Conclusions

From the analyses of provenance tests of muricata pine grown at 2 locations in Greece the following conclusions can be drawn:

There are significant differences between the provenances of muricata pine, in growth, bark thickness and branching characteristics. Mendocino inland blue provenance (09/2) is the fastest, while the Humboldt Trinidad Head (provenance 10) is the slowest in growth. At the early years (up to the age of 5 years) muricata and radiata pine have the same growth rate. However, later on, muricata is growing much slower. It is therefore recommended that the use of muricata pine in Greece must be restricted only on the hardier sites of higher elevation, where the growth of the faster growing radiata pine is rather problematic.

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Genetic Parameter Estimates for Production and Quality Traits of *Pinus elliottii* Engelm. var. *elliottii* in Zimbabwe

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Summary

P. elliottii Engelm. var. *elliottii* is an important exotic plantation species in Zimbabwe, where it is grown for saw-timber and resin production. Two progeny tests, originating from factorial matings between parents selected in plantations, were assessed at 5, 8 and 15 years. This paper reports genetic parameter estimates for important production and quality traits. All traits assessed were under a reasonable degree of additive genetic control, with the magnitudes of non-additive genetic variances almost invariably somewhat less than those of additive genetic variances. Narrow-sense heritabilities for growth traits, wood density and resin yield were moderate to high, ranging from 0.16 to 0.42; those for stem straightness and branching traits were lower, ranging between 0.04 and 0.17. Genetic correlations at each of the assessment ages were more variable; of most consequence for production were the slight negative correlations between wood density and both stem diameter and volume, and the slight positive correlation between density and height. Age-age correlations for growth traits were high, indicating potential for early selection. Age-age correlations for other traits were variable.

Key words: factorial mating design, genetic parameters, progeny tests, *Pinus elliottii*.

FDC: 232.11; 165.4; 174.7 *Pinus elliottii;* (689.1).

1. Introduction

Some 35 000 ha of *Pinus elliottii* Engelm. var. *elliottii* plantations have been established in Zimbabwe, where the commercial importance of the species is second only to *P. patula* Schiede and Deppe (Zimbabwe Forestry Commission[4]), pers. comm.). Under Zimbabwean conditions, *P. elliottii* has advantages over

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Table 1. – Families represented in the 2 progeny tests, where A and B refer to those present in tests 23a and 23b respectively. The A crosses in the inner block represent those in the 8×8 factorial sampled for resin yield in test 23a.

Females	Males								
	22	23	45	49	129	137	177	9	130
22		AB			AB	AB		AB	
23				AB	AB	AB	AB	AB	A
45	AB	A		AB	AB	AB	AB	AB	A
49	A	AB	AB		AB	AB		AB	
129	A	AB	AB	AB		AB		AB	AB
137	AB	AB	AB	AB	AB			AB	AB
177	AB	A	AB	AB	AB	AB		AB	AB
9	AB	AB	AB	AB	AB		AB		A
130									
58	AB	AB	AB	AB	AB	AB	AB	AB	
76	AB	AB	AB	AB	AB	AB	AB	AB	
87	A	AB	AB	AB	AB	AB	AB	AB	
126	AB	AB	AB	AB	AB	AB	AB	AB	
128	AB	AB	AB	AB	AB	AB	AB	AB	
174	AB	AB	AB	AB	AB	AB	AB	AB	
175	AB	AB	AB	AB	AB	AB	AB	AB	B
200	AB	AB	AB	AB	AB	AB	AB	AB	AB
28	AB	A		AB		A	AB	AB	
43	AB	AB		AB	AB			AB	
57	AB	AB	AB		AB	AB	AB	AB	
125	AB	AB		A	AB		AB	AB	
132	AB	AB	AB	AB	AB	AB	AB	B	
138	AB	AB	AB	AB	A		AB	AB	AB
172	AB	AB		AB			A	AB	
173		AB	AB	AB		AB	AB	AB	AB
176	AB	AB			AB	AB	AB		A
86		AB	AB				AB	AB	
88	AB	AB	AB	AB	A	AB		AB	
89	A	AB		AB	AB	AB	AB		
178				A			A		
203		AB		A			AB	AB	
224	A	AB		AB	AB		AB	AB	
234	AB	A		A	A	A	A	B	A

the alternative coniferous species, *P. patula* and *P. taeda* L., in terms of its capacity to withstand infertile soils and weed competition (MULLIN *et al.,* 1978). Saw-timber and pulpwood are the major wood products of Zimbabwean *P. elliottii* plantations; particle chipboards and veneers are also manufactured. The major non-wood product is resin, which is tapped commercially for the production of rosin and turpentine.

