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Additive and Dominance Genetic Effects in Pinus pinaster, P. radiata and P. elliottii and some Implications for Breeding Strategy

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Summary

Additive and dominance genetic variances were estimated for growth and stem straightness measured at around 8 years in control-pollinated progeny trials of *Pinus pinaster*, *P. radiata* and *P. elliottii* in South Africa. The progeny trials involved Design II matings among 13 female × five male parents in the case of *P. pinaster*, 11 × 5 for *P. radiata*, and 8× 8 for *P. elliottii*.

The levels of additive variance tended to be about the same or greater than the levels of dominance variance for growth of *P. pinaster* and *P. radiata*. Variance components for stem straightness of these two species were not reliably estimated. Additive variance was generally substantially greater than dominance variance for growth and straightness of *P. elliottii*.

An important finding was that the expected performance of full-sib families, as calculated by summing the general combining abilities of parents, proved to be a reasonable guide to the observed performance; even where levels of dominance variance were about the same as additive variance. Implications of this finding are discussed with particular reference to breeding strategies involving mass vegetative propagation.

Key words: Additive variance, dominance variance, *Pinus pinaster*, *Pinus radiata*, *Pinus elliottii*.

Zusammenfassung

In Südafrika wurden bei rund 8 Jahre alten frei abgeblühten Nachkommenschaftsprüfungen von *Pinus pinaster*, *Pinus radiata* und *Pinus elliottii* die additiven und die dominanten genetischen Varianzen für das Wachstum und die Geradschäftigkeit geschätzt. Die Nachkommenschaften umfassen im Design II Kreuzungen zwischen 13 weiblichen und 5 männlichen Eltern bei *Pinus pinaster*, 11 × 5 für *Pinus radiata* und 8 × 8 für *Pinus elliottii*.

Die Levels für die additive Varianz waren für das Höhenwachstum für *Pinus pinaster* und *Pinus radiata* genauso groß oder größer als die für die Dominanzvarianz. Die Varianzkomponenten für die Geradschäftigkeit dieser beiden Arten waren nicht zuverlässig zu schätzen. Bei *Pinus elliottii* war die additive Varianz sowohl für das Höhenwachstum als auch für die Geradschäftigkeit generell erheblich größer als die Dominanzvarianz.

Eine wichtige Feststellung war, daß die Leistungsfähigkeit der Vollgeschwisterfamilien, welche aus der Summe der generellen Kombinationseignungen der Eltern erwartet wurde, sich als ein guter Leitfaden für die beobachtete Leistungsfähigkeit erwies, besonders dort, wo die Levels der Dominanzvarianz etwa die gleichen waren, wie die, für die additive Varianz. Folgerungen aus dieser Erkenntnis werden besonders im Hinblick auf Züchtungsstrategien diskutiert, die eine vegetative Massenvermehrung mit sich bringen.

Introduction

Additive genetic effects are the only source of genetic variation which can be utilized in the cumulative improvement of trees by recurrent selection from one generation to the next. Non-additive genetic effects (such as dominance gene effects) can, however, be exploited when multiplying improved genetic material for use in establishing plantations. Afforestation using clones of superior individuals is clearly the most efficient method of exploiting

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dominance variance, but this type of clonal forestry presents practical and economic difficulties in pines (FIELDING 1969; CLARKE and SLEE 1985). Multiplication of seedlings of superior families by mass vegetative propagation is another method of exploiting dominance variance, and this approach is becoming increasingly important for species such as *Pinus radiata* (Anon. 1985; CARSON 1986), *P. caribaea* and *P. elliottii* (Anon. 1986). Estimates of the relative levels of additive and dominance variance are not well known for any species of pine. This dearth of information obviously needs to be rectified before the potential advantages of options such as mass vegetative propagation, or indeed clonal forestry, can be properly evaluated and exploited.

The aim of this study is to provide estimates of additive and dominance variance for some economic traits of *P. pinaster* AIT., *P. radiata* D. DON and *P. elliottii* ENGELM. var. *elliottii* grown in selected trials in the Republic of South Africa. The implications of these levels of additive and dominance variance are discussed in terms of breeding strategies which may be employed under mass vegetative propagation.

Materials and Methods

Parents, Sites and Field Designs

(1) *P. pinaster* Progeny Trial: Included a 13 × 5 (female × male) factorial or Design II (COMSTOCK and ROBINSON 1952) mating pattern with all 65 possible crosses completed. The 18 parents were selected as superior trees from unimproved plantations in South Africa, and for the purposes of this study these 18 parents are assumed unrelated.

The trial (identified locally as PF4109) was planted in May 1974 on one site at the Witfontein State Forest (latitude 33°58' S; longitude 22°32' E; altitude 223 m) near George in the Southern Cape of South Africa. The planting density was 2.7 × 2.7 m. The site was previously occupied by coastal forest. George has a warm-temperate (Mediterranean) type of climate with an average annual rainfall of about 860 mm (which falls all year round).

The field design was 10 randomised complete blocks with 5-tree row plots. A lattice layout was actually superimposed on the randomised blocks design of this progeny trial (as well as the *P. radiata* and *P. elliottii* trials), but these lattices have been ignored in order to simplify the models required for analyses of data. All surviving trees were measured for height, diameter (over-bark at 1.3 m) and stem straightness (eight-point subjective score with 8 = straight and vertical stem, 1 = crooked stem) in February 1983, at about 8½ years after planting. Stem volume was calculated from height and diameter measurements using the simple conical function — (1)

$$\text{volume} = \pi\ (\text{diameter}/2)^2\ (\text{height}/3). \qquad (1)$$

Table 1 gives the overall means and standard deviations of the above traits for all trees measured.

(2) *P. radiata* Progeny Trial: Included an 11 × 5 Design II mating with two crosses missing (out of 55 possible crosses). The 16 parents are assumed to be unrelated and were selected as superior trees from unimproved plantations in South Africa. The trial (local no. PF4611) was planted in October 1975 on one site at Witfontein State Forest. The planting density was 2.7 × 2.7 m. The site previously supported *P. radiata* plantation.

The field design was five randomised complete blocks with 5-tree row plots. All surviving trees were measured for height, diameter (over-bark at 1.3m) and stem straightness (eight-point score) in December 1983, at about 8 years.

Table 1. — Overall means and standard deviations of all individual trees measured in the *P. pinaster*, *P. radiata* and *P. elliottii* progeny trials.

Progeny trial	Height (m)	Diameter (cm)	Volume (dm^3)	Straigh. (point)
P. pinaster – (measured at 8½ years)	9.43 ±1.61	13.40 ±2.87	48.28 ±24.64	5.85 ±0.96
P. radiata – (measured at 8 years)	11.32 ±2.04	14.31 ±3.44	67.94 ±38.79	5.67 ±1.01
P. elliottii – (measured at 8½ years)	10.75 ±1.12	15.21 ±2.12	67.48 ±23.16	4.26 ±1.70

(3) *P. elliottii* Progeny Trial: Included an 8 × 8 Design II mating with six crosses missing (out of the 64 possible crosses). The 16 parents are assumed to be unrelated and were selected as superior trees from unimproved plantations in Zimbabwe, Australia and South Africa. The trial is part of a series of experiments initiated by Dr R. D. BARNES (Oxford Forestry Institute, England).

The trial (local no. PF1611) was planted in February 1976 at Wilgeboom State Forest (latitude 24°56' S; longitude 30°57' E; altitude 945 m) near Sabie in the Eastern Transvaal, South Africa. The planting density was 2.7 × 2.7 m. The site previously supported pine plantations. Sabie has a sub-tropical climate with an average annual rainfall (at Wilgeboom S.F.) of about 1340 mm, the majority of which falls between October and April.

