$$\sigma^2_{PF} = \frac{\sigma^2_w}{(k)(r)(p)} + \frac{\sigma^2_e}{(r)(p)} + \frac{\sigma^2_{pf(s)}}{p} + \sigma^2_{f(s)}$$

(See Table 3 for description of terms). Because of the imbalance in the experimental design, the coefficients k, r, and p used above were those given by the GLM procedure. Narrow-sense individual (h^2_i) and family heritabilities (h^2_f) were estimated following Falconer (1981):

$$h^2_i = \frac{\sigma^2_A}{\sigma^2_{PI}} \text{ and } h^2_f = \frac{\frac{1}{4}\sigma^2_A}{\sigma^2_{PF}}.$$

Standard errors of both types of heritability estimates were calculated following

Dickerson (1969).

Additive genetic correlations were estimated as,

$$r_A = \frac{Cov_f(x, y)}{\sqrt{\sigma^2_{f(x)}\sigma^2_{f(y)}}},$$

where $Cov_f(x, y)$ is the family component of covariance between traits x and y, and

$\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the respective family components of variance (Falconer, 1981). To

calculate phenotypic correlations, the covariance and variances in the above formula were

replaced with their phenotypic (individual tree) equivalents.

Objective 3. Breeding implications and efficiency of early selection:

To accomplish this objective, expected genetic gains from direct selection,

correlated response from indirect selection of correlated traits at the same or earlier age,

and relative efficiency of early selection were calculated. Genetic gain from direct

selection (G_y) was estimated as the amount of improvement in trait y expected in the

progeny of a seed orchard consisting of clones of parent trees selected on the basis of the

performance of their open-pollinated offspring (Namkoong, 1979):

$$G_y = 2ih^2_f \sqrt{\sigma^2_{PF}},$$

where i is the selection intensity. In all calculations it was assumed that the top 10% of

parent trees in each set were selected ($i = 1.755$). Correlated response to family selection

(CR_y) is the amount of improvement in a trait (y) when selection is applied to another

trait (x) (Falconer, 1981):

$$CR_y = 2ir_A\sqrt{h^2_{f(y)}h^2_{f(x)}\sigma^2_{PF(y)}} \, ,$$

where r_A is the genetic correlation between traits x and y, $h^2_{f(y)}$ and $h^2_{f(x)}$ are the respective family heritabilities, and $\sigma^2_{PF(y)}$ is the phenotypic variance of family means for trait y.

Efficiency of early selection was estimated as the ratio of the correlated response in a trait at age 24 (m) when selection was applied to a comparable (or different) trait at age 12 (j), to response expected from direct selection:

$$RE = \frac{CR_m}{G_m} = \frac{2ir_A\sqrt{h^2_{f(m)}h^2_{f(j)}\sigma^2_{PF(m)}}}{2ih^2_{f(m)}\sqrt{\sigma^2_{PF(m)}}} = \sqrt{\frac{h^2_{f(j)}}{h^2_{f(m)}}}r_A \, .$$

RESULTS and DISCUSSION

Trees were largest at the Clay and Coyote Creek sites in both 1984 and 1996, but the incidence of steep-angled branches was greater on these sites as well, with approximately one out of every two trees having at least one whorl with an SAB (Table 4). Trees at Oxbow were somewhat smaller, but had a much lower incidence of SABs, with only one out of every three (1984) or four (1996) trees having at least one whorl with an SAB. Mean sinuosity score was greatest at Coyote Creek in 1984, but was nearly equal at all sites in 1996.

Persistence of Stem Defects

Steep-angled branches - Although the proportion of trees with at least one steep-angled branch (SAB) was almost the same in 1984 (31.8%) and 1996 (32.3%), the distribution of SAB types (i.e., ramicorns or forks) was considerably different at the two ages (Table 5). The proportion of trees with only ramicorns increased from 24.5% at age-12 to 30.2% at age-24, while proportions with only forks, or bearing both types of SABs, decreased from 5% to 1.5%, and 2.3% to 0.6%, respectively. The majority of trees with only ramicorns at age-12 still had ramicorns at age-24 (61.7 + 0.03 = 62%), but most trees scored as having only forks at age 12 had lost them by the second measurement (53.4 + 30.2 = 83.6%). Interestingly, 53.4% of trees with only forks at age-12, and 55.8% of trees with both types of branches,

were recorded as having only ramicorns at age 24. The majority (83%) of the trees that were free of SABs at age 12 were also scored as having no SABs at age 24.

Table 4. Site means for all traits.

Trait[a]	Site					
	Clay Creek		Coyote Creek		Oxbow	
1996						
TSAB	0.70		0.53		0.28	
WSAB	0.58		0.45		0.25	
SABSC	0.90		0.61		0.33	
ISAB	1.02		0.93		0.40	
SIN	2.10		2.27		2.30	
BRS	2.29		2.46		2.10	
DBH (mm)	228.07		231.40		219.68	
1984						
WSAB	0.66[b]	0.66[c]	0.54[b]	0.50[c]	0.33[b]	0.35[c]
SIN	1.35	1.37	2.02	2.06	0.91	0.97
BRS	21.71	21.91	23.06	23.75	19.69	20.07
DBH (mm)	107.72	111.46	105.61	112.79	95.32	100.48
Number of trees	1225	1205	1277	955	1231	814

[a] See table 2 for description of traits. [b] All trees measured in 1984. [c] Only trees measured in 1984 that were still standing in 1996 (i.e., after losses due to thinning in 1995 or mortality).

Table 5. Proportions of trees with ramicorns (RA) and forks (FR) at ages 12 and 24.

Age-12		% of total	Age-24[a]			
			Only RA	*Only FR*	*RA & FR*	*Neither*
			30.2	*1.5*	*0.6*	*67.7*
Only RA	24.5		*61.7*	*0.7*	*0.3*	*37.3*
			50.0	**13.3**	**16.7**	**13.5**
Only FR	5.0		*53.4*	*13.7*	*2.7*	*30.2*
			8.9	**46.7**	**16.7**	**2.2**
RA & FR	2.3		*55.8*	*8.8*	*13.0*	*22.4*
			4.3	**13.3**	**50.0**	**0.7**
Neither	68.2		*16.3*	*0.6*	*0.1*	*83.0*
			36.8	**26.7**	**16.6**	**83.6**

[a] Light type in each cell refers to the proportion of trees with the designated branching type at age 12 that have the designated branching type at age 24. Bold type in each cell refers to the proportion of trees with designated branching type at age-24 that have the designated branching type at age 12. Proportions given are means over the three test sites.

The above results show that a high proportion of SABs persisted over time, but most of the largest SABs (i.e., forks) at age 12, became ramicorn branches by age 24. A likely explanation for the loss of forks is that differential growth between the forks results in one stem gaining dominance as trees age. 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 5m 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 remainder of this thesis, forks and ramicorns will be considered together in the single category of SABs.

Sinuosity - The distribution of sinuosity scores at age 24, among trees scored as perfectly straight at age 12, was nearly normal, with most trees scored in the middle sinuosity classes at the later measurement (Figure 2).

Figure 2. Distributions of sinuosity scores at age 24 among trees scored as straight and highly sinuous at age 12.[a]
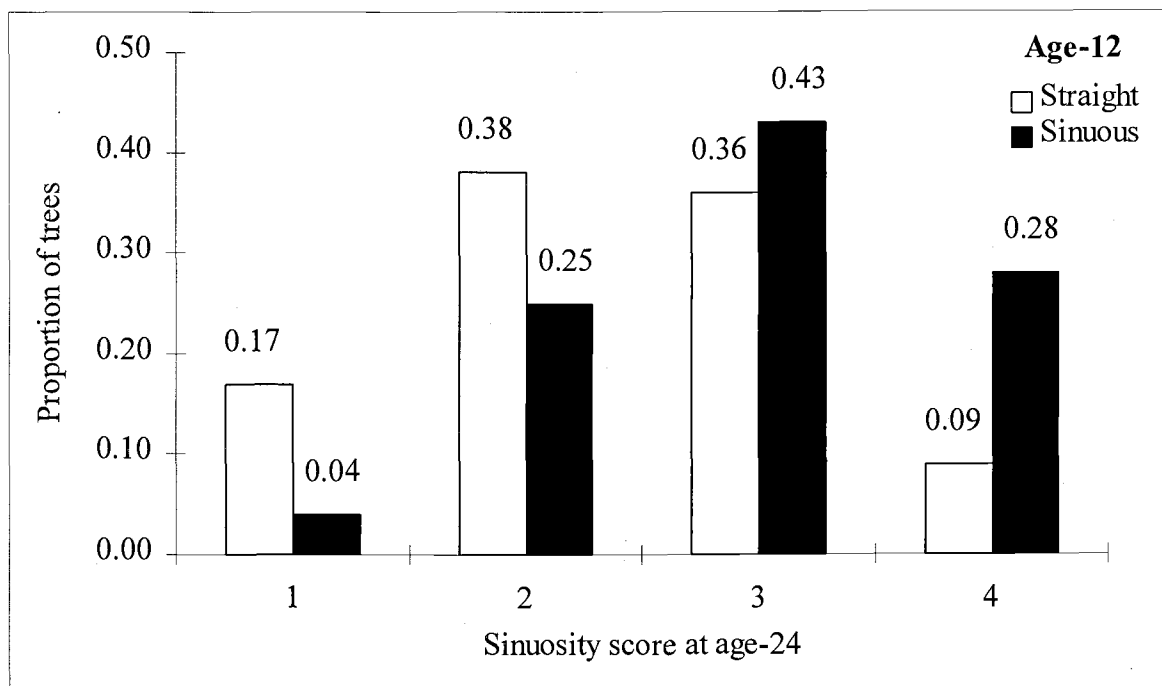
[a] "Straight" trees had a sinuosity index of 0 at age 12 (n = 171), while highly sinuous trees were the most sinuous 10% of all trees (n = 48) at this age.

