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Quantitative Genetic Structure of Stem Form and Branching traits in Douglas-fir Seedlings and Implications for Early Selection

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Abstract

Open-pollinated (OP) and full-sib (FS) families of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) were grown in two replicated nursery regimes in order to evaluate the magnitude and repeatability of genetic parameter estimates for stem form (stem sinuosity, forking) and branching (number, length and angle of branches) traits in 2-year-old seedlings, and the relationships of these traits with stem growth. With data from older trees of the OP families growing in the field (ages 12 and 24), genetic control of similar traits was compared at the different ages, and nursery-field correlations (r_{xy}) were estimated. With the exception of forking, estimates of family heritability (h^2_f) were moderate to strong for stem form and branching traits in seedlings ($0.32 \leq h^2_f \leq 0.94$; mean = 0.73), and similar to growth traits ($0.45 \leq h^2_f \leq 0.90$; mean = 0.75). Family performance and estimates of genetic parameters were relatively stable across nursery regimes and family type. Genetic relationships among traits in seedlings were similar to those observed in older field-grown trees, indicating that these traits are controlled by similar sets of genes in the two age classes. Nursery-field correlations between comparable traits were consistent across nursery regimes, but r_{xy} was strong enough to be useful for early testing purposes (i.e., $| r_{xy} | \geq 0.30$), only for number of whorls with steep-angled branches (WSAB), branch length, and branch angle in older trees. Predicted gains from early selection for these or correlated traits were at least 40–50% of those expected from selection at older ages. Because of unfavorable genetic correlations, selection for stem growth potential alone at the seedling stage is expected to produce unfavorable impacts on WSAB and stem sinuosity in older trees. To avoid such negative effects on wood quality, both stem form and branching traits should be included as selection criteria in Douglas-fir breeding programs.

Key words: Pseudotsuga menziesii, stem sinuosity, forking, repeatability, wood quality, nursery-field correlations.

Introduction

Stem form and branching traits have important economic impacts on both wood quality and productivity of forest trees. Stem sinuosity, stem forking, and occurrence of branches that

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are large in diameter, steep angled or numerous, reduce lumber yield and lower wood quality by increasing the amount of compression wood and number and size of knots (ZOBEL and VAN BUIJTENEN, 1989). These traits also unfavorably impact wood strength and uniformity, pulp yield, and processing costs (SHELBOURNE, 1970; ZOBEL and KELLISON, 1978). In addition, the number, size, and angle of branches influence stand competition and productivity, since both the amount of space required for individual trees and light interception of their crowns are affected by these traits (KUULUVAINEN, 1988; ST.CLAIR, 1994). Although some of the negative impacts of poor stem form and branch habit can be mitigated by silvicultural practices, such as selective thinning and bole pruning, genetic improvement provides a more efficient long-term solution, if enough genetic variation is available for these traits.

Given the long rotation cycle of most forest tree species, the possibility of testing and selection at the seedling stage in order to improve traits in older trees (i.e., early testing), is an important consideration in most tree breeding programs. Early testing provides the opportunity to reduce the length of the breeding cycle and increase average genetic gain per year (i.e., single-stage early selection; LAMBETH et al., 1983), or to eliminate genotypes with below-average genetic potential before field-testing (i.e., two-stage selection: early testing followed by field testing; WU, 1998; ADAMS et al., 2001). In the case of family selection, the efficacy of early testing depends on the magnitude of family-mean phenotypic correlations between traits measured in seedlings and target traits at older ages (r_{xy}) (ADAMS et al., 2001). In turn, the magnitude of r_{xy} is determined by the strength of genetic control (heritability) of the traits at the two ages and the genetic correlation (r_G) between the traits, a measure of the extent to which the traits in seedlings and in older trees are controlled by the same set of genes.

The choice of nursery test environment influences r_{xy} in two ways. First, if there is strong genotype-by-environment (GxE) interaction among nursery environments, the test environment can influence accuracy of prediction of field performance. A strong GxE interaction means that genotypes will be expressed differently in different environments, leading to changes in family rankings. Under these circumstances, some nursery environments will be better for predicting field performance than others. For practical reasons, the test environment chosen for early selection must be repeatable over years, organizations, etc., so that early testing predictions are consistent. If there is strong GxE over years or locations using the same testing regime, the practical value of early testing is questionable.

The choice of test environment can also influence the precision of ranking even if there is no significant GxE interaction, by affecting the heritability of seedling traits. For instance, in the study by ST.CLAIR and ADAMS (1991) the competitive environment had a large effect on estimates of variance components, leading to large differences between environments in heritability estimates. For early testing purposes, the ideal nursery regime would be one that is inexpensive, provides relatively accurate rankings of performance of target traits in older trees (strong r_{xy}), and is relatively insensitive to modest changes in environmental conditions (high heritability), so rankings are consistent across trial runs.

In 1986, the Pacific Northwest Tree Improvement Research Cooperative started a project on "Early Testing in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco)" utilizing relatively large numbers of two kinds of families (open- and control-pollinated) growing in two types of replicated nursery trials. The purpose of this study was to determine the magnitude and repeatability of nursery-field correlations that might

be reliably expected under operational conditions. In an earlier paper, ADAMS et al. (2001) showed that with r_{xy} as low as 0.30 to 0.40, early testing for growth potential could be very effective in either single- or two-stage selection scenarios. In this paper we evaluate the potential for early testing of stem form and branching traits in Douglas-fir using data from this study. Specifically, we: (i) estimate the degree of genetic control of stem form and branching traits in two-year old Douglas-fir seedlings and the genetic relationships between these traits and stem growth; (ii) evaluate the repeatability of these genetic parameter estimates across nursery tests; (iii) compare genetic parameters of traits in seedlings with those of similar traits in older trees, and estimate phenotypic and genetic correlations between these traits; (iv) evaluate responses in stem form and branching traits in older trees from early selection of comparable traits in seedlings; and (v) explore the implications of early selection for growth only on stem form and branching traits in older trees.

Materials and Methods

General Approach

Open-pollinated (OP) and full-sib (FS) families were grown in two replicated nursery regimes (bareroot and transplant). After two years of growth, seedlings were measured for a variety of growth, stem form and branching traits. This information was used to evaluate inheritance of traits and relationships between them at the nursery stage, as well as stability of rankings across nursery regimes. Field test measurements of stem form and branching traits in older trees were available only for the OP families, so comparison of quantitative genetic structure of traits at different ages, estimates of nursery-field correlations, and evaluation of the efficacy of early selection were restricted to these materials. Details of the study materials, nursery and field trials, and statistical methods are found in ADAMS et al. (2001). We present only a summary here.