Genetic improvement of *P. elliottii* in Zimbabwe began in 1958 (MULLIN *et al.,* 1978), in association with large-scale commercial afforestation in the Eastern Highlands. The focus of breeding activities has been on phenotypic selection, clonal seed orchard establishment, and the production of improved seed. Although series of progeny tests of full-sib families have been established, estimates of genetic parameters have so far been limited to preliminary investigations at early ages (BARNES and MULLIN, 1989). The study described here was initiated to derive the more comprehensive estimates that are essential for informed breeding decisions.

Data were available from progeny tests established across 2 sites with families originating from a factorial mating design. The tests had been assessed for important production and quality traits at 5, 8 and 15 years of age; this paper reports estimates of heritabilities, genetic correlations, and age-age

correlations for the important production traits of growth, stem straightness, branching traits, wood density and resin yield. Companion papers (PSWARAYI *et al.,* in prep., a and b) draw from these results to address 2 issues relevant to breeding decisions: assessment of the importance of genotype-environment interaction, and the development of combined selection indices.

2. Genetic Material, Test Design and Management

The progeny tests from which data originate are part of a series established in January and February 1976 by the Zimbabwe Forestry Commission. The 216 full-sib families represented in the tests derive from a factorial mating design involving 33 parents, which had been selected as superior phenotypes in unimproved plantations in Zimbabwe and South Africa. Little is known of their genetic origin or degree of relatedness, but it is assumed that they are unrelated since they were widely distributed within plantations. The South African plantations in which parents were selected originated from seedlots from Georgia, S. Carolina and Central Louisiana, USA; the Zimbabwean plantations were derived from seed collected in South African plantations. The crosses represented in the tests are shown in *table 1.*

The tests were planted at a spacing of 2.44 m x 2.44 m on 2 sites in Zimbabwe, in a randomized complete block design with 6 replications of 10-tree line plots of each family. The sites are identified locally as tests 23a and 23b; relevant details are summarised in *table 2*. The test sites are typical of those in the Zimbabwean Eastern Highlands on which commercial plantations of *P. elliottii* are established. Each test was thinned at 8 years by systematically removing every other tree, leaving 50% of the original trees standing.

Table 2. – Details of progeny tests used in this study.

Identification	Test	
	23a	23b
Location	Tarka, E. Highlands	Stapleford, E. Highlands
Latitude	19° 59′S	18° 44′S
Longitude	32° 56′E	32° 49′E
Altitude (m)	967	1760
Mean annual rainfall (mm)	2279	1836
Mean annual temperature (°C)	16.6	14.1
Soil type	Dolerite/quartzite-derived; varying from reddish brown fine grained sandy loams to red brown clays.	Quartzite/dolerite-derived; brown red clays.
Parental origin	Bulk commercial ex Georgia, Lousiana and South Carolina, USA, via South Africa.	
Mating design	Factorial 24♀ x 9♂	Factorial 23♀ x 9♂
Crosses represented	157 of possible 216	145 of possible 207

3. Assessment Procedures

The progeny tests were measured for height and diameter and assessed for stem straightness at 5, 8 and 15 years after planting. Branching characteristics were assessed only at 5 years, and wood density and resin yield only at 15 years. Height was measured with metre rods, from the base of the tree to the tip of the growing shoot. Stem diameter over bark was measured at 1.3 m (breast height) overbark with a girth tape. Stem volume over bark at 5, 8 and 15 years was calculated from the height and diameter measurements using the volume function:-

$$VOL_i = 0.45\pi(DBH_i/2)^2 HT_i \qquad (1)$$

where VOL_i = stem volume (dm³) at 5, 8 or 15 years;
$\quad DBH_i$ = stem diameter over bark (cm) at 1.3 m at 5, 8 or 15 years;
$\quad HT_i$ = the height (m) at 5, 8 or 15 years;
and 0.45 is the form factor appropriate for the species (MILLS[5] pers. comm.).