The distribution of age 24 scores among the most sinuous trees at age 12, however, was strongly skewed towards the two highest sinuosity classes; thus, the majority of the most sinuous trees at age 12 were still highly sinuous at age 24. The estimated family mean correlation between sinuosity scores at the two ages was low ($r_f = 0.22$) and non-significant.

These results indicate that while severe sinuosity may persist into older trees, stem sinuosity observed at age 12 has little bearing on sinuosity seen in old trees. Two reasons for the poor correlation in sinuosity scores between ages 12 and 24 can be offered. First, since the mean diameter of trees more than doubled in the 12 year period between measurements (Table 4), sinuosity observed at age 12 was probably covered up by radial growth. 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 entire 5m lower log was scored (Table 2).

Branch size - The distributions of branch diameter classes at age 24 among trees with the smallest (10%) and largest (10%) diameters at age 12, show that relative branch size was strikingly consistent over the 12 year period (Figure 3). This is confirmed by relatively strong family mean correlation between the two ages ($r_f = 0.70$, $p < 0.01$).

Figure 3. Distributions of branch size scores at age 24 among trees with the largest (10%) and smallest branch diameters at age 12.
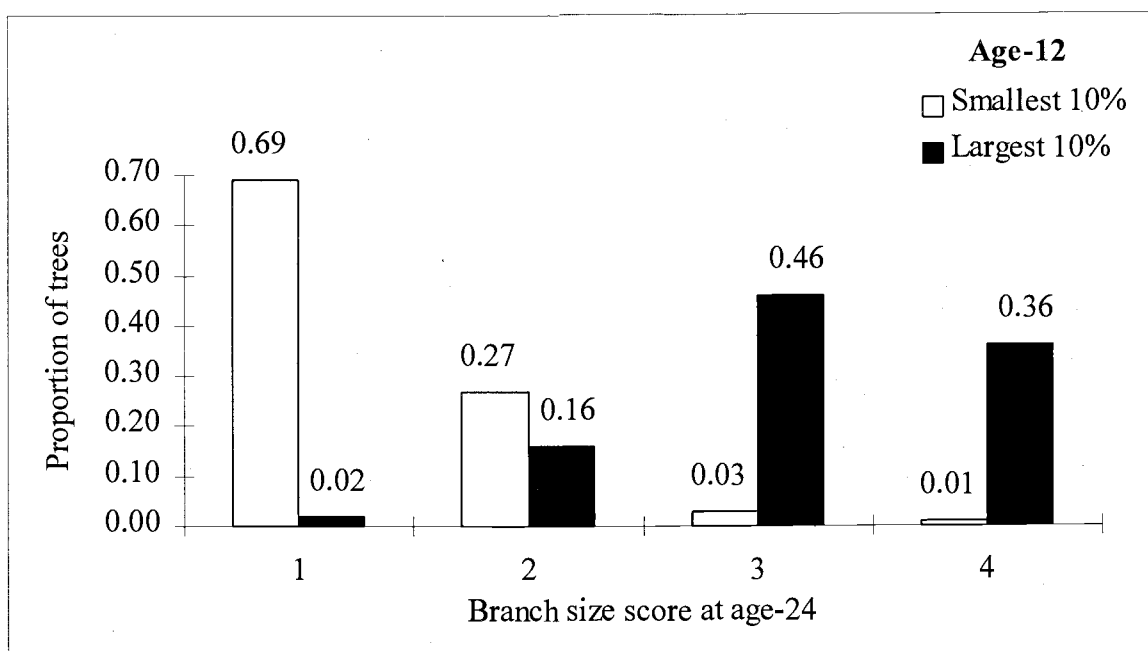
Genetics of Stem Form and Branching Defects and Interrelationships Among the Traits

Examination of the means and distributions of 1984 traits among all trees, versus among the trees remaining in 1996 (Table 4), suggests that thinning and mortality had little effect on the means and distributions of growth and stem form traits. Therefore, it is concluded that tree losses from 1984 to 1996 (mostly due to thinning in 1995) resulted in little or no bias in estimates of means, variances, and genetic parameters.

For all traits analyzed, tree-to-tree differences within plots accounted for the bulk of the total phenotypic variance (75% - 98%, Table 6). Estimated plot error variances, however, were very small or zero in all eleven cases. Although significant family-by-site

interactions were detected at age 12 for sinuosity, branch size, and DBH, this variance component at age 24 was only significant for DBH. This may, in part, be due to differences in the measurement techniques employed at the two ages. The average genetic correlation between the same trait expressed in pairs of sites can be estimated as

$$r_B = \sigma_f^2 \; / \; (\sigma_f^2 + \sigma_{f(s)}^2)$$

(Burdon, 1977). For the case of DBH in 1996, $r_B = 0.60$. This indicates that families have roughly similar rankings for DBH in the three test sites despite the significant family-by-site interaction.

Narrow sense individual heritability estimates for all traits were low, ranging from 0.04 to 0.13, with family heritabilities three to five times larger (Table 6). The steep-angled branch traits had consistently the lowest individual heritabilities at age 24, about half as great as for DBH. Despite the loss of nearly 30% of the trees at two sites due to thinning, individual and family heritabilities for traits measured at age 24 were roughly equivalent to the same or similar traits at age 12.

The family heritability for total number of steep-angled branches at age 24 (0.20, Table 6) is only about half of what Schermann et al. (1997) estimated for number of ramicorn branches ($h_f^2 = 0.43$) and number of forks ($h_f^2 = 0.35$) in a Washington Coastal breeding zone, although the incidence of trees with ramicorns and forks in the Washington test (46% and 26%, respectively), were higher than in this study. The estimated family heritability of sinuosity agrees at both ages with previous reports in Douglas-fir (0.48, Adams and Howe, 1985; 0.50, Adams and Bastien, 1994; 0.39, Schermann et al., 1997). Family heritability estimates for branch size were lower in this

Table 6. Estimated test means (range over families in parentheses), variance components (expressed as interclass coefficients), total phenotypic variances, and narrow-sense heritabilities for eleven traits measured at three sites.

Trait[a]	Means[b]	Variance Components (%)				Phenotypic Variance	Heritabilities (±SE)	
		Family	Family x Site	Plot	Within Plot		Individual	Family
Age-12								
WSAB	.50 (.1 - 1.16)	2.61*	0.60	0	96.76	.11194	.08 ± .03	.33 ± .11
SIN	1.47 (.37 - 3.57)	4.43*	1.62*	0	93.95	.35849	.13 ± .04	.41 ± .11
BRS	21.91 (19.86 - 24.73)	2.55*	2.50*	0	94.95	16.004	.08 ± .03	.30 ± .12
DBH (mm)	71.09 (96.34 - 120.16)	2.54*	3.96*	0	93.5	470.80	.08 ± .03	.28 ± .12
Age-24								
TSAB	.50 (.06 - 1.17)	1.48*	0	0	98.52	.20763	.04 ± .02	.20 ± .10
WSAB	.43 (.06 - 1.08)	1.75*	0	0	98.25	.10159	.05 ± .03	.23 ± .12
SABSC	.61 (.09 - 1.47)	1.91*	0	0	98.09	.26784	.06 ± .02	.24 ± .10
ISAB	.48 (.31 - 2.32)	1.80*	0	.51	97.69	1.7246	.05 ± .02	.23 ± .11
SIN	2.22 (.2 - 2.86)	3.65*	0	1.56	94.79	.67623	.11 ± .03	.36 ± .11
BRS	2.28 (.15 - 2.86)	3.23*	3.23	.29	93.25	.70287	.1 ± .03	.33± .11
DBH (mm)	226.38 (204.66 - 259.13)	3.74*	2.47*	0	93.79	1903.7	.11 ± .04	.34 ± .12

[a] See Tabe 2 for description of traits. [b] All means are before transformation. * Significant at 0.05 probablility level.

study than found previously in Douglas-fir (0.26, King et al., 1992; 0.34, St. Clair, 1994).

Heritability estimates for DBH were also lower than reported earlier ($h_i^2 = 0.27$, St. Clair, 1994; $h_f^2 = 0.55$, Scherman et al., 1997).

Estimated genetic correlations were usually of the same sign, but greater in magnitude, sometimes considerably so, than estimated phenotypic correlations between the same pairs of traits (Tables 7 and 8). The largest differences in genetic and phenotypic correlation estimates were found when SAB traits at both ages (i.e., TSAB, WSAB, SABSC, ISAB, WSAB) were compared with BRS and DBH. Genetic correlations in these cases were all moderately positive, while phenotypic correlations were near zero. All SAB traits in 1996 were highly intercorrelated (Table 8). Given the high intercorrelations and nearly identical heritabilities of these traits (Table 6), they all appear to be equal in information about SABs. Because WSAB is the easiest to score, this single trait is recommended for future assessment and selection of SABs in Douglas-fir.