Nursery Trials

Seeds of 67 OP families from sets 2, 4, and 5 of the Noti Breeding Unit (52,000 ha, below 650 m in elevation) in the central Oregon coast range, and 66 FS families from two series of crosses made by the B.C. Ministry of Forests Coastal Douglas-fir Tree Improvement Program were included in the nursery trials. In both cases, families were chosen among available seed lots in storage. Additionally, FS families were selected to minimize the relatedness of parentage among the progenies (in total, the families involved 74 parents, of which 50% were involved in only single crosses).

In the bareroot testing regime, germinants were sown directly into the beds of a nursery in the state of Washington at a spacing of 8.9 x 15.0 cm and grown for two years. Replicate trials were established in 1986 and 1987, using adjacent beds in the nursery. Within each trial, seed lots were sown in a split-split plot experimental design with nine blocks. Family types were allocated to the main plots, with family sets or series as subplots and families within sets as sub-subplots, each represented by a four-tree row. Seedlings were grown for two seasons using standard operational practices but without applying pre-emergent herbicide, nor top- or root-pruning the seedlings. Due to problems in emergence and survival in some blocks, only seven blocks in the 1986 and six blocks in the 1987 replicate were used in the final analyses. Survival in these blocks at the end of the experiment averaged 78% in the 1986 and 90% in the 1987 replicate.

In the transplant regime, germinants were sown in 1987 into Ray Leach containers (164 cc), using a standard growing medi-

um, in two (replicate) greenhouses, one in the state of Oregon (OR) and the other in the state of Washington (WA). The same split-split plot design as in the bareroot regime was used, with eight blocks in OR and six in WA. Seedlings were grown in the greenhouses for a single season using standard operational practices. Mild water stress was used to promote bud set, but it was applied sooner in WA (early July) than in OR (late July), so first-year height growth was lower in the WA greenhouse. In November 1987, seedlings were lifted from both greenhouses and stored in cold rooms. Next spring, in April 1988, half the blocks from each greenhouse (i.e., four from OR and three from WA) were transplanted into each of two nurseries, one in Oregon and the other in Washington (in WA, it was the same nursery used for the bareroot regime), and grown for an additional growing season at a similar spacing as in the bareroot regime. Cumulative survival at the end of the second growing season was 95% for the OR transplant nursery and 96.5% for the WA transplant nursery

In fall, after the end of the second growing season, shoot height, diameter, and fresh weight, and several stem form and branching traits (branch number, length, and angle; bole sinuosity; and, number of forks) were recorded for each seedling (*Table 1*). A branch was considered a fork if it was substantially thicker than other branches and had an angle of less than 30° from the main stem (i.e., steep-angled branches or SAB).

Estimation of Genetic Parameters

A separate statistical analysis was carried out for each nursery testing regime and type of family (i.e., OP and FS). Analyses of variance (ANOVA) were first done using the GLM procedure of SAS (SAS, 1990) to test for significance of family differences (type III sums of squares). All tests of significance in this study were at the 5% probability level.

Variance components were estimated with the REML method of the SAS VARCOMP procedure, using the following statistical model:

$$Y_{ijklm} = \mu + t_i + b_{j(i)} + s_k + ts_{ik} + bs_{j(i)k} + f_{l(k)} + tf_{il(k)} + e_{ijkl} + w_{ijklm}$$

where Y_{ijklm} is a trait's value in the mth seedling of the lth family within the kth set (or series) in the jth block within the ith replicate trial, μ is the trial mean, t_i is the random effect due to i^{th} replicate trial [$E(t_i)=0$, $Var(t_i)=\sigma^2_t$], $b_{j(i)}$ is the random effect due to j^{th} block within the ith trial [$E(b_{j(i)})=0$, $Var(b_{j(i)})=\sigma^2_b$], s_k is the random effect due to k^{th} set [$E(s_k)=0$, $Var(s_k)=\sigma^2_s$], ts_{ik} is the random interaction effect of the ith trial with the kth set [$E(ts_{ik})=0$, $Var(ts_{ik})=\sigma^2_{ts}$], $bs_{j(i)k}$ is the random interaction effect of the jth block within the ith trial with the kth set, or main-plot error [$E(bs_{j(i)k})=0$, $Var(bs_{j(i)k})=\sigma^2_{bs}$], $f_{l(k)}$ is the random effect due to l^{th} family within the kth set [$E(f_{l(k)})=0$, $Var(f_{l(k)})=\sigma^2_f$], $tf_{il(k)}$ is the random interaction effect of the ith trial with the lth family within the kth set [$E(tf_{il(k)})=0$, $Var(tf_{il(k)})=\sigma^2_{tf}$], e_{ijkl} is the random sub-plot error of the lth family within the kth set in the jth block of the ith replicate trial[$E(e_{ijkl})=0$, $Var(e^{ijkl})=\sigma^2_e$], and w_{ijklm} is the random error of the mth seedling in $ijkl^{th}$ sub-plot, or within-sub-plot error [$E(w_{ijklm})=0$, $Var(w_{ijklm})=\sigma^2_w$]. The REML VARCOMP estimation method is considered to provide more reliable variance component estimates than those obtained using GLM when there is imbalance in the data (SEARLE *et al.,* 1992). Stem sinuosity (SIN) and forking (SAB) indices were log-transformed (i.e., Log (SIN + 1) and Log (SAB + 1)) prior to analysis to conform to basic assumptions of ANOVA.

Table 1. – Description of growth, stem form, and branching traits measured in seedlings (age 2) and in older trees (ages 12 and 24).

