

pected alleles) detected in a sample must be considered a minimum estimate of contamination in a gametic pool; many contaminants may go undetected, especially if the alleles carried by the putative parents are fairly common in other potential sources of gametes. Indeed, the lack of *Glyd-3* in this sample suggests that contamination in the pollen pool of cross 65 × 66 was much greater than the three contaminants detected would indicate.

In cross 18 × 19, both gamete pools were *Questionable*, so the cross was classified as *Suspect*. If no error occurs in sampling for electrophoresis, *Suspect* crosses probably result from relatively minor pollen or seed contamination of otherwise valid crosses. If the initial sample is small, additional sampling may be warranted to rule out major contamination.

When none of the expected alleles at a locus is found in a gametic-pool sample, it can be concluded that the putative

parent was not involved in the cross. This was the case for several loci in the pollen pool of cross 26 × 27 (Table A1). Since the alleles at all loci in the pollen were consistent with expectations for a single parent, the pollen pool of this cross was classified *SWP* and the cross, *Invalid*.

The last two crosses in Table A1 illustrate crosses where no independent information on the genotype of one putative parent existed. For cross 19 × 18, there was no independently determined genotype for the seed parent, 19; but apparently only one parent contributed to the ovule pool, so it was classified *SP*. Since the pollen pool of this cross was *Acceptable*, the cross was declared *Credible*. No independent information was available on the genotype of the pollen parent (41) of the cross 40 × 41. In this case, the alleles in the pollen pool indicated multiple parentage, so this pool was classified *MP*, and the cross *Invalid*.

Selection of Wood Density and Diameter in Controlled Crosses of Coastal Douglas-fir

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Summary

Analyses of wood density and diameter in full-sib progeny of coastal Douglas-fir indicated additive genetic variance as the only important and significant genetic source of variation after 12 growing seasons. Individual tree heritability for wood density estimated by cores in a full-sib progeny trial of Douglas-fir was high (0.90). Pilodyn estimates were also high and correlated well with core estimates ($r_A = -0.95$). The efficiency of correlated response for half-sib family selection on the wood density core estimates by using the Pilodyn measure was 93%. Individual tree heritability for diameter was 0.23.

A strong negative correlation was shown to exist between wood density and diameter growth ($r_A = -0.53$). Index selection was used to highlight the options and trade-offs that can be made in the light of this adverse correlation.

Conservative options would restrict the loss in wood density or seek to improve both traits at the expense of maximising gain in any one trait. Less conservative options would allow that a loss in wood density was acceptable to gains in volume and overall dry weight.

Key words: Douglas-fir, wood density, diameter, Pilodyn, index selection

Zusammenfassung

Die Analysen der Holzdichte und des Durchmessers in Vollgeschwister-Nachkommenschaften der Küstendouglasie (*Pseudotsuga menziesii* (MIRB.) FRANCO) zeigten, daß die additive genetische Varianz die einzige wichtige und signifikante genetische Variationsursache nach 12 Vegetationsperioden war. Der individuelle Heritabilitätsschätzwert für die Holzdichte, ermittelt an Bohrspänen von Vollgeschwi-

ster-Nachkommenschaften der Douglasie, war hoch (0,90). Die Pilodyn-Schätzwerte waren ebenfalls hoch und eng mit den Bohrspän-Schätzwerten korreliert ($r_A = -0,95$). Die Effizienz für die Selektion von Halbgeschwister-Familien bei Verwendung der korrelierten Meßwerte von den Bohrspänen und dem Pilodyn-Verfahren war 93%. Die Einzelbaum-Heritabilität für den Durchmesser war 0,23.

Eine enge negative Korrelation wurde zwischen der Holzdichte und dem Durchmesserwachstum nachgewiesen ($r_A = -0,53$). Die Index-Selektion wurde benutzt, um die Selektionsoptionen und die Handelsgebräuche, die im Hinblick auf diese negative Korrelation getroffen werden können, herauszustellen. Konservative Optionen würden den Verlust bei der Holzdichte oder die Versuche, beide Merkmale zu verbessern, auf Kosten des maximierten Gewinnes bei jedem Einzelmerkmal beschränken. Weniger konservative Optionen würden ermöglichen, daß ein Verlust in der Holzdichte hinsichtlich der Gewinne bei Volumen und mittlerem Trockengewicht akzeptabel wäre.

