

The Genetics of Stem Volume, Stem Form, and Branch Characteristics in Sapling Noble Fir¹⁾

By D. L. DOEDE²⁾ and W. T. ADAMS

Department of Forest Science, Forestry Sciences Laboratory, Oregon State University,
Corvallis, OR 97331-7501, USA

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Summary

Genetic parameters for stem volume, stem form, and branching traits, along with the genetic interrelationships among these traits, were estimated from measurements on 60 open-pollinated families of noble fir (*Abies procera* REHD.) planted on three progeny test sites in southwest Washington (U.S.). Large family-by-site interactions were evident when all three sites were analyzed together; consequently, data for the two low-elevation sites (<1200 m) were analyzed separately from the high-elevation site (1402 m). Significant family variation was present in at least one environment for 10 of the 13 traits examined. Estimates of narrow-sense heritabilities were low to moderate (0.09 to 0.49) for all traits. With the exception of branch number and stem sinuosity, genetic correlations among stem growth, stem form, and branch traits were weak or favorable, so that selection for stem growth should have few unfavorable effects. Amounts of genetic and phenotypic variation present indicate that moderate gains from selection and breeding programs are possible for stem growth traits, while lesser gains can be achieved for stem form and branching traits.

Key words: *Abies procera*, heritabilities, stem form traits, branching characteristics, genetic correlations.

FDC: 165.3; 164.4; 181.63/65; 232.1; 561; 174.7 *Abies procera*; (797).

Introduction

Noble fir (*Abies procera* REHD.) is an important forest tree species in the Pacific Northwest of the United States, where it occurs at upper elevations (1000 m to 1700 m) in the Cascade Mountains of Oregon and Washington and on isolated peaks in the Oregon Coast Range and the Willapa Hills in southwestern Washington. It is valuable for timber, Christmas trees, and greenery products (FRANKLIN, 1982; DOUGLASS et al., 1986). Consequently, there are a number of noble fir breeding efforts in the Pacific Northwest aimed at improving this species for timber (QUALM, 1988; USDA Forest Service, 1991) and Christmas tree grade (BROWN and PROEBSTING, 1987). To date, within-population genetic variation has been reported only for early height growth, mortality, and Christmas tree grade. Noble fir is also of interest as an exotic in Europe and Canada, where provenance evaluations are underway in Great Britain, Germany, and British Columbia (FLETCHER and SAMUEL, 1990; RUETZ et al., 1990; XIE and YING, 1994; YING, 1992). XIE and YING (1994) found significant provenance differences in both survival and growth, but these differences were small when compared with site differences. Geographic variation in noble fir has also been investigated for monoterpenes (ZAVARIN et al., 1978), and for seedling traits, with strong family differences reported both among and within sources for early height

growth, date of bud set, and extension period (bud flush to final bud set) (SORENSEN et al., 1991).

Bole volume has historically been the focus of tree improvement programs; however, stem form and branch characteristics are also important because of their influence on product value (FAULKNER, 1970; SHELBOURNE, 1970; BENDTSEN, 1978; KELLOGG and WARREN, 1984). Straight stems with little taper have lower handling costs and higher recovery values for lumber and plywood (SHELBOURNE, 1970; KELLOGG and WARREN, 1984; ZOBEL and TALBERT, 1984). The presence of large ramicorn branches, as well as stem forking and crookedness, decreases lumber yields and increases the amount of compression wood in the stem, which lowers pulp yields and lumber quality. Branch size, the angle at which branches are attached to the bole, and number of branches influence the size and number of knots formed, and consequently the grade of lumber and plywood.

The goal of most tree improvement programs is to combine rapid stem volume growth with high quality stems (i.e., straight stems with small branches) to produce well adapted superior trees for lumber and plywood (SHELBOURNE, 1970; ZOBEL and TALBERT, 1984). Only a few traits, however, can be effectively improved at one time, and thus breeders must narrow the choice of traits upon which selections are based. The decision as to which traits to include in a selection program depends on the economic value of the traits, cost of measurement, potential response to selection, and direction and magnitude of changes that will occur in one trait as a result of selection for another. Predicting the responses and changes that may occur through selection requires estimates of several genetic parameters, including levels of phenotypic variation, heritabilities, family stability across environments, and genetic correlations among traits (BIROT and CHRISTOPHE, 1983).

Selection in genetic tests frequently occurs at young ages in the interest of saving time (LAMBETH, 1980). Measuring stem form and branch characteristics in sapling trees has additional advantages over measuring in older trees: the entire bole and crown is easily accessible from the ground, reducing measurement time and cost; juvenile bole defects can be evaluated before subsequent growth covers them up; and branch characteristics can be evaluated before inter-tree competition and shading affect branch size and angle. This study was undertaken to estimate the above genetic parameters for stem and branching traits of sapling noble fir in a southwest Washington population, and to interpret the estimated parameters with respect to including these traits in a breeding program.

