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Selection of Crown Form Traits in Controlled Crosses of Coastal Douglas-fir

By J. N. KING[1]), F. C. YEH, J. C. HEAMAN[1]) and B. P. DANCIK

Department of Forest Science, University of Alberta,
Edmonton, Alberta, Canada T6G 2H1

Summary

Genetic parameters for crown-form traits and bole taper were investigated in full-sib progeny of Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO). Significant amounts of additive genetic variance were shown for all traits except branch thickness. Non-additive genetic variance was statistically significant ($p < .05$) for three of the eight crown from traits investigated. High individual-tree heritability was expressed for branch angle, indicating that this trait could be improved through phenotypic selection. Progeny testing would be more effective for most other form traits. Branch thickness and branch length indicate stronger genetic differences when they are expressed as a proportion of stem size.

A positive association existed between yield and a fine branching form type. Path-analysis showed that branch number was associated with 42% of family differences for stem volume. Multi-trait index selection can be used to improve both yield and fine branching in Douglas-fir seed orchard progeny.

Key words: Douglas-fir, crown form, branching traits, bole taper, index selection.

Introduction

Mature Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) trees are characterized by a long, branch-free, cylindrical stem and a short, columnar, flat-topped crown, and young open-grown trees have narrow conical crowns that extend to the ground (HOSIE, 1973). In a closed stand, lower limbs die rapidly with increasing overhead shade, however, natural pruning of these limbs can take a long time (ISAAC and DIMOCK, 1965). Branching and crown-form traits are important for the effect they have on the quality of the clearwood resource; compression wood is increased with acute angled branching, and heavy branches produce persistent knots and retard the ability to produce clear stem wood (VON WEDEL et al., 1968). Clear stem wood is desirable not only for clearwood products and peeler logs (VON WEDEL et al., 1968; SHELFOURNE, 1970), but also in the production of uniform pulp products (BLAIR et al., 1974; ZOBEL and KELLISON, 1978). Large knot size is also one of the key factors in reducing structural strength in sawn pieces. Crown characteristics are likely to be important not only because of their effect on wood quality, but because biomass potential is more economically valuable when partitioned into stem wood than into undesirable branch wood.

This study characterizes the genetics of crown form traits and their interrelationships in juvenile Douglas-fir, and investigates ways in which selection can improve both crown form and volume.

Extreme phenotypic variability for limb and crown traits in natural populations of Douglas-fir was found by CAMPBELL (1961, 1963) who measured crown characteristics (branch numbers, angles, thicknesses and lengths) in 15- to 35-year-old Douglas-fir in each of 10 locations. Most of the variation of these traits could be explained by variation in stem volume, except in the case of branch angle. The relationships between stem volume and branch number, length, and thickness were all strong and positive. Age of the tree did not affect branch characteristics,

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except through its influence on volume. Campbell found the following relationships between branch characters:

1. trees with acute-angled branches had thicker and longer branches,
2. trees with fewer branches per whorl had thicker and longer branches,
3. when trees were of similar bole volume, taller (less tapering) trees had shorter and thinner branches.
4. the associations between the various branch traits were slight in comparison to the associations between branch traits and volume.

Environmental influences such as spacing, nutrient levels, and site quality exert a strong influence on form traits. Campbell (1961) found that the phenotypic variation in branching traits was most highly expressed on sites with good height growth. This has also been observed in studies of the effects of site factors on form characters in Douglas-fir (de Champs, 1978; Carter and Klinka, 1986).

Heritabilities for crown-form traits vary in conifers, but tend to be larger than those for growth traits. Estimates of 'narrow-sense' heritability (h^2_i, appropriate for mass selection) for branching-quality traits in Finnish trials of Scots pine (*Pinus silvestris* L.) were 0.4 to 0.7, whereas growth traits were low to moderate (< 0.3) and sometimes lower than 0.1 (Poykko, 1982). Merrill and Mohn (1985) found non-significant family differences in Lake States white spruce (*Picea glauca* (Moench) Voss) for total height and branch number per whorl; but significant family differences were observed for stem diameter ($h^2_i = 0.14$), branch thickness ($h^2_i = 0.16$), and branch angle ($h^2_i = 0.44$).

The inheritance of branch traits in Douglas-fir shows similar trends (Jarret, 1978; Birot and Christophe, 1983). A detailed study of crown-form traits was conducted by Jarret (1978) using 15 open pollinated (O.P.) families within one of the provenances of the French IUFRO provenance trial. Individual tree heritability for branch angle

was high (0.54) but moderate for branch thickness and knot index (0.3), where knot index was a ratio of cross-sectional areas of branches to the cross-sectional area of the stem 10 cm below the reference whorl (Campbell, 1961). As in white spruce (Merrill and Mohn, 1985) no family differences were detected in branch numbers per whorl which may reflect the difficulty in assessing this trait (Campbell, 1961). Branch angle assessed in other studies on the French provenance-progeny material (Birot and Christophe, 1983), showed strong additive genetic control similar to that reported by Jarret (1978) ($h^2_i = 0.49$) and together with large phenotypic variation indicated that response to selection for this trait would be good.

