Selection of Growth and Yield Traits in Controlled Crosses of Coastal Douglas-fir

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(Received 21st August 1987)

Summary

Growth and yield traits are among the most important selection criteria in the genetic improvement of Douglas-fir. Analysis of variance of several yield traits including height, height increment, diameter and volume in a full-sib progeny test on two sites in British Columbia revealed significant amounts of additive genetic variance but small and non-significant amounts of dominance genetic variance. Individual tree heritabilities were between .08 and .16 for growth traits and family heritabilities were between .55 and .73. Acceptable gains were predicted with progeny test re-selection (10% volume gain per unit selection intensity). Age 6 height was an effective selection trait, and correlated well with age 12 volume — 70% relative efficiency for family selection. Age 12 height measurement and height increment between 10 and 12 did not express significant genetic differences on the individual site analyses due in part to uncontrolled within-plot variation. Diameter showed higher heritabilities and was less sensitive to inadequacies in experimental design than the later height measurements. Index selection for stem volume also demonstrated that diameter was the most effective growth trait to predict the breeding value of parents for individual tree stem volumes.

Key words: Douglas-fir, growth and yield, selection, genetic parameters, index selection.

Zusammenfassung

Bei der genetischen Verbesserung der Douglasie sind Wachstums- und Ertragsmerkmale unter den Selektionskriterien mit die wichtigsten. Varianzanalysen verschiedener Ertragsmerkmale, wie Höhe, Höhenzuwachs, Durchmesser und Volumen in Vollgeschwister-Nachkommenschaftsprüfungen an zwei Standorten in Britisch-Kolumbien enthüllten signifikante additive genetische Varianzen, aber kleine und nicht signifikante genetische Dominanzvarianzen. Die Heritabilitäten für die Einzelbäume lagen für Wachstumsmerkmale zwischen 0,08 und 0,16, die Familienheritabilitäten zwischen 0,55 und 0,73. Akzeptable Gewinne wurden für die wiederholte Selektion nach Nachkommenschaftsprüfungen vorausgesagt (10% beim Volumen je Einheit Selektionsintensität). Die Höhe im Alter von 6 Jahren war ein effektives Selektionskriterium und eng mit dem Volumen im Alter 12 korreliert — 70% relative Effizienz für die Familienselektion. Messungen für die Höhe im Alter 12 und der Höhenzuwachs zwischen 10 und 12 zeigten bei den individuellen Standortanalysen aufgrund unkontrollierter Variation innerhalb von Parzellen. Der Durchmesser zeigte höhere Heritabilitäten und war weniger empfindlich gegenüber den Mängeln des Versuchsplanes als spätere Höhenmessungen. Die Index-Selektion für das Stammvolumen zeigte ebenfalls, daß der Durchmesser das effektivste Wachstumsmerkmal war, um den züchterischen Wert der Eltern für das individuelle Stammvolumen vorauszusagen.

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominates the most productive forest lands of western North America (Silen, 1978). The growth potential and high quality timber of Douglas-fir have made it the prime species for intensive forest management and tree improvement in the Pacific Northwest.

British Columbia's tree improvement programme for Douglas-fir began in 1957 with phenotypic selection of plustrees and seed orchard establishment (Orr-Ewing, 1969). Since 1973, a recurrent selection breeding programme has been developed (Heaman, 1978) and traits of growth and yield will be among the most important selection criteria.

Growth in coastal Douglas-fir can be quite vigorous, with up to 2 metres of annual height increment once established and 60 cm annual increment continuing for up to 100 years on the best sites (Silen, 1978). Total standing volumes of over 1500 m^3/ha occur regularly in stands of coastal Douglas-fir and may reach 2000 m^3/ha (Silen, 1978; Klinka and Carter, 1980). Coastal Douglas-fir is naturally associated with even-aged stand structure following fire (Schmidt, 1960). Height growth is therefore not only a trait of prime economic importance, but is also an important component of fitness and indicator of maladaptation. Suppression and eventual mortality will occur for genotypes that cannot remain in competition with their neighbours within the dominant and co-dominant canopy classes.

