

involving diameter at the Cardwell site are a general phenomenon or whether this study describes an unusual situation brought about by early grass infestation.

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## Genetic Parameters for Wood and Growth Properties in *Araucaria cunninghamii*

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#### Summary

All available information on genetic variation in wood properties of Queensland hoop pine is drawn together and examined. Results come from two half-sib progeny trials and one full-sib progeny trial, all about 15 years old.

Previously reported parameter estimates, from an earlier wood study on one of the half-sib progeny trials containing 25 families, were supported with new results from 22 families of which 17 were unrelated to the families in the earlier trial. Pooled narrow-sense heritability estimates obtained from the combined data of the two half-sib progeny trials were 0.60 for basic density, 0.19 for per cent compression wood, 0.36 for mean spiral grain, 0.17 for diameter and 0.58 for straightness. Approximate standard errors of the four estimates ranged from 0.10 to 0.16. Heritability of grain spirality at six equally spaced points from pith to bark averaged about 0.20 but peaked at 0.35 (approximate s.e. = 0.12) for the third sampling point from the pith, where average spirality was greatest.

Selection procedures that emphasize growth and straightness and ignore wood quality traits are likely to increase basic density, decrease spiral grain and lead to a small increase in compression wood. Improvements in spiral grain and compression wood can be ensured by further selecting plus tree candidates for these wood traits. However, genetically controlled increases in density can

probably only be restricted by decreasing the rate of improvement in straightness.

Estimation of non-additive or dominance variance, by comparing the components of variance of the full-sib and half-sib results, was not successful. Negative estimates of dominance variance for compression wood and mean spiral grain, as well as high standard errors associated with all estimates, call into question the value of this technique. It should be further examined in a larger data set, representing larger numbers of families, to better test its validity.

Offspring-parent regressions suggest that screening plus trees for basic density and spiral grain could be effective in providing a genetic ranking for these parameters, even though the plus trees may be of different ages and growing in different environments.

*Key words:* *Araucaria*, heritability, correlation, growth, straightness, wood properties.

#### Introduction

Hoop pine (*Araucaria cunninghamii* AITON ex D. DON) is noted for its high quality timber (SMITH, 1980) suited for veneer, joinery, particle board and structural products (DEAN *et al.*, 1988). However, for practical reasons, little emphasis has been placed on wood properties for first- and second-generation plus tree selections as part of a hoop pine breeding programme in south-east Queensland, Australia. Rather, selection has focussed on improving growth rate and tree form (NIKLES *et al.*, 1988), with a second-stage screening to eliminate trees with undesirable grain spirality. No changes in basic density have been

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sought, as its current level is regarded as satisfactory.

This paper summarises all available information on genetic variation in wood quality of hoop pine, examined in three parts. Firstly, the genetic parameters of wood properties estimated from the same progeny trial results by DEAN *et al.* (1988) and EISEMANN *et al.* (1990) also been augmented through the inclusion of information from another progeny trial, with the aim of providing more reliable estimates of genetic variation of wood properties in hoop pine. Secondly, the progeny trial reported by DEAN *et al.* (1988) and EISEMANN *et al.* (1990) also contains a large number of control-pollinated families for which wood results have not previously been reported. Wood property results from these full-sib families are included in this paper. As variances due to full-sib families contain a greater portion of non-additive genetic components than those due to half-sib families (BECKER, 1984), comparisons of the variance estimates from half-sib families with those from full-sib families are presented to indicate the extent of non-additive genetic variation. Thirdly, data are available on the wood characteristics of some of the parents of these families (Queensland Forest Service, unpublished results). These parents are of various ages and scattered over a wide geographic range, so the technique of offspring-parent regression has been used to indicate the value of sampling potential plus trees as a guide to their genotype when adjustments for environmental effects are not possible.

Published estimates of genetic parameters for growth and wood quality of hoop pine are very imprecise (DEAN *et al.*, 1988; EISEMANN *et al.*, 1990). Better information is required for making decisions on future strategies for wood quality improvement.