Introduction

The timber of Douglas-fir is highly prized for structural uses, pulp and veneer. It is straight-grained, moderately light to moderately heavy (wood density of 430 to 450 kg/m³) and of intermediate durability (COWN, 1976). Wood density is an important trait because of its close relationship to the strength, quality, and yield characteristics of pulp products (BAREFOOT *et al.*, 1970), and the strength and structural properties of clear-wood products (BARRETT and KELLOGG, 1984). With the emphasis on growth and yield traits in genetic improvement programmes and the increasing proportion of juvenile wood from fast-grown plantations the importance of wood density and its bearing on quality has often been emphasized (ZOBEL and KELLISON, 1978).

Wood density is not a single property, but is a complex of characteristics such as percentage of summerwood, cell-

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wall thickness, cell diameter, lignin content etc. (KOCH, 1972); however, it is convenient to treat it as a single trait. Single-tree estimates of wood density are complicated by substantial vertical within-tree variation, but much of this variation is predictable (COWN, 1976), and wood density estimates from breast-high increment cores can give a good indication of weighted tree mean density ($r = 0.91$; COWN, 1976).

Another consideration is the use of young trees to evaluate mature tree performance. Do early progeny evaluations of wood density offer reasonable guidelines for later, mature-tree wood density? Wood density increases with age and there are indications that this increase is linear and can be quite predictable. NORTHCOTT *et al.* (1964) in a study of variation patterns in a limited number (six) of Douglas-fir trees demonstrated this trend after an initial period of instability prior to the 10th year growth ring. KELLOGG (pers. comm.) in a recent study of Douglas-fir demonstrated a similar trend, with under 6-years being highly unpredictable, 8- to 12-year growth rings stabilising, and after 12 years demonstrating an increasing linear trend. KELLER and THOBY (1977) showed significant phenotypic correlations between mean density of the first ten rings to mean density of the outer ten rings in two stands of 30- and 60-year-old Douglas-fir, but non-significant correlations for another smaller population of 60-year-old Douglas-fir. Although McKIMMY (1966), working on the Douglas-fir Heredity Study (MUNGER and MORRIS, 1936), recommended that predictions of stem densities not be made before 25 years, McKIMMY and CAMPBELL (1982) suggested that tests on 10- to 15-year-old material could provide information applicable to older material. These and other studies (including RECK and SZIKLAI (1973) and COWN (1976)), have demonstrated that early wood density can be used to predict mature stem-wood density in Douglas-fir. Wood deposited after 15 years can be acceptable for whole-tree wood-density comparisons, but wood in the 8 to 12 year range may offer, with some caution, the earliest possible evaluation of whole-tree wood density.

Wood density has been consistently shown to be under strong genetic control and to have a high heritability. Heritability estimates appropriate for mass selection — were high (h^2 ; most provenances > 0.8) for wood mean density from 14-year-old provenance-progeny trials in France (BASTIEN *et al.*, 1985); genetic variability was much higher at the family level than the provenance level, confirming a similar observation made by McKIMMY and CAMPBELL (1982). In spite of high heritabilities BASTIEN *et al.* (1985) reported that potential gain for wood density would not be great because of the low phenotypic standard deviation; they also reported unfavourable correlations between mean wood density and growth traits and mean wood density and wood heterogeneity — wood heterogeneity referring to radial uniformity of wood density. Unfavourable genetic correlations between growth and wood density have also been reported in other conifers such as radiata pine (*Pinus radiata* D. DON) (DEAN *et al.*, 1983).

The objectives of this study were to estimate genetic parameters for wood density using both cores and Pilodyn estimates from full-sib progeny of Douglas-fir and to model selection strategies where negative and unfavourable correlations may exist between wood density and yield. Diameter has previously been shown in the same genetic test to be the best indicator for yield and biomass (KING, 1986).

Materials and Methods

Diameter and wood density measurements were made at the Cowichan Lake Research Station, British Columbia (Latitude 48.50°N, Longitude 124.10°S, elevation 165 m) on 12 year old coastal Douglas-firs averaging 6.5 m in height. The trees were full-sib progenies from the crossing of 22 seed parents (females) with 4 pollen parents (males) (North Carolina Design II; COMSTOCK and ROBINSON, 1952) randomly sampled from the breeding population. More details of the materials and planting are presented in YEH and HEAMAN (1982).