Materials and Methods

Materials

This study involved the full-sib progeny trial described earlier by King et al. (1988a). Eighty-eight full-sib families were generated using a factorial 'tester' mating design with 4 male parents and 22 female parents. These families were planted according to a randomized complete block design with three replications of nine-tree plots on each of two sites. The two sites on Vancouver Island were: the Cowichan Lake Experiment Station (CLES) and Greater Victoria watershed (GVWS). The trees were 12 years old and averaged 6 metres in height at assessment. The trees had full crowns and were still open-grown at 3 metre spacing, although at the CLES the canopy was nearly closed. Crown and form traits assessed in this study are summarized in *table 1*. *Figure 1* represents schematically the detailed measurements of the progeny trees.

Measurements

Branch measurements were taken at the branch whorls formed prior to the seventh and eighth growing seasons

Table 1. — Crown and form traits used in the study, means for individual and combined site, and ranges in family means based on the combined analysis.

Traits		unit of measure	CLES[a]	GVWS[a]	Combined	Family Range[b]		
					------ Means ------			
BN	branch number	number	5.13	5.73	5.34	4.82	-	5.97
BA	branch angle	°	64.82	67.43	65.74	59.38	-	71.24
BT	branch thickness	mm	19.95	18.51	19.44	18.42	-	20.42
BTT	branch/stem diameter ratio	%	26.36	28.94	27.28	25.64	-	29.16
BL	branch length	cm	164.69	139.57	155.78	143.43	-	165.28
BLT	branch length/ total height age 10	%	39.59	37.86	38.97	37.18	-	41.61
KI	knot index[c]	%	32.75	38.48	31.41	25.83	-	35.35
TAPER	bole taper[c]	mm/m	18.88	19.27	19.01	16.32	-	20.59

[a]) CLES is Cowichan Lake Experimental Station, GVWS is Greater Victoria Watershed.
  CLES had 2277 individuals measured, GVWS had 1251 (trees were not measured at GVWS due to browsing).
[b]) Range among 22 female half-sib families based on combined-site analysis.
[c]) See text for details.

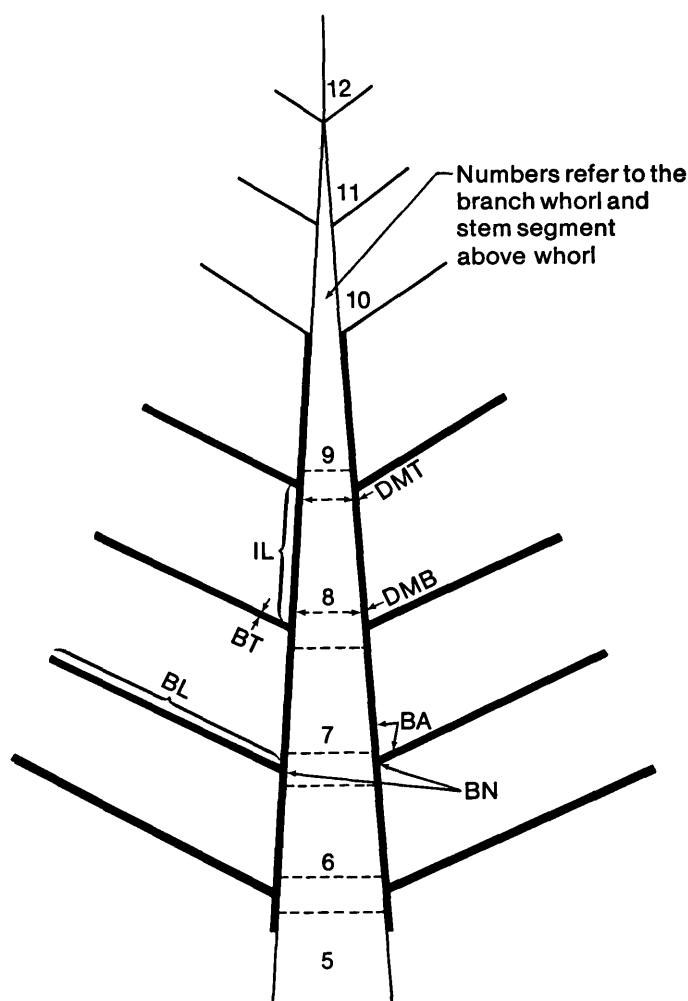Numbers refer to the
branch whorl and
stem segment
above whorl

Figure 1. — Schematic diagram of metric measurements made on
the progeny trees. IL is internode length, DMT is top diameter
of internode, DMB is bottom diameter of internode, BT is branch
thickness, BL is branch length, BA is branch angle, BN is branch
number.

