Analysis of Disconnected Diallel Mating Designs

II – Results from a Third Generation Progeny Test of the New Zealand Radiata Pine Improvement Programme

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Summary

Genetic parameters from a second generation (F_2) disconnected diallel progeny test of the New Zealand radiata pine improvement progamme are presented. Heritability estimates of growth and yield traits of 0.2 are similar to progeny test results of the previous generation (F_1). Coefficients of variation for additive genetic and phenotypic variances are also similar between generations. Quality traits are presented and parameters are also comparable to the F_1 generation tests. A trend of declining dominance genetic variance and increasing additive genetic variance with test age was noted. This trend probably represents artifacts affecting early growth of the full-sib cross – such as seed size effects or other environmental biases rather than changing gene action.

Key words: diallel analysis, radiata pine, heritability, GCA, SCA.

FDC: 165.3; 165.41; 181.6; 232.13; 812.31; 174.7 *Pinus radiata;* (931).

Introduction

There has been nearly 50 years of research into the genetic improvement of *Pinus radiata* in New Zealand (SHELBOURNE et al., 1986). The strategy for this improvement has been one of using large populations (hundreds) with recurrent selection (RS) for general combining ability (GCA) (BURDON and SHELBOURNE, 1971). Several generations of selection have now been performed using this strategy and although plans have been refined over the years (e.g. SHELBOURNE et al., 1991), RS-GCA is still the overlying improvement strategy. Earlier interest in using specific combining ability (SCA: that genetic variance attributable to dominance) (WILCOX et al., 1975) has declined with the realization that GCA is predominant in *Pinus radiata* (CARSON, 1986, 1991; COTTERILL et al., 1987) and GCA is more effectively realized as gain even in the production population (CARSON, 1986).

The "875"'s are one of the oldest advanced-generation series in New Zealand (SHELBOURNE et al., 1986) and were crossed in a diallel mating design. This series offers an ideal opportunity to review the RS-GCA strategy and monitor its effectiveness over generations.

Background to the "875" parental series

One of the largest of the older major series of progeny tests was represented by 588 open-pollinated (OP) families of the "268" parental series, which were selected in 1968 for tests established in 1969. The plus-tree selection for the "268" series emphasized fast diameter growth, freedom from malformation, straightness of stems and an even, multinodal branching habit (SHELBOURNE et al., 1986).

The "875" parental series were selected individuals from the OP progeny of the "268"'s. Two hundred "875"'s (100 from each of two sites) were identified using a multiple-trait among and within family selection index on data from an age-5 assessment of the "268"'s at Kaingaroa and Waimihia Forests of the Central North Island pumice plateau. Selection of the "875"'s emphasized tree volume, stem straightness, branch quality (combining freedom from malformation and branching habit) and wood density (WILCOX, FIRTH, LOW and MCCONCHIE, 1975, unpublished Genetics and Tree Improvement report No. 78). Economic weights for these traits were calculated by standardizing the variation of family means for each trait, rather than by applying economic principles. The 200 trees selected by the index were reduced to 95 based on additional culling for malformation, vigour, branching habit, needlecast and absence of pollen or female cones. The "875"'s were mated in a modified disconnected half-diallel design, which was planted out at two central North Island sites in 1980.

This paper reports results of assessments at 2, 4, and 7 years from the "875" series. CARSON (1986) reported age 4 estimates of heritabilities, GCA and SCA, and SCA/GCA ratios. The results of the later measurement (7 years) have been used for roguing purposes for seed orchard parents of the "875" series (JOHNSON and KING, 1988; unpublished co-op report) and for the selection of a third generation of parents. These third generation parents have been mated and established in progeny tests to provide for a fourth generation of selection for the improvement of radiata pine in New Zealand. This paper emphasizes the parameter estimates of GCA and SCA from this advanced generation material, and changes in these estimates over time. It also compares heritabilities and genetic correlations of the traits of improvement in the major breed of radiata pine developed in New Zealand over two generations of filial selection.

Materials and Methods

Diallel mating of the selected "875" parents

The final selected group of 95 "875"'s was mated in a modified, disconnected, 5-parent, partial half-diallel design totalling 18 diallels and 154 full-sib families. With the exception of diallel 1, the allocation of "875" parents to diallel crosses was at random and the parents were unrelated (for diallel 1, some first-cousin matings were included, to estimate inbreeding effects). Male parentage of the "875"'s was assumed to be unrelated.