Materials and Methods

Materials

In 1981 the Cowlitz Tree Improvement Cooperative in southwest Washington planted 11 noble fir progeny test sites to

¹⁾ Paper No. 3205 of the Forest Research Laboratory, Oregon State University

²⁾ Present address: USDA Forest Service, Trout Lake, WA 98650, USA

evaluate the open-pollinated progenies (families) of 120 'road-side' parent tree selections. The criteria for selecting parents were simply that they be well formed dominant or co-dominant trees and have evidence of previous cone production. These parents were located in the upper elevations of the Cowlitz and Lewis River drainages. The families were subdivided into four sets of 30 families for the purposes of testing, with families randomly assigned to sets. Sets One and Three (60 families total) were randomly chosen for this study. The mean elevation of parents in these sets was 1191 m (range: 1067 m to 1433 m).

Seeds for the progeny test were sown at the Industrial Forestry Association greenhouse facilities near Olympia, Washington, grown for 1 year as container seedlings in Leach 'supercells,' transplanted to larger 'd-pot' containers for another year, and then outplanted to the field sites at 2.8-m spacing. Each field site had a split-plot design replicated within each of three blocks, with sets as main plots and families nested within sets as subplots. Each family subplot consisted of four trees assigned at random to planting spots within the main plot (i.e., 4-tree non-contiguous subplots).

Table 1. — Description of traits.

Stem Growth Traits

Volume (VOL; cm^3): Calculated by using the formula $\text{VOL} = 0.0035(\text{HGT})^{1.1653}(\text{SDIA})^{1.6391}$ (see terms below).

Height (HGT; cm): Total height of the tree, measured with a telescoping pole.

Diameter (SDIA; mm): Stem diameter outside bark at the bottom of interwhorl 6, measured with vernier calipers. Interwhorls (Fig. 1) were numbered from the top of the tree down, beginning with the leader. Average height of interwhorl 6 was 1 m above ground level.

Stem Form

Taper (TAP; mm/cm): Decrease in stem diameter over a given stem length. Derived from diameter and height measurements by using the formula $\text{TAP} = (\text{SDIA} - \text{DIA3}) / (\text{HGT3} - \text{HGT6})$, where DIA3 is stem diameter (mm) outside bark at the top of interwhorl 3, HGT3 is the height (cm) at the top of interwhorl 3, and HGT6 is the height at the bottom of interwhorl 6.

Ramicorn branching: Total number of ramicorn branches (Fig. 1) on the tree.

Fork: Total number of forks (Fig. 1) on the tree.

Crook: Total number of crooks (Fig. 1) on the tree.

Sinuosity (SN): Scored visually from the ground in the second interwhorl (Fig. 1.).

Branching

Branch diameter ratio (BDIA; mm/mm): Diameter of the largest branch (mm) on the tree divided by SDIA.

Branch length ratio (BLEN; cm/mm): Length (cm) of the longest branch on the tree divided by SDIA.

Branch angle (ANGL; degrees): Average vertical angle of whorl branches from the main stem. Based on the whorl nearest mid-crown height and the next lower whorl, and visually estimated to the nearest 5° by using a clear plexiglass guide.

Branch number (BNUM): Average number of branches in the whorl nearest mid-crown height and the next lower whorl.

Knot index (KI; mm^2/mm^2): Ratio of the branch cross sectional area to the stem cross sectional area estimated as $\text{KI} = (\text{BNUM} * (\text{BDIA})^2) / (\text{SDIA})^2$.

Three of the 11 sites were selected for measurement based on high survival (88% to 93%). At the time of measurement (fall 1989), trees were 11 years old from seed, approximately 2 m tall, had full crowns that extended to the ground, and were not competing for light. The Lonetree (1128 m) and Section12 sites (1158 m) are at intermediate elevations for noble fir in this region, on moderate slopes (0% to 15%) facing south to southwest. At both of these sites the previous stand was a mixture of Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO), western hemlock (*Tsuga heterophylla* (RAF.) SARG.), noble fir, and Pacific silver fir (*Abies amabilis* (DOUGL.) FORBES). Natural regeneration has been primarily noble fir, Douglas-fir, and western hemlock. The Bishop site is about 250 m higher (1402 m) and slopes steeply (55%) to the northeast, resulting in lower year-round temperatures, more snow in winter, and a shorter growing season than the other two sites. Trees at this site were damaged by a dry, cold winter in 1982 to 1983; however, by the time of measurement they had recovered to the point where they had full crowns. The previous stand at Bishop consisted of Pacific silver fir and western hemlock, and natural regeneration has been primarily of these two species. Soils at all three sites are well drained and of volcanic origin.