There are several published accounts reporting that significant and important amounts of additive genetic variance are available for the improvement of growth traits in Douglas-fir. Campbell (1972) found significant differences but low heritabilities (h^2_i = 0.10—0.16) for height increments of four year old full-sib seedlings. Yeh and Heaman (1982) reported significant additive genetic variance for height and diameter at age six years in the same experiments used here. Heritability estimates were h^2_i = 0.14 and 0.19 for height and diameter respectively. Estimates of dominance genetic variance were non-significant.

Studies using open-pollinated (OP) families have in general shown much higher heritability estimates (Jarret, 1978; Birot and Christophe, 1983; Rehfeldt, 1983). Birot and Christophe (1983) reported heritability estimates from OP families of 26 provenances in the French Douglas-fir trials that ranged from 0.0 to 0.77 for height at 12 years. Most of the provenances had individual-tree heritabilities for height of around 0.3; and heritabilities of tree girth were similar. In contrast to results from these early height assessments Namkoong *et al.* (1972) found that family-within-provenance differences were non-significant ($P > .05$) in the older Douglas-fir Heredity Study (Munger and Morris, 1936).

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This study looks at growth annd yield traits: height, height increment, diameter, and volume, for several age classes up to 12 years in full-sib progeny of Douglas-fir on two sites. This is the age at which trees begin to deposit substantial bole volume and is the age at which preliminary selection decisions will be made in the progeny tests. The establishment of key growth traits that can be effectively measured at this age and used in progeny evaluations will facilitate these decisions. This study investigates additive and dominance genetic variances for growth and yield traits; looks at the pattern of changing variances during this crucial growth phase; establishes genetic parameters for growth and yield traits; looks at the relative efficiency of early height growth selection (age 6 $\cong$ 1 m) to later selection for growth and yield (age 12 $\cong$ 6 m); and compares the growth traits individually, and in a multiple trait index, for the efficiency of their indirect selection of parents for the breeding value of stem volume.

Materials and Methods

Materials

Twenty-six trees were randomly chosen from the first generation selections that make up the base breeding population of coastal British Columbia Douglas-fir. Twenty-two randomly chosen trees served as seed parents and were crossed with four trees (serving as pollen parents) in April 1971 (North Carolina Design II "tester"; COMSTOCK and ROBINSON, 1952).

Seeds from all 88 families were sown in the spring of 1972. In the autumn of 1973 a group of twenty seven seedlings from each of the 88 families was outplanted in the Greater Victoria Watershed (GVWS); in the following spring another group was outplanted at the Cowichan Lake Experimental Station (CLES). Families were planted at 3 m × 3 m spacing in a randomized complete block design with three replications of nine-tree plots at each site. Both sites were cleared and fenced prior to planting. The Cowichan Lake site (elev. 165 m) was planted with nine tree row plots and the Victoria Watershed site (elev. 488 m) was planted with nine-tree square plots. More details of the materials and planting are presented in YEH and HEAMAN (1982).

The growth and yield traits investigated include: height at 6 years (HT06); height at 12 years (HT12); diameter at 12 years (DM12); HTD representing the height increment of the trees from age 10 to age 12 (HTD = HT12—HT10); and volume (VOLM) at age 12 years was estimated by taking measurements of each internode length with top and bottom diameters of each internode — VOLM was the totalled volumes of all stem segments as tapering cylinders plus the cone volume from the highest diameter recorded to the top of the tree. In addition, intermediate heights and diameters at age 10 (HT10, DM10) were investigated to look at trends in the expression of variance components.

Analyses

Analyses of variance for a random model were performed on the growth and yield traits to test hypotheses about the significance of family related effects and also for the purpose of estimating variance components for these effects. The structure of this model for the combined-site analysis is detailed in *Table 1*. Where appropriate error terms were not available the approximation method of SATTERTHWAITE (1946) was used.

Variance components were estimated by equating the mean square for each effect with its expectation (*Table 1*) and solving for the component. Standard errors of variance components were calculated as per BECKER (1975). Components of covariances among traits were calculated by using the variance component model (*Table 1*) on the sum of the values for the pair of traits in question and solving for the covariance term (KEMPTHORNE, 1957:pg 264).