Genetic relationships between traits were similar at the two ages (Tables 7 and 8). Sinuosity was weakly correlated with all other traits (mean $r_g = 0.09$, range -0.11 to 0.21). Which agrees with what Schermann et al. (1997) found for Douglas-fir. WSAB (representing all SAB related traits), BRS, and DBH were positively intercorrelated to varying degrees (mean $r_g = 0.46$, range 0.20 to 0.65). The correlation between branch size and DBH is greater than found by King et al. ($r_g = 0.21$, 1992) for Douglas-fir, but correlations between WSAB and DBH are of similar magnitude to correlations of DBH with numbers of forks ($r_g = 0.59$) and ramicorns ($r_g = 0.42$) reported by Schermann et al.

Table 7. Estimated genetic (bold type, above diagonal) and phenotypic (regular type, below diagonal) correlations between age 12 traits: number of whorls with steep-angled branches (WSAB), sinuosity (SIN), branch size (BRS), and stem diameter (DBH).

	WSAB	SIN	BRS	DBH
WSAB	---	**0.20**	**0.20**	**0.61**
SIN	0.02	---	**-0.11**	**0.01**
BRS	0.09	0.19	---	**0.33**
DBH	0.10	0.18	0.70	---

Table 8. Estimated genetic (bold type, above diagonal) and phenotypic (regular type, below diagonal) correlations between age 24 traits: total number of steep-angled branches (TSAB), number of whorls with steep-angled branches (WSAB), steep-angled branch score (SABSC), impact of steep-angled branches (ISAB), sinuosity (SIN), branch size (BRS), and stem diameter (DBH).

	TSAB	WSAB	SABSC	ISAB	SIN	BRS	DBH
TSAB	---	**1.01**	**0.99**	**0.89**	**0.12**	**0.68**	**0.40**
WSAB	0.93	---	**1.04**	**1.03**	**0.21**	**0.65**	**0.41**
SABSC	0.91	0.91	---	**0.94**	**0.16**	**0.68**	**0.54**
ISAB	0.72	0.77	0.87	---	**0.39**	**0.73**	**0.75**
SIN	0.11	0.11	0.11	0.17	---	**0.12**	**0.12**
BRS	0.06	0.06	0.07	0.12	0.19	---	**0.56**
DBH	-0.03	-0.02	0.01	0.04	-0.001	0.55	---

(1997). Of particular concern to Douglas-fir breeders are the positive, but unfavorable, genetic correlations of DBH with WSAB and BRS. These correlations indicate that selection for increased stem size will indirectly increase the number of steep-angled branches and mean branch size on trees.

Breeding Implications and Efficiency of Early Selection

Because of the relatively low family heritabilities in this study, expected genetic gains from direct selection, at either age, are modest (Table 9). Percent gains in DBH progeny test in Washington based on the same selection intensity, about the same (age 12) and four times larger (age 24) for sinuosity, and only about one-half (age 24) and one-quarter (age 12) as much for WSAB. Gains in Schermann et al. (1997), however, were reported for transformed variables. As expected from the genetic correlation estimates, selection for DBH alone is predicted to have little or no influence on stem sinuosity at either age, but would increase mean branch size and number of whorls with SABs. Although these increases appear small, their economic impact may not be trivial. For example, the expected individual response in WSAB due to selection for DBH at age 12 is 0.05, or about one additional tree out of 20 with a SAB at age 12 in the next generation.

With the exception of SIN, estimated genetic correlations between comparable traits at the two ages were very strong ($r_g > 0.80$, Table 10), suggesting that early selection for these traits might be quite efficient. In fact, with exception of SIN, expected genetic gains in traits at age 24 by selection for comparable traits at age 12, are nearly as great as those predicted if selection is delayed until the later age (Table 9). The estimated

relative efficiencies of early selection were especially high for both BRS (0.85) and

WSAB (0.98), and quite good for DBH (0.76). Relative efficiency of early selections for

SIN, however, appears to be poor.

Table 9. Expected responses (gains) from direct selection of parent trees to increase DBH, and to decrease bole sinuosity (SIN), branch size (BRS), and number of whorls with steep-angled branches (WSAB), at ages 12 and 24; correlated responses (CR) in SIN, BRS, and WSAB at each of these ages if DBH is selected ignoring other traits; expected responses in each trait at age 24 if the corresponding trait is selected at age 12 (early selection); and, expected correlated responses in each trait at age 24 if DBH is the only trait selected at age 12.[a, b]

| Trait | Age-12 | | Age-24 | | | |
| | | | Select at age-24 | | Select at age-12 | |
	Direct Selection	CR from selection for DBH	Direct Selection	CR from selection for DBH	Response to early selection	CR from early selection for DBH
DBH	+5.60 (8.0)	---	+15.05 (6.7)	---	+11.44 (16.1)	---
SIN	-0.68 (46.3)	+0.00 (0.0)	-0.28 (11.2)	+0.03 (1.4)	-0.11 (4.95)	+0.05 (2.3)
BRS	-1.07 (4.9)	+0.34 (1.2)	-0.27 (11.7)	+0.15 (6.6)	-0.23 (10.1)	+0.16 (7.0)
WSAB	-0.05 (10.0)	+0.05 (10.6)	-0.09 (21.1)	+0.03 (6.8)	-0.08 (18.6)	+0.04 (9.3)

[a] Assuming top 10% of parent trees are selected in each family set based on the mean values of their offspring. Percent gains relative to test mean given in parentheses.
[b] In cases where traits were transformed, expected responses are given in the original units of the traits (i.e., calculated from backtransformed means expected after selection).

Table 10. Estimated genetic correlations between ages 12 and 24 in number of whorls with steep-angled branches (WSAB), sinuosity (SIN), branch size (BRS), and stem diameter (DBH).

Age-24	Age-12			
	WSAB	SIN	BRS	DBH
WSAB	**0.82**	0.20	0.16	0.42
SIN	0.08	**0.36**	0.15	0.20
BRS	0.34	-0.03	**0.89**	0.64
DBH	0.82	0.05	0.41	**0.84**

CONCLUSIONS

The main conclusions which can be drawn from this study are as follows:

1. While stem defects related to branching (i.e., SABs and branch size) persist over time, sinuosity appearing at young ages poorly predicts sinuosity in older trees. Due to differential growth of stems, many SABs observed as forks in young trees will become ramicorn branches later on. Thus, there seems to be little or no value in scoring ramicorns and forks as separate traits.

2. Although within plot variances made up the bulk of total variance, families were significant sources of variance for all traits. Heritabilities were equal to or lower than observed in previous studies.

3. Genetic correlations between the different traits used to describe the nature and severity of steep-angled branches were very high, indicating they are under nearly the same genetic control. It is recommended that only one SAB trait be scored in the future. The number of whorls with one or more SABs is the most likely candidate, since it is the easiest to score.

4. Comparable traits at age 12 and 24 seem to be under similar genetic control and are similarly interrelated genetically.

5. With the exception of SIN, comparable traits appear to be controlled by nearly the same set of genes at the two ages. Genetic gains from early selection for these traits are expected to be nearly as great as gains obtained from selection in more mature trees.

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6. Regardless of whether selection occurs early or is delayed to later, selection for stem

size (DBH) alone is expected to increase BRS and WSAB. Therefore, if an increase in

stem defects is intolerable, stem defect traits will need to be included as selection criteria

in Douglas-fir breeding programs.

7. Although BRS and WSAB are unfavorably correlated with stem growth (DBH), it is

still possible to improve stem growth without increasing the frequency of stem defects,

because small branches can occur in both small and big trees (Figure 4).

Figure 4. Scatter plot of mean DBH and mean BRS values of the 90 families over all
three sites at age 24. Solid data points indicate the top 10% of all families that can be
selected for DBH without increasing BRS.
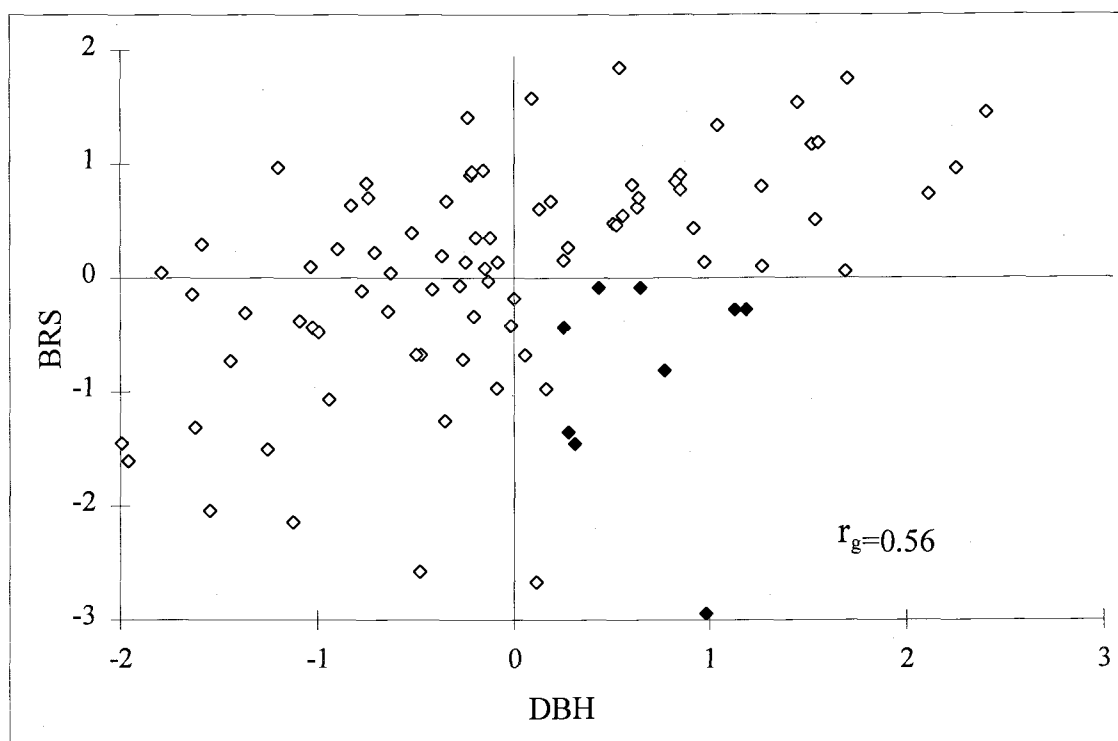
Additional Research.-. Since the selection based on stem growth alone, according to the results, will increase the incidence of stem form defects, it is important to determine impact of increased stem defects on wood quality. It is particularly important to determine impact of ramicorns on product recovery and internal wood properties. Impact of sinuosity observed at both ages also needs to be investigated. Given that early sinuous portions covered up by differential radial growth, it would be interesting to see what are the implications of sinuosity for internal wood characteristics. A project was undertaken by Dr. Barb Gartner at Oregon State University will help understanding the impact of sinuosity on inner wood properties.