Diameter (DM) was measured as a mid-diameter of the stem segment associated with the seventh growing season (measured as the fifth whorl from current leader: equivalent to breast height). Pilodyn estimation for wood density (PIN) was taken from two through-the-bark readings with a non-repeating Pilodyn of pin diameter 2.5 mm and spring strength of 6 joules. Increment core estimation of wood density (WD) was made by the maximum moisture content method (SMITH, 1954) on the last four growth rings of each core (years 8—12) from two diametrically opposed 5 mm cores. Samples with severe compression wood were excluded.

Analysis of variance and covariance for a random model were performed for DM, PIN, and WD to test hypotheses about the significance of family related effects and also for the purpose of estimating variance and covariance components for these effects. The structure of the analysis on individual trees is detailed in Table 1. Where direct F-tests could not be made for all sources of the variation, SATTERTHWAIT'S (1946) approximate test procedure was used to synthesise means squares and mean cross-products that had the same expected values except for the effect being tested. Standard errors of the variance and covariance components were calculated as per BECKER (1975).

Assuming no linkage, epistasis, and inbreeding, the components of variance among seed trees (σ_s^2) and pollen trees (σ_m^2) estimate one-quarter of the additive genetic variance. The component of variance among full-sibs (σ_{fm}^2) estimates one-quarter of the dominance genetic variance.

The number of seed parents (22) is much greater than the pollen parents (4) in this study. The selection unit and the source of information for additive genetic variance is, therefore, more appropriately the female seed tree. Where individual trees are the selection unit, the heritability (h^2) is:

$$4 \sigma_f^2 / (\sigma_m^2 + \sigma_f^2 + \sigma_{mf}^2 + \sigma_{fm}^2 + \sigma_p^2 + \sigma_w^2) \quad (1)$$

with the notations defined in Table 1. The expected response to mass selection per selection intensity unit "i" ($\% \Delta G_p/i$) is $h^2_i \times CV_{pi}$, where CV_{pi} is the coefficient of variation among individuals. The heritability appropriate for family selection (h^2_f) is:

$$\sigma_f^2 / (\sigma_f^2 + \frac{k_{11}}{k_{12}} \sigma_{rf}^2 + \frac{k_{10}}{k_{12}} \sigma_{mf}^2 + \frac{k_9}{k_{12}} \sigma_p^2 + \frac{1}{k_{12}} \sigma_w^2) \quad (2)$$

with the notations defined in Table 1. The expected response to progeny test selection per selection intensity unit "i" for a clonal seed orchard ($\% \Delta G_p/i$) is $2(h^2_f \times CV_{pf})$, where CV_{pf} is the coefficient of variation among female half-sib families. Genetic, phenotypic, and environmental correlations, and their standard errors were calculated following FALCONER (1982).

In constructing the index (I) for i traits ($i = 1$ and 2 , — representing wood density and diameter, respectively), a

Table 1. — Structure of the analysis of variance or covariance: σ_w^2 , within plot variance; σ_p^2 , plot variance; σ_{mf}^2 , variance due to male by female interaction; σ_{rf}^2 , variance due to replication by female interaction; σ_{rm}^2 , variance due to replication by male interaction; σ_f^2 , female variance; σ_m^2 , male variance; and σ_r^2 , replication variance.

Source of Variation	d.f.	Expected mean squares or mean cross-products
Replications (R)	2	$\sigma_w^2 + k_1^2 \sigma_p^2 + k_2^2 \sigma_{rf}^2 + k_3^2 \sigma_{rm}^2 + k_4^2 \sigma_r^2$
Males (M)	3	$\sigma_w^2 + k_5^2 \sigma_p^2 + k_6^2 \sigma_{mf}^2 + k_7^2 \sigma_{rm}^2 + k_8^2 \sigma_m^2$
Females (F)	21	$\sigma_w^2 + k_9^2 \sigma_p^2 + k_{10}^2 \sigma_{mf}^2 + k_{11}^2 \sigma_{rf}^2 + k_{12}^2 \sigma_f^2$
RxM	6	$\sigma_w^2 + k_{13}^2 \sigma_p^2 + k_{14}^2 \sigma_{rm}^2$
RxF	42	$\sigma_w^2 + k_{15}^2 \sigma_p^2 + k_{16}^2 \sigma_{rf}^2$
MxF	63	$\sigma_w^2 + k_{17}^2 \sigma_p^2 + k_{18}^2 \sigma_{mf}^2$
Plot	126	$\sigma_w^2 + k_{19}^2 \sigma_p^2$
Within plot	1909	σ_w^2
Total	2172	