Stem straightness (STR5, STR8, STR15) was assessed on a predetermined absolute scale of 1 (crooked) to 7 (straight), following the classification reported by BARRETT and MULLIN (1968). Three traits were assessed to characterise branching excellence. The branch count (BRCT5) involved counting all branches in the 2 whorls nearest breast height. This trait was assessed as a measure of the average number of branches per whorl on each tree. The average branch diameter (BRDM5) was calculated as the mean of the diameters of all branches in these 2 whorls, measured at approximately 5 cm from the base of each. It was assessed as an indication of branch size. The internode length (AIL) was measured as the average internode length along the stem, excluding the section between the ground and the first whorl (BARNES, 1973). This trait was assessed to characterise the frequency of whorls along the

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stem. As *P. elliottii* in Zimbabwe grows in a series of flushes throughout the year, internode length is not equivalent to annual height growth, as it might be for a temperate species.

Wood density was assessed in only three replicates of each test, and estimated following HEINRICHS and LASSEN (1971):-

$$\qquad\qquad\qquad\qquad (2)$$
$$DENS15 = \frac{dry\ weight(grams)}{green\ volume(cm^3)}.1000$$

where DENS15 = density in kg/m³.

Resin was tapped from living trees in a subset of families in test 23a which consisted of an 8 x 8 factorial design (*Table 1*). Resin was collected over a 3 month period (October to December) and the amount of resin produced (RESQ15) was expressed in grams per week.

4. Parameter Estimation Procedures

Parameters were estimated both from individual tree data at each site and from individual tree data pooled across the 2 sites. The case for the latter has been argued by WHITE and HODGE (1989), *viz* that more reliable estimates are likely to derive from the larger sample size of pooled data sets. As it is only these pooled parameters that are likely to be of more general interest, estimates for individual sites are not reported here, but are available from the authors.

Variance components were estimated by the Residual Maximum Likelihood (REML) methodology, as described by HARVILLE (1977), PATTERSON and THOMPSON (1971 and 1975) and SEARLE (1971 and 1987). The assumptions underlying the model are that the levels of each random factor are uncorrelated and normally distributed with a common variance. The residuals in the vector of random errors are also assumed to be normally distributed and uncorrelated with each other and with the other terms in the model (ROBINSON, 1987).

In the analyses, parents were treated as random effects, as they represented a sample of all parents of interest in the population about which inferences were made. The linear model used for analysis of the pooled data was:-

$$\qquad\qquad\qquad\qquad (3)$$
$$Y_{ijklm} = \mu + F_i + M_j + FM_{ij} + S_l + R_k:S_l$$
$$+ FS_{il} + MS_{jl} + FMS_{ijl} + FMSRijkl + e_{ijklm}$$

where Y_{ijklm} = individual tree observation;
$\quad \mu$ = population mean;
$\quad F_i$ = random effect of the ith female;
$\quad M_j$ = fixed effect of the jth male;
$\quad FM_{ij}$ = random effect of the ij^{th} family;
$\quad S_l$ = fixed effect of the lth site;
$\quad R_k:S_l$ = fixed effect of the kth replicate within the lth site;
$\quad FS_{il}$ = random effect of the ith female x l^{th} site interaction;
$\quad MS_{jl}$ = random effect of the jth male x l^{th} site interaction;
$\quad FMS_{ijl}$ = random effect of the ij^{th} family x l^{th} site interaction;
$\quad FMSR_{ijlk}$ = random effect of the ij^{th} family x fixed effect of the kth replicate within the lth site interaction;
$\quad e_{ijklm}$ = residual error.

In the case of resin yield, which was assessed at only one site, the model was reduced to the main effects of F_i, M_j and R_k, and their interactions.

Estimates of additive and dominance variances were derived from the covariances between half and full-sibs, as described by BECKER (1975) and COTTERILL *et al.* (1987). When the coefficient of inbreeding among the parents (F) is assumed to be zero and epistatic and maternal effects are assumed negligible, the additive variance can be directly derived from the female variance component:-

$$\sigma_A^2 = 4\,\sigma_f^2 \qquad (4)$$

where σ_a^2 = variance due to additive genetic effects;

σ_f^2 = random effect of the ith female parent.

Additive genetic variance may also be estimated from the male parents, as follows:-

$$\sigma_A^2 = 4\,\sigma_m^2 \qquad (5)$$

where σ_m^2 = random effect of the jth male parent and σ_a^2 is as defined above.

However, in factorial designs where the number of male parents is much less than that of the female parents, this estimate is likely to be less precise than that estimated from the variance due to female parents (BRIDGEWATER, 1992).

Dominance genetic variance was estimated as:-

$$\sigma_D^2 \approx 4\,\sigma_{fm}^2 \qquad (6)$$

where σ_d^2 = dominance genetic variance;

σ_{fm}^2 = random effect of the ij^{th} family.