Assuming no linkage, no epistasis, and no inbreeding, the components of variance among females (σ^2_f) and among males (σ^2_m) each estimate one-quarter of the additive genetic variance (σ^2_A). The component of variance among full-sibs (σ^2_{mf}) estimates one-quarter of the dominance genetic variance (σ^2_D). The female by site interaction (σ^2_{fs}) and the male by site interaction (σ^2_{ms}) estimate one-quarter of the additive genetic variance by site variance. The female by male by site interaction (σ^2_{fms}) estimates dominance genetic variance by site variance.

The number of seed parents (22) is much greater than the pollen parents (4). The selection unit and the source of information for additive genetic variance is, therefore, more appropriately the female seed tree parent (σ^2_f). Where individual trees in the combined progeny tests are the selection unit heritability (h^2_i is: σ^2_A/σ^2_{pi}, and the phenotypic variance of individuals, σ^2_{pi}, is:

$$\sigma^2_m + \sigma^2_f + \sigma^2_{mf} + \sigma^2_{sm} + \sigma^2_{sf} + \sigma^2_{rm} + \sigma^2_{rf} + \sigma^2_{smf} + \sigma^2_{rmf} + \sigma^2_w \qquad [1]$$

with the notations defined in *Table 1*. The expected response to mass selection as a percentage response per standard deviation unit of selection or per unit "i" (% $\triangle G_i/i$) is = $h^2_i \times CV_{pi}$, where CV_{pi} is the coefficient of variation among individuals.

In the selection of the best parent trees based on their progeny's performance, i.e. progeny test selection, the heritability (half-sib family — h^2_f) is σ^2_f/σ^2_{pf}, and the phenotypic variance of half-sib family means, σ^2_{pf} is:

$$\sigma^2_f + \frac{k_{11}}{k_{12}}\sigma^2_{sf} + \frac{k_{10}}{k_{12}}\sigma^2_{rf} + \frac{k_9}{k_{12}}\sigma^2_{mf} + \frac{k_8}{k_{12}}\sigma^2_{smf} + \frac{k_7}{k_{12}}\sigma^2_{rmf} + \frac{1}{k_{12}}\sigma^2_w \qquad [2]$$

with the notations defined in *Table 1*. Expected response to progeny test selection per selection intensity unit (% $\triangle G_f/i$) is 2 ($h^2_f \times CV_{pf}$), where both selected parents are used in a clonal seed orchard with no outside pollen contamination, and CV_{pf} is the coefficient of variation among female half-sib families.

Genetic correlations and associated standard errors were calculated using the formulae of FALCONER (1982). Index selection models were derived as per FALCONER (1982) and LIN (1978). The index investigated was for improving volume using the individual growth traits HT06, HT12 and DM12; and was for progeny test selection.

Results and Discussion

Significance and Trends in the Expression of Genetic Variances

Mean squares and their significance levels are presented for the combined site analysis in *Table 2*. The variance due to female parents that was used in estimating additive genetic variance was significant ($P < .05$) for all these growth traits. Dominance genetic variance = ($4 \times \sigma^2_{mf}$) was not significant for any of the growth traits and neither was additive genetic variance × environment interaction (σ^2_{sf}). These results indicate that recurrent selection for additive genetic variance will be the most effective way of genetically improving traits of growth and yield in Douglas-fir.

Table 1. — Structure of analyses of variance and covariance on combined sites.