The field design was six randomised complete blocks with 10-tree row plots, which were thinned in June 1984 to leave the five most commercially valuable trees per plot. All surviving trees were measured for height, diameter (over-bark at 1·3 m) and stem straightness (eight-point score) in August 1984, at 8½ years.

Analyses of Data

(1) Estimates of Variance Components: Data for each progeny trial (i.e. each Design II mating) were analysed using two analyses of variance: (a) an analysis of individual data to determine mean squares between and within-plots, and (b) an analysis of plot means to determine mean squares (and mean cross-products) due to female parents, male parents, and female × parent interactions. It will become apparent that the purpose of the analysis of individual tree data is to provide estimates of variance within plots which are necessary to express heritability on an individual tree basis. (These procedures for analysis of variance follow KEMPTHORNE 1969, Chapter 20.11; SNYDER and NAMKOONG 1978; BECKER 1985; and others. A detailed account of methods for estimating genetic variance components under Design II matings is given here as they are not readily accessible in the tree breeding literature).

The analysis of plot means was according to the model — (2)

$$\bar{Y}_{ijkl} = \mu + f_i + m_j + fm_{ij} + b_k + e_{ijkl} \qquad (2)$$

where $\bar{Y}_{ijkl}$ are the plot mean observations, μ the overall mean, f_i the effect of the ith female parent, m_j the effect of the jth male parent, fm_{ij} the female × male parent interaction, b_k the effect of the kth randomised complete block of the field layout, and the experimental error e_{ijkl} is the interaction between female-male parent combinations (i.e. full-sib families) and blocks. The effects of blocks are assumed fixed while those of female and male parents

Table 2. — Expectations of mean squares relevant to estimating genetic parameters from analyses of variance of Design II matings.

Sources of variation	d.f.	Expectations of mean squares[A)]
Analysis of individual tree data–		
Within-plots	N–bfm	σ^2_w
Analysis of plot mean data–		
Female	f–1	$\sigma^2_e + 1/k_1\sigma^2_w + k_5\sigma^2_{fm} + k_8\sigma^2_f$
Male	m–1	$\sigma^2_e + 1/k_2\sigma^2_w + k_6\sigma^2_{fm} + k_9\sigma^2_m$
Female x male	(f–1)(m–1)	$\sigma^2_e + 1/k_3\sigma^2_w + k_7\sigma^2_{fm}$
Female–male x block	(fm–1)(b–1)	$\sigma^2_e + 1/k_4\sigma^2_w$

A) There are f female parents, m male parents, b randomised complete blocks, and N trees in each progeny trial. The variance component σ^2_f is due to females, σ^2_m males, σ^2_{fm} female × male interactions, σ^2_e between-plot error, and σ^2_w within-plot error. Coefficients of variance components, computed according to the direct approach of Harvey (1960) were, for the *P. pinaster*, *P. radiata* and *P. elliottii* trials, respectively: k_4 = 4.90, 4.58 and 4.95; k_7 = 10.0, 4.97 and 5.86; k_8 = 50.0, 23.90 and 41.93; and k_9 = 130.0, 52.24 and 41.93.

are assumed random. Analyses were completed using a generalised least-squares program written by Harvey (1977).

Expectations of mean squares for both the analyses of individual tree and plot-mean data are given in *Table 2.* Note that the female-male × block error component of the plot mean analysis includes a between-plot error variance (σ^2_e) and a fraction of the variance among individuals measured within each plot (σ^2_w). An indirect estimate of σ^2_e can be obtained by equating the expectations of mean squares of the error terms of the two analyses of variance *(Table 2)* — (3)

$$\sigma^2_e = (\text{mean squares female-male x block error}) - (\text{mean squares within-plot error}/k_4). \quad (3)$$

The component σ^2_e may be thought of as the environmental portion of the variance between plots which is common to all the full-sib offspring within a plot.

Equating expectations of mean squares for the analysis of plot mean data provides estimates of variance due to female parents (σ^2_f), male parents (σ^2_m) and female × male parent interactions (σ^2_{fm}). Under the assumption of unrelated female and male parents (i.e. F = 0; F being the coefficient of inbreeding among the parents), the component σ^2_f is equal to the genetic covariance among maternal groups of half-sib offspring (cov HS_f) — (4)

$$\sigma^2_f = \text{cov } HS_f = 1/4\ \sigma^2_a + 1/16\sigma^2_{aa} + 1/64\sigma^2_{aaa} + \ldots + \sigma^2_c. \quad (4)$$

The σ^2_a represents variance due to additive gene effects; σ^2_{aa} and σ^2_{aaa} epistatic variance due to interactions of additive effects of two or more loci, and σ^2_c variance due to common environmental effects (in this case maternal effects). Epistatic effects are commonly assumed negligible and the component 4 σ^2_f used as an estimate of additive variance — (5)

$$4\sigma^2_f \simeq \sigma^2_a + 4\sigma^2_c. \quad (5)$$

The problem with 4 σ^2_f as an estimator is that it may seriously overestimate the true level of additive variance if the maternal component 4 σ^2_c happens to be important.

An independent estimator of additive variance is provided by the paternal component σ^2_m for Design II matings. The σ^2_m is equal to the genetic covariance among paternal groups of half-sibs (cov HS_m) and under the assumption of negligible epistasis — (6)

$$4\sigma^2_m \simeq \sigma^2_a. \quad (6)$$

This paternal estimate 4 σ^2_m usually has the advantage of being free from confounding with variance due to common environmental effects (including, of course, maternal effects).

The sum of the maternal and paternal components provides another estimator of additive variance, but again there is confounding with maternal variance (albeit less serious than the confounding in Equation 5) — (7)

$$2(\sigma^2_f + \sigma^2_m) \simeq \sigma^2_a + 2\sigma^2_c. \quad (7)$$

Note that this simple summation of σ^2_f and σ^2_m assumes that both components of variance are based on the same degrees of freedom (i.e. are equally reliable).

The female × male component σ^2_{fm} represents the variance among the full-sib families, and is equal to the genetic covariance among each of the full-sib groups of offspring (cov FS) minus the covariance among the half-sib offspring of the parents involved in each cross — (8)

$$\sigma^2_{fm} = \text{cov FS} - \text{cov } HS_f - \text{cov } HS_m = 1/4\sigma^2_d + 1/8\sigma^2_{aa} + 1/8\sigma^2_{ad} + 1/16\sigma^2_{dd} + 7/64\sigma^2_{aaa} + \ldots - \sigma^2_c. \quad (8)$$

Where σ^2_d represents the variance due to dominance gene effects, σ^2_{ad} epistatic variance due to interactions of additive and dominance effects at two loci, and σ^2_{dd} epistatic variance due to interactions of dominance effects at two loci. Under the assumption of negligible epistatic variance the component 4 σ^2_{fm} provides an estimator of dominance genetic variance with negative confounding (downward bias) from maternal variance — (9)

$$4\sigma^2_{fm} \simeq \sigma^2_d - 4\sigma^2_c. \quad (9)$$

An attempt may be made to adjust the above estimator 4 σ^2_{fm} for maternal effects by adding an approximate estimate of 4 σ^2_c determined as the difference between 4 σ^2_f and 4 σ^2_m — (10)

$$4\sigma^2_c \simeq 4\sigma^2_f - 4\sigma^2_m. \quad (10)$$

In other words, Equation 9 may be adjusted for maternal effects by adding Equation 10. The reliability of the estimate of maternal variance obtained from Equation 10 will of course depend on the reliability of the estimators 4 σ^2_f and, in particular, 4 σ^2_m. In tree breeding it is common for Design II matings to involve relatively few male parents (e.g. the *P. pinaster* and *P. radiata* matings studied here each involve only five males) and consequently estimates of the paternal component 4 σ^2_m may include substantial

sampling errors, leading to erratic estimates of 4 σ^2_c. For this reason the adjustment of 4 σ^2_{fm} (i.e. Equation 9) for maternal effects (Equation 10) has only been attempted in the case of *P. elliottii* where there are equal numbers of both female and male parents.