The total phenotypic variance was estimated as:-

$$\sigma_P^2 = \sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_{fs}^2 + \sigma_{ms}^2 + \sigma_{fmr}^2 + \sigma_w^2 \qquad (7)$$

where σ_p^2 is the total phenotypic variance, σ_f^2, σ_m^2, σ_{fm}^2 are as described above, σ_{fmr}^2 is the variance component due to family-replicate interaction (or plot mean), and σ_w^2 is that due to residual, which also contains the remainder of the genetic variance and the environmental variance, *ie*, the within-family variance.

Estimates of narrow-sense heritabilities on an individual tree basis could be derived separately from maternal and paternal half-sib covariances. However, the relatively small number of male parents compared to female parents represented here (9 *vs* 24, *Table 1*) limits the value of parameter estimates from the former, as BRIDGEWATER (1992) noted for tester designs more generally. It would also be possible to derive an average parameter from female and male estimates, either as an unweighted mean (*eg* COTTERILL *et al.,* 1987) or on some weighted basis – for example, weighting by the inverse of the standard error as described by CUNNINGHAM (1977). However, we followed the simpler and equally defensible (see discussion in COTTERILL *et al.,* 1987) approach of limiting parameter estimates to those from the female parents, which were calculated as:-

$$h_f^2 = \frac{4\,\sigma_f^2}{\sigma_p^2} \qquad (8)$$

where h_f^2 is the narrow-sense heritability estimated from the maternal variance. Standard errors were estimated by the program GENSTAT REML (MEYER, 1989). These heritability

estimates are block-adjusted, as discussed by COTTERILL (1987).

Phenotypic and genetic correlations between traits were estimated using generalised least-squares analysis, by the program LSLMLW (HARVEY, 1987). The genetic correlations were based only on the maternal half-sib variances and covariances, for the reasons described above. Additive genetic correlations for height at age 5 were estimated from the whole population; correlations at 8 years were estimated from that half of the population that was thinned systematically, as measurements were made only on this part of the population; correlations at 15 years were estimated from that half of the population that was left standing after the 50% thinning at 8 years. As the thinning at 8 years was systematic, it is expected that both 8 and 15 year data should still be representative of the whole population. The term "juvenile-mature correlation" is used subsequently to describe genetic correlations between traits at ages considered juvenile, *viz* 5 or 8 years, and that considered to approximate maturity, *viz* 15 years, which corresponds to around half the commercial rotation age.

Analyses followed the simplified linear model:-

$$(9)$$
$$Y_{ijklm} = \mu + F_i + M_j + FM_{ij} + S_l + R_k{:}S_l + e_{ijklm}$$

where Y_{ijklm} = individual tree observation;

μ = population mean;

F_i = random effect of the ith female;

M_j = fixed effect of the jth male;

FM_{ij} = random effect of the ij^{th} family;

S_l = fixed effect of the lth site;

$R_k{:}S_l$ = fixed effect of the kth replicate within the lth site;

e_{ijklm} = residual error.

A limitation in the program required the simplifying assumption that interactions of females or males with other fixed effects, such as replicates, are negligible. This assumption will render the estimates less precise than they would otherwise be, and illustrates the difficulty of realising good estimates of genetic correlations (*eg* HODGE and WHITE, 1992). Other assumptions are as for the REML analysis. Standard errors were calculated according to BECKER (1975).

As resin yield was assessed only at one site, wood density only in some replicates, and height recorded and volume estimates derived at 8 years for thinned trees only, it was not possible to estimate correlations involving these traits using the standard methodology described above. Correlations between family means were assumed to be the best proxy in these cases, and were estimated from the appropriate family data sets, following BURDON (1977), as:-

$$r_{G_{xy}} = \frac{r\,\overline{N}_{f_{xy}}}{(\sqrt{h_{fx}^2})\,(\sqrt{h_{fy}^2})} \qquad (10)$$

where r_{Gxy} = genetic correlation of family means of the traits x and y;

$r_{\overline{N}fxy}$ = correlation of family means between trait x and trait y;

h_{fx}^2, h_{fy}^2 = heritability of family means for traits x and y, respectively.

As the family mean correlations are estimated from full-sib families, they are actually total genetic rather than just additive genetic correlations (*ie*, r_G rather than r_A). They were used as the best proxy for the latter in this case.

5. Results and Discussion

Results of the pooled analysis are presented in *tables 3* and *4*: variance components and associated standard errors, trait means and associated standard deviations, additive and dominance genetic variances, ratios of additive to dominance variances, and narrow-sense heritabilities and associated standard errors are listed in *table 3*, and genetic and phenotypic correlations in *table 4*.