Source of variation	Degrees of freedom	Mean squares or mean cross products	Expected mean squares or mean cross products
Sites	s-1=1	MS_1	
Replications/sites	s(r-1)=4	MS_2	
Males	m-1=3	MS_3	$\sigma^2_w + k_1\sigma^2_{rmf} + k_2\sigma^2_{smf} + k_3\sigma^2_{mf} + k_4\sigma^2_{rm} + k_5\sigma^2_{sm} + k_6\sigma^2_m$
Females	f-1=21	MS_4	$\sigma^2_w + k_7\sigma^2_{rmf} + k_8\sigma^2_{smf} + k_9\sigma^2_{mf} + k_{10}\sigma^2_{rf} + k_{11}\sigma^2_{sf} + k_{12}\sigma^2_f$
Site x males	(s-1)(m-1)=3	MS_5	$\sigma^2_w + k_{13}\sigma^2_{rmf} + k_{14}\sigma^2_{smf} + k_{15}\sigma^2_{rm} + k_{16}\sigma^2_{sm}$
Site x females	(s-1)(f-1)=21	MS_6	$\sigma^2_w + k_{17}\sigma^2_{rmf} + k_{18}\sigma^2_{smf} + k_{19}\sigma^2_{rf} + k_{20}\sigma^2_{sf}$
Males x females	(m-1)(f-1)=63	MS_7	$\sigma^2_w + k_{21}\sigma^2_{rmf} + k_{22}\sigma^2_{smf} + k_{23}\sigma^2_{mf}$
Rep x males	s(r-1)(m-1)=12	MS_8	$\sigma^2_w + k_{24}\sigma^2_{rmf} + k_{25}\sigma^2_{rm}$
Rep x females	s(r-1)(f-1)=84	MS_9	$\sigma^2_w + k_{26}\sigma^2_{rmf} + k_{27}\sigma^2_{rf}$
Site x cross	(s-1)(m-1)(f-1)=63	MS_{10}	$\sigma^2_w + k_{28}\sigma^2_{rmf} + k_{29}\sigma^2_{smf}$
Plot	s(r-1)(m-1)(f-1)=252	MS_{11}	$\sigma^2_w + k_{30}\sigma^2_{rmf}$
Within plot	srmf(t-1)	MS12	σ^2_w

s = number of sites
r = number of replications within sites
m = number of male pollen trees
f = number of female seed trees
t = number of trees within plots
k_i = coefficient of the "i" th variance component

Although additive genetic variance remained significantly expressed ($P < .05$) for all the growth traits in the combined-over-sites analysis; for individual site analyses, additive genetic variances were non-significant for the later height measurement (HT12), height increment (HTD) and volume (VOLM) (especially at the Cowichan Lake site; *Table 3*). Inefficiencies of the plantation design with relatively few (three) replications of large (nine tree) row plots

Table 2. — Mean-squares and probability levels for combined-site analyses of variance of growth and yield traits.

Source of[1] Variation	d.f.[1]	Traits HT06	HT12	DM12	HTD	VOLM
[Males]	3	15543.07	221621	343.52	23356	67.71
Females	21	8416 **	72245 **	1458.35 **	9499 *	251.80 *
[SitexMales]	3	1091	59624	734.47	6460	5.22
SitexFemales	21	2343 NS	22511 NS	351.62 NS	3465 NS	69.60 NS
[RepxMales]	12	1868	30321	609.69	2325	129.85
RepxFemale	84	1901 NS	24965 NS	342.68 NS	2682 NS	72.75 NS
MalesxFemales	63	1988 NS	16870 NS	298.85 NS	3114 NS	117.13 NS
SitesxMalesxFemales	63	2159 NS	34200 *	509.05 NS	2622 NS	85.18 NS
Plot	252	1900 **	22813 **	448.82 **	2509 **	95.64 **
Within	3878	704	6948	118.13	1203	28.52

[1] based on d.f. for HT06; within Plot d.f: = 3684 for HT12, DM12 and HTD; within plot d.f. = 3010 for VOLM and plot d.f. = 242 for VOLM

NS $P > .05$

* $.05 > P > .01$

** $.01 > P$

could account for much of the error. Analyses of the error sources of variation used in detecting genetic differences were made to pinpoint specific experimental inadequacies.

The two major error sources of variation, that influence the sensitivities of detecting significant differences among genetic sources of variation in this experiment, are the error variance of the large-scale environmental heterogeneity within replications (σ^2_{rmf}) and the error variance of small-scale environmental variation within plots (σ^2_w). The large-scale error (σ^2_{rmf}) is caused by the failure of full-sib family plots to behave in the same way within environmental replication and can be reduced by re-blocking the experiment based on full-sib family plot performance. Correct blocking of an experimental site to reduce within-block heterogeneity is especially difficult in the rough topography of coastal British Columbia. To see if genetic differences could be more accurately determined, the site was re-blocked on the ranking of plot means and then re-analysed.

Although plot variation (σ^2_{rmf}) declined from 19.4% to 1.1% (*Table 3*) of total variation, the significance level of the female source of variation did not improve. Although this procedure restructured the blocks based on plot performance, the long, nine-tree row plots would appear to contain too much variability to prove effective.