## Materials and Methods

### Experimental design and management

Wood samples were obtained from two hoop pine progeny trial plantings established by the Queensland Forest Service. In the first, Experiment number 285, 25 open-pollinated (OP) and 31 control-pollinated (CP) families were sampled — these two categories of families are referred to below as progeny trials I and II respectively. In the second, a planting in the Experiment number 394 series — referred to below as progeny trial III — 22 OP families were sampled. Some details of these trials were provided in DEAN *et al.* (1988) but for completeness, the site, silviculture and sampling details for all trials discussed in this paper are summarised in table 1. Wood property results for the 25 OP families from progeny trial I have previously been reported by DEAN *et al.* (1988) for basic density only and by EISEMANN *et al.* (1990) for the same range of wood properties considered in this paper.

All trials were planted with two-year-old tubed seedling stock raised in local nurseries. The OP progeny were grown from seed collected from ortets which had been visually selected for superior growth, in routine wind-pollinated plantations in the Mary Valley, and the CP families came from hand-pollinations of mostly the same ortets. Five of the OP families in progeny trial III were also included in progeny trial I, but all other families were unrelated.

Table 1. — Site, silvicultural and sampling details of hoop pine trials sampled for wood analysis.

Details	Progeny Trial		
	I	II	III
Local number	285IM3	285IM1,2	394IM1
Stock type	Open-pollinated	Control-pollinated	Open-pollinated
Locality	Imbil	Imbil	Imbil
Latitude	26°31'S	26°31'S	26°34'S
Annual rainfall(mm)	1150	1150	1150
Soil type	Brown and red-brown clay loam	Brown and red-brown clay loam	Brown, silty loam
Elevation a.s.l.(m)	60	60	60
Slope	10-15°	5-15°	5-15°
Aspect	North-east to north-west	North-east to north-west	West to south-west
Previous vegetation	Closed-forest with hoop and bunya pine. Planted with <i>Agathis robusta</i> (Kauri Pine) in 1937. Kauri had been severely damaged by insects and was felled in 1968.		Transition forest, mainly brush box and grey ironbark.
Blocks	5*	5*	5†
Trees/line plot	10	10	10
Spacing(m)	2.8x3.4	2.8x3.4	2.8x3.4
Planting date	December 1968	December 1968	December 1971
Wood sampling date	March 1984	December 1984	March 1986
Age when wood sampled	15y 3m	16y	14y 3m
Families sampled	25	31	22
Trees sampled per family	15	15‡	15
Total trees sampled	375	444	330

\*) A sixth block planted on another site was not sampled

†) A sixth block badly affected by landslip was not sampled

‡) Two families were replicated in only 4 blocks resulting in 12 trees sampled for these families.

Note: (i) Five families were common between trials I and III.

Note: (ii) Table modified from DEAN *et al.* (1988).

### Wood Sampling Methods

Three trees from each family in each of five replicates (blocks) were sampled for both OP and CP studies, to give fifteen trees per family. A very small number of severely mis-shapen, damaged or runt trees that were unrepresentative of the progeny trial, or which appeared unlikely to produce marketable logs, were excluded.

The sampling was designed to be balanced across families and blocks. However, two CP families afforded less than the full 15 trees per family through these being omitted from one of the blocks sampled.

Data recorded for each sample tree were diameter over bark at 1.3 m above ground (DBHOB), tree total height, and bole straightness, which was scored on a scale from 1 (crooked) to 6 (straight). In addition a 12 mm diametral increment core of wood was removed from the inter-whorl immediately below the breast height measurement point (1.3 m above ground level) for wood properties assessment. Core sampling was at right angles to the lean of the tree or to the prevailing wind direction if no lean was detectable.

### Laboratory analysis of wood samples

Basic density was measured as the ratio of oven dry weight to maximum saturated volume for whole increment cores using the procedure of HEINRICHS and LASSEN (1970). Mean increment core values were obtained. These mean values were not weighted to adjust for whole-tree or cross-sectional disc differences in relative wood volumes.