All sources of variation had significant effects ($P < 0.05$) on all traits at all ages. The residual error was the most important source of variation for all traits, generally followed by the male and female effects. Branch diameters and stem straightness were exceptions, for which the family x site x replicate interaction was the next most important source of variation at all ages. In the case of resin yield, the family x replicate interaction effect was more important than both the female and male components. For growth traits, the magnitude of variance components increased with age (and size of the trees).

Ratios of additive to dominance genetic variances were greater than unity for all traits at the three ages, with the exception of stem straightness at 8 years, suggesting that additive genetic control is the more important. Whilst the magnitudes of both additive and dominance genetic variances increased with age, their ratio, in the case of growth traits, decreased over time, from around 4 at age 5 to 2 at age 15. Ratios for height at 5 and 8 years correspond to those reported by KRAUS (1973) for 6 year data of *P. elliottii* in Georgia, of 1.3 to 2.3. Those for growth traits generally and for stem straightness at 5 and 8 years are consistent with other published estimates for various pine species at similar ages, summarised by COTTERILL *et al.* (1987), and compare to ratios of between 2 and 4 reported by CARSON (1986) and VOLKER and CAMERON (1988) for height, diameter, sectional area, stem straightness and branch quality in *P. radiata* at 4 and 12.5 years, respectively.

5.1 Heritabilities

Growth traits, resin yield and wood density were under moderate to strong genetic control (*Table 3*). Heritability estimates for branch traits were moderate, in marked contrast to those for Zimbabwean *P. patula,* in which they were higher

Table 3. – Variance components and associated standard errors, estimates of additive and dominance variance and their ratio, and narrow-sense heritabilities and associated standard errors for all traits at 5, 8 and 15 years. Heritability estimates are based on female components of variance only.

Trait	Age	Source								Parameter			
		Female	Male	Fem x Male	Fem x Site	Male x Site	Fam x site	Fam x Site x Rep[2]	Residual	σ^2_a	σ^2_d	σ^2_a/σ^2_d	$h^2 \pm$ s.e.
HT	5	0.08±0.02	0.10±0.06	0.02±0.01	0.02±0.01	0.02±0.01	0.02±0.003	0.04±0.003	0.63±0.01	0.32	0.08	4.00	0.34±0.10
	8	0.15±0.05	0.14±0.11	0.07±0.02	0.07±0.02	0.10±0.06	0.03±0.01	0.09±0.01	1.54±0.02	0.60	0.29	2.06	0.27±0.09
	15	0.21±0.12	0.07±0.25	0.18±0.04	0.30±0.09	0.59±0.31	0.16±0.04	0.20±0.03	3.59±0.05	0.85	0.71	1.19	0.16±0.08
DBH	5	0.38±0.11	0.50±0.27	0.09±0.02	0.05±0.02	0.06±0.03	0.03±0.01	0.28±0.02	2.67±0.03	1.52	0.36	4.20	0.38±0.10
	8	0.75±0.23	1.16±0.68	0.30±0.06	0.13±0.05	0.30±0.16	0.07±0.04	0.36±0.06	6.83±0.10	3.01	1.22	2.47	0.30±0.09
	15	2.16±0.73	2.37±2.14	1.11±0.20	0.83±0.26	2.95±1.52	0.35±0.13	0.58±0.15	19.09±0.28	8.62	4.46	1.94	0.29±0.10
VOL	5	13.38±3.8	17.87±9.60	3.74±0.64	1.83±0.62	1.98±1.12	0.86±0.41	7.46±0.50	81.92±0.79	53.50	15.00	3.60	0.42±0.11
	8	158.1±47.63	211.0±127.3	64.4±11.5	27.2±9.50	61.88±33.55	11.5±7.68	71.8±10.8	1225.1±17.81	632.8	257.44	2.46	0.35±0.10
	15	2676.8±897.5	2403.8±2313.0	1402.7±240.8	870.2±269.4	3459.0±1762.4	372.5±152.1	901.9±189.0	22915.0±334.0	10709.6	5611.6	1.90	0.31±0.10
BRCT	5	0.11±0.04	0.13±0.09	0.01±0.01	0.03±0.01	0.10±0.05	0.03±0.01	0.08±0.01	3.01±0.03	0.44	0.04	11.00	0.13±0.04
BRDM	5	0.25±0.11	0.65±0.38	0.04±0.04	0.22±0.07	0.18±0.10	0.11±0.05	0.72±0.05	9.30±0.09	1.00	0.16	6.30	0.09±0.04
AIL	5	0.0004±0.0001	0.001±0.0004	0.0001±0.0001	0.0003±0.0001	0.0002±0.0001	0.0001±0.00003	0.0003±0.00003	0.01±0.0001	0.08	0.02	5.00	0.17±0.06
STR	5	0.02±0.01	0.02±0.01	0.004±0.002	0.01±0.004	0.01±0.01	0.0004±0.002	0.06±0.003	0.44±0.004	0.11	0.08	1.31	0.12±0.05
	8	0.01±0.01	0.01±0.02	0.01±0.003	0.03±0.01	0.03±0.02	0.0001±0.003	0.04±0.01	0.48±0.01	0.04	0.05	0.89	0.07±0.06
	15	0.01±0.01	0.0001±0.02	0.001±0.004	0.02±0.01	0.06±0.03	0.02±0.01	0.03±0.01	0.56±0.01	0.03	0.002	11.7	0.04±0.04
DENS	15	204.88±58.05	252.20±133.50	36.27±15.36	7.83±8.70	10.37±8.25	13.93±18.53	14.67±22.34	1947.1±40.34	819.50	145.08	5.65	0.36±0.09
RESQ[1]	15	17.03±10.71	10.73±7.35	0.02±5.67	–	–	–	39.76±9.15	156.2±8.04	703.7	0.54	1306.	0.37±0.20