Restructuring the experiment by reducing the small-scale environmental variation within plots (σ^2_w) was effective. Analysis of the four top trees of each full-sib family plot showed significant sources of variation of additive genetic effects and more substantial heritabilities ($h^2_i = 0.22$: *Table 3*). This micro-environmental variation within the row plots was quite noticeable at the Cowichan Lake site; with row plots running up and down a topographical gradient — mid-gradient trees were substantially bigger. Progeny test selection and estimations of GCA can be more efficiently made with smaller and more numerous (preferably single-tree) plots. In recurrent selection for additive genetic variance with long generation organisms such as conifers, effective selection is of paramount importance. Height measurements appear to be more sensitive to experimental inadequacies than diameter measurements.

Trends in the expression of environmental and genetic sources of variation are shown in *Table 4*. As trees become established during the juvenile growth phase, microsite influences that affect tree-to-tree variation decline in relation to large-scale macro-environmental sources. The relative proportion of the variation attributable to site effects rises steeply (7%—46%), whereas the proportion affecting tree-to-tree level variation (e.g. σ^2_w, σ^2_f) declines. In his model of trends in the expression of additive genetic variance FRANKLIN (1979) suggested that initial high levels of

Table 3. — Variance components as a percentage of the sum total of all effects and probability levels for final height and diameter at Cowchan Lake.

Source of variation	d.f.	Traits DM12	HT12	HT12 re-blocked	HT12 top 4 trees
Female	21	4.9 *	1.5 NS	0.9 NS	4.9 *
RepxFem	42	0.0 NS	0.0 NS	0.3 NS	0.0 NS
MalexFem	63	0.0 NS	2.5 NS	8.6 **	1.1 NS
Plot	126	26.0 **	19.4 **	1.1 NS	49.3 **
Within	2032	64.0	69.5	66.5	30.4
heritability (h^2_1)		0.20±0.09	0.06±0.06	0.05±0.07	0.22±0.13

NS $P > .05$, * $.05 > P > .01$, ** $.01 > P$

Table 4. — Trends in variance components: Variance components from combined-sites analyses expressed as a % of total and as a coefficient of variation (in brackets).

Source of Variation	Heights			Diameters		
	HT06	HT10	HT12	DM06	DM10	DM12
Site	7.2 (7.9)	36.2 (17.0)	46.1 (16.0)	17.3 (13.5)	38.8 (20.0)	53.2 (18.4)
Female	3.1 (5.2)	1.9 (3.9)	1.8 (3.2)	3.7 (6.3)	2.3 (4.9)	1.9 (3.4)
Plot	14.4 (11.2)	11.6 (9.7)	10.5 (7.7)	14.1 (12.2)	12.1 (11.2)	11.3 (8.5)
Within	69.7 (24.7)	44.5 (19.0)	36.2 (14.2)	57.9 (24.8)	43.1 (21.2)	31.1 (14.1)

additive genetic variance that are expressed early in the juvenile growth phase can decline as trees begin competing with each other. Trends of declining heritabilities (h^2_i) are not suggested in this study on the combined analyses (*Table 5*) but FRANKLIN's model may help to explain the inability at site CLES (where growth is more advanced) to detect significant family differences for the later height measurements.

Heritabilities and Correlations

Estimates of genetic and phenotypic variances, heritabilities and other selection parameters are shown in *Table 5*. Individual-tree heritabilities for growth and yield traits were low (0.08 to 0.19) but family heritabilities were high (0.55 to 0.77) for these traits. Individual tree heritability estimates were similar to CAMPBELL's (1972) estimate from full-sib material but were lower than the estimates from O.P. trials (JARRET, 1978; BIROT and CHRISTOPHE, 1983; REHFELDT, 1983). Open-pollinated material may be biased however because the assumption of half-sib mating is likely to be violated (NAMKOONG, 1966; SQUILLACE, 1974). Where open-pollinated seed is gathered from natural stands varying composition and effectiveness of the pollen clouds together with varying levels of natural inbreeding will add to this bias.