Field testing design

After sowing in replicated nursery blocks in 1979, the 154 "875" families (plus control seedlots) were planted in 1980 in tests at Onepu and Cpt. 327, Kaingaroa Forest. Onepu near Kawerau in the Bay of Plenty is on a rich and loamy ex pasture

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site. Cpt. 327 is in the South-Central part of the North Island central pumice plateau. The progeny test was planted in a "sets-in-replications" design with four sets each containing approximately 48 full-sib families plus controls. Trees were allocated as single-tree plots, with 46 and 50 replications at Onepu and Kaingaroa Forest respectively. Families from different diallels were mixed together in field sets to assist in the estimation of the breeding values of the "875" parents (since all progenies were randomized across environments). This also allowed the potential use of the trial as a *"seedling seed orchard"* by dispersing related progeny throughout the trial area. Survival at both sites was above 95% at the age-4 assessment and over 85% at the age-7 assessment.

Measurement of the „875" diallels

The traits that were analysed, together with plantation means are shown in *table 1* and are described as follows:

1. Age 2 assessment; the Onepu site showed exceptional fast early growth and was assessed for a 2 year height (HT02) (measured in 1982 was $2^1/_2$ years from seed).

2. Age 4 assessment; height and breast-height (1.4 m) diameter (HT04, DM04) were assessed at both Onepu and Kaingaroa.

3. Age 7 assessment; Assessment for height (HT07) and diameter (DM07) was made at Onepu; VOLM07 was calculated using a standard NZFRI volume equation with the Onepu height and diameters; at Kaingaroa only diameter (DM07) was recorded; qualitative scores for straightness, malformation and branching habit were made at both sites; a qualitative *Cyclaneusma* needle cast score was made at Kaingaroa and was based on number of branch whorls that retain needles; a pilodyn measure for wood density was made at Onepu and a wood density estimate using a regression equation of, WDPIN = 456.9 – PILO*6.52, where PILO is the pilodyn measure and WDPIN is the wood density estimate (kg/m^3). This wood density estimator was derived from pilodyn assessment and wood density core samples of 106 trees.

Reported results from the "268" parents and "880" cohorts

Results are reported from comparable measurements of the original "268" parental series and the "880"s which are cohorts of the "875"s. The original assessment of the "268"s at age-5 on the Kaingaroa and Waimihia sites was reported by WILCOX and FIRTH (unpublished Genetics and Tree Improvement report No. 71, 1974). At this time all 588 families were assessed for diameter, straightness and branch quality. The best 120 families were further assessed for height, volume and wood density (WILCOX, FIRTH, LOW and MCCONCHIE, unpublished Genetics and Tree Improvement report No. 78). From this assessment the "875"s were selected. In 1979 at age-10 years another assessment was made for diameter, straightness, branch quality and malformation; and needle cast and pilodyn at the Kaingaroa site only (SHELBOURNE, FIRTH and LOW, unpublished Genetics and Tree Improvement report No. 195, 1981). From this assessment the "880"s were selected. The "880" series are cohorts of the "875"s, selected from the same "268" progeny 5

Table 1. – Traits analysed and mean values at test sites.

Trait	Designation	Unit	Test site	
			Onepu	Kaingaroa
Height at 2 years	HT02	m	2.25	
Height at 4 years	HT04	m	7.51	5.49
Height at 7 years	HT07	m	13.9	
Diameter at 4 years	DM04	cm	13.7	9.57
Diameter at 7 years	DM07	cm	23.4	18.17
Volume at 7 years	VOLM07	cu dm	223	
Straightness score[1]	STR07	1-9	5.99	6.89
Malformation score[2]	MALF07	1-9	6.91	7.55
Branch habit score[3]	BRAN07	1-9	5.74	5.75
Wood density	WDPIN	kg/m^3	352.4	
Cyclaneusma score[4]	CYCLA	10-60		21

[1]) Straightness score 1-crooked to 9-straight
[2]) Malformation score 1-multiple forks and malformation to 9-none
[3]) Branch habit score 1-uninodal to 9-highly multinodal
[4]) Cyclaneusma score 10 to 60

Table 2. – Expected mean squares and genetic interpretations for yield measurements at Onepu.