(2) Estimates of Heritabilities: Individual heritability was estimated on a maternal (h^2_f), paternal (h^2_m) or maternal plus paternal (h^2_{f+m}) basis as — (11), (12) and (13)

$$h^2_f = 4\sigma^2_f/\sigma^2_P \quad (11)$$

$$h^2_m = 4\sigma^2_m/\sigma^2_P \quad (12)$$

$$h^2_{f+m} = 2(\sigma^2_f + \sigma^2_m)/\sigma^2_P. \quad (13)$$

The phenotypic component σ^2_P being calculated as - (14)

$$\sigma^2_P = \sigma^2_f + \sigma^2_m + \sigma^2_{fm} + \sigma^2_e + \sigma^2_w. \quad (14)$$

The interaction component σ^2_{fm} was occasionally negative in the progeny trials studied, and under these circumstances σ^2_{fm} was set to zero to solve Equation 14. Standard errors of the individual heritabilities were estimated according to Swiger *et al.* (1964).

(3) Estimates of Additive Genetic Correlations: The genetic correlations reported here were estimated according to Hazel *et al.* (1943) using only the maternal estimates of additive genetic variance and covariance. Standard errors of the genetic correlations were estimated according to Tallis (1959). Genetic correlations may also be estimated using paternal components of variance and covariance. However, preliminary analyses revealed that the relatively few male parents involved in the *P. pinaster* and *P. radiata* matings led to unreliable estimates of paternal correlations with very large standard errors.

(4) Estimates of Combining Abilities: The general combining ability (gca_i) of the ith female parent was estimated as the difference between the least-squares mean ($\bar{X}_{i.}$) of the half-sib offspring of the ith parent (i.e. the least-squares means fitted for female parent effects in the model) and the overall mean of the progeny trial ($\bar{X}_{..}$) — (15)

$$gca_{i.} = \bar{X}_{i.} - \bar{X}_{..}. \quad (15)$$

The general combining ability (gca_j) of the jth male parent was estimated in a similar way.

Least squares means differ from ordinary arithmetic means in that the former are minimum variance estimators adjusted for bias due to non-orthogonality of the data (Harvey 1960; Cotterill *et al.* 1983). In the case of the *P. pinaster* offspring there was a complete (orthogonal) mating pattern and the least-squares means of parents were almost exactly equal to the arithmetic means. However, the incompleteness (non-orthogonality) of the *P. radiata* and *P. elliottii* matings led to some (fairly small) differences between least-squares and arithmetic means. For example, the least-squares means for say volume growth of female parents in the *P. radiata* or *P. elliottii* progeny trials would be adjusted for the difference between the average volume of the male parents to which a particular female was crossed and the average of those males to which the female was not crossed.

The genetic value (gv_{ij}) of the full-sib family produced by mating the ith female and jth male parent was estimated as the difference between the least-squares mean ($\bar{X}_{ij}$) of the particular full-sib family and the overall mean — (16)

$$gv_{ij} = \bar{X}_{ij} - \bar{X}_{..}. \quad (16)$$

"Predicted" genetic values ($\hat{gv}_{ij}$) were also determined for each full-sib family as the sum of the female and male parents general combining abilities — (17)

$$\hat{gv}_{ij} = gca_{i.} + gca_{.j}. \quad (17)$$

Comparisons of rankings of full-sib families based on "observed" (or least-squares) and predicted genetic values have been used in this article to illustrate some of the practical implications of relative magnitudes of additive and dominance variance in tree breeding.

The specific combining ability (sca_{ij}) of the ith female parent mated to the jth male parent was calculated as the difference between the observed and predicted genetic values for the particular cross — (18)

$$sca_{ij} = gv_{ij} - \hat{gv}_{ij}. \quad (18)$$

Note that the variance of the general combining abilities of the female parents is equal to σ^2_f, while the variance of the gca's of the male parents is equal to σ^2_m. The variance of the sca's is equal to σ^2_{fm}.

Results and Discussion

Mean squares for analyses of variance of the *P. pinaster*, *P. radiata* and *P. elliottii* progeny trials are presented in *Table 3*. Components of additive and dominance variance, their ratios, and individual heritabilities are presented in *Table 4*, and genetic and phenotypic correlations in *Table 5*. General and specific combining abilities and genetic values for diameter of the *P. pinaster* and *P. elliottii* parents and full-sib offspring are presented in *Table 6* and *7*.

Variance Components, Ratios and Heritabilities

(1) Growth Traits: The effects of both female and male parents were highly significant ($P < 0.01$) for growth traits of *P. elliottii*, and significant ($P < 0.05$) or highly significant ($P < 0.01$) for growth traits of *P. pinaster (Table 3)*. The *P. radiata* male parents had a significant ($P < 0.05$) effect on all growth traits, but the female parents had a significant ($P < 0.01$) effect on height only *(Table 3)*. The only significant female × male parent interaction across all three species was for diameter of *P. pinaster*.

In keeping with the above levels of significance, the levels of additive genetic variance for growth traits (as estimated by 4 σ^2_f and 4 σ^2_m) were generally greater for the *P. elliottii* offspring (*Table 4*). These higher levels of additive variance were refleced in higher individual heritabilities for *P. elliottii* (e.g. h^2_{f+m} for growth traits of *P. elliottii* ranged from high values of 0.36 to 0.37; *Table 4)* compared with *P. pinaster* and *P. radiata* (h^2_{f+m} for the two species ranged from very low to moderate values of 0.04 to 0.19; *Table 4*).

In the case of *P. pinaster* the maternal, paternal and combined estimates of individual heritability for height were substantially higher than those for diameter (e.g. h^2_f, h^2_m and h^2_{f+m} values ranged from 0.11 to 0.27 for height compared with 0.03 to 0.05 for diameter; *Table 4*). However, the trend was not consistent across the other two species

Table 3. — Female, male, female × male interaction, full-sib family × block error and within-plot error mean squares for analysis of variance of the *P. pinaster*, *P. radiata* and *P. elliottii* progeny trials.