Measurement methods

Thirteen traits were measured or calculated, including three related to stem growth, five to stem form, and five to branching habit (Table 1, Figure 1). Large numbers of trees must be measured in selection programs; consequently, measurement techniques must be simple and inexpensive to apply, yet reasonably accurate in reflecting the traits of interest. Methods for measuring bole volume and branching traits in this study were developed from intensive measurements made on 35 trees in the Section12 plantation (DOEDE, 1993). Briefly, a single 'best measure' for a tree was estimated as precisely as possible based on these intensive measurements. A subset of simpler, less expensive measurements sufficiently well correlated with the 'best measure' was then chosen for use in the remainder of the study. For example, in the case of bole volume the best measure consisted of the sum of interwhorl stem segment volumes for interwhorls 1 to 6 plus the volume of the stem segment between whorl 6 and ground-level. A combination of easily measured height and diameter measurements that best predicted bole volume was then chosen by using multiple regression methods (Table 1).

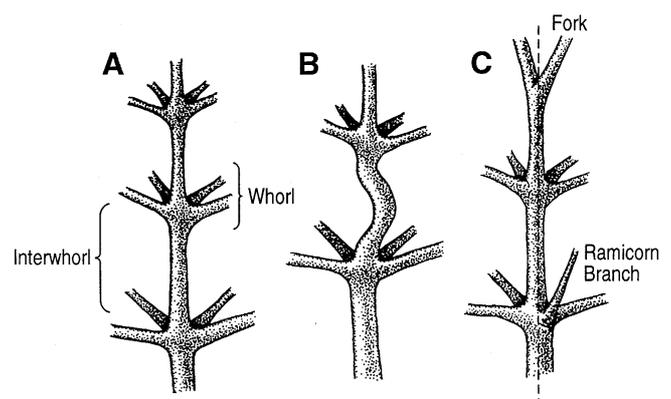


Figure 1. — Illustrations of terms used in defining branching habit and stem form in noble fir (see Table 1): A) whorl and interwhorl; B) sinuosity — maximum deviation from straightness within an interwhorl in units of one half stem diameter. In this example, the sinuosity score would be 2; C) Fork — either angle less than 30° from vertical; diameter of stems approximately equal. Ramicorn branch — branch angle less than 30° from the main stem with a diameter distinctly less than the main stem.

Statistical methods

Analyses of variance were performed on all 13 traits and analyses of covariance on all pairs of traits. For analyses involving two or more sites, the following linear model was used to represent individual trees:

$$y_{ijklm} = \mu + p_i + s_j + ps_{ij} + r_{ik} + sr_{ijk} + f_{jl} + fp_{ijl} + e_{ijkl} + w_{ijklm}$$

where

y_{ijklm} = observation on the m^{th} tree of the l^{th} family in the j^{th} set in the k^{th} block of the i^{th} test site.

μ = the overall mean;

p_i = random effect of the i^{th} test site, $E(p_i) = 0$, $\text{Var}(p_i) = \sigma_p^2$;

s_j = random effect of the j^{th} set, $E(s_j) = 0$, $\text{Var}(s_j) = \sigma_s^2$;

ps_{ij} = random interaction effect of the i^{th} test site with the j^{th} set, $E(ps_{ij}) = 0$, $\text{Var}(ps_{ij}) = \sigma_{ps}^2$;

r_{ik} = random effect of the k^{th} block within the i^{th} test site, $E(r_{ik}) = 0$, $\text{Var}(r_{ik}) = \sigma_r^2$;

sr_{ijk} = random interaction effect of the k^{th} block of the i^{th} test site with the j^{th} set, $E(sr_{ijk}) = 0$, $\text{Var}(sr_{ijk}) = \sigma_{sr}^2$;

f_{jl} = random effect of the l^{th} family within the j^{th} set, $E(f_{jl}) = 0$, $\text{Var}(f_{jl}) = \sigma_{f(s)}^2$;

fp_{ijl} = random interaction effect of the l^{th} family in the j^{th} set with the i^{th} test site, $E(fp_{ijl}) = 0$, $\text{Var}(fp_{ijl}) = \sigma_{f(s)p}^2$;

e_{ijkl} = random plot error of the l^{th} family in the j^{th} set in the k^{th} block of the i^{th} test site; $E(e_{ijkl}) = 0$, $\text{Var}(e_{ijkl}) = \sigma_e^2$;

w_{ijklm} = random tree error of the m^{th} tree in the $ijkl^{\text{th}}$ plot, $E(w_{ijklm}) = 0$, $\text{Var}(w_{ijklm}) = \sigma_w^2$, and the covariances between all pairs of factors are assumed to be zero.