(*Figure 1*). Douglas-fir does not have a definite whorl pat-
tern; instead, there often is a dominant upper portion of the
whorl originating from 1 to 5 lateral buds immediately
below the apical bud (major branches). A lower portion
of the whorl may include branches that originate from
lateral buds in the upper group of internodal buds (minor
branches) (CAMPBELL, 1961). The differentiation between
these types is not always so clear. A branch count was
made of all the major and minor branches within the
seventh and eighth whorls. Branch number (BN) repre-
sents the average number from these two whorls.

Two average major branches from each of the seventh
and eighth whorls were chosen to measure angle, length
and thickness. Branch angle was measured between the
bole and branch to the nearest 5°; branch length was
measured from the bole to branch tip to the nearest 5 cm;
and branch thickness (mm) was measured with calipers
placed away from the swelling of the trunk (approximately
3 cm from bole). The traits BA, BL, and BT represent the
average of the four measurements taken.

Proportional traits were also derived. Such proportional
traits, which use ratios to adjust for the size of the tree,
were found in Finnish Scots pine to have a stronger
genetic determination than direct branch measurements by
themselves (VELLING and TIGERSTEDT, 1984). BTT (*Table 1*)

represents branch thickness as ratio of the stem diameter
at the whorl:

$$BTT = \frac{BT}{DM} \qquad [1]$$

where DM is the average of the diameters measured
just above (DMB) and below (DMT) the whorl
(*Figure 1*). BLT (*Table 1*) represents branch length as a
ratio of the total height at age 10. CAMPBELL'S (1961)
measure of knot index (KI) — the ratio of the cross-
sectional areas of branches at a whorl to the cross-
sectional area of the stem at that whorl — was estimated
using the mean branch thickness, branch number and
diameter value for the two measurement whorls.

Live crown bole taper was also calculated. Internodal
lengths (IL) were measured between branch whorls from
the sixth through ninth growing seasons (*Figure 1*). Dia-
meters were measured by caliper at the top (DMT) and
bottom (DMB) of each internode but away from the nodal
swelling of the branch whorl (approximately 5 cm) (*Figure
1*). Taper in each internodal segment was calculated as
the difference between the bottom diameter of the inter-
node and the bottom diameter of the next higher inter-
node divided by the internodal length.

$$TAPER(i) = \frac{DMB(i) - DMB(i+1)}{IL(i)} \qquad [2]$$

TAPER (*Table 1*) is the average of the internodal tapers
measured.

Height (HT12) and diameter (DM12) were measured and
stem volume (VOLM) calculated as described in KING et al.
(1988a).

Analyses

Analyses of variance and covariance were completed
for the model:

$$Y_{ijklm} = \mu + S_i + R_{j(i)} + M_k + F_l + SM_{ik} + SF_{il} + FM_{kl} + RM_{ki(i)} + RF_{li(i)} + SMF_{ikl} + RMF_{kli(i)} + E_{m(ijkl)} \qquad [3]$$

where μ represents the general mean and S, R, M, F and
E represent the effects of sites, replicates (within sites),
male parents, female parents and within plot error
respectively. Details of the model and the estimation of
variance components are presented in KING et al. (1988a).

The assumptions and methods for estimating genetic and
phenotypic variances, individual 'narrow-sense' and half-
sib family heritabilities, and expected gain from individual
'mass' and family (progeny test) selection for this model
are detailed in KING et al. (1988a). Methods for estimating
the simple individual tree phenotypic correlation between
two traits, or partial correlation when another trait (in
this case VOLM) is fixed, is outlined in STEEL and TORRIE
(1980). Half-sib phenotypic and additive genetic correla-
tions between traits using the sib analysis model ([3])
and associated standard errors were calculated as given in
FALCONER (1982).

The genetic relationships between branch form associa-
tions and bole volume were investigated through path-
coefficient analysis. Path-coefficient analysis is a
standardized, partial regression analysis that provides a
method by which direct and indirect components of an
association can be segregated (LI, 1975). In this case it
was used to emulate the model of CAMPBELL'S (1963) cause-
and-effect of the phenotypic relationships between crown
characters and stem volume (*Figure 2*), except that ad-
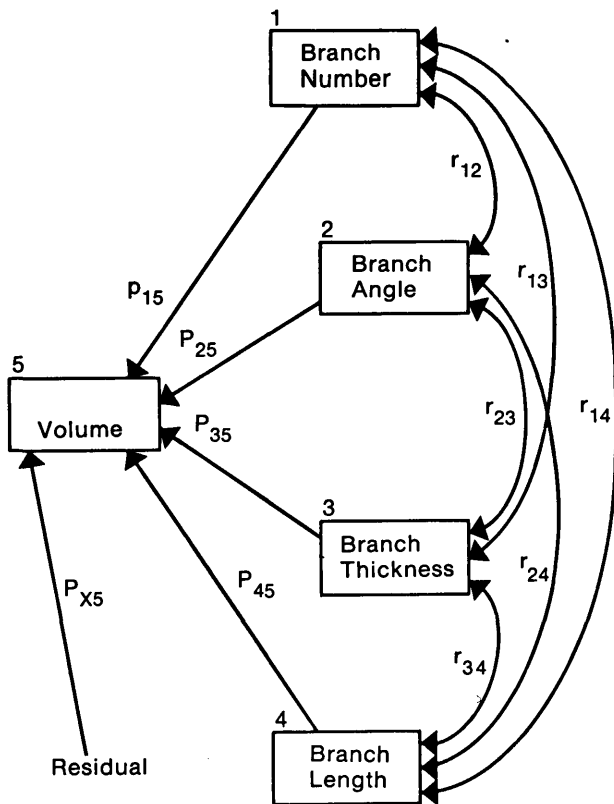ditive genetic relationships were used. Besides the model