Compression wood incidence and pith-to-bark grain angles were determined. Firstly, each increment core was planed as either a whole diametral strip or as radial samples to provide samples of about 7 mm thickness with regard to the longitudinal orientation of the fibres. To assess compression wood, a sector (originating at the pith) was drawn on the machined surface of each radial core from pith to cambium. The moist core was

then illuminated from below and the proportion of the sector affected by compression wood obtained by dot grid count. Results from the radial cores of each tree were averaged to provide a per cent compression wood value for the tree (at sampling height). After compression wood assessment, the radial cores were cut into six segments of equal length. Grain angles were measured at the cambial end of each of these segments to yield pith-to-cambium spiral grain profiles. Mean segment determinations used the methods of HARRIS (1984). The mean grain angle for the sampling height was calculated as the arithmetic mean of the segment values, i.e. ignoring any differences in sign due to changes in spirality from left- to right-handed direction or vice-versa (e. g. the mean of  $2^0$  and  $-3^0$  is taken to be  $2.5^0$ ).

### Analyses

#### Parameter estimates from OP progeny

EISEMANN *et al.* (1990) reported heritability estimates for wood quality traits from progeny trial I. To strengthen EISEMANN *et al.*'s estimates based on 25 families, the analyses in this paper include data from a further 22 families (17 unrelated) from another open-pollinated progeny trial at Imbil (progeny trial III). Data from these OP progeny trials were analysed using the method of least squares, fitting the statistical model:

$$Y_{ijk} = \mu + F_i + B_j + FB_{ij} + e_{ijk} \quad \dots \text{Equation 1}$$

Where  $Y_{ijk}$  is the observation on the  $k$ th tree in the  $j$ th block and the  $i$ th family  
 $\mu$  is the overall least-squares mean  
 $F_i$  is the random effect of the  $i$ th family  
 $B_j$  is the random effect of the  $j$ th block  
 $FB_{ij}$  is the random interaction effect of family  $i$  and block  $j$   
 $e_{ijk}$  is a random error, normally distributed, mean zero.

The analyses of EISEMANN *et al.* (1990) are directly comparable to those reported in this paper for progeny trial III as they are from trees of similar age and the same statistical model was fitted. In the current analyses, as in those of EISEMANN *et al.* (1990), it is assumed that data for wood quality traits are not adjusted for block effects. This is because, for these wood quality traits, it is unlikely that sufficient samples will ever be taken from each block to allow adjustments to be made. Therefore, heritability is estimated as:

$$h^2 = \sigma_a^2 / (\sigma_b^2 + \sigma_{fb}^2 + \sigma_a^2 + \sigma_e^2) \quad \dots \text{Equation 2}$$

Where  $h^2$  is the heritability estimate,  $\sigma_a^2$  is the additive genetic variance, calculated as four times the estimated between family variance,  $\sigma_b^2$  is the estimated block variance,  $\sigma_{fb}^2$  is the estimated interaction variance and  $\sigma_e^2$  is the error variance, assuming that there is no epistasis.

This heritability model includes block effects in the denominator so as to conform to the model advanced by EISEMANN *et al.* (1990). However, block effects are only included as an option which was not exercised in this study, in similar fashion to EISEMANN *et al.* (1990).

Respective variance components from the two analyses were checked for homogeneity using an F test, to deter-

mine the validity of combining the data for a pooled analysis. As reported below, these variances were found to be heterogeneous, so it was decided not to combine the two data sets but to pool the resultant parameter estimates by weighting each estimate by the inverse of its sampling variance. The distribution of wood property traits were closely approximated by a normal distribution, except for compression wood, which displayed a small amount of positive kurtosis. Two-stage selection index calculations were made, using the theory developed by CUNNINGHAM (1975).

#### Estimating non-additive variance

Data from 31 full-sib families (CP progeny) in progeny trial II were analysed using the model described by Equation 1, and 'heritability' was estimated using Equation 2. The between-family variance ( $\sigma_f^2$ ) from full-sibs is (BECKER, 1984):

$$\sigma_f^2 = 1/2\sigma_a^2 + 1/4\sigma_d^2 + 1/4\sigma_{aa}^2 + 1/8\sigma_{ad}^2 + 1/16\sigma_{dd}^2 + 1/8\sigma_{aaa}^2 \dots + \sigma_m^2$$

....Equation 3

Where  $\sigma_f^2$  is between-family variance  
 $\sigma_a^2$  is additive genetic variance  
 $\sigma_d^2$  is dominance variance  
 $\sigma_{aa}^2$  is additive  $\times$  additive epistatic variance etc.,  
and  $\sigma_m^2$  is variance due to maternal effects.

whereas that calculated from half-sib families is:

$$\sigma_f^2 = 1/4\sigma_a^2 + 1/16\sigma_{aa}^2 + 1/64\sigma_{aaa}^2 \dots + \sigma_m^2 \quad \dots \text{Equation 4}$$

Assuming maternal effects to be negligible by age 15 years, and the influence of epistatic effects in Equations 3 and 4 to be small, then the difference given by twice the between-family variance in full-sibs less four times the family variance in half-sibs roughly estimates half the dominance variance ( $0.5\sigma_d^2$ ).