Trait	Seedlings (age 2)	Age 12	Age 24
Height	Shoot height (mm).	Stem height (dm).	Not measured.
Diameter	Stem caliper just above root collar (0.1 mm).	Diameter at breast height (DBH) (mm).	DBH (mm).
Top weight/ Stem volume†	Fresh shoot weight (g).	Stem volume (dm³) estimated from height and DBH, using equation by Adams and Joyce (1990).	Not measured.
Number of branches	Total number of branches on the shoot.	Total number of branches at the whorl nearest to breast height and the interwhorl above it.	Not measured.
Branch length	Length of the longest branch at the base of the second-year shoot (mm).	Average length of the two longest branches at the whorl nearest to breast height (cm).	Not measured.
Branch diameter	Not measured.	Average diameter of the two longest branches at the whorl nearest to breast height, measured 3 cm from the bole (mm).	Average score of the thickest branch in both the lower and upper 5-m section of the stem, in a scale of 1 (thin) to 4 (thick).
Branch angle	Angle of the longest branch at the base of the second-year shoot, in 10° units, not including forks.	Average angle from the bole of main-whorl branches in the whorl nearest to breast height (visually estimated using angles etched on clear plastic as a guide).	Not measured.
Sinuosity (stem waviness or crookedness)	Maximum lateral displacement of the stem caused by the crooks (if any) on the second-year shoot, measured in 5-mm units.	Number of crooks in the second interwhorl from the top of the tree, multiplied by the maximum distance of lateral displacement of the stem caused by the crooks (measured in units of ½ diameter of the stem) (ADAMS and HOWE, 1985).	Average score of the most sinuous interwhorls in the lowest two 5-m sections of the bole, on a scale of 1 (straight) to 4 (very sinuous).
Forks/WSAB‡	Score of 0 (no forks in the main stem), 1(single fork), or 2 (multiple forks), measured in the first-year shoot.	Total number of whorls in the tree (without including the uppermost) with at least one steep-angled branch (diverging < 30° from the bole).	Total number of whorls with at least one steep-angled branch in the two lowest 5-m sections of the bole.

† Top weight at age 2, stem volume at age 12; ‡ Forking score at age 2, number of whorls with steep-angled branches (WSAB) at ages 12 and 24.

To compare the precision of early testing regimes, the heritability of family means, h^2_f, was estimated for each type of family as

$$h^2_f = (\sigma^2_f)/(\sigma^2_{\bar{p}})$$

where $\sigma^2_{\bar{p}}$ is the phenotypic variance of family means (NAMKOONG, 1979). Heritability of family means estimated this way evaluates repeatability of family performance within a particular test regime. If individuals within OP families are half-sibs, h^2_f is equivalent to the proportion of variation among family means due to additive genetic effects (i.e., narrow-sense family heritability). However, since individuals in OP families of Douglas-fir are likely to be related more closely than half-sibs (CAMPBELL, 1986), h^2_f probably overestimates narrow-sense family heritability. Some seedling traits were correlated with seed weight; however, seedling traits were not adjusted for seed weight in the analyses because adjustment did not influence nursery-field correlations (in the OP families). Without adjustment, h^2_f estimates were only slightly greater than with adjustment. In addition, adjusting for seed weight may reduce useful genetic variance in seedling traits (SORENSEN and CAMPBELL, 1993; SURLES et al., 1993).

Genetic correlations (r_G) between traits measured on the same individuals were estimated as

$$r_G = Cov_{f(x,y)}/(\sigma^2_{f(x)}\,\sigma^2_{f(y)})^{0.5}$$

where $Cov_{f(x,y)}$ is the family within set (or series) component of covariance between traits x and y, and $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the corresponding family variances for those traits. $Cov_{f(x,y)}$ was estimated by performing a REML VARCOMP analysis on the sum of traits x and y, and using the relationship (FREUND, 1962)

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

Phenotypic correlations between family-means ($r_{\bar{p}}$) for each pair of traits were also estimated as the Pearson product-moment correlation using the family mean values for each trait. Phenotypic correlations were first estimated separately for each set (or series) of families and then weighted estimates of $r_{\bar{p}}$ across sets (or series) were obtained for each testing regime using the methods described in STEEL et al. (1997; Section 11.5).

Repeatability of Nursery Trials

To evaluate the repeatability of family performance for seedling traits between replicates of the same testing regime, the significance of the family-by-trial interaction for each trait was determined for both OP and FS families in the GLM analyses. In addition, type-B genetic correlations (r_B) between replicate trials were estimated from REML variance components in the VARCOMP analysis using the equation

$$r_B = \sigma^2_f/(\sigma^2_f + \sigma^2_{tf}).$$

To evaluate the repeatability of family performance between testing regimes, similar GLM and VARCOMP analyses were done for all pairwise combinations involving a replicate from each testing regime in the model. Significance of family-by-testing regime interaction and rB estimates were obtained as above.

To further evaluate the repeatability of genetic control of traits across nursery trials, correlations between all pairs of traits within a trial (i.e., correlation structure) were compared between nursery regimes. The Pearson product-moment correlations between paired elements in the correlation matrices of the testing regimes were obtained, after transforming each element to a 'z-score' (STEEL et al., 1997). Given that genetic correlations have an unknown distribution, and large standard errors are generally associated with them (CHEVERUD, 1988),

$r_{\bar{p}}$, rather than r_G matrices were used for this similarity test. Pearson's correlation coefficients between r_G and $r_{\bar{p}}$ of the same traits, after transforming them to z-scores, were very high for both nursery regimes and family types ($r \geq 0.96$; $r = 0.97$ overall).

Quantitative Genetic Structure of Traits in Field Tests

Field data from 43 families in two of the OP sets (sets 2 and 4) were available from other studies (ADAMS and HOWE, 1985; TEMEL and ADAMS, 2000) to compare genetic structure of stem and branching traits in older trees with that of similar traits in seedlings. These data came from measurements of these families in three test plantations established in the same breeding zone as the parent trees. At each test site, each set of families was planted as a separate randomized complete block experiment with four replications; families were represented originally by four-tree, non-contiguous plots in each block. A detailed description of conditions and management of the test plantations is provided elsewhere (TEMEL and ADAMS, 2000).

Stem form and branching traits in these trees were measured in 1984 and 1996, at ages 12 and 24 years, respectively. Measurements at age 12 were: bole sinuosity; number of whorls with steep-angled branches (WSAB); branch number, length, diameter, and angle; tree height; diameter at breast height (DBH); and, bole volume, estimated using the equation described by ADAMS and JOYCE (1990) (Table 1). At age 24 only DBH, bole sinuosity, WSAB and branch size were measured. Note, however, because of the difficulty of reaching branches or seeing the entire crown at age 24, sinuosity, WSAB and branch size were measured/scored differently at the two age classes (Table 1; TEMEL and ADAMS, 2000). Steep-angled branches were defined as branches that diverged less than 30° from the bole and included both forks (similar in diameter to the main bole) and ramicorns (smaller diameter than the main bole).