Source of variation	d.f.	Height (m)	Diameter (cm)	Volume (dm^3)	Straigh. (point)
P. pinaster -					
Female parent	12	8.42**	8.17*	1061**	0.692**
Male parent	4	8.69**	12.64*	1224**	0.504ns
Female x male parent	48	0.67ns	3.43*	244ns	0.226ns
Family x block error	576	0.81	2.42	177	0.176
Within-plot error	2524	1.59	6.82	478	0.877
P. radiata -					
Female parent	10	5.92**	7.04ns	975ns	0.433ns
Male parent	4	7.46*	27.60*	3317**	0.566ns
Female x male parent	38	2.05ns	4.82ns	671ns	0.303ns
Family x block error	207	2.19	4.50	598	0.287
Within-plot error	955	2.49	9.07	1089	0.916
P. elliottii -					
Female parent	7	3.86**	22.06**	2069**	6.915**
Male parent	7	5.92**	12.60**	2050**	3.922**
Female x male parent	43	0.35ns	1.37ns	188ns	0.961ns
Family x block error	278	0.37	1.08	135	0.690
Within-plot error	1351	0.75	2.88	331	2.452

** $P < 0.01$; * $P < 0.05$; ns not significant.

studied. Another feature of the heritabilities of *P. pinaster* is that the maternal estimates h^2_f were consistently higher than the paternal estimates h^2_m (*Table 4*). The obvious explanation is that the maternal heritabilities were biased upward by maternal variance, but the trend was again not consistent across the other species. The heritabilities reported here for height of *P. pinaster* at around 8 years are similar to values of 0.17 and 0.20 reported by KREMER (1981) for absolute height of *P. pinaster* at the same age in France. The literature appears to contain no other published estimates of individual heritability for growth or form of *P. pinaster*.

The individual heritabilities observed in the present study for growth of *P. radiata* are similar to unpublished estimates calculated by Dr G. VAN WYK using data from three open-pollinated progeny trials (local nos. PF4610, PF4612 and PF4615) in the same region of the Southern Cape. For instance, the combined heritabilities $h^2_{f+m} = 0.12$ for height and 0.09 for diameter at 8 years correspond with individual heritabilities of 0.16, 0.17 and 0.20 calculated by VAN WYK for height, and 0.02, 0.05 and 0.07 for diameter.

In general, the individual heritabilities for height of *P. radiata* in South Africa agreed fairly closely with the averages of published estimates from other countries, but the heritabilities for diameter appear to be consistently low in South Africa. For instance, pooled (or average) estimates of individual heritability of 0.29 (COTTERILL and ZED 1980), 0.16 (DEAN *et al.* 1983) and 0.23 (MATHESON and RAYMOND 1984) have been reported for height of *P. radiata* between 4½ and 11 years in Australia. Corresponding average estimates for diameter were 0.18 (COTTERILL and ZED 1980), 0.23 (DEAN *et al.* 1983) and 0.18 (MATHESON and RAYMOND 1984). SHELBOURNE and LOW (1980) also report a moderately high average individual heritability of 0.19 for diameter of *P. radiata* in New Zealand.

The fairly high estimates of individual heritability reported for growth of *P. elliottii* at 8½ years in South Africa (e.g. $h^2_{f+m} = 0.36$ to 0.37; *Table 4*) are comparable with estimates in Australia. For instance, ALLEN (1985) found individual heritabilities of 0.44, 0.24 and 0.26, respectively, for height, diameter and volume of *P. elliottii* at 15 years in Queensland, Australia. SLUDER (1983) reported lower individual heritabilities of between 0.19 and 0.25 for growth traits of *P. elliottii* in Georgia, USA, but these estimates were based on within-family deviations.

Estimates of dominance variance ($4\sigma^2_{fm}$) were negative for the height of all three species studied (*Table 4*). These consistently negative estimates may reflect very low (true) levels of dominance variance for height of *P. pinaster*, *P. radiata* and *P. elliottii* in South Africa, but this conclusion is not supported by other trends for *P. radiata* and *P. elliottii* (discussed below). The negative components of dominance variance obviously make it impossible to calculate ratios of additive to dominance variance for height.

In the case of *P. pinaster* the estimated level of dominance variance for diameter proved to be marginally greater than the additive variance, leading to low ratios of $\sigma^2_f/\sigma^2_{fm} = 0.9$ and $\sigma^2_m/\sigma^2_{fm} = 0.7$ (*Table 4*). Indeed, there were no lower ratios of additive to dominance variance recorded for growth traits across any of the three species studied. The estimated level of dominance variance for volume of *P. pinaster* was substantially less than the maternal estimate of additive variance ($\sigma^2_f/\sigma^2_{fm} = 2.4$; *Table 4*) and marginally less than the paternal estimate of additive variance ($\sigma^2_m/\sigma^2_{fm} = 1.1$). KREMER (1981) reported high levels of dominance variance for early height growth of *P. pinaster* in France, but by 8 years the level of dominance was substantially less than the additive variance. There appear to be no other published estimates of dominance variance for *P. pinaster*.

Table 4. — Additive genetic variance as approximated by four times the variance due to female ($4\sigma^2_f$) or male parents ($4\sigma^2_m$), dominance genetic variance as approximated by four times the variance due to female × male parent interactions ($4\sigma^2_{fm}$), ratios of additive to dominance variance, and individual heritabilities estimated on a maternal (h^2_f), paternal (h^2_m) or maternal *plus* paternal basis (h^2_{f+m}) for the *P. pinaster*, *P. radiata* and *P. elliottii* progeny trials. Ratios of additive to dominance variance are also presented for *P. elliottii* using female × male interaction variance ($\hat{\sigma}^2_{fm}$) adjusted for maternal effects.

Parameter estimate	Height (m)	Diameter (cm)	Volume (dm^3)	Straigh. (point)
P. pinaster -				
$4\sigma^2_f$	0.6200	0.3788	65.340	0.0372
$4\sigma^2_m$	0.2468	0.2832	30.142	0.0084
$4\sigma^2_{fm}$	negative	0.4072	26.779	0.0200
σ^2_f/σ^2_{fm}	*	0.9	2.4	1.9
σ^2_m/σ^2_{fm}	*	0.7	1.1	0.4
h^2_f	0.27±.11	0.05±.03	0.11±.05	0.04±.02
h^2_m	0.11±.09	0.03±.03	0.05±.05	0.01±.01
h^2_{f+m}	0.19±.10	0.04±.03	0.08±.05	0.03±.02
P. radiata -				
$4\sigma^2_f$	0.6476	0.3728	50.965	0.0220
$4\sigma^2_m$	0.4140	1.7452	202.644	0.0200
$4\sigma^2_{fm}$	negative	0.2520	58.698	0.0128
σ^2_f/σ^2_{fm}	*	1.5	0.9	1.7
σ^2_m/σ^2_{fm}	*	6.9	3.5	1.6
h^2_f	0.15±.11	0.03±.05	0.03±.05	0.02±.03
h^2_m	0.09±.10	0.14±.12	0.13±.12	0.02±.03
h^2_{f+m}	0.12±.11	0.09±.09	0.08±.09	0.02±.03
P. elliottii -				
$4\sigma^2_f$	0.3341	1.9739	179.555	0.5681
$4\sigma^2_m$	0.5309	1.0707	177.647	0.2825
$4\sigma^2_{fm}$	negative	0.2004	35.703	0.1852
σ^2_f/σ^2_{fm}	*	9.9	5.0	3.1
σ^2_m/σ^2_{fm}	*	5.3	5.0	1.5
$\sigma^2_m/\hat{\sigma}^2_{fm}$	*	1.0	4.7	0.6
h^2_f	0.28±.15	0.47±.20	0.36±.17	0.20±.11
h^2_m	0.45±.21	0.26±.14	0.36±.17	0.10±.07
h^2_{f+m}	0.37±.18	0.36±.17	0.36±.17	0.15±.09

The estimate of dominance variance for diameter of *P. radiata* was marginally less than the maternal estimate of additive variance ($\sigma^2_f/\sigma^2_{fm} = 1.5$; *Table 4*), and very much less than the paternal estimate ($\sigma^2_m/\sigma^2_{fm} = 6.9$). The corresponding rations of additive to dominance variance for volume of *P. radiata* were substantially lower than those for diameter, with the dominance variance for volume actually exceeding the maternal estimate of additive variance ($\sigma^2_f/\sigma^2_{fm} = 0.9$; *Table 4*). This finding of lower additive to dominance ratios for volume compared with diameter is surprising in view of the negative component of dominance variance estimated for height. If the true level of dominance variance for height was actually very small, the additive to dominance variance ratios for volume (calculated as a function of height and diameter) should be greater than the corresponding ratios for diameter.