The full-sib families in progeny trial II were not structured appropriately to analyse them using an incomplete diallel or factorial model, as there were too many missing cells.

#### Estimating parameters from offspring-parent regression

Wood samples were taken from sixteen of the ortets whose progeny were represented in progeny trials I and II. The mean basic density of these parents was 451.9 kg/m<sup>3</sup> ( $\pm$  standard deviation 20.6) and their mean spiral grain was 3.28 degrees ( $\pm$  1.43). Of these parents, 14 were represented in the half-sib families. The variances for these two traits in the parents were not significantly different from the respective variances in their half-sib progeny, allowing the technique of offspring-parent regression to be used to estimate heritabilities (BECKER, 1984).

All standard errors were calculated according to BECKER (1984), except those given for pooled estimates, where the method described by CUNNINGHAM *et al.* (1977) was used.

## Results and Discussion

### Half-sib families

A summary of the means and standard deviations of OP families in both progeny trials I and III are presented in table 2. Mean squares from the analysis of variance of the half-sib families in progeny trial III are shown in table 3. Family was a significant source of variation

( $P < 0.05$ ) for all traits except compression wood and DBHOB. Block effects were insignificant for all traits except DBHOB ( $P < 0.05$ ).

Tests of homogeneity of variance indicated significantly different error variances between progeny trials I and III for straightness score, compression wood, sg1 (spiral grain segment 1), sg4, sg5 and sg6 ( $P < 0.01$ ), with a difference approaching significance ( $P < 0.08$ ) for density and radial average spiral grain. The estimates of heritability from this study, together with those from EISEMANN *et al.* (1990), and the resultant pooled estimates with standard errors, are shown in table 4.

Basic density and straightness were strongly controlled by additive genetic effects ( $h^2 = 0.60$ , Table 4). Estimated heritabilities of compression wood and diameter were lower (0.19 and 0.17 respectively), with mean spiral grain intermediate (0.36). Although basic density appeared to have a high heritability, the trait was characterised by a low variability (coefficient of variation, c. v. = 6%), so genetic change in this trait, should it be considered desirable, would not be rapid if measured on a percentage basis. By contrast, this measure of compression wood was highly variable (average c. v. = 99%) and proportional changes in this trait could be achieved relatively quickly, despite its lower heritability. Of the six spiral grain segments, the third segment yielded the highest heritability estimate (0.35).

Table 2. — Estimates of overall means and standard deviations for wood, growth and form traits assessed in half-sib hoop pine from progeny trials I and III.

Property	Progeny trial I†		Progeny trial III	
	Mean	Standard deviation	Mean	Standard deviation
Basic density (kg/m <sup>3</sup> )	459.60	29.55	453.00	27.93
Compression wood (%)	8.09	6.88	7.76	8.84
Spiral grain (°)				
— radial mean	3.59	1.35	3.40	1.36
— segment 1	3.85	1.76	3.27	2.11
— segment 2	3.92	1.53	3.69	2.19
— segment 3	4.15	2.05	3.69	2.22
— segment 4	3.83	1.53	3.92	2.22
— segment 5	3.49	1.60	3.42	2.07
— segment 6	2.31	1.22	2.69	1.73
Standard deviation of spiral grain (°)	1.46	0.57		
DBHOB (cm)*	17.45	2.21	18.52	3.15
Straightness (1-6)	2.21	0.76	3.20	1.41
Height (m)	15.92	1.62	Not available	

\*) DBHOB = diameter at breast height (1.3 m) over bark  
†) From the same data set discussed by EISEMANN *et al.* (1990)

Table 3. — Mean squares for diameter, straightness and wood quality traits in open-pollinated families from progeny trial III.