linear function of an individual's phenotypic value (X_i) is weighted by coefficients (b_i) designed to maximise the correlation between the function and the individual's genetic worth (H). H is an aggregate consisting of a linear function of the breeding values (g_i) weighted by the economic weights (a_i). The least-squares partial regression coefficient of H on X_i provides the weighted coefficient for the index and is of the form $I = \sum b_i X_i$.

The least-squares solution for the vector of regression coefficients b is $P^{-1}Ga$, where P is the matrix of variances and covariances among the X_i , G is the matrix of genetic covariances between X_i and g_i , and a is the vector of economic weights. The variance of the index (σ_I^2) is $b'Pb$ and the variance of H (σ_H^2) is $a'Ga$.

Genetic gain of each trait in the aggregate genotype as a result of selection on the index is $i(b'G_i/\sigma_I)$, where i is the selection intensity and G_i is the i th column in the G matrix or the vector of genetic covariances between the i th trait and each component trait in the index (LIN, 1978). One ap-

proach of the selection strategy when the economic weights are not known with certainty is to examine the sensitivity of the response of a trait to changes in a_i (BARADAT, 1982).

Results and Discussion

Wood density measures averaged 363.01 kg/m³ (CV = 7.16%), and family means ranged from 339.5 to 382.8 kg/m³ (Table 2). The female source of variation used in estimating additive genetic variance was significant ($P < .001$) and accounted for over 20% of the total variation (Table 2). Sources of variation for dominance genetic variance (σ_{mf}^2) and environmental block by additive genetic variance (σ_{rf}^2) were non-significant for the core estimates of wood density (WD), and although the dominance genetic effect of the parent trees was significant for the Pilodyn estimates (PIN) it only accounted for 19% of the additive genetic variance (Table 2).

Mean diameter for the plantation was 86.3 mm (CV = 14.58) and families ranged from 80.6 to 94.6 mm. Additive genetic variance was also the only significant source of genetic variance expressed for this trait. The predominance of additive genetic variance in this test corroborates other findings in both wood traits (BASTIEN *et al.*, 1985; MCKINNY and CAMPBELL, 1982) and juvenile growth (CAMPBELL, 1972; YEH and HEAMAN, 1982) and suggests that recurrent selection schemes for additive genetic variance will be important for both growth and wood quality in Douglas-fir.

The individual tree heritability for wood density (WD) was high ($h^2_i = 0.90$), and a low comparative error of within-family variation ($\sigma_w^2 = 60\%$) suggests that this trait should respond well to phenotypic selection (Table 3). The expected response to individual (mass) selection for wood density (6.2%) is very nearly equivalent to the expected response to progeny test (family) selection (6.4%) (Table 3). The high individual tree heritability of wood density agrees with other published reports (BASTIEN *et al.*, 1985).

Heritability estimates for diameter from this trial were 0.23 and 0.66 on the basis of individual tree and female half-

Table 2. — Variance components (v.c.) and standard errors (s.e.), plantation mean, and range of parents for diameter (DM) and wood density^a in coastal Douglas-fir after 12 growing seasons.