Wilcox *et al.* (1975) analysed a 4 × 4 Design II mating (which was actually part of a larger 4 × 23 Design II) of *P. radiata* in New Zealand, and although the authors did not calculate variance components, the mean squares from analysis of variance suggest ratios of additive to dominance variance of less than 1.0 for height, diameter and volume at 5 years. However, later analyses of the completed 4 × 23 Design II across two sites showed ratios of additive to dominance variance of 0.9 and 2.0 for diameter at 5 or 6 years, and higher ratios of 3.6 and 2.0 for diameter at 10 years

(Dr R. D. BURDON, New Zealand Forest Research Institute, personal communication). CARSON (1986) analysed data collected at 4½ years from eighteen 5 × 5 disconnected half-diallel matings of *P. radiata* established across two sites in New Zealand and reported levels of dominance variance which almost equalled the additive variance for diameter and volume at one site. However, the dominance variance for growth traits was far less important at the other site.

As mentioned previously, *P. elliottii* exhibited the highest levels of additive variance of any of the three species studied, and the ratios of additive to dominance variance (unadjusted for maternal effects) for both diameter and volume were consistently large (exceeding 5.0; *Table 4).* (The ratios of additive to dominance variance for volume were again less than those for diameter, suggesting higher than estimated levels of true dominance variance for height). When an attempt was made to adjust for maternal effects in *P. elliottii* the ratio of additive to dominance variance declined to unity in the case of diameter, but the ratio for volume remained about the same. This large reduction in the adjusted ratio for diameter, but not volume, is a conflicting result which tends to confirm previous doubts about the reliability of the adjustment procedure itself.

The only other estimates of additive and dominance variance for *P. elliottii* appear to be those of KRAUS (1973) who analysed 14 × 5 and 9 × 5 Design II matings in Georgia, USA. This author found ratios of additive to dominance variance of between 1.3 and 2.3 for height at 6 years, which are lower than the ratios reported for *P. elliottii* in the present study. (Note that the ratios quoted above for *P. elliottii* in Georgia are half the ratios of combined female plus male additive variance over dominance variance calculated by KRAUS).

In conclusion, the levels of additive variance for growth to around 8 years were generally about the same, or greater than, the levels of dominance variance across the three species of pines studied in South Africa. The dominance effects tended to be greatest in the case of *P. pinaster* and least in the case of *P. elliottii,* with *P. radiata* approximately intermediate.

(2) Stem Straightness: The effects of both female and male parents were highly significant ($P < 0.01$) for stem straightness of *P. elliottii* (*Table 3*). Female parents only had a significant ($P < 0.01$) effect on straightness of *P. pinaster,* while neither the female or male parents significantly affected the straightness of *P. radiata.* There were no significant female × male parent interactions for stem straightness of any of the species studied.

In the case of *P. pinaster* and *P. radiata* the estimated levels of both additive and dominance variance were very low for straightness *(Table 4).* Although the additive variance generally exceeded the dominance variance (except in the case of σ^2_m/σ^2_{fm} for straightness of *P. pinaster),* the absolute magnitudes of the additive variance across the two species were sufficient only to produce very low individual heritabilities (e.g. $h^2_{f+m} = 0.03$ for straightness of *P. pinaster,* and $h^2_{f+m} = 0.02$ for *P. radiata; Table 4).* This reduced variation for straightness of *P. pinaster* and *P. radiata* is almost certainly due to the way the subjective scores were assigned for stem form in these progeny trials. A disproportionate majority of trees were assigned scores in the upper end of the range and the variation of the form trait was therefore restricted (as evidenced by the high mean values and lower standard deviations of straightness of *P. pinaster* and *P. radiata; Table 1).* In assigning form scores it is important to use the full range of the point-score (including extreme scores on both ends of the scale) and thereby create a reasonably normal distribution across the entire range of the scale.

Published estimates of individual heritability for straightness of *P. radiata* in Australia and New Zealand are consistently moderate to high (e.g. pooled or average values of 0.21, COTTERILL and ZED 1980; 0.17, SHELBOURNE and LOW 1980; 0.21, DEAN *et al.* 1983; and 0.39, MATHESON and RAYMOND 1984). In the previously mentioned 4 × 23 Design II mating of *P. radiata* measured across two sites in New Zealand the ratios of additive to dominance variance for straightness were found to be 1.9 and 5.7 at 5 or 6 years, and 1.0 and 4.0 at 10 years (BURDON, personal communication). Corresponding ratios for a subjective score of the number of branch whorls were 1.9 and 5.3 at 5 or 6 years, and 10.1 and 9.0 at 10 years. CARSON (1986) reported moderate levels of dominance variance for straightness at 4½ years in the 18 disconnected half-diallel matings of *P. radiata* in New Zealand.

In the case of *P. elliottii* the range of the eight-point subjective score for straightness was used more fully (see standard deviation for straightness of *P. elliotii; Table 1).* Consequently, the absolute magnitudes of the additive and dominance variance were much higher for *P. elliottii* compared with *P. pinaster* or *P. radiata* (*Table 4*), and the combined heritability for straightness of *P. elliottii* was a moderate $h^2_{f+m} = 0.15$. This estimate is similar to the individual heritability of 0.14 reported by ALLEN (1985) for straightness of *P. elliottii* in Queensland. SLUDER (1983) reported within-family heritabilities of 0.13 and 0.28 for *P. elliottii* across two sites in Georgia.

The estimated dominance variance of straightness of *P. elliottii* was less than the additive variance ($\sigma^2_f/\sigma^2_{fm} = 3.1$ and $\sigma^2_m/\sigma^2_{fm} = 1.5$; *Table 4*), except when the adjustment was made for maternal effects. The problem, as mentioned previously, is that there is no way of checking the reliability of this adjustment for maternal effects. These appear to be the first published estimates of ratios of additive to dominance variance for straightness of *P. elliottii.*

In conclusion, the level of additive variance appears to be somewhat greater than the dominance variance for straightness of *P. elliottii* at around 8 years in the Eastern Transvaal of South Africa. However, if maternal effects are taken into account the relative proportion of dominance variance may increase. The absolute magnitudes of the genetic variances for straightness of *P. pinaster* and *P. radiata* were substantially reduced by the manner in which form traits were evaluated.

Correlations

Phenotypic correlations and additive genetic correlations (the latter estimated using maternal components of additive variance and covariance) were consistently positive between all traits examined across the three species of pine in South Africa (*Table 5*). The genetic correlations between height and diameter were moderately strong for *P. radiata* (0.67 ± 0.38; *Table 5*) and very strong (with relatively low standard errors) in the case of *P. pinaster* (0.88 ± 0.12) and *P. elliottii* (0.78 ± 0.16). Genetic correlations between volume and height or diameter were very strong (values of 0.87 to 0.98) across the three species studied. The phenotypic correlations between growth traits followed similar trends to the genetic correlations but were generally lower in magnitude (values of 0.61 to 0.97; *Table 5*).

Table 5. — Genetic correlations and their standard errors estimated using maternal components of additive genetic variance and covariance, and phenotypic correlations for the *P. pinaster*, *P. radiata* and *P. elliottii* progeny trials.