Figure 2. — Model of path-coefficient analysis of the association of crown form traits with stem volume.

using direct branch measures BT and BL, another model was analysed that used the proportional traits BTT and BLT. These path analysis models were also used as a heuristic aid to identify key crown traits for inclusion in multi-trait selection indices to aid selection for form type and stem volume.

Selection models were analyzed for the improvement of stem volume and the promotion of fine branching crown form type. Genetic gains were determined for progeny test selection, where half-sib family information is used for backwards selection of parents (FALCONER, 1982). The growth trait chosen was stem diameter (DM12), because it is an easy trait to measure, and allows accurate interpolation of comparative stem volumes (KING et al., 1988a). Crown-form traits were chosen for their ease of measurement, for their heritabilities, for economic values in their own right, and for their genetic correlations with other traits in the fine-branching form type. Four selection strategies were investigated:

1. a multi-trait index that selects for diameter and branch number (IBN),
2. a multi-trait index that selects for diameter, branch number, and against proportional branch thickness (IBNT),
3. a multi-trait index that selects for diameter, and against knot index (IKI),
4. selection only for diameter (DM 12), and using correlated response to improve form traits.

Relative efficiencies showing the expected gains of the component traits (DM12, BN, BTT, BA, and KI) in these selection index models as a percentage of gain for direct selection of individual traits are presented. Formulae for estimating gains for direct progeny test selection using this experimental design are shown in KING et al. (1988a).

Expected correlated response (gain) in one trait when selection is applied to another was estimated using equation presented in FALCONER (1982). Index selection gains were estimated as shown by LIN (1978). Economic weights for the traits used in multi-trait selection were varied and the genetic gains plotted in order to determine the desired economic weights that both maximizes stem volume and promotes good form types (e. g. KING et al., 1988b). Where the estimates of gain involve traits not used in the index (e. g. BA in IBN) a BINET-type restriction was used (BINET, 1965). This imposes a constraint that index weights, b elements, whose measurements are not in the index must equal zero. The use of such restrictions are illustrated by COTTERILL and DEAN (1988) and BURDON (1989).

Results and Discussion

Means for the traits assessed and ranges of family means are presented in *table 1*. Estimates of variance components for significant sources of variation of interest are presented in *table 2*. Genetic and phenotypic variances and selection parameters are presented in *table 3*. The female-parent source of variation, which was used in the estimation of additive genetic variance, was significant ($p < .05$) for all traits except branch thickness (BT) (*Table 2*). The male x female interaction component which was used in estimating non-additive genetic variance, was significant for three of the eight crown-form traits reported in this study. Of these three traits, the magnitude of non-additive genetic variance in BA, the trait with the highest individual tree heritability ($h^2_i = 0.73$), was only about 10% that of additive genetic variance. The relative magnitude of non-additive genetic variance for BL and TAPER was close to that of additive genetic variance, but both these traits had low estimates of individual tree heritability ($h_i^2 = 0.10$; *Table 3*). Because of the small number of pollen parents (four), the precision for estimating non-additive genetic variance with the 'tester' mating design is low, especially for low heritability traits (PEDERSON, 1972). Genotype x environment interaction sources of variation (site x female) were non-significant for all the traits assessed in this study.

The significant between-family variation observed for branch number (accounting for 4% of the total variance, *Table 2*) contrasts to JARRET's (1978) work in Douglas-fir and MERRILL and MOHN's (1985) in white spruce where non-significant family differences were found. With moderate heritabilities ($h^2_i = 0.19$; $h^2_f = 0.82$) expected response to selecting the best parent trees for a seed orchard offers gains of nearly 9% per selection intensity unit for this trait (*Table 3*).

Between-family variation for branch angle (BA) was highly significant ($p < .001$); 16% of the total variation was attributable to family differences (*Table 2*), making BA the most highly heritable trait in the study ($h^2_i = 0.73$; *Table 3*). High individual-tree heritabilities have been expressed for this trait both in Douglas-fir (JARRET, 1978; BIROT and CHRISTOPHE, 1983) and in other conifers (MERRILL and MOHN, 1985; POYKKO, 1982; VELLING and TIGERSTEDT, 1984). This high individual-tree heritability value suggests that mass selection would be quite effective for improving branch angle in juvenile Douglas-fir.