Source	df	Expected Mean Squares
Diallel	14	$\sigma^2_e + 30.98\sigma^2_{sca} + 210.69\sigma^2_{gca} + 254.7\sigma^2_{gca}$
GCA/Diall	60	$\sigma^2_e + 30.69\sigma^2_{sca} + 74.86\sigma^2_{gca}$
SCA/Diall	50	$\sigma^2_e + 30.45\sigma^2_{sca}$
Error	3674	σ^2_e

narrow sense heritability

$$h^2_t = \frac{4\,\sigma^2_{gca}}{\sigma^2_{dial} + 2\,\sigma^2_{gca} + \sigma^2_{sca} + \sigma^2_{error}}$$

genetic correlation

r_A = additive genetic correlation of traits X and Y

$$= \frac{COV_{gca}\,X,Y}{\sqrt{(\sigma^2_{gca}\,X * \sigma^2_{gca}\,Y)}}$$

years later (emphasizing the same traits for the growth and form breed; SHELBOURNE et al., 1986). The open-pollinated progeny of the "880"s were reported for an age-4 assessment for volume, straightness, malformation and branch habit (JOHNSON and BURDON, 1990). A final assessment of the "268"s was made for diameter at age-17 (KING and BURDON, 1991).

Statistical analysis

Individual tree measurements were analysed on each site using the following model:

$$Y_{ijkl} = \mu + R_i + D_j + G_{k(j)} + G_{l(j)} + S_{kl(j)} + E_{ijkl} \quad ...[1]$$

where Y_{ijkl} is the individual tree observation, μ is the overall mean and; R_i = effect of the *i*th replication; D_j effect of the *j*th diallel; $G_{k(j)}$ and $G_{l(j)}$ are the general combining ability (GCA) effects of the *k*th and *l*th parents within the *j*th diallel; $S_{kl(j)}$ is the specific combining ability (SCA) effect of the *k*th and *l*th parents within the *j*th diallel; and E_{ijkl} is the error associated with the *ijkl*th tree. All effects were considered random (Model II, GRIFFING, 1956). An additional model using location and GCA by location effects was also analysed for the diameters and qualitative scores of straightness, branching and malformation. Field sets were excluded from the model after set differences were found to be non-significant in an ANOVA. The analysis was done using PROC GLM and PROC VARCOMP (SAS Institute, 1989).

Genetic analysis

Estimation of components of variation and their genetic interpretation followed this random model. Expected mean squares and genetic interpretations of this model are shown in JOHNSON and KING (1998). Because of the imbalance in the data (differential survival of individuals in families and incomplete crosses) expectations based on means or harmonic means for coefficients of variance components will be incorrect (SCHAFFER and USANIS, 1969; JOHNSON and KING, 1998). A common method of overcoming this problem is to use the DIAL program of SCHAFFER and USANIS (1969) (e.g. YANCHUK, 1995) which will provide the correct solution. Our analysis was conducted using a modification of the procedure outlined by SANDERS (1987) that produces an equivalent least-squares solution to the DIAL program but allows the flexible model construction found in common SAS procedures such as PROC GLM or PROC VARCOMP (SAS Institute, 1989). Details of this procedure for calculating Sums of Squares, estimating variance components and the genetic interpretation of variance components are found in JOHNSON and KING (1998). The following genetic parameters were estimated (details of their calculation along with an example of Expected Mean Squares are shown in *Table 2*).

Heritability, in the narrow sense (h^2_t), was estimated as four times the GCA component, divided by the phenotypic variance of the individual values adjusted to the replicate mean;

included in this estimate are variance components for diallels (because families in replicates can be from several diallels), two times GCA within diallels (because the two parents of a given individual are assumed to have the same GCA variance), SCA within diallels, and the within replicate error (*Table 2*). σ^2_{sca} was also reported as a percentage of σ^2_{gca} (*Table 2*).

Genetic correlations were formulated as in FALCONER (1989: pg. 317; *Table 2*). Estimates of variances and covariances were made from the expected mean squares and cross products (MANOVA).

Standard errors are not reported in this paper. Precision in estimating variance components and derived genetic parameters is reliant on high numbers for both degrees of freedom and for individuals to make the sample mean (BECKER, 1975). Both these conditions are well met in the New Zealand trials (*Table 2*) and standard errors around heritability estimates are therefore low (e.g. VOLM07 at Onepu: $h^2_i = 0.292 \pm 0.07$ (*Table 3*); "268" DM05 $h^2_i = 0.34 \pm 0.04$: KING and BURDON, 1991). Sampling errors around parameter estimates are thus less of a concern than sources of potential bias which are discussed in more detail later.