The linear model for individual test site analyses was essentially the same as the above, but with terms involving test sites deleted. Analyses were done on plot means, with within-plot variances estimated separately for each plot and pooled. There were no missing plots because of the high survival on all sites. Quasi F ratios for site and set effects were calculated by using SATTERTHWAIT'S method (STEEL and TORRIE, 1980). Data for taper, ramicorn branching, crook, and sinuosity were transformed prior to analysis. Taper was transformed to $\text{LOG}(\text{Taper} + 1)$, while ramicorn branching, crook, and sinuosity were transformed to $\text{SQRT}(\text{Trait} + 0.5)$ (STEEL and TORRIE, 1980). Variance components were estimated by equating observed mean squares to those expected and solving for the desired component. Components of covariance were estimated by a similar procedure, except that mean crossproducts were used instead of mean squares.

Genetic variability and interrelationships between traits were quantified by estimating family variances, individual and family heritabilities, and genetic and phenotypic correlations between traits. Genetic parameter estimates were not calculated in cases where family variances were not significant ($p < 0.05$). Total phenotypic variation on an individual tree basis was calculated as $\sigma_{PI}^2 = \sigma_w^2 + \sigma_e^2 + \sigma_{f(s)p}^2 + \sigma_{f(s)}^2$ and total phenotypic variation on a family basis as

$$\sigma_{PF}^2 = \frac{\sigma_w^2}{(n)(r)(p)} + \frac{\sigma_e^2}{(r)(p)} + \frac{\sigma_{f(s)p}^2}{p} + \sigma_{f(s)}^2$$

(there are p sites, r blocks per site, and n is the harmonic mean of trees per plot). Narrow-sense individual and family heritabilities were estimated as

$$h_i^2 = \frac{4\sigma_{f(s)}^2}{\sigma_{PI}^2} \text{ and } h_f^2 = \frac{\sigma_{f(s)}^2}{\sigma_{PF}^2},$$

respectively (FALCONER, 1981). Note that these equations assume all traits are corrected for main plot (i.e., set within

block) means and that open-pollinated families are true half-sibs. Relationships between traits were assessed by estimating phenotypic correlations among family means and genetic (Type A) correlations and their standard errors (BECKER, 1984).

Family stability across environments (genotype-by-environment interaction) was evaluated by examining the size and significance of the family(set) X site interaction variance component (SHELBOURNE, 1972). Also, genetic (Type B) correlations between the same trait expressed at different sites were calculated according to BURDON (1977).

In order to evaluate the implications of the above genetic parameter estimates with regard to breeding programs, expected genetic gains and correlated responses to selection were calculated. Genetic gain was estimated as the amount of improvement 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), with 20% of the population selected or a selection intensity of 1.376. Correlated response to selection was calculated according to FALCONER (1981).

Results and Discussion

Combined sites analyses

When all three sites were analyzed together, family(set) X site interaction was significant for all stem growth traits, and the associated variance component was large, often larger than the family(set) component. SHELBOURNE (1972) gives as a rule of thumb that if the interaction variance component reaches 50% or more of the family component, genotype-by-environment interaction is likely to have serious effects on a breeding program. Further investigation revealed that there were indeed changes in family rankings; however, the changes were mostly due to families ranking differently at Bishop than at the other two sites. Genetic correlation estimates support this observation.

Family differences were not significant for bole volume at Lonetree; consequently, genetic correlations for this trait could not be estimated between Lonetree and the other two sites. Nevertheless, the estimated genetic correlation for bole volume between Bishop and Section 12 was only 0.22. For height, pairwise correlations for Bishop with Lonetree and Section 12 were 0.66 and 0.31, respectively, and 1.18 between Lonetree and Section 12 (DOEDE, 1993). For stem diameter, estimated pairwise correlations for Bishop with Lonetree and Section 12 were only 0.46 and 0.30, but were 0.77 between Lonetree and Section 12.

Bishop is located at the upper elevation limits for noble fir in this area and is on a northeast-facing slope, resulting in a much colder environment and shorter growing season than at the other two sites. Indeed, this site may be too cold for noble fir, as this species was not part of the original stand nor is it part of the natural regeneration on the site. Although noble fir is considered a high-elevation species, it shows a preference for warmer microclimates at upper elevations (FRANKLIN, 1982). Because Bishop appears to represent a distinctly different planting environment from the Lonetree and Section 12 sites, this site and the pooled data for the other two sites are analyzed separately.