Branch thickness (BT) showed non-significant family differences and branch length (BL) demonstrated weak expression of additive genetic variation. However, when

Table 2. — Results of analyses of variance for crown form traits and bole taper expressed as variance components and percentages of the total variance for each trait.

Trait[a]	Source (d.f.)									
	Female (21)		Site x Female (21)		Male x Female (63)		Plot/Full sib family (242)		Within Plot (3010)	
	σ^2_f	%	σ^2_{sf}	%	σ^2_{mf}	%	σ^2_{rmf}	%	σ^2_w	%
BN	0.06 ± 0.02	4	N.S.	0	N.S.	0	0.15 ± 0.03	10	1.11 ± 0.03	71
BA	8.85 ± 2.88	16	N.S.	1	1.00 ± 0.50	2	2.94 ± 0.75	5	33.58 ± 0.86	62
BT	N.S.	1	N.S.	0	N.S.	1	1.92 ± 0.28	16	7.57 ± 0.19	65
BTT	0.66 ± 0.26	5	N.S.	0	N.S.	1	1.34 ± 0.22	9	7.12 ± 0.18	49
BL	15.92 ± 8.24	2	N.S.	1	13.93 ± 8.35	2	144.10 ± 18.82	16	408.01 ± 10.51	44
BLT	1.00 ± 0.39	4	N.S.	0	N.S.	1	2.07 ± 0.29	9	17.00 ± 0.44	72
KI	2.80 ± 1.30	2	N.S.	1	N.S.	0	6.35 ± 1.43	5	60.05 ± 1.55	45
TAPER	0.59 ± 0.31	2	N.S.	1	0.44 ± 0.21	2	1.80 ± 0.45	7	20.32 ± 0.52	85

[a]) BN is branch number, BA is branch angle, BT is branch thickness, BTT is branch thickness to stem diameter ratio, BL is branch length, BLT is branch length to height ratio, KI is knot index, TAPER is bole taper.

N.S. — non-significant component, $P > 0.05$.

± represents standard errors of variance components (BECKER, 1975).

Table 3. — Estimates of genetic and phenotypic variances, heritabilities, coefficients of variation and expected response to selection for key crown form traits.

Parameter	Traits[a]						
	BN	BA	BTT	BL	BLT	KI	TAPER
Individual selection							
$b_{\sigma^2_A}$	0.25 ± 0.09	35.40 ± 11.50	2.64 ± 1.05	63.68 ± 32.96	3.98 ± 1.55	11.18 ± 5.19	2.35 ± 1.25
σ^2_{pi}	1.35	48.64	10.09	593.66	21.12	72.19	23.89
h^2_i	0.19 ± 0.07	0.73 ± 0.24	0.26 ± 0.10	0.11 ± 0.06	0.19 ± 0.07	0.15 ± 0.07	0.10 ± 0.05
CV_{pi}	21.76	10.61	11.64	15.64	11.80	21.82	25.70
$\%\Delta G_{i/i}$	4.10	7.72	3.04	1.68	2.22	3.36	2.53
Parent (progeny test) selection							
σ^2_f	0.06 ± 0.02	8.85 ± 2.88	0.66 ± 0.26	15.92 ± 8.24	1.00 ± 0.39	2.80 ± 1.30	0.59 ± 0.31
σ^2_{pf}	0.08	9.66	0.84	30.81	1.30	4.03	1.03
h^2_f	0.82 ± 0.30	0.92 ± 0.30	0.78 ± 0.31	0.51 ± 0.27	0.76 ± 0.30	0.69 ± 0.32	0.57 ± 0.30
CV_{pf}	5.21	4.73	3.36	3.56	2.93	5.16	5.35
$\%\Delta G_{f/i}$	8.56	8.66	5.27	3.68	4.48	7.15	6.08

[a]) (Same as in *Table 2*) except BT branch thickness — is not included because of non-significant family differences.

[b]) σ^2_A is additive genetic variance, σ^2_f is the female parent variance component, σ^2_{pi} and σ^2_{pf} are the phenotypic variance of individuals and half-sib family means respectively. h^2_i is the individual tree heritability, h^2_f is the half-sib family mean heritability. CV_{pi} and CV_{pf} are the coefficients of variation of individuals and half-sib family means respectively. $\%\Delta G_{/i}$ is percent expected gain per unit of selection intensity ("i") (KING et al., 1988a).

these crown-form traits were expressed as proportional traits — branch thickness as a ratio of stem diameter (BTT) and branch length as a ratio of total height (BLT), significant family differences were observed and moderate heritability estimates obtained (*Tables 2* and *3*).