[1]) data available for one site only, therefore no site interaction terms.

[2]) similarly, Fam x Rep in the case of RESQ15.

Table 4. – Genetic correlations and associated standard errors (upper triangle), and phenotypic correlations (lower triangle), between all traits at 5, 8 and 15 years.

Trait	HT5	DBH5	VOL5	BRCT5	BRDM5	AIL5	STR5	HT8	DBH8	VOL8	STR8	HT15	DBH15	VOL15	DENS15	STR15	RESQ15
HT5		0.80±0.07	0.88±0.04	-0.46±0.17	0.08±0.18	0.12±0.18	0.41±0.15	1.00	0.95	0.98	0.79	0.92±0.04	0.74±0.10	0.80±0.08	0.09±0.18	0.06±0.23	0.07±0.41
DBH5	0.71		0.99±0.01	-0.55±0.16	0.42±0.15	0.23±0.17	0.32±0.16	1.00	1.00	0.93	0.43	0.64±0.13	0.87±0.05	0.88±0.05	-0.31±0.17	0.08±0.23	0.06±0.41
VOL5	0.85	0.94		-0.54±0.16	0.34±0.16	0.19±0.17	0.32±0.16	1.00	1.00	0.98	0.31	0.75±0.10	0.89±0.05	0.91±0.04	-0.21±0.18	0.07±0.23	0.11±0.40
BRCT5	-0.03	-0.05	-0.07		-0.21±0.21	-0.56±0.16	-0.09±0.21	0.01	-0.55	-0.27	-0.08	0.42±0.15	0.45±0.15	0.43±0.15	-0.08±0.19	0.10±0.19	0.21
BRDM5	0.13	0.32	0.24	0.01		0.30±0.17	-0.03±0.18	0.10	0.23	0.21	0.04	0.05±0.19	0.33±0.17	0.27±0.17	-0.13±0.19	-0.03±0.19	0.34
AIL5	0.21	0.20	0.19	-0.002	0.24		0.05±0.18	0.14	0.08	0.10	0.06	0.21±0.18	0.17±0.18	0.15±0.18	0.07±0.19	0.13±0.19	0.12
STR5	0.31	0.23	0.24	0.02	-0.02	0.06		0.28	0.20	0.21	0.83	0.41±0.18	0.15±0.21	0.18±0.21	0.16±0.19	0.73±0.16	0.59±0.30
HT8[1]	0.79	0.79	0.72	0.01	0.43	0.36	0.51		0.78±0.07	0.86±0.05	0.28±0.17	1.00	0.87	0.92	0.14	0.85	0.10
DBH8[1]	0.78	0.86	0.83	-0.20	0.42	0.27·	0.42	0.82		0.98±0.01	0.12±0.18	0.64±0.13	0.95±0.02	0.94±0.03	-0.30±0.17	0.39±0.17	0.08±0.41
VOL8[1,2]	0.79	0.85	0.89	-0.13	0.42	0.31·	0.47	0.84	0.95		0.10±0.18	0.88	1.00	1.00	-0.17	0.87	0.32
STR8[1]	0.61	0.60	0.52	-0.15	0.39	0.34·	0.64	0.40	0.33	0.29		0.14±0.22	-0.09±0.22	-0.09±0.22	-0.06±0.20	0.88±0.06	0.55±0.36
HT15	0.65	0.54	0.56	0.14	0.12	0.416	0.24	0.92	0.66	0.77	0.34		0.75±0.10	0.81±0.08	0.18±0.18	0.21±0.22	0.24±0.42
DBH15	0.61	0.69	0.69	0.17	0.24	0.12	0.23	0.77	0.89	0.91	0.30	0.73		0.99±0.004	-0.22±0.18	0.19±0.22	0.10±0.42
VOL15	0.61	0.66	0.69	0.16	0.20	0.12	0.22	0.82	0.85	0.94	0.27	0.74	0.96		-0.19±0.18	0.19±0.22	0.09±0.42
DENS15[3,4]	0.01	-0.13	-0.10	-0.07	-0.05	-0.02	0.002	0.13	-0.10	-0.16	0.003	0.08	-0.04	-0.04		-0.43±0.17	-0.42
STR15	0.32	0.30	0.29	0.06	0.07	0.04	0.34	0.59	0.40	0.62	0.56	0.46	0.48	0.43	0.01		0,60±0,34
RESQ15[4]	0.13	0.06	0.09	0.11	-0.16	-0.08	0.02	0.14	0.10	0.31	-0.06	0.06	0.09	0.09	-0.36	0.03	