The field data were first analyzed to test for significance of family differences and then to estimate variance components, using the GLM and VARCOMP procedures described for the nursery trials. The data set combined over the three sites was used for all analyses, since the goal was to evaluate overall performance of families in the field tests. The statistical model was similar to that used for seedling data but with "blocks" nested within family sets and test sites.

Prior to statistical analyses of the field data, the sinuosity index (SIN) at age 12 was transformed to Log (SIN + 1) (ADAMS and HOWE, 1985), and WSAB at both ages was transformed to $(WSAB + 0.5)^{0.5}$ (TEMEL and ADAMS, 2000). Family heritability (h^2_f) and genetic correlations between traits were estimated using the same equations described for the nursery trials.

Nursery-Field Correlations and Implications for Early Selection

Associations of stem form and branching traits between seedlings and older (field-grown) trees were first assessed by estimating Pearson's correlation coefficients (r_{xy}) between OP family means (total 43 families) for comparable traits at the two ages. These correlations were calculated separately for each set of families (i.e., sets 2 and 4) and then simple weighted means of r_{xy} across sets were obtained for each nursery trial replicate. A χ^2 test of heterogeneity was used to compare mean r_{xy} estimates across seedling test replicates and nursery regimes.

The effectiveness of early (single-stage) selection for stem form and branching traits was evaluated by comparing the predicted responses of these traits in older trees (i.e., target trait at age 12 or 24) when comparable (or correlated) traits are selected at age 12 (typical selection age) and age 2 (early testing). We used selection at age 12 as a reference because final

selections in Douglas-fir are likely to occur at age 15 or earlier (SILEN and WHEAT, 1979; JOHNSON *et al.*, 1997).

Response in target trait (Ry) was calculated as:

$$R_y = ih_xh_yr_G\sigma_{\bar{p}y}$$

where i = selection intensity, h_x and h_y = square-root of family heritabilities for the selected and the target traits, respectively, r_G = genetic correlation between the selected and the target traits, and $\sigma_{\bar{p}y}$ = phenotypic standard deviation among family means for the target trait. We assumed for a selection scenario that the top 20% (i=1.40) of the families are selected and deployed in plantations without further mating. Note that when the target trait and the selected trait are the same (e.g., branch length at age 12), x and y are the same, and $h_xh_yr_G = h^2_y$ (FALCONER and MACKAY, 1996). Similarly, assuming there is no environmental covariance between the nursery and the field environments, when selection is done in early tests (at age 2), $h_xh_yr_G = r_{xy}$ (ADAMS *et al.*, 2001), so $R_y = ir_{xy}\sigma_{\bar{p}y}$. In this case, the average r_{xy} of the two separate replicate trials in each testing regime for each pair of traits was used, assuming that under operational conditions a single nursery trial would be employed. The relative efficiency of early testing was calculated as the ratio of predicted response in a target trait from selection at age 2 divided by predicted response if selection were at age 12, assuming the same selection intensity at both ages.

To evaluate impacts of early selection for growth on stem form and branching traits at the target age, correlated responses in these traits when stem height is selected at ages 2 and 12 were calculated. Response in target traits (R_y) was estimated using the above equation where y is the target trait and x is height at age 12 or 2. At age 12, we used selection for height as a reference because in our data set this trait had stronger genetic control than other growth traits at that age and had a strong genetic correlation with volume growth.

Results and Discussion

Genetic Variation of Stem Form and Branching Traits in Seedlings

Seedlings in the transplant regime were, on average, 15 cm smaller, with about 35% fewer branches at age two than those grown in the bareroot regime, but had straighter stems (i.e., less sinuosity) (*Table 2*). Height differences were primarily due to reduced growth of seedlings after transplanting, since at the end of the first growing season, greenhouse-grown seedlings were on average 5 cm taller and had similar numbers of branches to seedlings grown in the bareroot regime. The reduced growth in the transplant regime seems to be related to the phenomenon of "transplant shock" (HAASE and ROSE, 1993). Trial means for traits other than height, number of branches and sinuosity were similar and relatively consistent across testing regimes and family types (*Table 2*).

Significant family variation was observed for all seedling traits, except forking (*Table 2*). The frequency of seedlings scored as forked was low in the nursery trials (ranging between 8 and 20% over the two testing regimes and family types) and there was a large environmental component of variation; thus, it appears family differences in forking cannot be adequately assessed in two-year-old seedlings. The recurrence of forking is also low in older Douglas-fir trees established in field test plantations, but the frequency of forks and ramicorns (i.e., all SAB) together can exceed 30%, particularly on sites favorable to growth (TEMEL and ADAMS, 2000). In contrast to the low family variation observed in forking, the range in average height among families was about 30% of the trial mean, and stem sinuosity varied about two-fold with respect to its mean. Coefficients of family variation were above 5% for most traits (*Table 2*). Differences among traits in family variation were consistent over testing regimes and family types; stem sinuosity always showed the largest coefficient of family variation (above 30%), while branch angle had the lowest (about 3–5%).

Family means were found to be under moderate to relatively strong genetic control for most seedling traits. Among growth traits, estimates of family heritability for height were consistently greater across nursery trials than for diameter and top weight (*Table 2*). It is well known that diameter growth is very sensitive to environmental factors, even in seedlings grown under nursery conditions (CAMPBELL and WILSON, 1973; DURYEA, 1984), so the lower h^2_f for diameter is not unexpected. Seedling biomass, on the other hand, was previously found to have stronger genetic control than height growth in Douglas-fir (LAMBETH *et al.,* 1982), but it is also sensitive to competition

Table 2. – Estimated trial means ($\bar{x}$), ranges of family means, coefficients of family variation (Fcv), and family heritabilities (h^2_f) for growth, stem form, and branching traits of two-year-old seedlings in bareroot and transplant nursery trials of open-pollinated and full-sib families.