This study addressed stem defects, which have external effect on wood properties, however, wood density is the most important wood quality trait. Thus, it is important to investigate relationships between stem form defects and wood density. Although both stem form and wood density are unfavorably correlated with fast growth (Vargas-Hernandez and Adams, 1991), it is necessary to determine the degree to which wood quality traits intercorrelated. This will aid in determining which traits need to be included as selection criteria in Douglas-fir breeding programs, and emphasis to be placed on each.

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APPENDIX

This appendix contains two tables and twelve figures. Appendix Table 1 displays mean values of each family for all eleven traits. Analysis of variance tables for all traits over the three test plantations are presented in Appendix Table 2. Distribution of the traits are given in the Appendix Figures 1 to 9. Distribution of age 12 traits among all trees, and for the subset of trees remaining after thinning at age 23, are also presented. Appendix Figures 11 to 13 display scatterplots of the 90 families between their DBH and BRS and WSAB at the both ages.

Appendix Table 1. Family means (30 in each of 3 sets) for all eleven traits included in this study[a].

Fam. No.	Age 12				Age 24						
	WSAB	SIN	BRS	DBH	TSAB	WSAB	SABSC	ISAB	BRS	SIN	DBH
Set 1											
1601	0.29	1.23	21.53	101.26	0.31	0.16	0.31	0.31	2.19	1.78	226.97
1602	0.22	1.21	22.90	105.03	0.45	0.39	0.45	0.39	2.27	1.91	223.97
1603	0.23	1.00	22.70	104.97	0.28	0.24	0.28	0.40	0.40	0.20	222.44
1604	0.57	1.05	20.71	96.86	1.10	0.76	1.28	1.17	2.17	2.34	220.48
1605	0.56	1.20	19.86	96.34	0.61	0.46	0.71	0.71	1.64	2.39	209.50
1606	0.28	1.04	21.82	113.25	0.26	0.26	0.32	0.74	2.24	2.26	232.26
1607	0.70	2.83	22.27	109.07	0.39	0.39	0.96	1.39	2.78	2.65	259.13
1608	0.54	1.18	20.27	97.14	0.75	0.67	1.29	1.50	2.17	2.46	204.75
1609	0.40	1.06	23.40	104.10	0.35	0.29	0.47	0.65	2.29	2.06	219.32
1610	0.34	1.89	23.86	110.31	0.35	0.27	0.42	0.62	2.46	1.19	235.65
1611	0.40	1.11	22.61	112.94	0.47	0.38	0.47	0.62	0.35	2.50	230.41
1612	0.71	0.84	23.00	103.21	0.29	0.29	0.46	0.71	2.75	2.46	225.92
1616	0.35	1.27	22.30	104.86	0.31	0.28	0.44	0.56	2.06	2.44	218.50
1619	0.41	0.55	22.64	104.35	0.47	0.35	0.47	0.50	2.23	2.12	225.62
1620	0.37	2.63	21.30	102.15	0.30	0.30	0.48	0.65	2.09	2.35	225.13
1621	0.56	1.86	21.52	112.78	0.42	0.38	0.42	0.96	2.23	2.15	241.88
1624	0.24	1.08	20.68	97.52	0.70	0.53	0.83	0.80	1.93	2.03	210.50
1627	0.60	0.47	22.34	115.06	0.54	0.38	1.00	0.88	2.63	2.04	257.29
1628	0.32	2.11	23.08	117.16	0.53	0.39	0.61	0.76	2.66	2.53	240.24
1631	0.19	1.43	21.74	106.71	0.06	0.06	0.09	2.32	0.15	2.29	242.00
1632	0.24	1.39	22.62	109.95	0.44	0.28	0.44	0.44	2.59	1.94	231.44
1633	0.77	2.29	23.10	106.89	0.53	0.47	0.65	1.09	2.59	2.38	224.26
1634	0.16	1.12	23.24	106.79	0.37	0.30	0.47	0.60	2.40	2.36	221.83
1635	0.52	1.26	22.64	113.00	0.68	0.64	0.76	1.28	2.56	2.12	237.28
1638	0.56	1.62	21.48	104.30	0.79	0.46	0.82	0.71	2.32	2.46	232.61
1639	0.33	1.48	21.82	97.83	0.30	0.26	0.30	0.70	2.04	2.33	206.93
1642	0.31	1.50	22.29	109.38	0.41	0.38	0.41	0.72	2.45	2.41	235.90
1643	0.10	1.72	21.02	104.34	0.38	0.27	0.38	0.38	2.31	2.35	216.85
1644	0.41	1.97	22.61	113.30	0.42	0.27	0.70	0.58	2.48	2.21	249.45
Set 2											
1647	0.39	0.92	23.47	111.19	0.38	0.34	0.38	0.72	2.69	2.48	237.00
1650	0.43	1.42	22.45	11.86	0.71	0.58	0.84	0.90	2.19	1.87	222.42

Appendix Table 1. (continued).

Fam. No.	W S A B	S I N	B R S	D B H	T S A B	W S A B	S A B S C	I S A B	B R S	S I N	D B H
1653	0.53	1.76	24.19	118.45	0.69	0.56	0.83	0.92	2.53	2.11	254.67
1655	0.80	1.80	24.50	113.56	1.06	0.91	1.27	1.46	2.55	2.18	241.03
1656	0.66	1.50	23.97	117.37	0.75	0.53	0.84	0.84	2.41	2.38	252.50
1657	0.43	1.47	22.67	110.03	0.60	0.52	0.72	0.88	2.08	2.08	237.64
1658	0.40	1.55	23.93	109.00	0.69	0.50	0.73	0.92	2.46	2.15	231.85
1659	0.51	1.24	21.74	112.41	0.70	0.55	0.76	0.94	2.15	2.06	229.67
1660	0.49	1.43	21.67	103.65	0.56	0.50	0.56	0.74	2.09	2.12	221.71
1662	0.32	2.84	23.85	112.70	0.39	0.30	0.39	0.79	2.30	2.21	224.79
1663	0.27	1.55	22.66	108.38	0.68	0.55	0.74	0.71	2.23	2.10	215.81
1664	0.58	1.32	22.89	103.58	0.58	0.42	0.58	0.77	2.08	1.96	222.46
1665	0.53	0.37	21.93	108.63	0.70	0.60	0.70	0.87	2.10	2.10	232.17
1666	0.39	1.18	21.43	108.08	0.44	0.37	1.00	1.00	2.00	2.59	243.67
1667	0.26	0.95	22.65	108.74	0.46	0.32	0.54	0.46	2.36	1.75	232.11
1669	0.64	1.79	22.83	119.08	0.79	0.75	1.04	1.36	2.18	1.93	254.61
1670	0.37	0.86	22.14	120.16	0.31	0.31	0.44	0.56	2.19	2.00	249.56
1671	0.74	0.69	23.04	109.94	0.73	0.63	0.93	1.27	2.20	2.27	233.63
1672	0.76	1.86	23.32	118.08	0.65	0.53	0.68	0.73	2.26	2.08	245.44
1673	0.84	2.13	23.14	121.36	0.63	0.50	1.00	1.16	2.47	1.81	263.03
1675	0.59	1.05	22.17	107.08	0.78	0.75	1.16	0.88	2.34	2.06	225.75
1676	0.45	1.46	22.35	108.10	0.33	0.28	0.33	0.53	1.95	2.53	223.43
1682	0.44	2.38	22.34	107.97	0.60	0.53	0.63	0.67	2.03	2.30	229.07
1683	0.45	1.53	21.15	116.79	0.32	0.29	0.32	0.45	1.87	1.81	238.29
1684	0.86	0.92	23.54	113.30	1.17	0.93	1.50	1.20	2.37	2.40	220.47
1685	0.50	1.47	21.38	108.00	0.85	0.65	0.96	1.04	1.73	1.96	221.38
1687	0.55	0.87	22.28	113.26	0.39	0.39	0.42	0.61	1.97	2.10	236.55
1688	0.24	1.48	23.30	110.34	0.49	0.41	0.68	0.68	2.11	2.22	227.03
1690	0.50	1.85	22.48	113.15	0.43	0.37	0.66	0.86	1.97	1.77	233.60
1691	0.63	2.09	22.36	109.26	0.61	0.58	1.06	1.32	2.03	2.26	235.32
1692	0.89	2.71	21.23	116.29	0.54	0.43	0.71	0.91	1.89	2.03	237.94
Set 4											
1717	0.53	0.93	21.60	109.22	0.65	0.58	0.77	1.23	2.61	2.26	226.77
1718	0.50	1.50	21.61	103.88	0.56	0.44	0.56	0.63	2.44	2.11	217.04
1719	0.50	1.76	21.76	110.24	0.59	0.53	0.81	1.16	2.66	2.63	230.81
1720	0.53	1.46	23.14	110.58	0.45	0.41	0.48	0.77	2.68	2.32	220.10
1721	0.51	2.39	23.10	109.83	0.55	0.39	0.71	0.84	2.65	2.23	235.97
1722	0.72	1.88	23.68	115.17	0.56	0.50	0.81	1.16	2.72	1.19	239.59
1723	0.44	2.75	23.22	110.63	0.52	0.52	0.74	0.84	2.68	2.03	237.00
1724	0.34	1.73	20.31	97.19	0.19	0.19	0.42	0.54	2.12	2.23	210.23