Source	df	BD†	Comp. wood	Mean sg	sg1	sg2	sg3	sg4	sg5	sg6	dbh	st
Family (F)	21	2135 ***‡	108.6 ns	6.73 **	7.74 *	8.91 *	11.44 **	11.59 **	7.43 *	5.22 *	9.56 ns	5.98 **
Block (B)	4	535 ns	68.0 ns	1.03 ns	5.79 ns	5.44 ns	0.78 ns	1.63 ns	4.74 ns	0.41 ns	20.51 ns	4.06 ns
FxB	84	929 ns	86.6 ns	2.58 ns	4.65 ns	4.85 ns	4.96 ns	5.02 ns	4.23 ns	3.12 ns	6.50 ns	2.09 *
Error	215	626	73.5	2.33	3.92	4.10	4.40	4.32	3.85	2.82	6.45	1.49

†) BD = basic density (kg/m<sup>3</sup>), Comp. wood = compression wood (%), Mean sg = mean radial spiral grain (°), sg1, sg2, sg3, sg4, sg5, sg6 = spiral grain of segments 1 to 6 respectively (°), dbh = diameter at breast height (1.3 m) over bark (cm) and st = straightness (scored from 1, crooked, to 6, straight).

‡) ns Not significant

\*)  $P < 0.05$

\*\*)  $P < 0.01$ .

Table 4. — Heritability estimates from progeny trial III and the pooled heritability estimates from combining results from progeny trials I and III.

Trait	Progeny trial I†	Progeny trial III	Pooled ± standard error
Basic density	0.83	0.40	0.60 ± 0.16
Compression wood	0.44	0.07	0.19 ± 0.11
Spiral grain (°)			
— radial mean	0.33	0.42	0.36 ± 0.12
— segment 1	0.29	0.19	0.26 ± 0.10
— segment 2	0.12	0.24	0.15 ± 0.09
— segment 3	0.35	0.35	0.35 ± 0.12
— segment 4	0.17	0.36	0.21 ± 0.10
— segment 5	0.19	0.21	0.20 ± 0.10
— segment 6	0.15	0.19	0.16 ± 0.09
DBHOB*	0.22	0.12	0.17 ± 0.10
Straightness	0.61	0.53	0.58 ± 0.16

\*) DBHOB = diameter at breast height (1.3 m) over bark  
†) From EISEMANN *et al.* (1990)

Table 5. — Selected phenotypic correlations ( $r_p$ ) and estimates of genetic correlations ( $r_g$ ) of wood, growth and form traits, pooled across progeny trials I and III.

Traits		Pooled genetic correlation (s.e.)*		Mean phenotypic correlations
Basic density (kg/m <sup>3</sup> )	Compression wood	-0.36	(0.24)	0.08
	Diameter	0.10	(0.26)	0.02
	Straightness	0.48	(0.18)	-0.02
	Mean spiral grain	0.26	(0.22)	0.14
Compression wood (%)	Diameter	-0.16	(0.32)	0.06
	Straightness	0.10	(0.26)	0.00
	Mean spiral grain	0.23	(0.27)	0.03
Diameter (cm)	Straightness	0.57	(0.21)	0.14
	Mean spiral grain	-0.69	(0.28)	0.14
Straightness	Mean spiral grain	-0.66	(0.18)	-0.21

\*) s.e. = approximate standard error (given in parentheses)

Pooled estimates of genetic and phenotypic correlations are also tabulated (Table 5).

Most phenotypic correlations were small, with that of the greatest magnitude being between straightness and mean spiral grain ( $r_p = -0.21$ ). Over half the genetic correlations presented have high standard errors associated with the result to the extent that their utility is severely limited. Of the genetic correlations with relatively low standard errors, diameter and straightness had a strong favourable genetic association ( $r_g = 0.57$ , Table 5), as did diameter and mean spiral grain ( $-0.69$ ) and straightness and mean spiral grain ( $-0.66$ ). Also basic density had a positive genetic correlation with straightness (0.48) and a negative genetic correlation with compression wood ( $-0.36$ ). These stronger genetic correlations are generally very favourable when considered in relation to the aims of the tree breeding programme, which emphasise both large diameter and improved stem straightness. To have decreased mean spiral grain strongly associated which both diameter and straightness is very desirable.