Results and Discussion

Parameter estimates and trends for growth and yield traits

From *table 1* it can be seen that growth has been especially vigorous in the Onepu trial with a mean height at 7 years of nearly 14 metres, diameter of 23.4 cm and a mean volume per tree of 223 dm^3. Volume per hectare was 185 cubic metres. The Kaingaroa Forest site, on the cooler less fertile plateau was also growing vigorously with a mean dbh of 18.2 cm which is slightly more than 75% of that at the Onepu site.

The parameters estimated for growth and yield traits are shown in *table 3*. The estimates for height in the "875"s indicate that although the early height heritability at 2 years was low (0.071), by age-4 it had increased (0.235), and showed signs of levelling off at age-7 height (0.254). The diameter

Table 3. – Genetic parameters estimated for growth and yield trait.

Traits		σ^2_{gca}	CV_A	σ^2_{sca}	SCA%	h^2_i	CV_{pi}
Onepu	HT02	0.0023	4.3%	0.003	130%	0.071	16%
	HT04	0.0264	4.3%	0.0016	6%	0.235	9.0%
	HT07	0.0738	4.0%	0.0067	9%	0.254	7.7%
Kaingaroa	HT04	0.0166	4.7%	0.00287	17%	0.173	11.3%
Combined Sites	HT04	0.0221	4.7%	0.0011	5%	0.204	10.5%
"880" series[1]	HT04		5.2%			0.20	11.5%
"268" series[2A]	HT06		4.2%			0.18	10%
Onepu	DM04	0.0474	3.2%	0.0492	103%	0.089	11%
	DM07	0.443	5.7%	0.1076	24%	0.284	11%
Kaingaroa	DM04	0.0372	4.2%	0.0212	57%	0.068	11.8%
	DM07	0.1462	4.0%	0.0631	43%	0.128	15.4%
Combined Sites	DM04	0.0478	4.0%	0.0257	54%	0.086	13%
	DM07	0.259	5.0%	0.0792	31%	0.187	12%
"880" series[1]	DM04		6.4%			0.18	15%
"268" series[2B]	DM05		7.6%			0.34	13%
"268" series[2B]	DM10		7.5%			0.28	14%
Onepu	VOLM07	181.0	12%	31.406	17%	0.292	22.3%
"880" series[1]	VOLM04		16%			0.20	38%
"268" series[2A]	VOLM06		14%			0.24	30%

[1]) "880" estimates 4 years – JOHNSON and BURDON, 1989 – pumice sites only.
[2A]) "268" estimates height and volume at 6 years on re-selected best 120 of 588 families (WILCOX, FIRTH, LOW and MCCONCHIE, 1975, unpublished Genetics and Tree Improvement report, N. 78).
[2B]) "268" estimates on 410 of 588 families at 5 years and 10 years from planting (KING and BURDON, 1991).

heritability was slower in showing this trend and was only 0.089 at age-4 but had increased to 0.284 by age-7 (at Onepu or 0.086 to 0.187 on Combined Sites (*Table 3*)). Diameter often reflects earlier height growth (R.D. BURDON, pers. comm.) and such delays in diameter to height heritabilities have been shown in other species (e.g. HODGE and WHITE, 1992). Later trends may show a slight decline (KING and BURDON, 1991) but interpreting trends in heritabilities over time needs careful consideration. Environmental as well as biological factors can add various biases to the estimation of genetic and phenotypic variances. Examples of how these biases might operate are discussed below.