Genetic variability and inheritance

For both data sets, plot error was usually zero; within-plot error accounted for the bulk of the phenotypic variance between individuals (>84%) for all traits (Table 2).

When only the two low-elevation sites were analyzed together, family(set) X site interaction was significant for three

traits (stem diameter, branch length ratio, and branch angle). Genetic correlations between Lonetree and Section 12 were 0.77 for stem diameter and 0.78 for branch length ratio (DOEDE, 1993), suggesting that family rankings are relatively consistent between the two sites, despite the significant interaction for these two traits. The estimate of genetic correlation between these sites for branch angle, however, was low (0.38), indicating that for this trait, family rankings on one site are quite different from those on the other.

Significant family differences were detected for stem growth traits in both analyses; however, the proportion of phenotypic variance due to family(set) effects was usually higher for Bishop (Table 2). Family variance estimates are probably inflated in the analysis of the single site because family differences there are confounded with the family(set) X site interaction. Taper and most branching traits showed significant family differences only in the Lonetree and Section 12 analysis, perhaps because either 1) the ANOVA on the two sites

has more precision for detecting family differences; and/or 2) family differences for these traits are better expressed at sites that are typical of noble fir and are more productive.

One trait, sinuosity, showed significant family variation at Bishop, but not at the lower elevation sites (Table 2). The ability to detect family differences in sinuosity at Bishop is probably due to the higher frequency of sinuous trees (sinuosity score > 0) on this site (39.6%) than on the other sites (12.3%). Bishop also has a higher frequency of crooks (18% vs. 9%). The crooks at Bishop occurred just below the whorl formed in 1983, indicating that the tops of trees were killed during the winter of 1982 to 1983 (possibly by winter desiccation, as this was a year with a very low snowpack in the local area). Thus, at Bishop, families expressed variation in their ability to maintain straight stems in a harsh winter climate. This may help explain why most branch traits did not show significant family differences; that is, damage to stems and crowns obscured family differences in branching characteristics. These traits

Table 2. — Estimated means, estimated variance components (expressed as intraclass coefficients), total phenotypic variances, and narrow-sense heritabilities for 13 traits measured in (A) low-elevation (Lonetree and Section 12) and (B) high-elevation (Bishop) test environments.

Trait	Test env.	Mean	Variance components (%) ^a				Total phenotypic variance ^b	Heritabilities (± SE) ^c	
			Family (set)	Family (set) X site	Plot error	Within-plot error		Individual	Family
Volume (cm ³)	A	1279.4	4.15*** ^d	1.80	0	94.05	570,399.90 (59.0)	0.17 ± 0.08	0.43 ± 0.20
	B	698.7	6.51**	—	0	93.49	214,768.04 (66.3)	0.26 ± 0.12	0.41 ± 0.19
Height (cm)	A	244.04	7.31**	0.41	0.29	91.99	3,933.53 (25.7)	0.29 ± 0.20	0.61 ± 0.20
	B	181.7	8.29**	—	0	91.71	2,592.11 (28.0)	0.33 ± 0.12	0.47 ± 0.18
Stem diameter (mm)	A	47.10	4.32**	3.86*	0	91.82	108.36 (22.1)	0.17 ± 0.09	0.41 ± 0.20
	B	39.7	6.37**	—	0	93.63	108.52 (26.2)	0.25 ± 0.12	0.40 ± 0.20
Taper (mm/cm)	A	0.2278	2.27*	0	0	97.73	0.005192 (35.1)	0.09 ± 0.05	0.33 ± 0.17
	B	0.2624	0	—	4.25	95.75	0.012914 (48.4)	—	—
Ramicorn branch (count)	A	0.10	0	1.44	0	98.55	0.036806 (25.1)	—	—
	B	0.26	0	—	4.79	95.21	0.110870 (38.2)	—	—
Fork (count)	A	0.05	0.28	0	0	99.72	0.022882 (20.3)	—	—
	B	0.04	0.48	—	0	99.52	0.017663 (18.0)	—	—
Crook (count)	A	0.09	0.18	0	0	99.82	0.033551 (23.8)	—	—
	B	0.18	3.32	—	0	96.68	0.049130 (26.9)	—	—
Sinuosity (score)	A	0.10	0.20	2.33	0	97.48	0.069616 (31.3)	—	—
	B	0.46	8.13*	—	0	91.87	0.141850 (38.4)	0.33 ± 0.13	0.47 ± 0.18
Branch diameter ratio (mm/mm)	A	0.34	3.71*	2.85	4.05	89.40	0.005567 (22.2)	0.15 ± 0.09	0.37 ± 0.22
	B	0.35	2.25	—	0	97.75	0.009374 (27.8)	—	—
Branch length ratio (cm/mm)	A	1.66	12.23**	3.71*	0	84.06	0.095293 (18.6)	0.49 ± 0.13	0.67 ± 0.19
	B	1.95	3.07	—	0	96.93	0.194680 (22.7)	—	—
Branch angle (degrees)	A	80.0	4.19*	3.34*	0	92.47	50.268 (8.9)	0.17 ± 0.08	0.40 ± 0.20
	B	76.5	6.93*	—	0	93.07	73.607 (11.2)	0.28 ± 0.11	0.42 ± 0.17
Branch number (count)	A	4.6	2.38*	0	0.75	96.87	1.0048 (21.9)	0.10 ± 0.06	0.33 ± 0.21
	B	4.5	0.46	—	0	99.54	1.3205 (25.6)	—	—
Knot index (mm ² /mm ²)	A	0.53	3.37*	3.04	1.11	92.48	0.06637 (48.5)	0.13 ± 0.08	0.35 ± 0.22
	B	0.56	3.42	—	0	96.59	0.11194 (59.8)	—	—