As mentioned previously, the current level of basic density in hoop pine is regarded as satisfactory, for both current and predicted end-users. Therefore, higher basic density resulting from selection pressure for improved stem straightness (due to their positive genetic correlation) is not required, as it might be for some *Pinus* species which have negative genetic correlations between growth traits and basic density. However, this would not really be

regarded as an unfavourable association unless the increase in basic density became quite large.

Compression wood has an important effect on the utilisation of hoop pine (SMITH, 1980). As the shrinkage of compression wood is higher than that of normal wood, compression wood is trimmed from veneer sheets and can cause significant seasoning defects in machined joinery and cabinet pieces. However, compression wood incidence is difficult to measure effectively, as relationships between assessments based on increment core observations are not consistently well correlated with those on cross-sectional discs at the same sampling height, or with multiple stem assessments, in trees of this age (Queensland Forest Service, unpublished results). This probably, in part, reflects the bias against compression wood in the standard procedure of taking increment cores in the direction least likely to encounter compression wood, so as to avoid biasing the basic density assessment (by inclusion of compression wood which has higher basic density than normal wood). Increment core samples thereby avoid the maximum incidence of compression wood at the sampling point, with unknown effects on estimates of genetic parameters. Therefore it would not be feasible to measure a large number of trees in a breeding programme.

Selection index calculations were undertaken to examine the feasibility of a two-stage selection procedure, assuming the parameters shown in tables 2, 4 and 5. For a breeding objective which places equal emphasis on diameter and straightness, an optimum index may lead to an increase in basic density, a moderate decrease in spiral grain and a very slight increase in compression wood. Selection for an alternative objective was examined which gave equal emphasis to improving diameter and straightness, and reducing compression wood and spiral grain. A two-stage selection procedure was assumed whereby potential plus trees are identified using diameter and straightness data first; then candidates are further screened on the basis of their compression wood, spiral grain and basic density. Selection indices based on this approach may not only give similar improvement in diameter and straightness to that in the first objective, but may also reduce compression wood, further increase basic density and give a greater reduction in spiral grain. However, it should be emphasised that the magnitude of these possible changes depends on the proportion of candidates tested for wood quality.

Further analyses indicated that genetic changes in basic density cannot be restricted from increasing without a considerable reduction (by about 40%) in the rate of gain in straightness, with would be undesirable. Improvements in other traits are relatively unaffected by maintaining basic density at current levels.

Table 6. — Estimate of overall means and standard deviations for wood properties assessed in full-sib families (progeny trial II).

Property	Mean	Standard deviation
Basic density (kg/m <sup>3</sup> )	466.52	23.35
Compression wood (%)	7.23	4.41
Spiral grain (°)		
— radial mean	3.23	0.96
— segment 1	3.61	1.27
— segment 2	3.61	1.27
— segment 3	3.76	1.32
— segment 4	3.34	1.27
— segment 5	3.00	1.20
— segment 6	2.06	0.96

Table 7. — Mean squares for wood quality traits in full-sib families (progeny trial II).

Source	df	Basic density (kg/m <sup>3</sup> )	Compression wood (%)	Mean spiral grain (°)
Family (F)	30	5888.06 **†	122.03 **	7.06 **
Block (B)	4	524.96 ns	85.31 ns	2.64 ns
FxB	118	652.43 *	44.19 ns	1.96 *
Error	321	500.71	42.68	1.48

†) ns Not significant

\*) P < 0.05

\*\*\*) P < 0.01

Table 8. — Components of variance estimated from full-sib and half-sib families.

Analysis	Variance component	Basic density (kg/m <sup>3</sup> ) <sup>2</sup>	Compression wood (%) <sup>2</sup>	Mean spiral grain (degrees) <sup>2</sup>
Full-sibs	Family	342.91	5.09	0.33
	s.e.*	96.90	2.04	0.12
	Additive + 1/2 dominance	685.82	10.18	0.66
	s.e.	193.80	4.08	0.24
Half-sibs	Family	146.77	6.33	0.18
	s.e.*	50.61	3.06	0.09
	Additive	586.08	25.32	0.72
	s.e.	202.44	12.24	0.36
	1/2 Dominance	98.74	-15.14	-0.06
	s.e.	280.25	12.90	0.43
	Dominance/additive (%)	33.6%	-119.6%	-16.7%

\*) s.e. = standard error

#### Full-sib families

A summary of the full-sib means from progeny trial II is presented in table 6. Mean squares from the analysis of variance of the full-sib families in progeny trial II are presented in table 7. Families were a significant source of variation for density, compression wood and spiral grain (P < 0.01), while the interaction of family and block affected density and spiral grain (P < 0.05) but not compression wood. Block effects were not significant for any of the traits reported suggesting that within block variation may have contributed to the interaction.