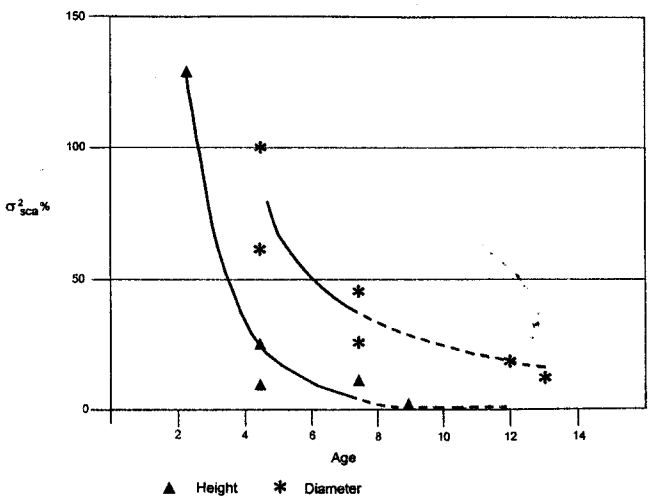
In general, yield traits showed similar heritabilities to their "268" series parents and "880" series cohorts. Heritabilities for a 6-year assessment of the original "268" parents from which the "875" filial generation was selected was 0.18 for height (WILCOX, FIRTH, LOW and MCCONCHIE, 1975, unpublished) which compares favorably with the age-4 estimates of 0.20 and the estimate from the "880" cohorts of 0.20. The coefficients of variation both for the additive genetic variance and individual phenotypic variance are also quite similar between these three intragenerational series. This "268" estimate was made however on the re-selected best 120 of the 588 original parents and may be expected to have reduced variances due to truncation selection (FALCONER, 1989, pg. 203).

The diameter figures reported here do show markedly higher heritabilities (0.34 vs 0.187) and coefficients of variation for additive genetic variance (7.6% vs 5%) for the "268"s over the "875"'s. The estimates shown for the "268"s are from the published estimates of the age-5 diameters (KING and BURDON, 1991) which are from a thinned population (usually leaving the 5 best trees per row plot). Unpublished estimates of the age-5 diameter unthinned gives a heritability of 0.18 and a coefficient of variation of the additive genetic variance of 6.3% (WILCOX and FIRTH, 1974, unpublished; KING and BURDON, 1991). Although this heritability is the same, the estimation of the coefficient of variation of the additive genetic variance is still higher than the "875" estimate, but is similar to the "880" estimate (6.4%, *Table 3*). Both of the "268" and "880" are OP matings and use the common assumption that the genetic covariance within the OP families is that of half-sibs and use a coefficient of relationship of 4 (FALCONER, 1989, pg. 156). The bias implicit in this assumption (SQUILLACE, 1974) could explain the slightly higher estimates from the OP series compared to the full-sibs (*Table 3*). The unthinned "268" diameter phenotypic coefficient of variation is 14.6% and is similar to the thinned value (13%) and the "875" and "880" values (13% and 15%).

The volume figures show similar results (h^2_i: 0.20–0.29): i.e. there are no strong or consistent results regarding intragenerational changes in genetic variances and parameters that could not most likely be explained by experimental design and stand history. Most of the differences reflect timing of assessments (i.e. the increasing then levelling out of the expression of additive genetic variance, *Table 3*) or the thinned or unthinned status of the stand. Selective thinning often shows increased heritability estimates (MATHESON and RAYMOND, 1984). In simulated thinning this was caused by declining phenotypic variances but in "actual" heavy selective thinning inflated additive genetic variance may be more of an influence on increased heritability (MATHESON and RAYMOND, 1984). An intensive low thinning which leaves the best trees, through either good genotype or favorable microenvironment, will compromise the independance between genotypic and effects. Thus a major assumption in the model is violated. In cases where thinning from below is less intensive biases in heritabilities may be not so apparent (COTTERILL and DEAN, 1988) or as much a problem for the model assumptions.

Although no strong intra-generational trends were observed, there is expected to be a decline in genetic and phenotypic variances that affects the between family component in the initial generations of selection due to gametic phase disequilibrium. This is because selected genotypes would be more likely to have similar genotypic values (BULMER, 1985, Ch. 9). This decline stabilizes when the increase of disequilibrium due to selection is balanced by the loss due to recombination. There is no real evidence of decline in this work between the generations shown in *table 3*. Explanations might include: 1) the "268"s are already selected individuals (P_1) and their F_1 progeny already have already reached this balanced phase as is shown in the fact that variances are similar to the F_2 progeny (the "875"s); and unpublished realized gain data have shown the effectiveness of the plus tree selection in New Zealand radiata pine; 2) The selection of the "875"s from the F_1 progeny was not really at a very high selection intensity. Although the selection intensity appears high (200 "875" P_2's from a potential of 90,000 F_1 "268"s). Restrictions involving site location, restrictions to family selection and the multiple-trait restriction quite significantly reduced this selection intensity and 3) Biases inherant in estimating these variances including those mentioned above quickly mask weak generational trends in genetic variances.