^a) Negative estimates set to zero.

^b) Total phenotypic variance is the variance among individual seedlings after adjustment for plot means; phenotypic coefficient of variation given in parentheses.

^c) Heritabilities were not estimated when Family(set) effects were not significant.

^d) Corresponding variance significant at the p = 0.05 (*), and p = 0.01 (***) levels.

Table 3. — Genetic (below diagonal) and phenotypic (above diagonal) correlations between traits measured in (A) low-elevation (Lonetree and Section 12) and (B) high-elevation (Bishop) test environments.

		VOL ^a	HGT	SDIA	TAP	SN	BDIA	BLEN	ANGL	BNUM	KI
VOL	A	1.00	0.92 ^b	0.93	-0.62	0.36	-0.51	-0.19	-0.11	0.27	-0.39
	B	1.00	0.90	0.95	0.17	0.57	-0.41	-0.38	-0.03	0.05	-0.41
HGT	A	0.93*	1.00	0.80	-0.44	0.43	-0.39	0.03	-0.03	0.29	-0.26
	B	0.93*	1.00	0.81	0.08	0.54	-0.40	-0.15	0.13	0.05	-0.38
SDIA	A	0.92*	0.73*	1.00	-0.04	0.30	-0.66	-0.38	-0.15	0.27	-0.55
	B	0.92*	0.89*	1.00	0.24	0.53	-0.45	-0.54	-0.14	-0.02	-0.49
TAP	A	-0.13	-0.56*	0.16	1.00	-0.16	-0.07	-0.29	-0.27	-0.14	-0.13
	B	— ^c	—	—	1.00	0.07	0.08	-0.18	-0.10	0.04	0.03
SN	A	—	—	—	—	1.00	-0.06	0.20	-0.02	0.09	-0.05
	B	0.54*	0.54*	0.49*	—	1.00	-0.10	-0.02	-0.22	0.04	-0.10
BDIA	A	-0.41	-0.29	-0.65*	-0.15	—	1.00	0.66	0.03	-0.15	0.90
	B	—	—	—	—	—	1.00	0.50	-0.23	-0.21	0.90
BLEN	A	-0.04	0.17	-0.30	-0.44*	—	0.75*	1.00	0.05	0.00	0.64
	B	—	—	—	—	—	—	1.00	0.40	0.06	0.57
ANGL	A	-0.07	-0.01	-0.15	-0.80*	—	-0.32	-0.16	1.00	0.02	0.04
	B	-0.20	-0.06	-0.25	—	-0.43	—	—	1.00	0.18	-0.12
BNUM	A	0.23	0.33	0.23	-0.35	—	-0.05	0.23	0.40	1.00	0.21
	B	—	—	—	—	—	—	—	—	1.00	0.26
KI	A	-0.28	-0.10	-0.56*	-0.30	—	0.93*	0.84*	-0.13	0.30	1.00
	B	—	—	—	—	—	—	—	—	—	1.00

^a) Key to traits: VOL=Stem volume; HGT=Height; SDIA=Stem diameter; TAP=Taper; SN=Sinuosity; BDIA=Branch diameter ratio; BLEN=Branch length ratio; ANGL=Branch angle; BNUM=Branch number; KI=Knot index.

^b) Phenotypic correlations with an absolute value greater than or equal to 0.25 are statistically significant at the $p=0.05$ probability level.

^c) Means not calculated because the family variance was not significant for one or both traits ($p < 0.05$).

^{*}) Absolute value of correlation exceeds twice its standard error.

expressed in one environment and not the other underscore the importance of measuring traits where they can be expressed.