[1]) genetic correlations with 5-year traits approximated by Type B correlations.

[2]) genetic correlations with 15-year traits approximated by Type B correlations.

[3]) genetic correlations with RESQ15 approximated by Type B correlation.

[4]) estimates from sub-samples of complete data set.

than for any other trait (BARNES, 1973; BARNES *et al.,* 1992a). Heritabilities estimates for stem straightness were generally low, and decreased with age, as did those for growth traits. The low estimates reported for stem straightness may be a consequence of assessment on an absolute rather than a site-specific scale (COTTERILL *et al.,* 1987; RAYMOND and COTTERILL, 1990). Although selective thinning has been found to affect the magnitude of additive and phenotypic variances, increasing the former and decreasing the latter (MATHESON and RAYMOND, 1984), the thinning practised here was systematic and should have had no such effects.

These estimates of heritability are generally consistent with those reported elsewhere for *P. elliottii* – for example, by ALLEN (1985), COTTERILL *et al.* (1987), DORMAN and SQUILLACE (1974), or SOHN and GODDARD (1974) – and for other *Pinus* species – for example, by BARNES *et al.* (1992a and b) for *P. patula,* COTTER-ILL *et al.* (1987) for *P. pinaster* and *P. radiata,* DEAN (1990) for *P. radiata,* FOSTER (1986) for *P. taeda,* or WOOLASTON *et al.* (1990) for *P. caribaea.* Those for growth traits tend to be higher than the estimates reported by HODGE and WHITE (1992) from a large series of open-pollinated trials of *P. elliottii* in the south-eastern USA, but consistent with estimates from other studies summarised therein.

The estimate of the heritability of wood density (0.36 ± 0.09) is within the range reported previously for *P. elliottii* (0.16 to 0.65, with standard errors ranging from 0.10 to 0.23; GODDARD and COLE, 1966; HODGE and PURNELL, 1993; Institute of Paper Chemistry, 1962; SOHN and GODDARD, 1974). The estimate is lower than those reported for Zimbabwean *P. patula,* which ranged from 0.51 and 0.63 with standard errors of between 0.21 and 0.32 (BIRKS, 1990; BARNES *et al.,* 1992b). Generally, heritabilities of wood density in conifers have varied between 0.4 and 0.7, with standard errors ranging between 0.1 and 0.3 (MEGRAW, 1985; ZOBEL and VAN BUIJTENEN, 1989).

5.2 Correlations

Additive genetic correlations between growth traits were large and positive, above 0.65 at all ages, with moderate or low standard errors. Phenotypic correlations were generally of comparable magnitude to genetic correlations. Additive genetic correlations between growth traits generally increased between the ages of 5 and 8 and decreased between 8 and 15 years. These estimates are generally similar to those reported in the literature for *P. elliottii* (ALLEN, 1978; COTTERILL *et al.,* 1987; SMITH *et al.,* 1993; SOHN and GODDARD, 1974).