Trait	Height	Diameter	Volume	Straigh.
P. pinaster -				
Height		0.88±.12[A]	0.97±.04	0.66±.22
Diameter	0.64[B]		0.98±.03	0.39±.36
Volume	0.78	0.94		0.62±.25
Straightness	0.37	0.33	0.32	
P. radiata -				
Height		0.67±.38[A]	0.87±.22	0.99±.35
Diameter	0.77[B]		0.95±.09	0.57±.71
Volume	0.83	0.97		0.73±.59
Straightness	0.58	0.50	0.53	
P. elliottii -				
Height		0.78±.16[A]	0.89±.09	0.78±.20
Diameter	0.61[B]		0.98±.02	0.46±.36
Volume	0.77	0.96		0.59±.30
Straightness	0.27	0.22	0.26	

[A]) Genetic correlations presented above the diagonals.
[B]) Phenotypic correlations below the diagonals.

Straightness was strongly correlated genetically with height across all three species (values of 0.66 to 0.99; *Table 5*) and moderately correlated with diameter (0.39 to 0.57). The standard errors of the genetic correlations between straightness and diameter were high. Cotterill and Zed (1980) and Dean *et al.* (1983) also report strong positive genetic correlations between straightness and growth traits of *P. radiata* in Australia. Phenotypic correlations between straightness and growth in the present study were much lower in magnitude (values of 0.22 to 0.58; *Table 5)* compared to corresponding genetic correlations.

Combining Abilities and Genetic Values

Combining abilities and genetic values have not been presented for every trait of all three species examined. Instead, as an example, these parameter estimates are presented only for diameter of *P. pinaster* (*Table 6*) and *P. elliottii* (*Table 7*). Diameter across these two species was, in the present study, controlled by widely contrasting levels of additive and dominance variance. For instance, diameter of *P. pinaster* exhibited marginally lower levels of additive relative to dominance variance (i.e. $\sigma^2_f/\sigma^2_{fm} = 0.9$ and $\sigma^2_m/\sigma^2_{fm} = 0.7$; *Table 4*), while the diameter of *P. elliottii* exhibited over five times more additive relative to dominance variance ($\sigma^2_f/\sigma^2_{fm} = 9.9$ and $\sigma^2_m/\sigma^2_{fm} = 5.3$).

Table 6 lists the 13 female parents involved in the *P. pinaster* matings in order of decreasing general combining abilities (gca) for diameter. For instance, female parent 68 had the highest gca of 0.64 cm for diameter at 8½ years (or 0.64 cm above the progeny trial mean of 13.40 cm; *Table 6*). The female parent 43 had the lowest gca of −0.85 cm for diameter (or 0.85 cm below the trial mean). The five male parents are likewise listed in order of decreasing gca.

Assuming a strictly additive genetic model (with no dominance or epistatic variance) the best full-sib families for diameter would be expected to be the crosses between the female and male parents having the highest gca's. In other words, under the assumption of additivity the performance of each cross should equal the predicted genetic value (i.e. the sum of the parents gca's). Therefore, in the case of the *P. pinaster* matings, the cross between the best female parent 68 and the best male 12 had the highest predicted genetic value of 1.15 cm for diameter (1.15 cm above the trial mean; *Table 6*). The cross 51 × 12 had the next highest predicted genetic value, and so on. A ranking is actually given in *Table 6* beside the 10 families having the highest predicted genetic values. The best families on the basis of predicted performance are, of course, clustered in the top left corner of *Table 6*.

In practice, the diameter of *P. pinaster* clearly defies the assumption of a strictly additive model (having more dominance variance relative to additive variance, as well as a very low heritability) and the observed (or least-squares) genetic values were often very different from the predicted values. (The difference between the observed and predicted genetic values being the specific combining ability, sca). As already mentioned, the cross 68 × 12 was expected to be the best for diameter having a predicted genetic value 1.15 cm. However, this family failed to rank in the top 10 on actual performance with a rather mediocre observed genetic value of 0.48 cm (due to a strong negative specific combining effect of −0.67 cm; *Table 6*). The best cross for diameter turned out to be 68 × 46, which ranked fourth on predicted genetic value, but had a high observed genetic value of 1.74 cm due to a very strong positive sca of 1.04 cm (*Table 6*). The next best cross proved to be 25 × 12, which ranked fifth on predicted genetic value, but had a fairly high observed value 1.34 cm (*Table 6*). The third best cross for diameter was 71 × 12 which also had the third highest predicted value.

In the case of the diameter of *P. elliottii* the additive variance was much greater than the dominance variance, and therefore observed genetic values tended to conform more closely to predicted values (*Table 7*). (In other words, the trait tended to conform more closely to a strictly additive genetic model). For instance, cross 126 × 137 had the highest predicted genetic value of 2.00 cm for diameter

Table 6. — General combining abilities (gca) for diameter of female and male parents in the *P. pinaster* progeny trial, observed and predicted genetic values of full-sib families, and specific combining abilities (sca). All values are expressed as deviations from the overall mean diameter of 13.40 cm for the progeny trial. The top 10 full-sib families according to observed or predicted genetic values are identified by rankings in square brackets.

Female parent (gca)		Male parent (gca)				
		12 (0.51)[A]	46 (0.06)	19 (-0.13)	33 (-0.17)	90 (-0.27)
68 (0.64)	Obs.[A]	0.49	1.74[1]	0.36	0.80[10]	-0.18
	Pred.[B]	1.15[1]	0.70[4]	0.51[9]	0.47	0.37
	(sca)[C]	(-0.67)	(1.04)	(-0.15)	(0.33)	(-0.55)
51 (0.62)		1.07[6]	0.00	1.10[5]	0.06	0.85[9]
		1.13[2]	0.68[6]	0.49[10]	0.45	0.35
		(-0.06)	(-0.68)	(0.61)	(-0.39)	(0.50)
71 (0.37)		1.29[3]	1.10[4]	0.02	-0.15	-0.41
		0.88[3]	0.43	0.24	0.20	0.10
		(0.41)	(0.67)	(-0.22)	(-0.35)	(-0.51)
25 (0.19)		1.34[2]	-0.19	0.18	-0.62	0.23
		0.70[5]	0.25	0.06	0.02	-0.08
		(0.64)	(-0.44)	(0.12)	(-0.64)	(0.31)
73 (0.12)		1.03[8]	0.16	-0.19	0.30	-0.70
		0.63[7]	0.18	-0.01	-0.05	-0.15
		(0.40)	(-0.02)	(-0.18)	(0.35)	(-0.55)
77 (0.01)		1.05[7]	0.23	-0.35	-0.68	-0.22
		0.52[8]	0.07	-0.12	-0.16	-0.26
		(0.53)	(0.16)	(-0.23)	(-0.52)	(0.04)
63 (-0.06)		0.36	-0.97	-0.16	0.13	0.35
		0.45	0.00	-0.19	-0.23	-0.33
		(-0.09)	(-0.97)	(0.03)	(0.36)	(0.68)
76 (-0.13)		0.32	0.41	-0.60	0.00	-0.79
		0.38	-0.07	0.26	-0.30	-0.40
		(-0.06)	(0.48)	(-0.86)	(0.30)	(-0.39)
59 (-0.20)		-0.69	0.58	0.58	-0.65	-0.81
		0.31	-0.14	-0.33	-0.37	-0.47
		(-1.00)	(0.72)	(0.91)	(-0.28)	(-0.34)
27 (-0.20)		-0.32	0.45	-0.07	-0.85	-0.22
		0.31	-0.14	-0.33	-0.37	-0.47
		(-0.63)	(0.59)	(0.26)	(-0.48)	(0.25)
75 (-0.23)		-0.10	-0.16	-0.70	0.49	-0.70
		0.28	-0.17	-0.36	-0.40	-0.50
		(-0.38)	(0.01)	(-0.34)	(0.89)	(-0.20)
69 (-0.28)		0.50	-0.86	-0.53	-0.08	-0.45
		0.23	-0.22	-0.41	-0.45	-0.55
		(0.27)	(-0.64)	(-0.12)	(0.37)	(0.10)
43 (-0.85)		0.25	-1.78	-1.30	-0.87	-0.49
		-0.34	-0.79	-0.98	-1.02	-1.12
		(0.59)	(-0.99)	(-0.32)	(0.15)	(0.63)

[A]) Standard errors are approximately 0.26 cm for gca estimates and approximately 0.48 cm for observed genetic values.