Heritabilies for height growth were not improved when it was expressed as the height increment between age 10 and age 12 rather than overall height. In fact the low heritabilities and marginal levels of significance for additive genetic variance for height increment were very disappointing. Heritability estimates were higher for diameter than for height growth. Expected gain from progeny test reselection for volume at age 12 is expected to be quite high, with 10% gain per unit selection intensity. A unit of selec-

Table 5. — Estimates of variance components, standard errors, and heritabilities from combined-site analyses; and predicted gain for growth and yield traits.

Parameter	Traits				
	HT06	HT12	HTD	DM12	VOLM
Individual selection					
σ^2_A	124.81±52.90	1411.97±494.99	115.72±64.80	28.188±9.763	3.880±2.054
σ^2_{pi}	904.76	10090.92	1446.90	171.460	40.764
h^2_i	0.14±0.06	0.14±0.05	0.08±0.05	0.16±0.06	0.10±0.05
CV_{pi}	28.00	17.12	18.12	16.94	44.764
% $\Delta G_i/i$	3.9	2.4	1.4	2.8	4.3
Progeny test re selection					
σ^2_f	31.20±13.22	352.99±123.75	28.93±16.20	7.047±2.441	0.970±0.513
σ^2_{pf}	42.89	538.97	49.23	9.709	1.763
h^2_f	0.73±0.3[illegible]	0.66±0.23	0.59±0.33	0.73±0.25	0.55±0.29
CV_{pf}	6.10	3.96	3.34	4.031	9.31
% $\Delta G_f/i$	8.9	5.2	3.9	5.9	10.2

Table 6. — Genetic (r_A), phenotypic (r_{pi} and r_{pf}) and environmental (r_E) correlations and correlated response to early height family selection with corresponding relative efficiencies to this early height selection.

	Traits for correlations			Correlated response on HT06	
Trait	HT06	HT12	DM12	$CR_{f/i}$	R.E.
VOLM				6.9	6.9/10.2 = 70%
r_A	.68±.21	.47±.28	.86±.09		
r_{pi}	.80	.80	.88		
r_{pf}	.74	.61	.92		
r_E	.81	.84	.89		
DM12				2.8	2.8/5.6 = 50%
r_A	.51±.20	.45±.21			
r_{pi}	.66	.81			
r_{pf}	.57	.58			
r_E	.69	.88			
HT12				3.6	3.6/4.7 = 75%
r_A	.73±.13				
r_{pi}	.75				
r_{pf}	.76				
r_E	.76				

All terms significant $P < .001$

$CR_{f/i}$ — correlated response on yield traits — VOLM, DM12 and HT12 for family selection on height at age 6 per selection intensity unit — FALCONER 1982.

R.E. — relative efficiency of indirect selection given by CR_f/G_f as a percentage — FALCONER, 1982.

tion intensity is equivalent to selecting the top 8 of the 22 seed tree clones.

Phenoypic and genetic correlations of growth and yield traits were strong, positive, and significant (*Table 6*). The early strong genetic correlation between height at 6 years and diameter ($r_A = 0.81$; YEH and HEAMAN, 1982) was much less evident between height and diameter at 12 years ($r_A = 0.45$; *Table 6*), although phenotypic correlation on an individual tree basis remained strong ($r_{pi} = 0.81$). The association between later height and diameter becomes increasingly a reflection of growth in a common environment rather than of a strict genetic association.

The genetic correlations between age 6 height and height, diameter and volume at age 12 were strong. Early selection of families for height at age six (mean height $\simeq$ 1 m) proved reasonably effective for a correlated response for height at age 12 (mean height $\simeq$ 6 m) or for volume, with efficiencies for indirect family selection in the order of 75% (*Table 6*). Correlated response to diameter was less efficiently selected through early height selection (approximately 50%, *Table 7*). For overall volume at age 12 the correlated response of selecting families when the average height was only 1 metre was quite effctive (70%, *Table 7*).

Comparison of Growth Traits for Indirect Selection for Volume and Yield

Growth traits were compared for their effectiveness for indirect selection of overall yield or stem volume. The age six height (HT06), the age twelve height and diameters (HT12, DM12), and an index (IVOL) using these three growth measures (HT06, HT12, DM12) were compared in their ability to predict the correct breeding values for stem volume. The index, IVOL, used the phenotypic variance-covariance matrix based on the heights and diameter (HT06, HT12, and DM12) and the additive genetic covariances of the heights and diameter traits to predict the breeding value of stem volume (VOLM). The index weightings for IVOL were:

HT06	HT12	DM12
0.78	0.03	3.90

The coefficient of HT12 ($\simeq 0$) shows that it has a negligible influence in predicting the breeding value of stem volume when used in conjunction with HT06 and DM12.