Appendix Table 1. (continued).

Fam. No.	WSAB	SIN	BRS	DBH	TSAB	WSAB	SABSC	ISAB	BRS	SIN	DBH
1725	0.21	1.37	23.07	113.35	0.31	0.31	0.38	0.53	2.53	2.28	227.59
1726	0.61	1.88	21.68	103.76	0.59	0.52	0.59	0.83	2.28	2.17	224.90
1727	0.54	1.84	22.18	104.56	0.58	0.48	0.61	0.79	2.73	2.33	227.27
1728	0.90	1.44	24.73	119.49	0.69	0.56	0.75	1.09	2.81	2.38	241.94
1729	0.92	2.58	23.04	114.79	0.97	0.80	1.47	1.43	2.70	1.43	244.70
1730	0.63	1.60	23.55	107.57	0.89	0.71	1.18	1.32	2.71	2.32	239.28
1732	0.62	0.84	21.53	102.31	0.54	0.46	0.88	0.75	2.50	1.92	229.25
1733	0.69	1.57	22.80	110.80	0.63	0.59	0.66	0.94	2.78	2.44	248.25
1735	0.81	1.18	22.29	115.61	0.64	0.48	0.97	1.18	2.48	1.94	243.70
1736	0.47	1.10	21.21	102.50	0.41	0.33	0.44	0.48	2.52	2.04	234.52
1737	0.60	1.51	21.73	101.43	0.53	0.47	0.60	0.87	2.40	1.87	223.13
1738	0.69	3.57	22.67	112.07	0.52	0.44	0.52	1.04	2.52	2.81	237.07
1740	0.39	1.92	20.05	96.45	0.43	0.43	0.46	1.14	2.21	2.64	205.11
1741	0.57	1.48	22.52	103.23	0.43	0.43	0.43	0.76	2.86	2.14	230.33
1742	0.46	1.59	22.04	102.00	0.43	0.37	0.47	0.63	2.23	2.37	213.77
1743	0.43	1.14	21.64	101.78	0.64	0.54	0.75	0.93	2.61	2.25	227.71
1744	0.41	1.98	21.59	98.75	0.28	0.28	0.28	0.52	2.24	2.41	204.66
1745	0.65	1.21	21.66	106.06	0.39	0.39	0.39	0.82	2.39	2.61	226.00
1746	0.49	2.63	22.34	115.60	0.36	0.32	0.40	0.64	2.48	2.40	242.96
1749	1.20	1.34	23.16	113.44	1.04	1.10	1.19	1.96	2.85	2.35	246.88
1750	0.91	2.14	22.77	109.91	0.52	0.48	0.65	0.84	2.45	1.94	229.03
1751	0.48	1.82	22.36	101.93	0.23	0.23	0.27	0.41	2.27	1.82	209.27

[a] Key for the traits: TSAB = Total number of steep-angled branches, WSAB = Number of whorls with steep-angled branches, SABSC = Steep-angled branch score, ISAB = Impact of steep-angled branches, SIN = Sinuosity, BRS = Branch size, DBH = Diameter at breast height.

Appendix Table 2. Analyses of variance for 11 traits over all test sites.

Age 24 Traits:

A. Total Number of Steep-angled Branches[a]

Source	Df	SS	MS	F	Prob.
Site	2	0.22277	0.11139	0.12	0.8904
Set	2	15.02540	7.51270	7.83	0.0004
Site x Set	4	14.37776	3.59444	3.75	0.0048
Rep(Site x Set)	27	43.23891	1.60144	1.67	0.0170
Family(Set)	87	124.67449	1.43304	1.49	0.0026
Site x Family(Set)	174	184.66708	1.06131	1.11	0.1734
Plot error	760	745.63521	0.98110	1.02	0.3539
Error	1628	1561.24029	0.95900		

B. Total Number of Whorls with Steep-angled Branches[b]

Source	Df	SS	MS	F	Prob.
Site	2	0.40208	0.20104	0.21	0.8104
Set	2	17.69995	8.84997	9.25	0.0001
Site x Set	4	13.25511	3.31378	3.46	0.0079
Rep(Site x Set)	27	40.76687	1.50988	1.58	0.0301
Family(Set)	87	127.43720	1.46480	1.53	0.0015
Site x Family(Set)	174	190.50677	1.09487	1.14	0.1057
Plot error	760	732.96212	0.96442	1.01	0.4439
Error	1628	1557.11945	0.95646		

C. Total Steep-angled Branch Score[b]

Source	Df	SS	MS	F	Prob.
Site	2	0.24368	0.12184	0.13	0.8795
Set	2	13.47529	6.73765	7.10	0.0008
Site x Set	4	14.70002	3.67500	3.87	0.0039
Rep(Site x Set)	27	46.83523	1.73464	1.83	0.0059
Family(Set)	87	134.80476	1.54948	1.63	0.0003
Site x Family(Set)	174	181.15975	1.04115	1.10	0.1937
Plot error	760	752.23868	0.98979	1.04	0.2447
Error	1628	1544.51906	0.94872		

[a] Transformed for analysis as SQRT(X + .5).
[b] Transformed for analysis as LOG(X + 1).

Appendix Table 2. (continued).

D. Impact of Steep-angled Branches

Source	Df	SS	MS	F	Prob.
Site	2	0.68209	0.34105	0.36	0.6990
Set	2	9.77639	4.88820	5.13	0.0060
Site x Set	4	8.97570	2.24392	2.36	0.0517
Rep(Site x Set)	27	53.32440	1.97498	2.07	0.0010
Family(Set)	87	123.21198	1.41623	1.49	0.0029
Site x Family(Set)	174	154.74186	0.88932	0.93	0.7152
Plot error	760	775.76064	1.02074	1.07	0.1288
Error	1628	1550.04370	0.95212		

E. Sinuosity

Source	Df	SS	MS	F	Prob.
Site	2	0.00928	0.00464	0.01	0.9946
Set	2	18.61619	9.30809	10.88	0.0001
Site x Set	4	48.49154	12.12288	14.17	0.0001
Rep(Site x Set)	27	203.72587	7.54540	8.82	0.0001
Family(Set)	87	134.78524	1.54926	1.81	0.0001
Site x Family(Set)	174	133.78125	0.76886	0.90	0.8171
Plot error	760	678.85477	0.89323	1.04	0.2419
Error	1628	1393.06172	0.85569		

F. Branch Size

Source	Df	SS	MS	F	Prob.
Site	2	0.73049	0.36525	0.44	0.6445
Set	2	88.25465	44.12733	53.09	0.0001
Site x Set	4	94.81600	23.70400	28.52	0.0001
Rep(Site x Set)	27	130.29952	4.82591	5.81	0.0001
Family(Set)	87	135.07924	1.55263	1.87	0.0001
Site x Family(Set)	174	169.50292	0.97415	1.17	0.0712
Plot error	760	660.08291	0.86853	1.04	0.2371
Error	1628	1353.25135	0.83124		

Appendix Table 2. (continued).

G. Diameter at Breast Height

Source	Df	SS	MS	F	Prob.
Site	2	0.84570	0.42285	0.45	0.6400
Set	2	9.16047	4.58024	4.83	0.0081
Site x Set	4	12.62973	3.15743	3.33	0.0100
Rep(Site x Set)	27	60.14633	2.22764	2.35	0.0001
Family(Set)	87	171.03783	1.96595	2.08	0.0001
Site x Family(Set)	174	197.04772	1.13246	1.20	0.0495
Plot error	760	661.52810	0.87043	0.92	0.9112
Error	1628	1542.32324	0.94737		

Age 12 Traits:

H. Number of Whorls with Steep-angled Branches[c]

Source	Df	SS	MS	F	Prob.
Site	2	1.26838	0.63419	0.68	0.5077
Set	2	20.41132	10.20566	10.91	0.0001
Site x Set	4	10.30283	2.57571	2.75	0.0267
Rep(Site x Set)	27	70.22472	2.60092	2.78	0.0001
Family(Set)	87	162.61792	1.86917	2.00	0.0001
Site x Family(Set)	174	183.78710	1.05625	1.13	0.1275
Plot error	772	739.94252	0.95847	1.02	0.3377
Error	2081	1946.57182	0.93540		

I. Sinuosity[d]

Source	Df	SS	MS	F	Prob.
Site	2	0.08844	0.04422	0.06	0.9394
Set	2	8.66473	4.33236	6.13	0.0022
Site x Set	4	38.32246	9.58061	13.55	0.0001
Rep(Site x Set)	27	670.92866	24.84921	35.14	0.0001
Family(Set)	87	175.99145	2.02289	2.86	0.0001
Site x Family(Set)	174	165.55109	0.95144	1.35	0.0025
Plot error	772	541.38098	0.70127	0.99	0.5516
Error	2081	1471.48053	0.70710		

[c] Transformed for analysis as SQRT(X + .5).
[d] Transformed for analysis as LOG (X + 1).