Narrow-sense individual heritabilities (Table 2) are low to moderate for all traits where estimates were possible. Family heritabilities are often twice the magnitude of individual heritability estimates. Where comparable, both individual and family heritabilities in the lower elevation sites were similar to those at Bishop.

Individual heritability estimates were similar for the three stem growth traits and are comparable to those reported for other species (KING et al., 1988; ERIKSSON et al., 1987; ZOBEL and TALBERT, 1984). As in Douglas-fir (KING et al., 1992) and Scots pine (*Pinus sylvestris* L.) (ERIKSSON et al., 1987), taper is weakly heritable in noble fir. Heritability of sinuosity in noble fir is similar to that in Douglas-fir ($h^2_i = 0.39$, BIROT and CHRISTOPHE, 1983; $h^2_f = 0.39$, SCHERMANN et al., 1997).

Individual tree heritabilities range from 0.09 to 0.49 among traits, with the highest heritability being for branch length ratio ($h^2_i = 0.49$). This heritability is higher than observed for branch length in other conifers, regardless of whether branch length has been adjusted for tree size (as in this study) ($h^2_i = 0.12-0.20$, STRICKLAND and GODDARD, 1965; POYKKO, 1982; KING et al., 1992). POLK (1972), however, found heritability for branch length to be high in jack pine (*Pinus banksiana* LAMB.). Heritabilities for branch diameter ratio, branch number, and knot index in noble fir are comparable to those found in other species (STRICKLAND and GODDARD, 1965; POYKKO, 1982;

MERRILL and MOHN, 1985; ERIKSSON et al., 1987; KING et al., 1992). Branch angle heritability appears to vary greatly among conifers. While it is high in Douglas-fir ($h^2_i = 0.73$, KING et al., 1992) and white spruce (*Picea glauca* (MOENCH) VOSS) (0.44, MERRILL and MOHN, 1985), it is lower in slash pine (*Pinus elliottii* ENGELM.) (0.33, STRICKLAND and GODDARD, 1965) and noble fir (Table 2).

Interrelationships among traits

Where comparable, genetic and phenotypic correlation estimates were similar in sign and magnitude for the two data sets (Table 3). Correlations among stem growth traits were all large and positive (≥ 0.73), which agrees well with findings for other species (KING et al., 1988; ERIKSSON et al., 1987; SCHERMANN et al., 1997). The moderate negative correlation of taper with height in the low-elevation test sites agrees with findings in Douglas-fir, as do the weak correlations of volume and stem diameter with taper (KING et al., 1992). Sinuosity, however, had positive correlations with stem growth at the high-elevation site; larger, faster growing trees were more sinuous. This relationship is similar to that in Douglas-fir and Scots pine (ERIKSSON et al., 1987; KING, 1986), although the correlations between sinuosity and stem growth traits are somewhat higher in noble fir than reported in these species.

Correlations between branch traits and stem growth traits were generally weak and negative (Table 3), although branch number had weak positive correlations with growth traits. Larger trees showed a slight tendency to have more branches

that were smaller relative to stem diameter and that intersected the stem at a steeper angle. These relationships among branch and stem growth traits are similar to those observed in Douglas-fir and Scots pine, where stem size was positively associated with the production of numerous fine branches (ERIKSSON et al., 1987; KING et al., 1992). Knot index was strongly and positively correlated with branch diameter ratio and branch length, but only weakly correlated with branch or angle number. Thus, knottiness in noble fir appears to be largely a function of branch size relative to stem diameter. Furthermore, weak negative correlations were found between knot index and stem growth traits, indicating that knottiness is greatest in small trees. All branch traits were negatively correlated with taper, which agrees with results for Scots pine (ERIKSSON et al., 1987) but contrasts with the weak positive correlations found between these traits in Douglas-fir (KING et al., 1992).

Implications for breeding

Significant family(set) X site interaction was observed in this study, which suggests that it may be necessary to subdivide the breeding population into two sets of families, those suitable for lower (<1372 m) and higher elevation planting sites. An alternative to subdivision is to maintain one breeding population for all planting sites and select for broadly adapted genotypes; however, this may be difficult given the strength of interaction found. Another alternative would be to apply the breeding program only to the lower elevations of the breeding zone, where higher growth rates may justify the investment. Higher elevations could be reforested with seed from wild stand collections, seed production areas, or plantations suitable for mass selection (ZOBEL and TALBERT, 1984). Also, the cold high-elevation sites may be better suited to reforesting with other species, such as Pacific silver fir, ENGELMANN spruce (*Picea engelmannii* PARRY), or mountain hemlock (*Tsuga mertensiana* (BONG.) CARR.).