Relationships between crown form and growth traits

Simple (individual tree phenotypic) correlations between crown and growth traits are presented in *table 4*. As expected, traits related to tree size (e. g.: bole volume (VOLM), branch thickness (BT) and length (BL), were

highly intercorrelated. Partial correlations (controlling for bole volume (VOLM)) are presented in *table 5*. The results of these phenotypic correlations are similar to CAMPBELL's (1963), except: branch number was not so highly correlated to bole volume (0.04 compared to CAMPBELL 0.51); branch angle showed a small but significant negative correlation with bole volume (—0.14 compared to CAMPBELL — non significant); and the partial correlation between branch number and angle was significant and positive (0.13 compared to CAMPBELL — non significant). Even so, the phenotypic associations between branch and upper-

Table 4. — Simple (individual tree phenotypic) correlation coefficients between growth and crown form traits[a]).

PEARSON CORRELATION COEFFICIENTS

	DM12	VOLM	TAPER	BN	BA	BT	BTT	BL	BLT
HT12[a]	.81***	.83***	-.18***	.03*	-.13***	.69***	-.22***	.80***	-.22***
DM12		.88***	.03*	.01 NS	-.14***	.77***	-.31***	.84***	.05**
VOLM			.02 NS	.04*	-.14***	.80***	-.26***	.83***	-.06***
TAPER				.03*	-.07***	.10***	.11***	.03 NS	-.31***
BN					.13***	-.03 NS	-.04**	-.03 NS	-.16***
BA						-.19***	-.02 NS	-.17***	-.07***
BT							.22***	.83***	.12***
BTT								-.07***	.09***
BL									.25***

[a]) HT12 is height at 12 years, DM12 is diameter at 12 years, VOLM is bole volume (see KING et al., 1988a), TAPER is bole taper (see text), BN is branch number, BA is branch angle, BT is branch thickness, BTT is proportional branch thickness (see text), BL is branch length, BLT is proportional branch length (see text).

*), **), ***) = significant at 0.05, 0.01, 0.001 levels of probability, NS = non-significant $P > 0.05$.

crown attributes are similar to CAMPBELL's observations:
1. trees with fewer branches have thicker branches,
2. trees with fewer branches have proportionally longer branches,
3. acute-angled branches are thicker,
4. acute-angled branches are longer, and

and in addition to CAMPBELL's dissertation
5. trees with fewer branches have branches with more acute angles,
6. thicker branches are longer, even accounting for stem volume.

Although the partial correlations are not strong enough to have one or a few of the traits explain the majority of the variation in any of the others, there is a significant association of high branch numbers with comparatively light branching (thickness and length) and flat branch angle (fine branching). The contrasting association in form is for few, but heavy and acute-angled branches (coarse branching).

Genetic relationships are summarized in table 6. Although CAMPBELL's (1963) strong correlation between bole volume and branch number was not apparent in the simple in-

Table 5. — Partial correlation coefficients between crown form traits, for constant stem volume.

	BA	BT	BL
BN[a]	-.13***	-.10***	-.11***
BA		-.13***	-.11***
BT			.48***

[a]) BN = branch number, BA = branch angle, BT = branch thickness, BL = branch length.

*), **), ***) Significant at 0.05, 0.01, 0.001 levels of probability.

dividual tree phenotypic correlation (Table 4), it is shown in the additive genetic correlations ($r_A = 0.71 \pm 0.18$).

Of the aforementioned association of crown characters for the fine branching form type, the strongest genetic basis appears to be that between branch number (BN) and branch thickness as a proportion of stem thickness (BTT) ($r_A = -0.59 \pm 0.18$). Thus the contrast between trees with many but light branches can be utilized effectively for selection. Branch angle shows a moderate, negative genetic relationship ($r_A = -0.29 \pm 0.23$) with proportional branch thickness, further supporting the genetic association of these form types. JARRET's (1978) observation of a strong positive genetic correlation between vigour (height) and branch angle ($r_A = 0.96$) is not corroborated by these data, but branch number (BN) and proportional branch thickness (BTT) both show strong genetic associations with growth variables, especially diameter and volume ($r_A \geq 0.7$; Table 6). The correlation of BTT with VOLM is to be expected of course because DM is a component of both measures, but the negative relationship ($r_A = -0.75$) indicates larger trees have comparatively smaller branches. Strong positive genetic correlations exist between bole taper and branch number, and bole taper and branch thickness ($r_A > .5$; Table 6). Bole taper increases when woody material is shifted from the bole to the branches.

The genetic relationships between branch form associations and bole volume were further investigated through path-coefficient analysis. The additive genetic relationships among branch traits can be evaluated, in this model, for their direct and indirect influences on stem growth. The path-coefficient model, similar to CAMPBELL's (1963), except using additive genetic correlations, is presented in figure 2.