Trait	Bareroot				Transplant			
	$\bar{x}$	range	Fcv (%)[†]	h^2_f[‡]	$\bar{x}$	range	Fcv(%)[†]	h^2_f[‡]
Open–pollinated families								
Height (cm)	64.1	52.3 – 73.2	6.27 *	0.81	49.6	44.5 – 56.5	5.40 *	0.80
Diameter (mm)	9.2	7.4 – 10.9	6.92 *	0.73	10.4	9.5 – 11.6	2.42 *	0.41
Top weight (g)	671.2	425.8 - 976.4	13.56 *	0.73	656.4	525.8 – 784.3	6.74 *	0.58
No. of branches	34.5	26.6 – 40.4	8.07 *	0.78	23.5	18.3 – 29.3	7.34 *	0.75
Branch length (cm)	22.4	17.6 – 26.3	6.88 *	0.76	19.6	17.6 – 22.4	4.83 *	0.70
Branch angle (°)	64.0	56.2 – 72.8	4.58 *	0.77	65.5	60.0 – 70.1	2.85 *	0.73
Sinuosity[§]	1.9	0.2 – 4.8	34.17 *	0.59	0.3	0.0 – 1.3	50.69 *	0.32
Forking[§]	0.2	0.0 – 0.5	0.58	-----[£]	0.3	0.1 – 0.6	0.00	-----[£]
Full-sib families								
Height (cm)	62.4	49.2 – 75.6	7.05 *	0.90	47.5	32.8 – 57.2	8.07 *	0.83
Diameter (mm)	8.7	7.2 – 10.2	7.26 *	0.85	10.0	7.7 – 11.1	5.58 *	0.71
Top weight (g)	614.5	355.9 - 905.1	16.47 *	0.86	574.5	306.6 – 807.0	13.79 *	0.80
No. of branches	29.7	19.6 – 38.8	14.51 *	0.94	18.9	11.5 – 24.3	15.51 *	0.90
Branch length (cm)	21.6	18.3 – 25.5	7.95 *	0.86	18.6	14.3 – 21.2	6.49 *	0.76
Branch angle (°)	65.9	53.8 – 77.4	5.51 *	0.88	64.1	56.4 – 71.1	3.03 *	0.75
Sinuosity[§]	2.9	0.3 – 7.3	39.12 *	0.78	0.3	0.0 – 1.8	60.45 *	0.36
Forking[§]	0.1	0.0 – 0.4	0.38	-----[£]	0.2	0.1 – 0.5	12.73	-----[£]

[†] Fcv(%) = $(\sigma_f/\bar{x})(100)$, where σ_f is the square root of family variance within sets or series. [‡] Upper bound estimates of the standard error of h^2_f (DICKERSON, 1969) ranged 0.17 to 0.21 (mean=0.18). * Significant family variation (p ≤ 0.05). [§] Means and ranges are given in original (untransformed) variables; Fcv and h^2_f are for transformed variates (see text). [£] Not estimated because family differences were not significant.

effects (St.Clair and Adams, 1991), and using "fresh" instead of "dry" weight might have introduced additional environmental noise.

Estimates of h^2_f for branching traits were generally intermediate between those for height and diameter growth (*Table 2*). Stem sinuosity had consistently the lowest estimated heritability ($h^2_f \leq 0.59$ in the OP families), despite a large coefficient of family variation. St.Clair (1989) found a similar pattern in the magnitude of heritabilities for growth (seedling biomass) and branching traits in Douglas-fir seedlings, but no previous reports for heritability of stem sinuosity in seedlings of this species were available for comparison.

The bareroot regime consistently produced higher h^2_f estimates than the transplant regime for both types of families, although the differences were usually small (0.80 vs. 0.67, on average). Despite differences in average values, the relative magnitudes of heritability estimates were consistent among traits across testing regimes; correlation of h^2_f estimates between regimes was 0.90 in OP families and 0.93 in FS families. The lower h^2_f estimates obtained in the transplant regime were primarily associated with a larger relative component of within-plot error variance, although in some traits a higher between-plot error variance also contributed to the differences in precision among testing regimes. Seedling mortality in the transplant regime was lower than in the bareroot regime, so the increase in both within- and between-plot variance in the transplants must be related to other causes. Some of the increase in environmental noise might be due to the transplanting process, either as a result of variation in "transplant shock" effects on seedlings, or from variation in seedling response to changes in growing conditions from the greenhouse to the nursery, as described by Hahn (1984). The greater genetic precision (higher h^2_f estimates) observed with the bareroot versus transplant regimes suggests that the bareroot regime should be favored in early testing, although the final decision needs be based on relative values of r_{xy} (see below).

GxE Interaction and Stability of Traits in Nursery Trials

There were only a few cases (4 out of 28) of significant GxE interaction between replicates of the same testing regime, even though the plantings were done in different years (bareroot) or in different nurseries (transplant), indicating high repeatability of family means in the traits evaluated. Type-B genetic correlations (r_B) between trial replicates varied from 0.74 to 1.00, with average values across traits of 0.93 (bareroot) and 0.92 (transplant) in the OP families, and 0.97 (bareroot) and 0.93 (transplant) in the FS families. Between testing regimes, significant GxE interaction was detected in all cases, but r_B estimates were at least moderate, varying from 0.48 to 0.80 (mean = 0.59) in OP families, and from 0.47 to 0.87 (mean = 0.62) in FS families. Thus, family rankings for growth and branching traits seem to be sensitive to different testing regimes in the nursery, but not greatly so. Possible implications of small changes in family rankings for early selection will be addressed later.

Correlation Structure Between Traits in the Nursery Trials

Estimated genetic correlations (r_G) were very similar to corresponding phenotypic correlations among family means ($r_{\bar{p}}$); average values of r_G and $r_{\bar{p}}$ across testing regimes and type of families (n=84) were 0.42 and 0.39, respectively, and the correlation between r_G and $r_{\bar{p}}$ values was 0.97, so only r_G matrices are presented here (*Table 3*). Relative magnitudes of r_G between traits were similar across nursery regimes and family types; the correlation between corresponding elements of matrices from the two regimes was 0.84 in OP families and

0.89 in FS families, and was > 0.93 between OP and FS families within each regime.

Table 3. – Estimated genetic correlations between growth, stem form, and branching traits of two-year-old seedlings in bareroot (above the diagonal) and transplant (below the diagonal) trials of open-pollinated and full-sib families[†].