	DM			WD			PIN		
	v.c.	s.e.	%v.c.	v.c.	s.e.	%v.c.	v.c.	s.e.	%v.c.
Replications (R)	6.8**	5.6	-	75.5**	55.2	-	48.9**	35.6	-
Males (M)	0.0ns	0.9	0.0	31.1**	21.9	4.8	20.4**	14.8	5.0
Females (F)	7.9**	3.3	5.9	143.1**	45.3	22.4	81.6**	26.6	20.1
RxM	3.0ns	2.6	2.2	4.6ns	5.2	0.7	3.4ns	3.3	0.8
RxF	0.0ns	2.3	0.0	0.0ns	7.5	0.0	0.0ns	3.6	0.0
MxF	0.2ns	3.5	0.2	0.0ns	8.8	0.0	15.3**	7.4	3.8
Plots	37.8**	6.0	28.2	75.3**	15.4	11.8	40.5**	8.9	10.0
Within plots	85.2	2.8	63.5	385.5	12.5	60.3	244.3	7.9	60.3
Total ^b	134.1		100.0	639.6		100.0	405.5		100.0
Plantation mean		86.3 mm			363.0 kg/m ³			16.7 mm	
Range of parents		80.6-94.6 mm			339.5-382.8 kg/m ³			14.9-18.5 mm	

* $p < 0.05$; ** $p < .01$; ns not significant

^a) Wood density measures based on increment cores (WD) and Pilodyn pin penetration (PIN).

^b) Excluding variance component for replication.

Table 3. — Genetic (σ_a^2 , σ_f^2) and phenotypic (σ_{pi}^2 , σ_{pf}^2) variances, heritabilities (h_i^2 , h_f^2), coefficients of variation (CV_{pi} , CV_{pf}), and expected response to mass (% ΔG_i) and family selection (% ΔG_f) per selection intensity unit "i" for diameter (DM) and wood density traits.

Parameter	Traits		
	DM	WD	PIN
Individual selection			
σ_A^2	31.41 ± 13.24	572.32 ± 181.20	326.55 ± 106.27
σ_{pi}^2	134.08	639.65	405.47
h_i^2	0.23 ± 0.10	0.90 ± 0.28	0.80 ± 0.26
CV_{pi}	13.33	6.97	12.06
% $\Delta G_{i/1}$	3.12	6.23	9.71
Family selection			
σ_F^2	7.85 ± 3.31	143.08 ± 45.30	81.64 ± 26.57
σ_{pf}^2	11.89	153.20	91.26
h_f^2	0.66 ± 0.28	0.93 ± 0.30	0.90 ± 0.29
CV_{pf}	3.97	3.41	5.72
% $\Delta G_{f/1}$	5.24	6.37	10.23

sib family means, respectively (Table 3). For diameter individual tree selection was much less efficient than family selection ($\Delta G_i = 3.12$ compared to 5.24; Table 3). In multiple stage selection schemes, high heritability traits such as wood density should be stressed at the phenotypic and individual tree selection stage, and low heritability growth traits should use the added efficiencies of genetic selection. The potential gains for wood density from both individual or family selection would appear to be at least as good as diameter selections. Our results suggest that there is enough variability to make effective progress for the selection of wood density.

Heritability estimates for the Pilodyn values were also very high $h_i^2 = 0.80$, $h_f^2 = 0.90$; Table 3). The value of PIN for predicting genetic differences as demonstrated by the high heritability estimates is in contrast to the results of BASTIEN *et al.* 1985, whose heritability estimates for the Pilodyn were low.

The genetic correlation between the Pilodyn measure (PIN) and wood density (WD) was high ($r_A = -0.95$; Table 4). Because of the high genetic correlation and high heritability, the efficiency of correlated response of wood density (WD) to family selection was 93% ($(5.93/6.73) \times 100$; Tables 3 and 4), and it would appear from this study that the Pilodyn is a valuable instrument for family selection of wood density in 12 year old Douglas-fir. It would also appear from our results that the Pilodyn is a useful instrument for individual tree selection in young Douglas-fir plantations. This is in contrast to the results of BASTIEN *et al.* (1985) and caution may be needed in using this instrument. SPRAGUE *et al.* (1983) found that certain types of Pilodyn configurations (e.g., different pin sizes) (and/or spring strength) are more effective than others. It may therefore be wise to test the efficiency of Pilodyn selection with some sampling by cores.

Unfortunately strong negative genetic correlations exist between wood density and diameter (Table 4; $r_A = -0.53$). A strong negative relationship between growth and mean

wood density was also reported in the French Douglas-fir provenance-progeny tests (BASTIEN *et al.*, 1985). They also found a negative genetic correlation of mean wood density vs wood heterogeneity, but no unfavourable correlations of wood heterogeneity and growth. Such results are discouraging for the simultaneous improvement of growth traits, wood quality, and wood density in Douglas-fir.