Families were ranked by their phenotypic values for volume (VOLM) and a selection differential (SD) was recorded for selecting the best 8:22 parents (equivalent to $i = 1$). Comparisons were made of the selection differentials obtained for direct volume selection compared to selections on rankings based on the aggregate breeding value of the index IVOL, and by the indirect selections of volume using the individual growth traits (*Table 7*). This selection

Table 7. — Volume means of selected progeny ($i = 1$), selection differential, selection differential as a percentage of direct volume selection and Spearman rank correlations of family rankings for volume for different selection traits.

	Selection Trait				
	VOLM	IVOL	HT06	HT12	DM12
$\bar{x}$	15.414	15.399	14.777	14.826	15.298
SD	1.181	1.166	0.544	0.593	1.065
SD as % Direct Selection	100	99	46	50	90
r_s	1.000	0.988	0.508	0.553	0.889

differential was also expressed as a percentage of the direct volume selection differential (*Table 7*). The Spearman rank correlation coefficients, r_s (Steel and Torrie, 1980), of the family rankings for volume for the different selection criteria was also calculated (*Table 7*).

Diameter was the most accurate single growth trait in predicting and ranking the breeding values of the parents for stem volume (90% of the SD of stem volume direct selection). If a single character such as diameter can accurately predict the breeding value for the desired character the inclusion of other growth traits in an index gives little extra benefit; in fact, errors of estimation will make it more unreliable (Sales and Hill, 1976; Falconer, 1982). The age 12 height was a poor predictor of breeding values for overall biomass (50 % of the SD of volume) and in fact the early height measure was almost as good for predicting volume selections.

Our study suggests that selections for overall yield and biomass production in Douglas-fir of 6 metres or more is best made using diameter although seedling height of as low as one metre is effective for preliminary selection. Height growth, however, can be sensitive to inadequacies in experimental design.

Conclusions

1. Additive genetic variance (σ^2_A) was significant for height, diameter, and volume, combined over sites. Dominance genetic variance was not significant ($P > .05$) for any of the growth traits. There were no significant genotype × environment interactions of site × female (σ^2_{sf}) for any growth trait. Recurrent selection for additive genetic variance would appear most effective for the improvement of growth and yield traits.
2. Individual sites were less accurate for demonstrating genetic differences. Site CLES was especially insensitive and family differences for later height and growth measures (excepting diameter) were non-significant ($P > .05$) at this site. This was in part due to too few replications and to excessive uncontrolled environmental variation within the 9 tree row plots. Smaller and non-contiguous plots will more efficiently detect differences in breeding values of parents.
3. Individual tree heritabilities for growth and yield traits were low to moderate (0.08 ± 0.05 — 0.19 ± 0.07) but family heritabilities were high (0.55 ± 0.29 — 0.77 ± 0.28) for these traits. Individual tree heritability estimates were similar to published estimates from full-sib trials but were lower than estimates from open-pollinated trials. Heritability estimates were higher for diameter than height growth. With large phenotypic standard deviations, expected response to selection for the better parents in a clonal seed orchard appeared good with up to 10% gain for individual tree stem volume (per unit of selection intensity).
4. Correlation of growth traits was good and correlated response for family selection for age 12 height (HT12 $\cong$ 6 m), diameter, or volume could well be made from an early height measurement (HT06 $\cong$ 1 m).
5. The most effective growth trait to use in making volume and yield selections in Douglas-fir of six metres or more would be breast-high stem diameter.

Acknowledgements

This paper represents a portion of a dissertation submitted by J. N. King to the University of Alberta in partial fulfilment of the requirements for the Doctor of Philosophy degree. The research was supported by grants from the Natural Sciences und Engineering Research Council of Canada, A2282 (F.C.Y.), and the Canadian Forestry Service. Drs C. J. A. Shelbourne and M. J. Carson provided helpful comment and criticism.

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