Appendix Table 2. (continued).

J. Branch Size

Source	Df	SS	MS	F	Prob.
Site	2	0.82484	0.41242	0.46	0.6341
Set	2	4.82124	2.41062	2.66	0.0700
Site x Set	4	21.46988	5.36747	5.93	0.0001
Rep(Site x Set)	27	157.86450	5.84683	6.46	0.0001
Family(Set)	87	158.14297	1.81773	2.01	0.0001
Site x Family(Set)	174	198.00460	1.13796	1.26	0.0158
Plot error	772	672.05651	0.87054	0.96	0.7398
Error	2081	1883.59709	0.90514		

K. Diameter at Breast Height

Source	Df	SS	MS	F	Prob.
Site	2	0.34478	0.17239	0.19	0.8241
Set	2	26.26097	13.13048	14.73	0.0001
Site x Set	4	17.70854	4.427136	4.97	0.0006
Rep(Site x Set)	27	137.37166	5.08784	5.71	0.0001
Family(Set)	87	177.66223	2.04209	2.29	0.0001
Site x Family(Set)	174	235.22365	1.35186	1.52	0.0001
Plot error	772	667.49938	0.86464	0.97	0.6901
Error	2081	1854.45738	0.89114		

Appendix Figure 1. Distributions of number of steep-angled branches at age 24, for all trees at age 12 (BT), and for the subset of trees at age 12 that remained after thinning at age 23 (AT).
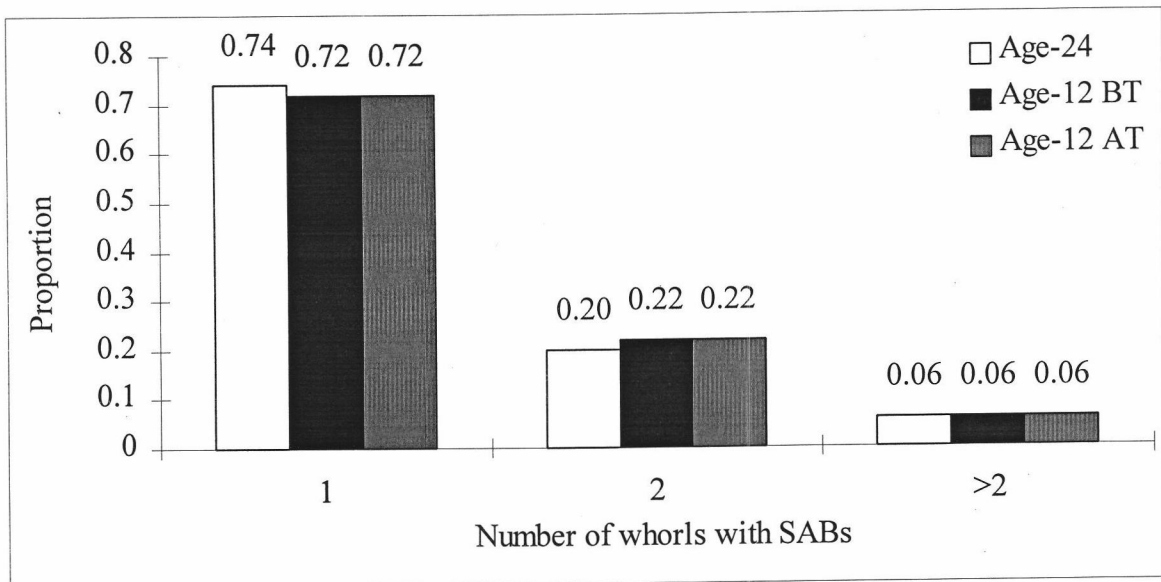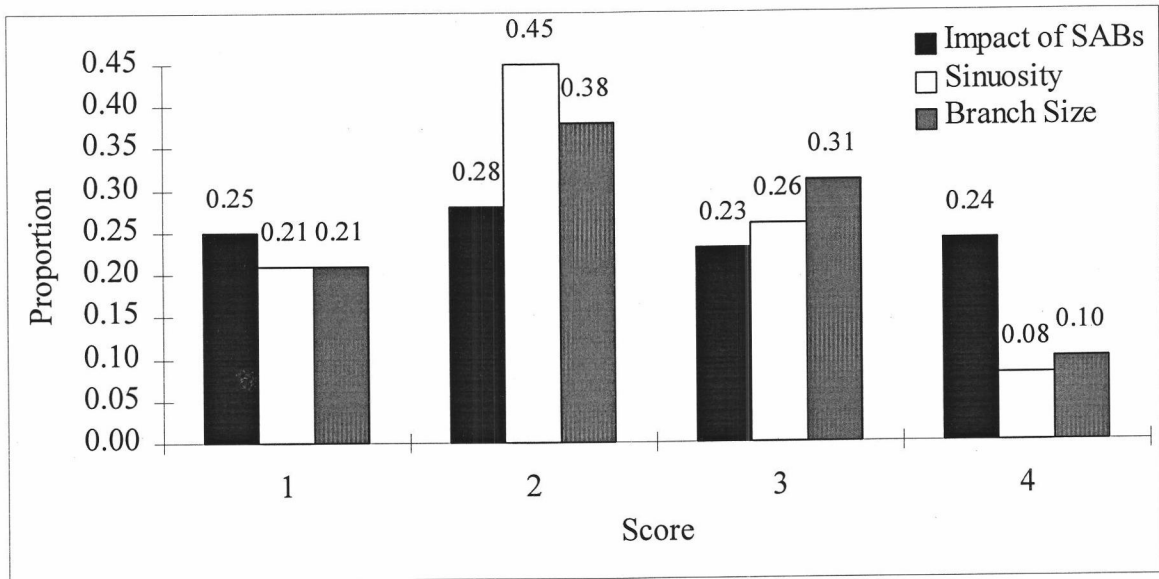