The trends over time in the additive genetic variance for height and diameter as indicated by the heritabilities is even more distinct when σ^2_{gca} is compared to σ^2_{sca} (*Table 3*). Early significant components of variance for both diallel effects and SCA for height growth declined into non-significance with time; with σ^2_{sca} changing from 130% of the GCA variance to under 10%. This trend also showed for diameter but was more delayed, and although SCA variance declined to 25% of the GCA variance it remained as a significant source of variation. This trend of declining SCA variance relative to GCA variance over time is similarly recorded in an NC-II design with 10-year data (C.D. LOW, unpublished data) and in measurements up to 13 years in a 25 parent diallel (CARSON, unpublished data and CARSON, 1991). σ^2_{sca} as a percentage of σ^2_{gca} was plotted over time for height and diameter with data points extended from the 7 year assessment using these older trials (*Figure 1*). There



Dotted line interpolated from data presented by S. D. CARSON and C. D. LOW.

Figure 1. – Percentage of non-additive to additive genetic variance over time.

Table 4. – Genetic parameters estimated for wood density, form and crown health traits.

Traits		σ^2_{gca}	CV_A	σ^2_{sca}	SCA%	h^2_i	CV_{pi}
Onepu	STR07	0.1371	12%	0.0165	12%	0.176	29%
Kaingaroa	STR07	0.0166	8%	0.00287	17%	0.173	24%
Combined sites	STR07	0.1021	10%	0.053	52%	0.14	26%
"880" series[1]	STR04		13%			0.15	34%
"268" series[2A]	STR06		10%			0.14	26%
Onepu	BRAN07	0.205	15%	0.0	0%	0.28	29%
Kaingaroa	BRAN07	0.1595	14%	0.0609	38%	0.187	32%
Combined sites	BRAN07	0.1756	15%	0.031	18%	0.21	32%
"880" series[1]	BRAN04		15%			0.185	35%
"268" series[2B]	BRAN10		20%			0.33	34%
Onepu	MALF07	0.0776	7.7%	0.1032	133%	0.06	31%
Kaingaroa	MALF07	0.0609	6.5%	0.1195	196%	0.046	31%
Combined sites	MALF07	0.0779	7.5%	0.06179	79%	0.06	31%
"880" series[1]	MALF04		7.0%			0.06	37%
"268" series[2B]	MALF10		7.0%			0.10	22%
Onepu	WDPIN	3.503	1.0%	1.889	54%	0.195	2.5%
"268" series[2B]	WDPIN		6.1%			0.40	9.6%
Kaingaroa	CYCLA	8.019	27%	1.735	22%	0.32	48%
"268" series[2C]	CYCLA		32%			0.32	56%

[1]) "880" estimates 4 years – JOHNSON and BURDON, 1989 – pumice sites only.
[2A]) "268" estimates height and volume at 6 years on re-selected best 120 of 588 families (WILCOX, FIRTH, LOW and MCCONCHIE, 1975, unpublished Genetics and Tree Improvement report, N. 78).
[2B]) "268" estimates after 10 years (SHELBOURNE, FIRTH and LOW, 1981, unpublished Genetics and Tree Improvement report, No. 195).
[2C]) "268" estimates on 410 of 588 families at 5 years and 10 years from planting (KING and BURDON, 1991).

is every indication from these data that the observed decline in SCA variance over time will continue. The final volume showed strong and significant amounts of GCA, and although SCA was significant ($P<0.05$), the SCA variance was less than 20% of the GCA variance for volume at this age. Diallel effect in volume, as for the component traits of height and diameter, was non-significant.

BALOCCHI et al. (1993) noted that nonadditive gene effects were most prominent in the control of early tree height (full-sib progeny of nonselected loblolly pine) but later on was supplanted by additive gene effects. DIETER et al. (1995) showed a doubling of additive to dominance genetic variation between 5 and 14 years in full-sib tests of slash pine. Not all studies have shown this trend of decling SCA and increasing GCA, however. BOYLE (1987) reported increasing SCA with age in full-sib families of black spruce and SAMUEL (1991) reported strong declining GCA relative to SCA at least on one of the sites of a Sitka spruce complete diallel.