[B]) Predicted genetic values for each full-sib family are calculated as the sum of the parental gca's.

[C]) Sca estimates for each full-sib family are calculated as the difference between observed and predicted genetic values.

at 8½ years, and proved also to have the highest observed value of 2.43 cm (*Table 7*). The cross 174 × 137 had the second highest predicted genetic value of 1.91 cm for diameter and the third highest observed value of 1.83 cm (*Table 7*). However, substantial levels of sca were evident for diameter in many crosses of *P. elliottii*. For instance, the crosses 126 × 9 and 88 × 137 were predicted to rank third and fourth for diameter but, due to strong negative sca's, these families actually performed below average having negative observed genetic values. These two crosses exhibited far greater sca than any of the other *P. elliottii* matings. The cross 174 × 9 ranked fifth on predicted genetic value but actually produced the second highest observed genetic value for diameter because of strong positive sca.

Table 7. — General combining abilities (gca) for diameter of female and male parents in the *P. elliottii* progeny trial, observed and predicted genetic values of full-sib families, and specific combining abilities (sca). All values are expressed as deviations from the overall mean diameter of 15.21 cm for the progeny trial. The top 10 full-sib families according to observed or predicted genetic values are identified by rankings in square brackets.

Female parent (gca)		Male parent (gca)							
		137 (1.13)[A]	9 (0.42)	49 (0.22)	45 (−0.23)	177 (−0.29)	23 (−0.33)	129 (−0.44)	22 (−0.48)
126 (0.87)	Obs.[A]	2.43[1]	−0.01	1.19[5]	0.93[6]	0.76	0.39	0.36	0.93[7]
	Pred.[B]	2.00[1]	1.29[3]	1.09[7]	0.64	0.58	0.54	0.43	0.39
	(sca)[C]	(0.43)	(−1.30)	(0.10)	(0.29)	(0.18)	(−0.15)	(−0.07)	(0.54)
174 (0.78)		1.83[3]	2.03[2]	0.79[9]	0.06	0.43	0.52	0.39	0.17
		1.91[2]	1.20[5]	1.00[8]	0.55	0.49	0.45	0.34	0.30
		(−0.08)	(0.83)	(−0.21)	(−0.49)	(−0.06)	(0.07)	(0.05)	(−0.13)
87 (0.32)			0.53	0.65	−0.21	0.57	−0.26	−0.24	0.13
			0.74[10]	0.54	0.09	0.03	−0.01	−0.12	−0.16
			(−0.21)	(0.11)	(−0.30)	(0.54)	(−0.25)	(−0.12)	(0.29)
88 (0.12)		−0.23	0.76	0.49	−0.31		0.39		−0.41
		1.26[4]	0.54	0.34	−0.12		0.22		−0.36
		(−1.49)	(0.22)	(0.15)	(−0.19)		(0.17)		(−0.05)
128 (0.02)		0.66	1.26[4]	−0.23	−0.34	−0.22	−0.11		−0.47
		1.16[6]	0.44	0.24	−0.22	−0.28	−0.32		−0.46
		(−0.50)	(0.82)	(−0.47)	(−0.12)	(0.06)	(0.21)		(−0.01)
57 (−0.31)		0.79[10]	0.63		0.07	−1.14	−0.44	−0.81	−1.51
		0.82[9]	0.11		−0.54	−0.60	−0.64	−0.75	−0.79
		(−0.03)	(0.52)		(0.61)	(−0.54)	(0.20)	(−0.06)	(−0.72)
58 (−0.47)		0.89[8]	−0.38	0.03	−0.44	−1.07	−1.24	−0.50	−1.01
		0.66	−0.05	−0.25	−0.70	−0.76	−0.80	−0.91	−0.95
		(0.23)	(−0.33)	(0.28)	(0.26)	(−0.31)	(−0.44)	(0.41)	(−0.06)
76 (−1.33)		0.49	−1.44		−1.61	−1.44	−1.85	−2.01	−1.68
		−0.20	−0.91		−1.56	−1.62	−1.66	−1.77	−1.81
		(0.69)	(−0.53)		(−0.05)	(0.18)	(−0.19)	(−0.24)	(0.13)

[A]) Standard errors are approximately 0.33 cm for gca estimates and approximately 0.53 cm for observed genetic values.
[B]) Predicted genetic values for each full-sib family are calculated as the sum of the parental gca's.
[C]) Sca estimates for each full-sib family are calculated as the difference between observed and predicted genetic values.

Implications for Breeding Strategy

Carson (1986) identified two fundamental strategies for mass vegetative propagation. The first strategy, called the "tested cross" option, involves crossing all new-generation selections (chosen in the breeding population) in as many combinations as possible and progeny testing the large number of full-sib families generated to determine which are the most outstanding. Mass controlled-pollinations would then be carried out in seed orchards ("control-pollinated seed orchards", using Carson's terminology) or clone banks to produce commercial quantities of seed of the few outstanding full-sib families, and the ensuing seedlings would be multiplied by mass vegetative propagation. (Two-clone orchards or supplementary mass pollination might also be used to produce the commercial quantities of seed required.) The main practical problem with the tested cross option is the substantial labour required to complete controlled-pollinations among new-generation selections and screen the potentially very large number of families generated.

The second strategy, called "general combiner selection", involves an initial polycross or open-pollinated progeny test to determine the gca's of all new-generation selections in the breeding population. Mass controlled-pollinations (or perhaps supplementary mass pollination) would then be used to produce commercial quantities of seed of crosses involving only those parents having the very best gca's, and the ensuing seedlings would be multiplied by mass propagation. General combiner selection is less labour intensive and operationally simpler because it requires testing of the parents only, not every possible cross among those parents. Carson (1986) found that general combiner selection produced marginally greater expected genetic gains than the tested cross option under circumstances where progeny testing capacity is limited (i.e. where the total number of offspring which can be tested is limited).

The results of the present study lend some support to general combiner selection (or relying solely on additive genetic variance) for species which are mass propagated. However, *Tables 6* and *7* indicate that additional gains may be achieved from an integrated approach involving general combiner selection followed by testing the limited number of possible crosses among the very best general combining parents only. In other words, a two-stage approach involving stage-1 general combiner selection and stage-2 limited tested cross.