Trait	Height	Diameter	Top weight	No. of branches	Branch length	Branch angle	Sinuosity
Open–pollinated families							
Height		**0.77**	**0.88**	**0.62**	**0.78**	0.22	**0.41**
Diameter	0.56		**0.95**	**0.56**	**0.67**	0.09	**0.33**
Top weight	0.75	0.82		**0.73**	**0.75**	0.18	**0.45**
No. of branches	0.34	0.42	0.86		**0.53**	0.16	**0.47**
Branch length	0.94	0.48	0.69	0.21		0.19	**0.51**
Branch angle	-0.06	-0.19	0.07	0.23	-0.01		0.27
Sinuosity	0.42	0.43	0.31	0.26	0.52	-0.13	
Full-sib families							
Height		**0.70**	**0.77**	**0.60**	**0.51**	0.03	**0.35**
Diameter	0.75		**0.94**	**0.63**	**0.62**	-0.20	**0.33**
Top weight	0.89	0.90		**0.76**	**0.60**	-0.18	**0.42**
No. of branches	0.55	0.67	0.78		**0.27**	-0.18	0.28
Branch length	0.89	0.63	0.70	0.30		-0.07	**0.40**
Branch angle	-0.05	-0.16	-0.17	-0.22	-0.01		-0.04
Sinuosity	0.67	0.54	0.57	0.40	0.56	-0.21	

[†] Values in "bold" indicate that the corresponding phenotypic correlation between family means was significantly different from zero ($p \leq 0.05$).

Growth traits in seedlings (height, diameter and top weight) were strongly and positively interrelated, with r_G estimates between 0.56 and 0.95 (mean=0.81). With the exception of branch angle, branching and stem form traits were also positively interrelated, but only moderately so ($0.21 \leq r_G \leq 0.56$; mean=0.39). Branch angle appears to be practically independent of all other branching traits ($-0.22 \leq r_G \leq 0.27$; mean= -0.01) (*Table 3*). Number and length of branches were positively correlated with growth traits ($0.34 \leq r_G \leq 0.94$; mean=0.66). Thus, as expected, growth potential in Douglas-fir seedlings is tied to both the number and length of branches (i.e., total photosynthetic area). Stem sinuosity, on the other hand, was also positively associated with growth, but only moderately so ($0.31 \leq r_G \leq 0.67$; mean=0.44). These genetic relationships between growth and branch traits are consistent with the results described by St.Clair (1989) for two-year old Douglas-fir seedlings grown in mixture at a close spacing. In that study, however, r_G estimates between traits differed in magnitude across competitive regimes.

The genetic correlations found between growth, stem form and branching traits imply that early selection for growth potential in the nursery will also increase the number and length of branches and stem sinuosity in seedlings, but will have little or no impact on branch angle at this age. The implications of early selection for growth potential on stem form and branching traits at older ages depend on the strength of early-mature correlations between these traits (discussed later in this section).

Quantitative Genetic Structure of Stem Form and Branching Traits in Older Trees

As in the nursery trials, most growth, stem form, and branching traits measured on older trees in the field showed significant family variation (*Table 4*). On average, estimates of Fcv and h^2_f in the older trees were nearly equivalent to those for seedlings in the transplant trial, but were lower than in the bareroot trial. Genetic parameter estimates obtained from the nursery trials using only data for the 43 OP families evaluated in the field were very similar to those obtained using all 67 families; thus, all seedling comparisons are based on estimates derived from the larger sample.

Table 4. – Estimated means (x̄), ranges of family means, coefficients of family variation (Fcv)), and family heritabilities (h²f) for growth, stem form, and branching traits at ages 12 and 24 (43 open-pollinated families) grown in three field sites.

Trait	x̄	range	Fcv(%)†	h²f‡
Age 12				
Height (m)	7.8	6.7 - 8.6	3.60 *	0.62
DBH (cm)	10.9	9.4 - 12.1	3.21 *	0.33
Bole volume (dm³)	34.6	24.5 - 44.2	8.20 *	0.44
No. of branches	10.1	8.6 - 11.4	4.09 *	0.41
Branch diameter (cm)	2.2	19.6 - 24.2	3.09 *	0.42
Branch length (m)	2.2	1.9 - 2.4	3.18 *	0.49
Branch angle (°)	70.0	64.0 - 76.0	3.78 *	0.76
Bole sinuosity§	1.1	0.6 - 2.1	10.91 *	0.36
WSAB§	0.5	0.2 - 1.1	5.12 *	0.42
Age 24				
DBH (cm)	23.0	20.6 - 25.6	3.44 *	0.34
Branch size	2.4	1.8 - 3.0	4.52	---£
Bole sinuosity	2.5	2.0 - 3.0	5.86 *	0.49
WSAB§	0.9	0.3 - 2.0	7.16 *	0.51

† Fcv(%) = $(\sigma_f/\bar{x})(100)$, where σ_f is the square root of family variance within sets. ‡ Upper bound estimates of the standard error of h²f (DICKERSON, 1969) ranged 0.20 to 0.23 (mean = 0.22). * Significant family variation (p ≤ 0.05). § Means and ranges are given in original (untransformed) variables; Fcv and h²f are for transformed variates (see text). £ Not estimated because family differences were not significant.

Relative rankings of variation and h²f estimates among traits in older trees were similar to those obtained for seedlings. For instance, bole sinuosity had the largest coefficient of family variation in the field at age 12 and branch angle was among the traits with the lowest (*Table 4*). In addition, h²f for height growth was greater than for diameter, and h²f estimates for branching and stem form traits were comparable in magnitude to those for growth traits. The only exception is branch angle, which appears at age 12 to have much stronger genetic control relative to other traits, than it does in seedlings. Our estimates of genetic control of stem form and branching traits in older trees are consistent with those obtained in previous reports for young (sapling-age) coastal Douglas-fir grown in field tests (BIROT and CHRISTHOPHE, 1983; KING *et al.,* 1992; ADAMS and BASTIEN, 1994; ST.CLAIR, 1994; TEMEL and ADAMS, 2000).

The structure of genetic correlations between traits in the field tests (*Table 5*) was similar to that described for seedlings. As in seedlings, growth traits were strongly and positively interrelated (0.61 ≤ rG ≤ 0.95), while branching and stem form traits were less so. In addition, branch angle was essentially uncorrelated with all other traits. Branch length was positively correlated with stem size, as in seedlings; but unlike seedlings, the number of branches at breast height and stem sinuosity were uncorrelated with growth rate in older trees (*Table 5*). Thus, it appears that as trees get older and crown closure occurs, the influence of branchiness per se on stem growth diminishes, particularly when only the branches at breast height are considered. WSAB was also strongly and positively correlated with growth traits in 12-year old trees. Based on a larger data set including the 43 open-pollinated families used in this study, TEMEL and ADAMS (2000) pointed out that fast growing trees have tendency to produce more steep-angled branches. Despite a couple of exceptions, the similarities in genetic control and genetic correlations between traits in seedlings and older trees of coastal Douglas-fir suggest that these traits are under similar genetic control at the two ages.