Index selection

Table 5 shows index weightings (b's), and expected gain (ΔG) expressed in number of standard deviation units which the selected population has been shifted and as a percentage of the mean at different economic value weightings of wood density (a_{WD}) to diameter (a_{DM}).

The gain values, as elsewhere, are expressed per unit of selection intensity "i". For the seed parents in this population $i = 1.00$ at a selection intensity of 8:22 or 36.4%. ΔG as a % of means is plotted against changes in the economic weighting of wood density relative to diameter (Figure 1). This plot provides a basis for applying selection strategy and highlights four different selection options that might be made on his population in the face of the adverse correlation between wood density and diameter. These different selection options (shown on Figure 1) are:

1. Option I: When a unit of wood density is of equal value to a unit of diameter, the overall aggregate value would favour wood density response to diameter response because of its higher heritability. However, the assumption of equal values, or any other known value relationship, even if it were known to be true in present market conditions could not be predicted for the future.
2. Option II: The optimum strategy when economic values are highly uncertain is one of maximizing the minimum response to selection for both traits (NAMKOONG, 1979). The optimum point in this selection strategy is at the curve intersection point. Neither trait is maximized at this point; indeed because of the strong negative genetic relationships between these two traits this point achieves less than 50% of the maximum response to both of these traits. However, this point is the maximum/minimum (maximin) response point for both traits — at any other point one of the traits would have a lower response — and is the most appropriate if we believe both traits are economically valuable, but there is high uncertainty as to their specific value functions. By selecting for positive response in both traits at this point the selection process can begin to break the negative genetic correlation caused by the pleiotropic action of genes between these traits.

Table 4. — Genetic correlation (r_A) with standard errors, phenotypic correlation among individuals (r) and families (r_{pf}), and correlated response to family selection per selection intensity unit "i" (% C. R.) on wood density (WD) using diameter (DM) and Pilodyn assessments (PIN).

WD Parameter	Correlation Traits	
	DM	PIN
r	-0.46 ***	-0.70 ***
r_A	-0.53 ± 0.19	-0.95 ± 0.02
r_{pf}	-0.49	-0.94
% C.R./1 for WD	-2.85	-5.93

*** = significant at 0.001 levels of probability.

Table 5. — Response to index selection expressed in both standard deviation units and percentages of means per selection intensity unit, "I", for changing economic weights of wood density (WD) to diameter (DM). The selection options of Figure 1 are noted.

Option	Economic Weight		Index Weight		ΔG (S.D. units)		ΔG (% mean)	
	a_{WD}	a_{DM}	b_{WD}	b_{DM}	WD	DM	WD	DM
I	2.00	: 1	3.77	1.96	1.86	-0.69	6.35	-2.72
	1.00	: 1	1.85	1.58	1.84	-0.58	6.27	-2.28
	0.75	: 1	1.37	1.48	1.81	-0.49	6.18	-1.94
	0.50	: 1	0.89	1.39	1.72	-0.30	5.87	-1.19
	0.30	: 1	0.51	1.31	1.40	0.13	4.78	0.52
II	0.19	: 1	0.30	1.27	0.77	0.67	2.63	2.63
III	0.117	: 1	0.16	1.24	0.00	1.09	0.00	4.30
IV	0.00	: 1	-0.07	1.20	-1.10	1.34	-3.73	5.30
	-0.50	: 1	-1.03	1.01	-1.81	1.03	-6.17	4.09
	-1.00	: 1	-1.99	0.82	-1.85	0.93	-6.31	3.69

- Option III: This option maximizes response in diameter at the same time restricting any loss in wood density. This restriction is imposed by applying an economic value that will not let the response in wood density (ΔG) go below zero and is equivalent to the restricted index of KEMPTHORNE and NORDSKOG (1959). This option can be chosen where there is more certainty as to the value of diameter in relation to wood density. Diameter is seen as the trait of value and it is maximized to the point where a loss in overall wood density occurs. This was determined at an economic weighting of 0.117 for wood density over a weighting of 1.0 for diameter.
- Option IV: This strategy assumes that a decline in wood density in the population by selecting for maximum diameter is economically acceptable. For growers that are interested primarily in biomass production — pulp and fibre — this may be a quite acceptable option. BRIDG-

WATER *et al.* (1983) found that wood density had little impact on dry weight production compared to volume. Investigation of dry weight in our data showed the same result.