#### Estimation of non-additive variance

Components of variance estimated from analysis of full-sib and half-sib families are shown in table 8.

Estimates of additive variance are given by four times the between family variance in half-sibs (Table 4), whereas twice the between-family variance in full-sibs provides an estimate of additive plus half dominance variance (assuming the effects of epistatic variance to be negligible). For basic density, the estimate of dominance variance was 197.4 (sg/m<sup>3</sup>)<sup>2</sup>, or 34% of the additive variance. The estimates of dominance variance for compression wood and mean spiral grain were negative. However, it should be noted that these estimates are associated with very high standard errors and should therefore be treated cautiously.

One explanation for the negative estimates of dominance variance could be that maternal effects (which were confounded with nursery effects) are large. When estimating half the dominance variance, four times Equation 4 was deducted from twice Equation 3. The difference also contains twice the variance due to maternal effects. How-

ever, other evidence in hoop pine (Queensland Forest Service, unpublished results) indicates that although maternal effects accounted for 11% of the variation in height shortly after planting, this declines to around 3% by age eight years. Also at eight years, maternal effects accounted for only 1% of the variation in diameter and 4% of the variation in straightness. Even assuming comparable figures at age 15 years for spiral grain and compression wood, the effect is not large enough to cause a negative estimate of dominance variance. Considering these results and those of comparable analyses in other species (Queensland Forest Service, unpublished results), the value of this method as a means of estimating non-additive variance is questionable.

#### Offspring-parent regression

The estimated heritability of basic density derived from the offspring-parent regression was 0.99 ( $\pm$  0.25), and of mean spiral grain was 0.64 ( $\pm$  0.26). These estimates do not differ significantly from those derived using sib-analysis in the same experiment (progeny trial II), shown in table 4.

The theoretical expectation of heritabilities estimated from offspring-parent regression differs in several respects to those estimated by sib-analysis. Firstly, bias can arise using the latter technique either through the algebraic properties of the estimation procedure (ROBERTSON, 1977; PONZONI and JAMES, 1978) or through gametic disequilibrium due to selection (BULMER, 1971). Offspring-parent regression, on the other hand, provides estimates unaffected by selection (HILL and THOMPSON, 1977). For the families reported here, no selection pressure was exerted on wood characteristics when the parents were selected, except via the correlations with vigour and form (Table 6). According to PONZONI and JAMES (1978), both these effects should be relatively small.

Secondly, a potential disparity arises between the two methods of estimation in that the parents are not growing together under trial conditions, and they range in age at sampling. Environmental effects, if appreciable, would therefore tend to increase the variance of the traits measured in the parents. This in turn could be expected to decrease the offspring-parent regression. Estimates derived using this technique would therefore be appropriate to individual trees of various ages and in various environments, as opposed to trees growing in similar environments and of the same age such as in a replicated progeny trial. As reported above, the variances for basic density and mean spiral grain were not significantly different in the parents and progeny, so this source of disparity is also likely to be negligible.

These results give a strong indication that age and site effects do not appreciably affect basic density or spiral

grain. The relatively small effect of block effects on wood quality traits (Tables 3 and 7) adds support to this argument. This implies that for the purposes of providing a genetic ranking for basic density and spiral grain, it may be satisfactory to directly compare plus trees of different ages and growing in different environments. Should this be the case, considerable time and effort could be saved by screening plus trees on the basis of their phenotype for basic density and spiral grain, regardless of whether or not they are grown in replicated progeny trials. However, more data are needed from a wider range of environments and ages to fully test the generality of this hypothesis. Studies currently underway should provide the data necessary to better test this hypothesis.

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## Hybridization Studies in the Eurasian Species of Elm (*Ulmus* spp.)

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#### Summary

This paper presents data on crossability, and rate of selfing derived from crossing trials carried out for four years among 11 species of elm. Crossability barriers among