**Appendix Figure 2.** Distribution of trees with given numbers of steep-angled branches at age 24.
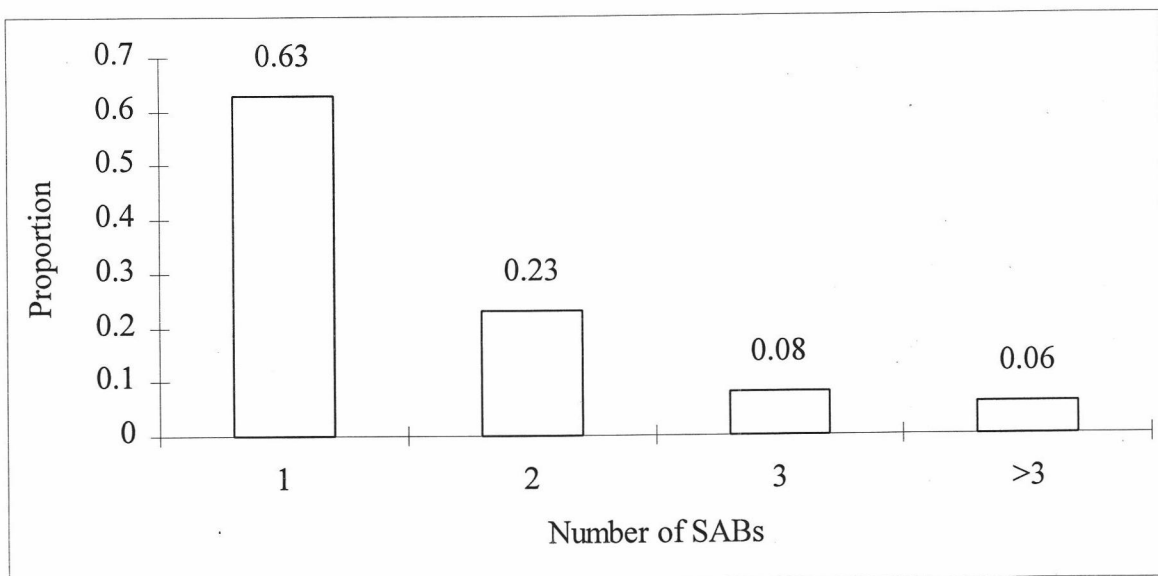
Appendix Figure 3. Distribution of steep-angled branch size classes at age 24.
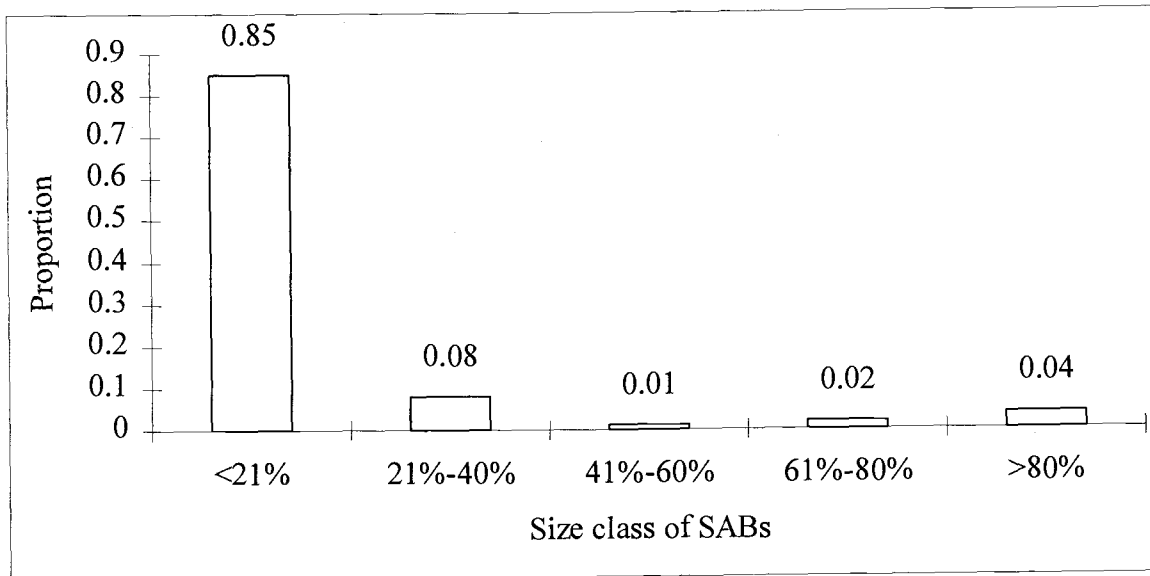
**Appendix Figure 4.** Distribution of total steep-angled branch scores at age 24.
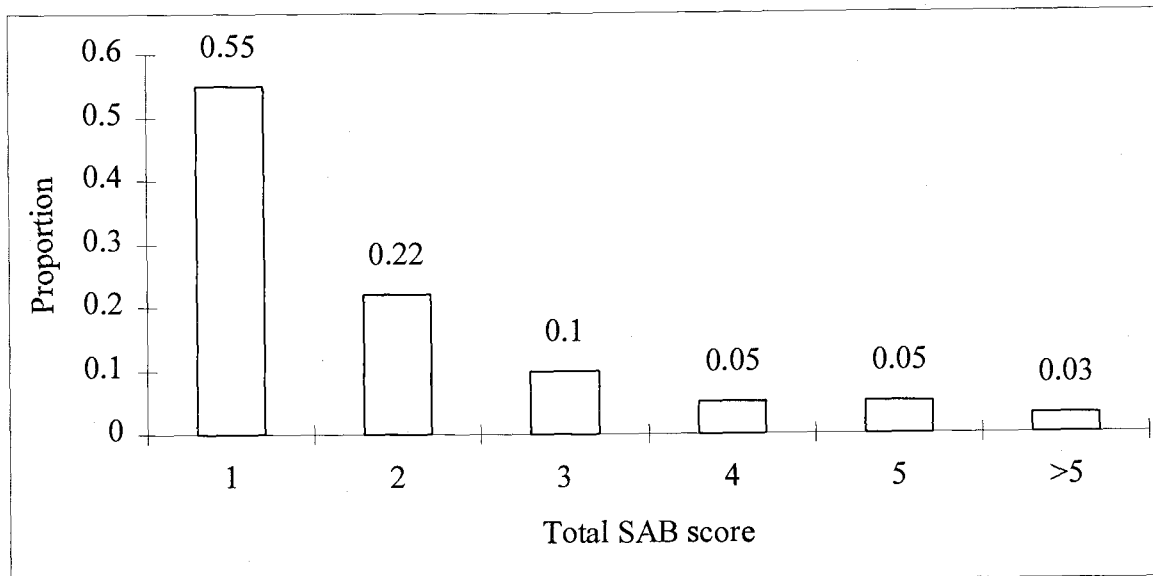
Appendix Figure 5. Distributions of impact of steep-angled branches, sinuosity, and branch size scores at age 24.

**Appendix Figure 6.** Distribution of diameter at breast height at age 24.
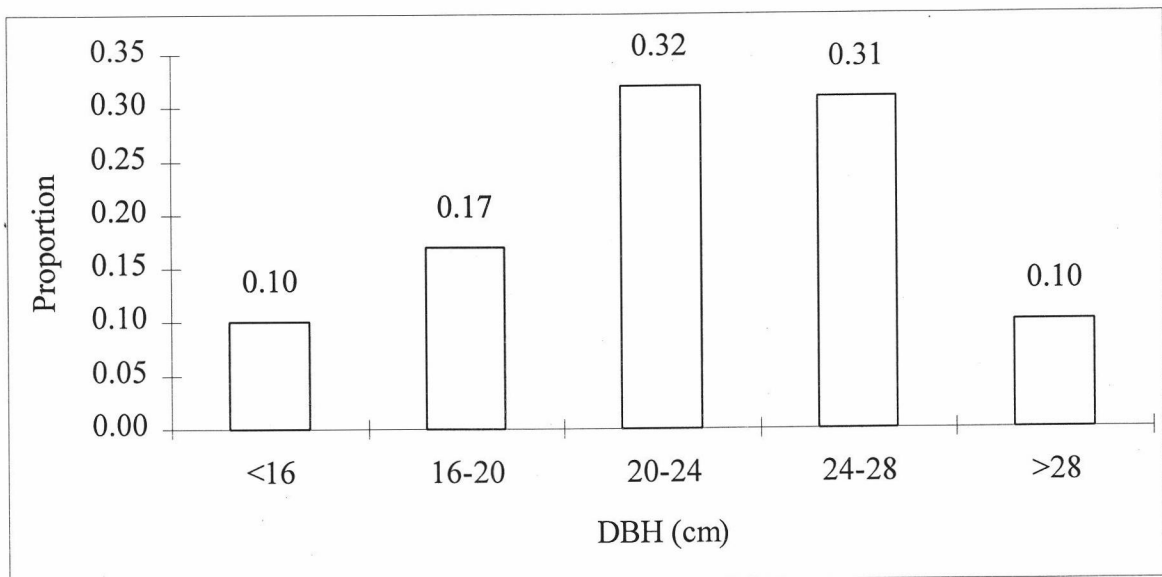
Appendix Figure 7. Distributions of sinuosity index scores among all trees at age 12 (BT), and among age 12 trees remaining after thinning at age 24 (AT).
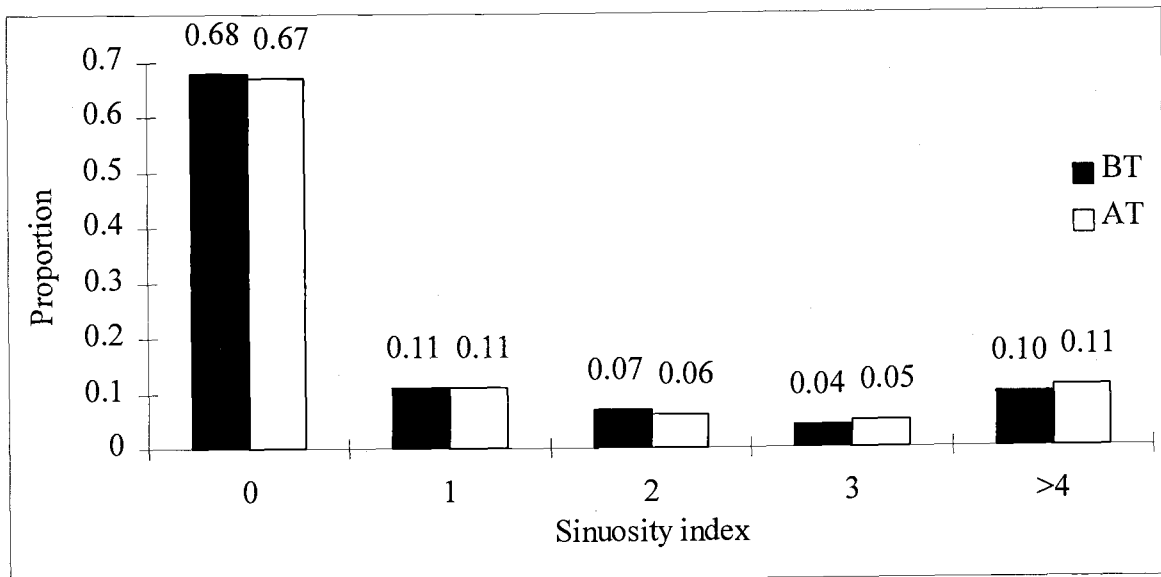