Additive genetic correlations between juvenile heights or diameters and mature height, diameter or volume were generally high, at 0.6 and above, with low to moderate standard errors (0.5 and below). Correlations were generally higher between 8 and 15 years than between 5 and 15 years. Phenotypic juvenile-mature correlations between growth traits were generally high (0.6 and above), and of lesser magnitude than genetic correlations. The high juvenile-mature correlations found here are consistent with those reported by PASCHKE (1979) for *P. taeda,* and WAKELEY (1971) for a variety of southern pines.

Genetic correlations between stem straightness and growth traits ranged from weakly negative to strongly positive, generally with large standard errors. Highly positive genetic correlations between stem straightness and growth traits were also reported for *P. elliottii* by COTTERILL *et al.* (1987). Juvenile-mature correlations between stem straightness and growth traits were also variable and were associated with large standard errors. Phenotypic correlations between stem straightness and growth traits were generally low to moderate

but always positive. As discussed above, these results may in part be an artifact of the straightness scoring system.

Additive genetic correlations between wood density and height were weakly positive, ranging from 0.09 ± 0.18 to 0.18 ± 0.18. Correlations between wood density and diameter or volume were negative, ranging from low to moderate (-0.19 ± 0.18 to -0.31 ± 0.17); the magnitude of correlations with diameter decreased with increasing age. Correlations between wood density and stem straightness ranged from being weakly positive (0.16 ± 0.19) to moderately negative (-0.43 ± 0.17). These results are consistent with those reported in the literature for *P. elliottii,* where slightly positive correlations between height and density and negative correlations between density and diameter have been observed, for example by SOHN and GODDARD (1974) and SQUILLACE and KRAUS (1962). Phenotypic correlations between density and growth traits were generally low, also as reported previously.

The positive genetic correlations found here between height at each age and wood density, and the negative correlations between diameter and density, are consistent with those reported, for example, by DEAN (1990) and MEGRAW (1985). MEGRAW (1985) has suggested that these results may be a consequence of the relationship between the position of the live crown and diameter growth at any given height up the stem.

Additive genetic correlations between branching traits and other traits were variable. Additive genetic correlations between the branching traits and growth traits were generally strongly negative, ranging from $r_a = 0.42 \pm 0.15$ to $r_a = -0.55 \pm 0.16$, with no particular pattern. Correlations between the number of branches per whorl and stem straightness at 5 years were negative; those between BRCT5 and AIL5 with stem straightness at 15 years were positive. Correlations between BRCT5 and AIL5 were high and negative; correlations between internode length and volume at 15 years were positive. Standard errors of correlations involving branching traits were generally high.

Correlations between resin yield and height were moderate and positive, while those with diameter or volume were low, but also positive. COPPEN *et al.* (1984) reported that trees with large diameters yielded more resin, but this relationship was not strongly evident here. Rather, resin yield was most strongly correlated with stem straightness at 15 years (0.60 ± 0.34). The correlation between resin yield and wood density was moderately negative. All correlations involving resin yield were associated with high standard errors, and it is possible that too few trees were sampled for reliable estimates. Phenotypic correlations with resin yield were generally low, with the exception of that with wood density, which was moderately negative.

Juvenile-mature correlations between resin yield and growth traits ranged from low to moderate, and those with stem straightness were high and positive (0.5 and above). Correlations with each trait were reasonably consistent over time, but associated with high standard errors. Phenotypic correlations were moderate and similarly consistent over time.

6. Conclusions

In the Zimbabwean breeding population of *P. elliottii,* growth traits, wood density and resin yield are under moderate to strong additive genetic control. Stem straightness and branching traits are under less strong additive genetic control, although the magnitude of the heritability estimates never-theless suggests a substantial response to selection. Additive genetic variances are greater than non-additive genetic vari-

ances for all traits but branch diameter. The magnitude of the estimates, and the preeminence of additive genetic effects, are broadly consistent with results reported elsewhere for *P. elliottii* and other industrial pines.

The favourable genetic correlations between early and late growth, between early growth and resin yield, and between early height and wood density suggest that early selection should be feasible for *P. elliottii* in Zimbabwe. The favourable additive genetic correlations between height and wood density, between stem straightness and resin yield, and between growth traits and resin yield, suggest that timber production and resin yield could be improved in the same population. These estimates are used in an associated paper (Pswarayi *et al.,* in prep. b) to develop selection indices for both saw-timber and resin production in Zimbabwe.

8. Literature

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