Results using the direct measurements for branch thickness and branch lengths are presented in table 7. Stem volume is affected mainly by the number of branches (42%, $P^2_{15} = 0.416$). Other effects are minor in comparison,

Table 6. — Estimated additive genetic (r_A) and phenotypic half-sib (r_{phs}) correlations between crown form traits, and additive genetic correlations between crown form and growth.

	BN[a]	BA	BT	BTT	BL	BLT	KI	TAPER

Between crown traits ... r_A above diagonal, r_{phs} below diagonal.

	BN[a]	BA	BT	BTT	BL	BLT	KI	TAPER
BN		.19	.16	-.59	.18	-.11	.36	.57
BA	.37		-.05	-.29	-.10	.12	-.10	-.05
BT	.22	-.23		.38	.33	.11	.56	.73
BTT	-.46	-.25	.33		-.04	.14	.52	.26
BL	.27	-.16	.66	.01		.61	NC	NC
BLT	-.07	.0	.22	.06	.46		NC	NC
KI	.46	-.10	.37	.59	NC	NC		NC
TAPER	.40	-.12	.52	.28	NC	NC	NC	

Between crown traits and growth traits...r_A

	BN[a]	BA	BT	BTT	BL	BLT	KI	TAPER
HT12	.26	-.03	-.03	-.31	.38	-.59	NC	-.38
DM12	.67	.18	.21	-.82	.22	.21	-.32	.15
VOLM	.71	.18	.29	-.75	.28	-.19	NC	.17

[a]) BN = branch number, BA = branch angle, BT = branch thickness, BTT = proportional branch thickness (see text), BL = branch length, BLT = proportional branch length (see text), KI = knot index (see text), TAPER = taper (see text), HT12 = height at 12 years, DM12 = diameter at 12 years, VOLM = bole volume (see KING et al., 1988a).
NC — not calculated.

and they affect volume mainly through their indirect effect on branch number. The residual variation leaves nearly 45% of the variation in volume unexplained by these traits.

The second analysis (Table 8) used the proportional branch measure traits to predict volume. In this analysis, proportional branch thickness (BTT) has at least as important a direct effect on volume as does branch number. These traits also have a strong indirect influence on each other. Branch number (BN) and proportional branch thickness (BTT) together account for 42% (P^2_{15} = 0.165 + P^2_{35} = 0.257) of the genetic differences in stem volume by their direct influences. This is no more, however, than 42% accounted for by branch number alone in the model using direct measurements. Branch angle and proportional branch length do not appear to have important effects on stem volume. The additive genetic relationships between branch angle and proportional branch length with both branch number and proportional branch thickness (Table 6) mean that selecting for high branch number and light branching (BTT) will also improve branch angle and branch length.

A positive association of a fine branching form type with growth characters is encouraging, and the promotion of more branches per whorl will be less detrimental due to the relative reduction of branch size, flatter branch angle and increased volume for this form type. A positive relationship between volume and a similar complex of form characters was found in Scots pine by VELLING and TIGERSTEDT (1984). They concluded that reduction in proportional branch diameter was of great importance for wood quality, and more than offset the promotion of branch number.

Selection for multinodal branching habit has been important in improving both growth and form for radiata pine (Pinus radiata D. DON) in New Zealand (SHELBOURNE et al., 1986; CARSON, 1987). Multinodal branching in radiata pine refers to increased periodicity of branch whorls (SHELBOURNE et al., 1986) as opposed to branch number per whorl, but the effect is similar. The favourable correlation between branch number and stem volume is also shown in radiata pine between multinodality and stem volume. Increased knotiness in multinodal trees reduces clearcutting grades but increases premium framing grades in unpruned radiata pine by having more but smaller knots (CARSON, 1987).

Where silviculture regimes call for pruning, small but numerous branches may be more economically pruned than few but large branches. Where untended silviculture is practised, self-pruning is more likely to occur on small branches than large branches (unlike radiata pine, Douglas-fir is self pruning, thus clearwood production should not have an advantage in unimproved over improved trees as it does in radiata pine (CARSON, 1987)). Selection for the combination of volume and fine (but numerous) branching, compared to volume on its own, may be better justified for the development of 'special-purpose' breeds that are tied to silvicultural regimes and products (such as premium framing grades). than for 'general-purpose' breeding.

Number[b]	-------------------- Crown Variables ------------------------				
	[a]BN 1	BA 2	BT 3	BL 4	X
Due to direct effect: P.5	.645	.074	.140	.128	.675
Due to indirect effects:					
via branch number P$_{15}$		.123	.106	.114	
via branch angle P$_{25}$	.014		-.004	-.008	
via branch thickness P$_{35}$	.023	-.007		.047	
via branch length P$_{45}$	.023	-.013	.044		
Totals (additive genetic correlations)	.705	.177	.286	.282	

[a]) BN is branch number, BA is branch angle, BT is branch thickness, BL is branch length, X is residual variation.

[b]) See *figure 2*, bole volume is trait 5.