YANCHUK (1995) found no differences in comparative amounts of SCA to GCA in two ages of Douglas-fir. But he noted the many potential errors and biases that may occur in estimating non-additive genetic variances. These are more likely caused by genetic or non-genetic factors other than a true dominance interaction. Epistasis is one gene effect that cannot be readily differentiated from SCA. Linkage disequilibrium is another problem especially in small population sizes originating from nonselected or plus-tree selected wild populations (YANCHUK, 1996). Regardless of the genetic cause (dominance or epistatsis) these are estimated as non-additive genetic variance, however non-genetic factors might also be important in this estimation especially in interpreting trends over time.

One possible explanation for the observed trend of declining SCA and increasing GCA (*Figure 1*) is that the early high levels of SCA in fact represent extraneous effects that cannot be readily removed from the full-sib cross effect. The basic treatment unit is the specific full-sib cross. After removal of the parental GCA effect the remaining variance is assigned to a specific combining ability effect, although there may well be other factors in the full-sib cross effect. If, for example, full-sib seedlots are not adequately replicated in the nursery prior to lifting for field planting, or if there are seed size or other types of maternal effects present (e.g. GRIFFIN, 1972; PERRY, 1976; ROBINSON and VAN BUIJTENEN, 1979; KAHLIL, 1981) then early full-sib cross variances could be inflated. As these extraneous effects disappear over time and additive gene effects express themselves more fully in field conditions, the trends noted in *figure 1* would be observed. In OP or half-sib matings similar non-genetic effects would bias upwards early estimates of additive genetic variance.

Trends in the other direction might also be explained by non-genetic or genetic factors other than by increasing SCA over time. BOYLE's (1987) black spruce estimates of GCA and SCA were generated with 9-tree block plots with only three replicates. If the replication effect is not adequate to remove the common environmental effect found in the large plots, tree growth over time and could be interpreted as increasing SCA. SAMUEL's (1991) study used a complete diallel mating design so the estimates of SCA should be clean. High estimates of SCA for height growth could be caused by linkage disequilibrium in a small population size (only 7 parents were used by SAMUEL (1991)). Presence of nonadditive gentic variances and strong trends should be interpreted cautiously and may point to the need for more detailed investigation (SAMUEL, 1991).

Parameter estimates for wood quality traits

The parameter estimates for quality traits, including the wood density estimate and crown health scores, are shown in *table 4*. Straightness score with a heritability of 0.14 was similar to that recorded in the tests of the earlier generation (*Table 4*). The single site analyses of the "268"s reported by SHELBOURNE and LOW (1991) (h^2_i : 0.18–0.25) was also close to our estimates of 0.17–0.18. GCA was much higher than SCA, but diallel effects were quite significant for the straightness score ($P < .001$). Coefficients of variation of both the phenotypic and additive genetic variances are quite similar. Malformation score, as with earlier generation tests, had a low heritability (0.06) and this trait appeared to have a strong expression of SCA (*Table 4*). But the low heritability and often highly skewed distribution of malformation score make any genetic interpretations difficult. Branching habit had strong GCA expression with an individual tree heritability of approximately 0.20. The wood density estimate (using the pilodyn) had a quite low heritability (0.195) compared to the "268" estimate and although SCA was significant the GCA variance was almost twice as high (*Table 4*). The poor *r-square* (0.34) in the regression of cores (106 cores) to pilodyn reading may go some way in explaining the poor heritability compared to the 10-year "268" pilodyn estimate. This trait also showed very low estimates of additive and phenotypic coefficients of variation. Crown health, by way of the *Cyclaneusma* score, had the highest individual tree heritability (0.32) and GCA variance was 4 times that of the SCA variance. The heritability of this trait in the "268" progeny test was also 0.32. Phenotypic and genetic variances for quality traits (as shown by the CV's, *Table 4*) do not show strong differences or trends between generations and are more likely to be affected by stand history and design than show any true intra-generational differences.

Correlations among traits are reported in *table 5*. A slight negative genetic correlation between growth and straightness ($r_A = -0.2$) is noted also in the "880" cohorts and is reported similarly in the "268" ($r_A = -0.1$) at least at the 5-year measure on the pumice sites (the 6-year measure with height and volume had this correlation at about -0.4 (WILCOX, FIRTH, LOW and MCCONCHIE, 1975, unpublished Genetics and Tree Improvement report No. 78) and the 10-year correlation was 0 or slightly positive (SHELBOURNE, FIRTH and LOW, 1981, unpublished Genetics and Tree Improvement report No. 195). There is a low but positive correlation ($r_A = 0.2$) between malformation score and yield on the pumice sites and a moderate correlation between yield and branch habit ($r_A = 0.45$). This moderate correlation ($r_A = 0.3$–0.6) is shown between the trait combination of straightness, malformation and branching habit and between branching habit and yield. A multinodal form type was directly selected in the original "268"s P_1 selections and in the F_1 selections that formed the "875" and "880" parents (SHELBOURNE et al., 1986). The F_2 progeny have also maintained the moderate but favourable correlations for this multinodal branching habit type.