Options II and III are the more conservative of the selection strategies. Option II is the most conservative and most appropriate for use when there is a high level of uncertainty as to the relative value of wood density to diameter. Option III is more attractive when here is less uncertainty and we wish to maximise diameter but only wish to hold wood density. Option IV is a high risk option, or is appropriate when there is a good deal of certainty as to an economic decision that has wood density valued negligibly in regards to diameter. Most current decisions regarding wood density vs diameter will lie between Options II and IV. An extreme positive (Option I) or negative emphasis on wood density is not at all likely.

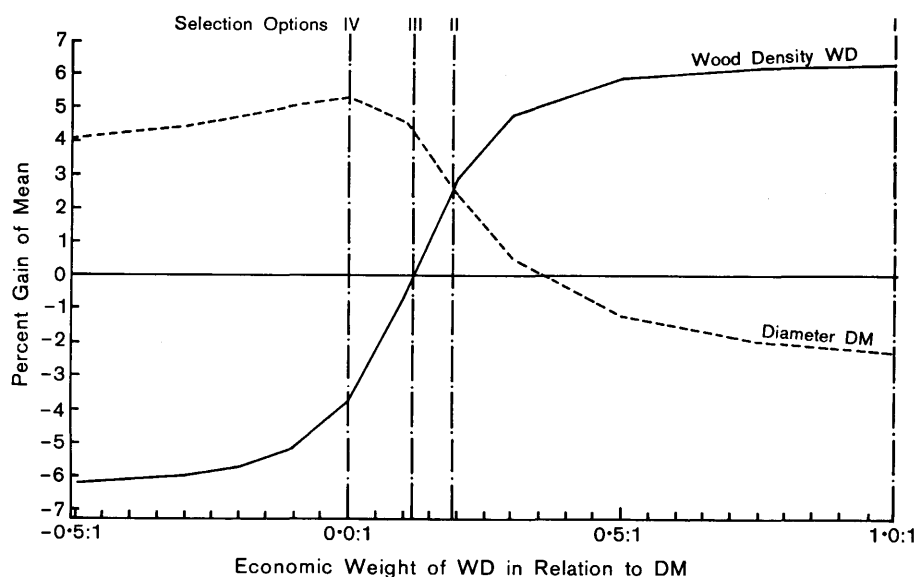


Figure 1. — Plot of expected percentage gains for wood density and diameter to changing emphasis on the economic weighting of wood density, highlighting the selection options of Table 5.

The process here highlights the selection strategies that can be employed to counteract the adverse negative genetic correlation that exists between wood density and diameter. Each of the options, however, requires some trade offs, and final decisions regarding how wood density is incorporated as a selection trait will require more information in regards to its contribution to the value of the wood resource of coastal Douglas-fir. One thing the breeder can do is to offer wood density in a multiple population context (BURDON and NAMKOONG, 1983) and allow the forest managers to weight the trade-offs and make the economic decisions.

Conclusions

1. Heritabilities for wood density were high ($h^2_i = 0.90 \pm 0.28$) — wood density is a trait that can be effectively improved through mass selection as well as family selection.
2. The Pilodyn proved very effective for selecting for wood density. With a genetic correlation of -0.95 the efficiency of using the correlated response for family selection was 93%.
3. Wood density correlation with diameter was strongly negative ($r_A = -.53 \pm .19$).
4. An antagonistic relationship between wood density and heterogeneity of wood density (BASTIEN *et al.*, 1985) is also of concern considering the importance of producing a uniform product (ZOBEL *et al.*, 1982).
5. Index selection is highly effective for selection involving negative correlations and can be used to minimize the impact of the negative relationship between wood density and growth. Several selection strategies were examined. Options that maximize the minimum expected response to both traits or restrict the loss in wood density are the most appropriate if wood density has some significant non-zero value. Options that maximize diameter and allow a loss in wood density are also considered.

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