Growth and Crown Form Selections

The selection process presented here is designed to maximize growth and also promote the fine branching form type association. Three different multiple trait selection indices and selection for diameter by itself were compared. The selection indices included: IBN — for DM and BN; IBNT — for DM, BN and BTT; and IKI — for DM and KI.

Table 9 presents a comparison of expected gains from these four different selection strategies. The results for different traits are presented as the relative efficiencies (R. E.) of the correlated response, compared to the direct response, expressed as a percentage. The increased diameter response from the index (IBNT) over direct response (104:100) reflects the strong correlations of BN and BTT helping with indirect selection for diameter. These results indicate the clear benefit of using multi-trait index selection, especially index IBNT, for increasing stem volume, and promoting fine branching in Douglas-fir. Some of these gains could also be made through correlated response from selecting for diameter, on its own.

Conclusions

1. Additive genetic variance (proportional to σ^2_f) was significant (P < 0.05) for all 8 crown-form traits, except branch thickness. Although significant (P < 0.05) amounts of non-additive genetic variance (proportional to σ^2_{mf}) was expressed for branch angle, branch length and bole taper; this was a less important source of genetic variance for crown traits in general. Genotype x environment interac-

tion effects (estimated using σ^2_{sf}) were not significant for any trait.

2. Branch angle (as has been reported in other studies) should respond well to mass selection (h^2_i = 0.73). Most of the other form traits would respond best to family selection. Moderate heritability ($h^2_i \approx 0.2$) were found for branch number, branch thickness to diameter ratio and branch length to height ratio. Low heritability ($h^2_i \approx 0.10$) was found for branch length and bole taper.

3. Branch thickness and branch length showed stronger genetic differences when used as proportional traits —

Number[b]	------------------------- Crown Variables ------------------				
	[a]BN 1	BA 2	BT 3	BL 4	X
Due to direct effect: P.5	.406	-.038	-.507	-.073	.575
Due to indirect effects:					
via branch number P$_{15}$		.077	-.239	-.044	
via branch angle P$_{25}$	-.007		-.011	-.004	
via branch thickness P$_{35}$	.299	.146		-.072	
via branch length P$_{45}$	.008	-.008	-.010		
Totals (additive genetic correlations)	.705	.177	-.746	-.193	

[a]) BN is branch number, BA is branch angle, BTT is proportional branch thickness (see text), BLT is proportional branch length (see text), X is residual variation.

[b]) See *figure 2*, bole volume is trait 5.

Strategy[a]	Trait				
	DM12	BN	BTT	BA	KI
1. Index IBN[b]	96	80	-71	17	-2
2. Index IBNT	104	85	-93	24	-23
3. Index IKI	98	43	-77	15	-65
4. DM12	100	58	-72	14	-20

[a]) DM12 is diameter at 12 years, BN is branch number, BTT is proportional branch thickness (see text), BA is branch angle, KI is knot index (see text).

[b]) IBN is a multiple trait index using DM12 and BN;
IBNT is a multiple trait index using DM12, BN, and BTT;
IKI is a multiple trait index using DM12 and KI.

branch thickness as a ratio to stem thickness at the measuring point, and branch length as a ratio of total height.

4. There was an association among high branch number, light branch size (thickness and length), and flat branch angle — in contrast to low branch number, heavy branch size (thickness and length) and steep-angled branches. Genetic relationships were established for a fine-branching form type and were shown to be positively associated with stem volume.

5. Path-analysis demonstrated that 42% of the additive genetic variation in stem volume could be accounted for by the additive genetic variation in branch number.

6. A negative genetic correlation is demonstrated between height and bole taper. Strong positive genetic correlations exist between bole taper and branch number, and bole taper and branch thickness. Higher bole taper exists where more wood is shifted from the bole to branches.

7. Multi-trait selection for the improvement of form and growth traits can accentuate the positive association of the fine-branching form type of profuse/light/flat branches with stem volume. Selecting key traits (branch number, proportional branch thickness, and knot index) in the tree-form-complex, along with stem diameter, can favourably affect all traits. Selecting for diameter on its own can improve form, but is not as effective as multi-trait selection for pursuing a fine branching form type.

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Effect of Geographical Transfer on Growth and Survival of Jack Pine (Pinus banksiana Lamb.) Populations

By C. MÁTYÁS[1]) and CHR. W. YEATMAN[2])

Summary

Heights and mortality at age 15 were analysed in Ontario tests of a range-wide provenance experiment.

[1]) Professor and head, Plant Sciences Dept., Sopron University, POB 132, H-9401 Sopron, Hungary

[2]) Senior scientist, Petawawa National Forestry Institute, Chalk River, Ontario, KOJ 1JO, Canada

The analysis confirmed that the between-sources variaton pattern of height growth in jack pine populations is shaped by thermo- and photoperiodic effects. The geographical pattern is latitudinally clinal but weakly expressed.

For calculating the response regression surface, the variable "ecological distance" was introduced as a measure of environment change for the transferred sources. The