There seems little point in a tested cross option which involves crossing all the individuals selected in the breeding population in as many combinations as possible and screening the many full-sib families generated in a rather hit-or-miss attempt to find a few exceptionally outstanding families for mass propagation. Considerable time and effort

may be saved by first identifying those parents having the very highest gca's (stage-1 general combiner selection) and then testing only crosses among these parents (stage-2 limited tested cross). This approach ignores the vast majority of potential crosses which involve parents having sufficiently high gca's to be selected in the breeding population, but are not among the very top general combiners. The results given here suggest that these good, but not outstanding parents, are not very likely to produce outstanding families. For instance, in the case of diameter of both *P. pinaster* and *P. elliottii* the top five crosses (out of 65 and 64 crosses, respectively) on predicted genetic value (the sum of the parental gca's) turned out to include the families which ranked first, second and third on observed genetic values (*Tables 6* and *7*). This is despite the fact that diameter of *P. pinaster* exhibited substantial levels of dominance genetic variance. Although results are not presented, similar trends were found between predicted and observed genetic values for height, volume and stem straightness of the three species examined. The single cross between the female and male parents which ranked first on gca for a particular trait did not always produce the most outstanding family (as evidence in the case of diameter of *P. pinaster; Table 6*). However, the crosses between the best two or three female and male parents invariably included top ranking families.

It is possible to use genetic values estimated in the present study to calculate gains expected from general combiner selection used alone, compared with general combiner selection followed by limited tested cross. Consider general combiner selection to retain say four *P. elliottii* parents (out of 16 parents) having the highest gca's for diameter. Genetic gain in this instance can be calculated as twice the average of the gca's of the four parents retained (or the average of their breeding values). The best four *P. elliottii* parents for diameter happen to be the female parents 126 and 174 and male parents 137 and 9 (*Table 7*), and twice the average of their gca's is 1.60 cm. A genetic gain of 1.60 cm represents an increase of 10.5% in the overall mean for diameter of *P. elliottii*. If, however, the six possible crosses (excluding self and reciprocal crosses) between these four selection were subsequently tested and the best cross 126 × 137 used for mass vegetative propagation, the genetic gain would be 2.43 cm (which is the observed genetic value of 126 × 137; *Table 7*). This gain represents a 16.0% increase in the overall mean for diameter of *P. elliottii*. If the two best crosses (126 × 137 and 174 × 9) were mass propagated the gain would be 2.23 cm (the average of the observed genetic values of the two families), or 14.7%. This moderate gain advantage for general combiner selection followed by limited tested cross was found to be approximately the same for all traits across all three species studied. (Note that only four of the six possible crosses between the top four *P. elliottii* parents for diameter are completed in the Design II matings in *Table 7*. The above calculations of gain for general combiner selection followed by limited tested cross would, therefore, be biased downward if the missing crosses happened to be superior. However, the bias should be fairly slight.)

In circumstances where general combiner selection is on multiple-traits the gca's of each parent for individual traits may be weighted for relative economic importance, and then summed to provide an estimate of the parental "net worth" or "net merit". Parents having the greatest net merit would be selected as best. Alternatively, the predicted genetic values of a particular cross for individual traits may be weighted and then summed to provide an estimate of the expected net merit of the resulting family, before the controlled-pollinations actually begin. Crosses having the greatest net merit would be completed in the subsequent controlled-pollination program. This latter approach is equivalent to the "net merit index" described by Allaire (1980). The group of parents which are selected and mated would be the same under both approaches, except where the economic weightings of traits are non-linear. In other words, where relative economic importance changes with increasing or decreasing phenotypic value of traits. Under conditions of non-linear weights the net merit index can be far more efficient (Allaire 1980). Cotterill (1984) recommended routine use of the net merit index in breeding *P. radiata* in South Australia.

Conclusions

Additive variance tended to be about the same or greater than dominance variance for growth of *P. pinaster* and *P. radiata* at around 8 years in the Southern Cape of South Africa. By contrast, additive variance was generally much greater than dominance variance for growth and straightness of *P. elliottii* at 8½ years in the Eastern Transvaal. Additive genetic associations between growth traits and between growth traits and straightness were positive across all three species.

An important finding of this study is that mating best gca parents with best gca parents appears reasonably likely to produce outstanding families, even where levels of dominance variance are about equal to the additive genetic variance. This approximate adherence to an additive genetic model, at least for practical breeding purposes, has important implications for breeding stratgey of species which are mass vegetatively propagated.

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Genetic Differentiation among Seed Samples from Provenances of Pinus sylvestris L.

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Summary

Differentiation is studied among seed samples from nine Scots pine forest stands or seed orchards. The results are based on the allele frequencies obtained at ten enzyme gene loci. Pairwise statistical comparisons between the samples indicated significant deviations for nearly all pairs. The genetic distances reflected similar tendencies but were shown to allow more reliable interpretations of the genetic differences between samples and the efficiency of single loci in revealing such differences. A new method of subpopulation differentiation was applied to measure and illustrate the genetic differentiation among the samples and their complements instead of in pairs. The presented graphs clearly point out loci reflecting maximum differentiation and thus can serve as a criterion for the selection of the best-suited single locus or multilocus combination. The proposed methods can be utilized equally well for genotype frequencies, which, lowever, requires larger sample sizes. As a result of the measure of subpopulation differentiation, the seed orchard crops were proven to show greater genetic differentiation than the samples representing the seed of forest stands.

Key words: Differentiation, allele frequency, provenance, forest, seed, *Pinus sylvestris* L.

Zusammenfassung

Bei *Pinus sylvestris* L. wurde die Differenzierung zwischen Samenstichproben aus neun Beständen bzw. Samenplantagen untersucht. Die Ergebnisse basieren auf den an zehn Enzym-Genorten ermittelten Allelhäufigkeiten. Der paarweise statistische Vergleich zwischen den Proben zeigt für nahezu alle Paare signifikante Abweichungen. Die genetischen Abstände spiegeln ähnliche Tendenzen wider, sie gestatten jedoch zuverlässigere Interpretationen der genetischen Unterschiede zwischen den Proben und verdeutlichen die Effektivität einzelner Genorte für den Nachweis solcher Unterschiede. Es wird eine neue Methode der Differenzierung von Subpopulationen angewendet, um genetische Differenzierung nicht paarweise sondern zwischen Einzelproben und der jeweiligen Komplemente zu messen und zu veranschaulichen. Die verwendeten Darstellungen zeigen deutlich, welche Genorte größte Differenzierung reflektieren und können daher als Kriterium für die Auswahl der am besten geeigneten Einzel-Genorte oder deren Kombinationen dienen. Die vorgeschlagene Methode kann gleichermaßen gut für die Häufigkeiten von Genotypen verwendet werden, jedoch erfordert dies größere Stichprobenumfänge. Als ein Ergebnis der Messung der Differenzierung von Subpopulationen kann festgehalten werden, daß die aus Plantagen stammenden Proben eine größere genetische Differenzierung zeigen als diejenigen aus Waldbeständen.

Introduction

In this country, the marketed reproductive material of coniferous species still originates exclusively from generative propagation. By law, this category is termed "selected reproductive material". In effect, such seed originates from collections in phenotypically selected forest stands or from particular breeding populations, i.e. seed orchards, which are laid out to reduce pollination from the outside and are managed to produce abundant crops of seed. At present, in Scots pine (*Pinus sylvestris* L.), clonal seed orchards cover nearly 500 ha or 0.4% of the total area of selected Scots pine seed stands. The area devoted to clonal seed orchards, is, however, increasing continuously, as is the productivity. Seed stands are located in designated regions of provenance which are supposed to be ecologically homogeneous. The clones being used for seed orchard establishment descend vegetatively from phenotypically selected trees in forest stands within regions of provenance. In the present paper,