Another important relationship is that between growth and *Cyclaneusma* score ($r_A = 0.4$ or $r_A = -0.4$ if the trait refers to *Cyclaneusma* infection rather than branch retention) in which high *Cyclaneusma* infection correlates with poorer growth. This correlation was explored in detail in the later assessments of the original "268"s (KING and BURDON, 1991). A negative correlation increases with age of assessment (from 0.10 at age-5, to -0.24 at age-10, to -0.38 at age- 17). Early growth assessments can be increased in their efficiencies by about 15% if CYCLA is added as an indirect selection trait for final yield (KING and BURDON, 1991). However by the time a negative genetic correlation has arisen (showing the growth reduction effect of *Cyclaneusma*) little or no extra efficiency can be added. In the case with a moderate genetic correlation with growth rate the impact of cyclaneusma will already be felt in the plantation.

The negative relationship between pilodyn pin penetration and volume ($r_A = 0.15$) is lower than the earlier generation estimates ($r_A = 0.4$), but may be misleading considering the poor heritability estimates obtained with the pilodyn. The "875"'s are already heavily selected for wood density, so that correlations of these traits may not reflect those that occur in unselected populations.

Conclusions

We would like to draw attention to three conclusions from this work. The first is that that these progenies resulting from two generations of selection exhibit large amounts of additive genetic variance, and genetic parameters are very similar to those estimated in earlier generation progeny tests ($h^2 = 0.2$ for growth and yield traits). This would appear to confirm the strategy of population improvement using recurrent selection for GCA and indicate substantial gains should be possible over multiple generations of improvement.

The second conclusion is that dominance genetic variance for growth traits, although large and significant for early measurements, tends to disappear with time. Proposals for the exploitation of SCA based on early results (WILCOX et al., 1975) would not appear warranted and the results here further confirms CARSON (1986) who suggested that selection for the best general combiners would be most profitable for radiata pine improvement.

The third conclusion is that trends over time and between generations should be interpreted with caution. Explanations

Table 5. – Additive genetic correlations between traits above diagonal indicates genetic correlations of 875's (880's where available in italics) below diagonal are the genetic correlations of the 268 parents.

Trait	YIELD	STR	MALF	BRAN	WDPIN	CYCLA
YIELD		-0.2 *(-0.25)* [1]	0.2 *(0.3)* [1]	0.45 *(0.3)* [1]	0.15	0.4
STR	-0.1 [2A]		0.3 *(0.35)* [1]	0.4 *(0.2)* [1]	N.C.	N.C.
MALF	0.2 [2C]	0.5 [2C]		0.6 *(0.45)* [1]	N.C.	N.C.
BRAN	0.25 [2A,C]	0.4 [2A, B, C]	0.55 [2C]		N.C.	N.C.
WDPIN	0.4 [2C]	N.C.	N.C.	N.C.		N.C.
CYCLA	0.25 [2D]	N.C.	N.C.	N.C.	N.C.	

[1]) "880" estimates 4 years – JOHNSON and BURDON, 1989 – pumice sites only.
[2A]) "268" estimates all 588 families at 5 years from planting (SHELBOURNE and LOW, 1980; after WILCOX and FIRTH, 1974, unpublished).
[2B]) "268" estimates height and volume at 6 years on re-selected best 120 of 588 families (WILCOX, FIRTH, LOW and MCCONCHIE, 1975, unpublished Genetics and Tree Improvement report, No. 78).
[2C]) "268" estimates after 10 years (SHELBOURNE, FIRTH and LOW, 1981, unpublished Genetics and Tree Improvement report, No. 195).
[2D]) "268" estimates on 410 of 588 families at 10 years from planting (KING and BURDON, 1991), shows as positive correlation here.

for trends may better be explained by potential biases in the experimental design and estimation procedures rather than by the effects of gene action changing over time.

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