Nursery-Field Correlations and Implications for Early Selection

In our analysis of nursery-field correlations we generally considered stem form and branching traits in field-grown trees at the oldest age they were measured (i.e., bole sinuosity and WSAB at age 24, and number, length, and angle of branches at age 12). The only exceptions were that we used branch diame-

Table 5. – Estimated genetic correlations between growth, stem form, and branching traits measured in the field at ages 12 and 24 (43 open-pollinated families)†.

Trait	DBH	Bole volume	No. of branches	Branch diameter	Branch length	Branch angle	Bole sinuosity	WSAB
Age 12								
Height	0.61	0.84	-0.13	0.04	0.52	0.19	0.15	0.50
DBH		0.95	-0.03	0.45	0.72	-0.07	0.02	**0.93**
Bole volume			-0.04	0.36	0.68	0.08	0.09	**0.88**
No. of branches				-0.32	-0.07	0.33	-0.35	-0.34
Branch diameter					**0.69**	-0.36	-0.13	0.57
Branch length						-0.04	0.34	**0.57**
Branch angle							0.26	-0.07
Bole sinuosity								0.59
Age 24								
DBH							-0.02	0.56
Bole sinuosity								0.11

† Values in "bold" indicate that the corresponding phenotypic correlation between family means was significantly different from zero (p ≤ 0.05).

ter at age 12 rather than branch size scored at age 24 because family differences in branch size score were not statistically significant (*Table 4*). Also, we included sinuosity at both ages because TEMEL and ADAMS (2000) found that sinuosity measured near the top of the tree at age 12 (i.e., sinuosity in rings near the pith in older trees) was only weakly correlated (rG = 0.36) with sinuosity observed in the outer bole at age 24.

For seemingly similar traits measured in seedlings and older trees (i.e., sinuosity, number of branches, branch length, branch angle), estimated nursery-field correlations (rxy) were consistent across nursery trial replicates and testing regimes (*Table 6*); for all traits, χ² tests of heterogeneity of rxy estimates across replicates and nursery regimes were non-significant at the p=0.05 level. Correlations between branch length at ages 2 and 12 and branch angle at these two ages, although relatively weak, were significantly different from zero (p ≤ 0.05) and positive (mean rxy=0.38). Estimated correlation coefficients between stem sinuosity at ages 2 and 24 were negative, and positive between ages 2 and 12, but in both cases the average correlation was very weak (|rxy| ≤ 0.20). The correlation between number of branches at breast height in 12-year-old-trees and total branches observed at age 2 was essentially zero (mean rxy = 0.04).

Traits equivalent to WSAB at age 24 or branch diameter at age 12 were not measured in seedlings. Nevertheless, a low and negative, but significant, association (mean rxy=−0.30) was found between WSAB at age 24 and seedling branch angle (i.e., families with flatter-angled branches in 2-year-old seedlings

Table 6. – Estimated family mean correlations (rxy) between stem form and branching traits in older, field-grown (ages 24 and 12) trees and two-year old seedlings grown in two nursery regimes (bareroot and transplant), and predicted responses in older trees (i.e., in field trait at age 24 or age 12) from selection of the corresponding field trait at age 12 (R$_{y-12}$) or a correlated nursery trait at age 2 (R$_{y-2}$).

Trait Field	Trait Nursery	R$_{y-12}$(%)†	r$_{xy}$‡ Bareroot	r$_{xy}$‡ Transplant	R$_{y-2}$(%)† Bareroot	R$_{y-2}$(%)† Transplant
Age 24						
Bole sinuosity	Sinuosity	-0.6	-0.05	-0.21	-0.6	-2.6
WSAB§	Branch angle	-24.3	-0.28	-0.33	-14.9	-17.5
Age 12						
No. of branches	No. of branches	-3.7	0.11	-0.03	-1.0	-0.3
Branch diameter	Branch length	-2.8	0.17	0.35	-1.1	-2.3
Branch length	Branch length	-3.1	0.33	0.43	-2.1	-2.7
Branch angle	Branch angle	4.6	0.39	0.36	2.4	2.2
Bole sinuosity§	Sinuosity	-11.7	0.31	0.09	-10.1	-3.0

† Percent change in target trait with respect to mean in original population when 20% of the families are selected (i = 1.40) for a similar trait at age 12 (R$_{y-12}$) or at age 2 (R$_{y-2}$). ‡ Average phenotypic correlation of family means between nursery and field traits from two replicated nursery trials; rxy estimates ≥ 0.30 are significantly different from zero (p ≤ 0.05). § Percent change was estimated from back-transformed means after selection.
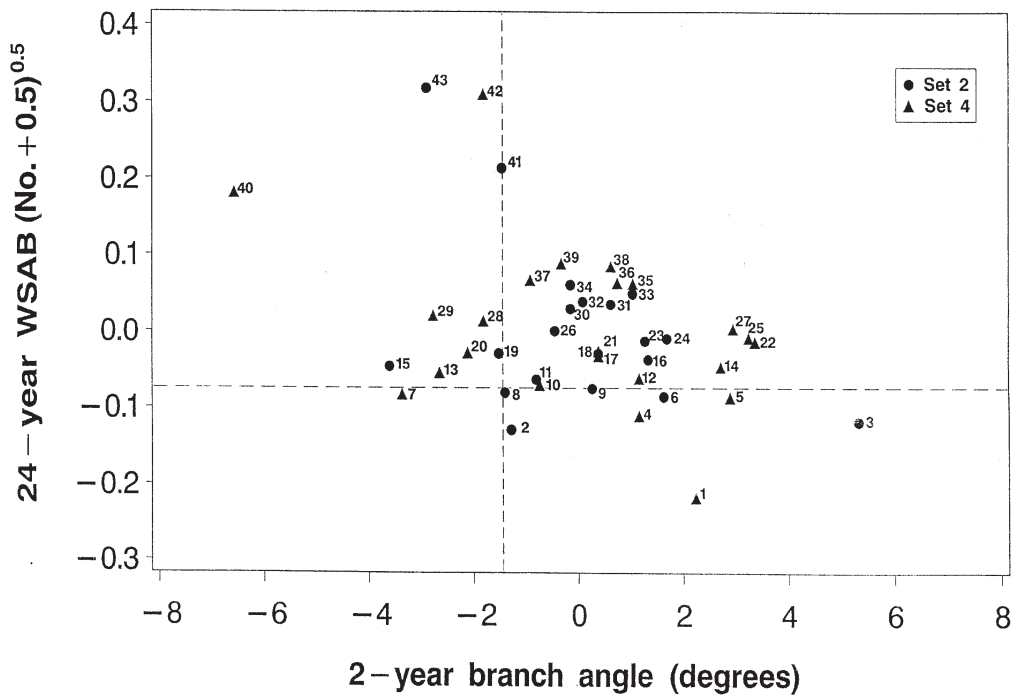
Figure 1. – Scatter plot of family means (expressed as deviations from set means (see text)) for number of whorls with steep-angled branches (WSAB) at age 24 versus branch angle in two-year old seedlings (grown in the transplant regime). The 25% of the families in the nursery trial with the steepest branch angle occur to the left of the vertical dashed line, while the 20% of the families with the lowest number of WSAB at age 24 occur below the horizontal line. Families are ranked best (1) to worst (43) for WSAB at age 24.