The amounts of genetic and phenotypic variation in noble fir indicate that breeding programs would be successful in improving a variety of stem and branching traits. Ten of the 13 traits originally examined showed significant genetic variation in at least one planting environment. Expected genetic gains from selection of parents based on the mean performance of their progeny at the Lonetree and Section 12 sites indicate that moderate responses are possible for stem growth traits such as volume (21.7%) (Table 4).

The genetic interrelationships among traits in noble fir indicate that there would be few, if any, unfavorable responses in stem quality and branching habit if selection was applied only to stem volume at the low-elevation sites. Selection for stem volume at Lonetree and Section 12 is expected to decrease stem taper and knottiness (Table 4), both favorable effects. However, selection for volume alone at Bishop would result in a large, unfavorable increase in sinuosity (47.1%).

It appears that stem diameter might be an acceptable trait for indirect volume selection in noble fir. Genetic correlations between diameter and volume were very high (≥ 0.92), and diameter is easy to measure. However, the height of the trees in this study averaged less than 2.5 m, while similar recommendations for Douglas-fir were based on trees greater than 6 m (KING et al., 1988). The relationship between stem diameter and volume may weaken in older trees, and thus it may be too early to draw conclusions about the value of stem diameter for indirect selection of stem volume.

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Table 4. — Expected genetic gains when selection is applied directly to individual stem and branching traits, and correlated gains in these traits when selection is applied to stem volume^a.

Trait	Direct gain ^b	(%) ^c	Correlated gain ^b	(%) ^c
Volume (cm ³)	277.9	(21.72)	—	—
Taper (mm/cm)	0.0214	(9.39)	-0.0031	(1.36)
Sinuosity	0.4396	(95.56)	0.2167	(47.12)
Knot index (mm ² /mm ²)	0.0767	(14.46)	-0.0238	(4.49)

^a) Gains for sinuosity calculated for selection at the Bishop site; other traits calculated for selection at Lonetree and Section 12 sites.

^b) Gain expected in seed orchard offspring when the top 20% of parental clones are selected.

^c) Gain relative to population mean before selection.

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Genetic Variability in Anatomical, Physiological and Growth Characteristics of Hybrid Poplar (*Populus x euramericana* DODE (GUINIER)) and Eastern Cottonwood (*Populus deltoides* BARTR.) Clones

By S. ORLOVIĆ¹), V. GUZINA¹), B. KRSTIĆ²) and L. MERKULOV²)

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Summary

Anatomical and physiological parameters of rooted cuttings of eight black poplar clones (4 *Populus x euramericana* and 4 *Populus deltoides*) were evaluated in three field experiments on different soil types (humofluvisol, fluvisol f. loamy and fluvisol f. sandy). Measurements were taken on the thickness of assimilation tissues (palisade and spongy) on the cross section, and on net photosynthesis, dark respiration and leaf area. At the end of the vegetation period, the main plant growth elements were measured: diameter, height and biomass. The results showed a high interclonal variability for most parameters. Statistically significant differences among clones, regardless of site, indicated that the majority of study characters are controlled by genetic factors, specific to each clone. Most characteristics showed a statistically significant genotype x environmental interaction, as clone rankings at the three locations were not identical. The thickness of spongy tissue and plant height exhibited the highest genotype x environmental interaction, while the number of stomates per mm² of the adaxial surface of the leaf, leaf area, and biomass showed the

least sensitivity to environmental change. Strong correlations were shown between the number of stomates on leaf adaxial surface and biomass, thickness of palisade layer and biomass, leaf area and with height and biomass respectively. Leaf area, also was strongly correlated with height. The results indicate that the stomata number adaxial, thickness of palisade tissue, net photosynthesis, and leaf area can be used in the selection of nursery stock for the desired characteristics, that will result in higher biomass production. Construction of high yielding hybrids with desirable anatomical features was considered to be feasible.

Key words: poplar clone, anatomy, physiology, variability, genotype x environment interaction.

FDC: 165.5; 161.2/.3; 164.5; 168; 232.13; 232.328.1; 532; 537; 561; 176.1 *Populus euramericana*; 176.1 *Populus deltoides*.

Introduction

The genus *Populus* L. is broadly distributed in Europe, North America, and Asia (CEULEMANS *et al.*, 1988). The ability of spontaneous and controlled intra- and interspecies hybridization within the genus has, enabled the creation of a high number of subspecies and transient forms, i.e. simple and complex hybrids. This has resulted in a great natural variability which enables *Populus* species to inhabit a variety of

¹) Poplar Research Institute, Antona Čehova 13, P.O. Box 117, 21000 Novi Sad, Yugoslavia. Email: sasao@polj.ns.ac.yu

²) University of Novi Sad, Faculty of Natural Science, Institute of Biology, Novi Sad, Yugoslavia