Appendix Figure 8. Distributions of branch size scores among all trees at age 12 (BT), and among age 12 trees remaining after thinning at age 24 (AT).
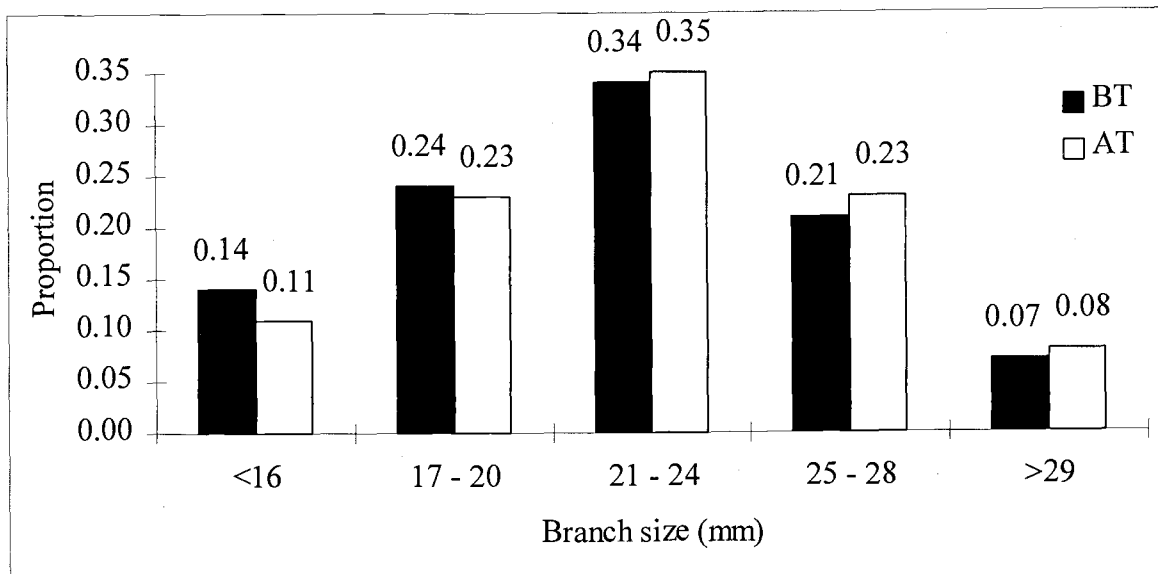
Appendix Figure 9. Distributions of diameter at breast height among all trees at age 12 (BT), and among age 12 trees remaining after thinning at age 24 (AT).
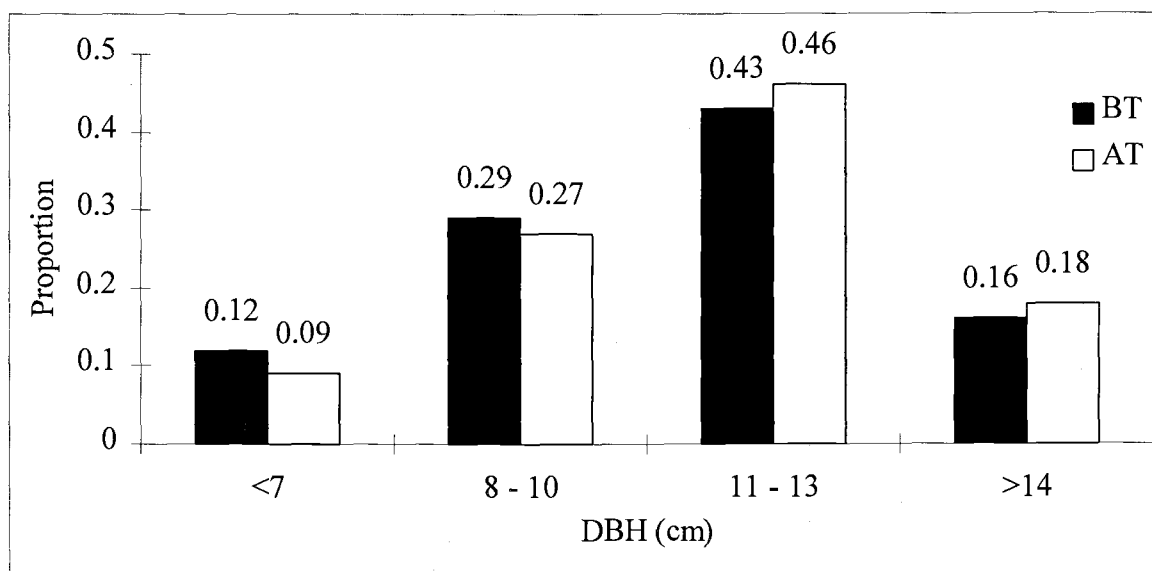
Appendix Figure 10. Scatter plot of mean DBH and mean WSAB of the 90 families over all three sites at age 24. Solid data points indicate the top 10% of all families that can be selected for DBH without increasing BRS.
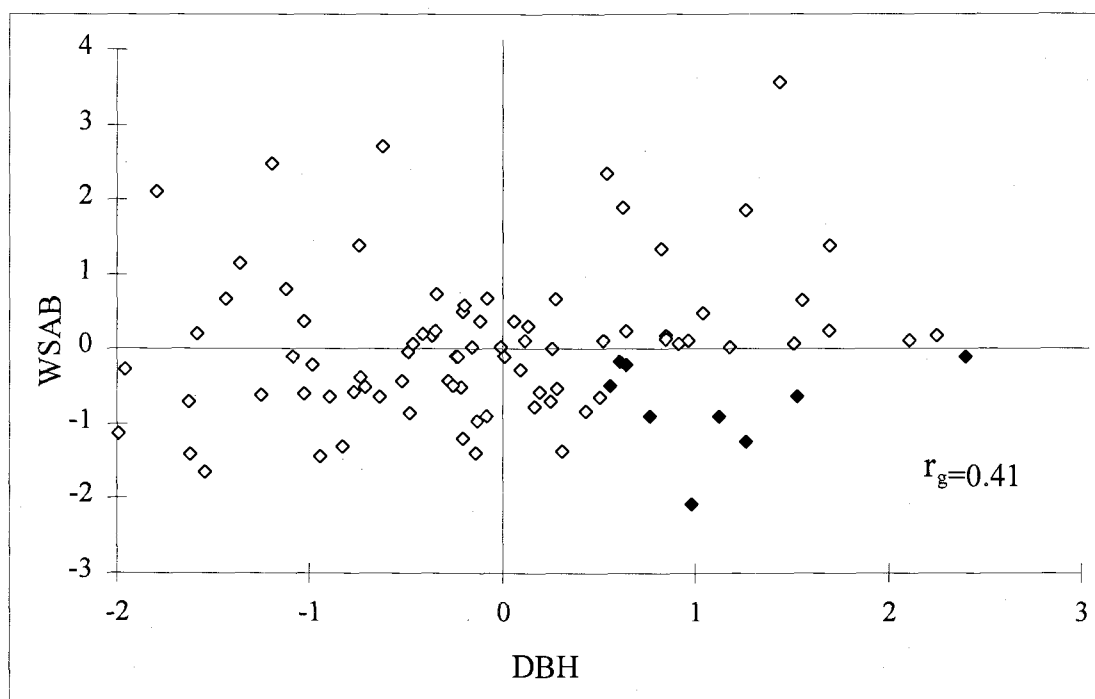
Appendix Figure 11. Scatter plot of mean DBH and mean BRS values of the 90 families over all three sites at age 12. Solid data points indicate the top 10% of all families that can be selected for DBH without increasing BRS.
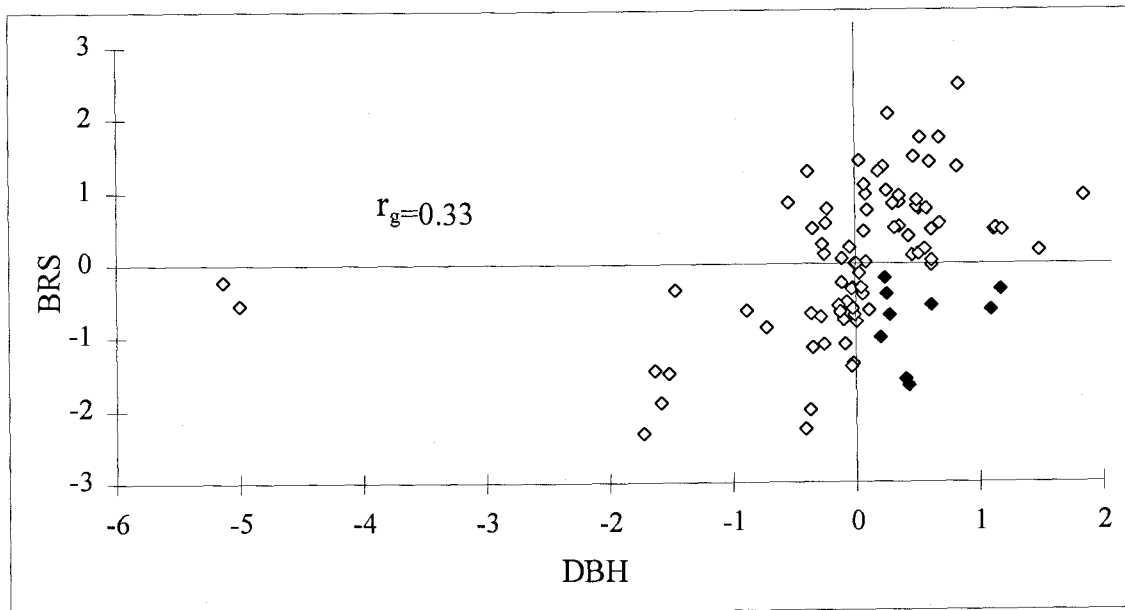
Appendix Figure 12. Scatter plot of mean DBH and mean WSAB values of the 90 families over all three sites at age 12. Solid data points indicate the top 10% of all families that can be selected for DBH without increasing WSAB.