had fewer WSAB at age 24) (*Table 6*). In addition, a weak and positive correlation was observed between branch diameter at age 12 and branch length in seedlings (mean $r_{xy} = 0.26$). These associations seem to have reasonable explanations. It is not hard to imagine that families with steeper-angled branches in seedlings would have a tendency towards a higher frequency of WSAB in older trees. Likewise, because longer branches require larger diameters for support, the association between branch diameter at age 12 and branch length in seedlings is logical.

Only modest responses (i.e., genetic gains) in branching traits are expected from selection at age 12 because of the weak genetic control observed for these traits in the field. For most traits, response of less than 5% of the population mean are predicted under the assumed selection scenario (*Table 6*). Responses in WSAB and internal bole sinuosity from selection at age 12, however, are predicted to be much greater, with WSAB at age 24 reduced by 24.3% and internal sinuosity (as measured at age 12) reduced by 11.7%.

Despite low nursery-field correlations, responses in WSAB, branch diameter, branch length and branch angle in older trees from early testing are predicted to be at least 40–50% of the gains predicted if selections were made at age 12. Although there were some differences in family rankings of seedling traits between the bareroot and transplant trials, predicted responses in older trees from early selection were relatively similar for the two regimes. From an operational point of view, however, bareroot trials are preferable to the transplant regime because they are simpler, less costly, and avoid management problems associated with seedling transplants.

The magnitude of nursery-field correlations found for WSAB, branch length and branch angle in this study (i.e., $|r_{xy}| \geq 0.30$) might also be useful for early testing in two-stage selection scenarios. In *Figure 1*, we illustrate the potential of using branch angle in seedlings as the first stage of two-stage selection to reduce WSAB in older trees. Culling 25% of the families with the steepest branch angle in the nursery would remove most of the families with highest WSAB at age 24, without removing any of the best 20% families for this trait (i.e., those with the fewest number of WSAB at age 24), except for the family ranked 7th. Thus, early testing makes it possible to substantially reduce the size and cost of field testing, with little or no loss of genetic gain that would have been obtained if all families were tested in the field.

We showed previously, using a larger sample of families from the same study, that early testing of family performance for bole volume could be effectively based on height of one-year-old seedlings (ADAMS *et al.*, 2001). In this paper, we used information from two-year-old seedlings to evaluate the efficiency of early testing because most of the stem form and branching traits in seedlings were measured only at this age. However, two traits measured at age 1 (height and number of branches) were strongly correlated with the same trait at age 2 ($r_G > 0.80$), and heritabilities were similar at the two ages. If the same holds for branch angle and branch length, early selection for these traits and for WSAB might just as effectively be done on one-year-old seedlings. In addition to cost savings with only one year of testing rather than two, early testing at age 1 has the practical advantage that test results are available in the same amount of time that it typically takes to raise seedlings for progeny testing in the field. Thus, early testing could be accomplished without delaying the field testing program.

Because of the relatively strong, unfavorable genetic correlations of stem growth traits with branch length and WSAB (*Tables 3* and *5*), it is expected that selection for stem size alone will have unfavorable impacts on these branching traits, regardless of whether selection is done at age 12 or 2 (*Table 7*). Indeed, it is predicted that selection and deployment of the top

Table 7. – Predicted correlated responses of stem form and branching traits in older trees when selection is based on stem height at age 12 or at age 2 (in bareroot and transplant nursery regimes).

Trait	Selection at age 12 (%)[†]	Selection at age 2 (%)[†]	
		Bareroot	Transplant
Age 24			
Bole sinuosity	-1.17	2.32	3.14
WSAB[§]	9.49	20.71	16.41
Age 12			
No. of branches	-0.59	2.39	1.70
Branch diameter	0.14	1.47	2.27
Branch length	1.83	1.82	2.93
Branch angle	0.79	0.74	0.96
Bole sinuosity[§]	2.50	6.42	13.26

[†] Percent change in field trait with respect to mean in original population assuming 20% of the families are selected (i = 1.40). [§] Percent change was estimated from back-transformed means after selection.

20% of the families based on height at age 12, would result in a small increase in branch length (1.83%) and internal bole sinuosity (2.50%), but perhaps more importantly, a 10% increase in WSAB (*Table 7*). Unfavorable responses in these stem form and branching traits are predicted to even be greater (sometimes 2 to 3 times as much) if selection is based on height at age 2 (*Table 7*).

Results of this study confirm earlier reports in Douglas-fir which show that genetic response in growth potential in this species cannot be maximized without negatively influencing stem form and branching traits (KING *et al.,* 1992; ADAMS and BASTIEN, 1994; ST.CLAIR, 1994; SCHERMAN *et al.,* 1997; TEMEL and ADAMS, 2000). Because growth, stem form, and branching traits seem to be largely influenced by the same sets of genes in seedlings and in older trees, selection for stem growth alone in early tests is also expected to negatively impact wood quality in older trees. Thus, if reduction in wood quality is unacceptable, and a single stage of selection is used, then stem form or branching traits with greatest impact on wood quality should be included along with growth traits as selection criteria. In a two-stage selection scenario, a decision needs to be made at which stage (or both) is it best to include stem form and branching traits. It might be desirable to include both growth and stem quality traits in the first stage of selection in the nursery. Alternatively, initial culling of families could be done on the basis of growth potential alone, and traits affecting stem quality handled in the final stage of selection in the field. The merits of various alternatives can be explored using index selection methods (WHITE and HODGE, 1991; CAMERON, 1997).

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