

## INTERSPECIFIC PINE HYBRIDS. I. GENETIC PARAMETER ESTIMATES IN AUSTRALIA

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### ABSTRACT

Genetic parameter estimates are presented for hybrids between *Pinus caribaea* var. *hondurensis* (PCH) and both *P. oocarpa* (POOC) and *P. tecunumanii* (PTEC). Estimates were derived from factorial matings between these species established at two test locations in Queensland, Australia. Data from a total of seven genetic tests (four PCH × PTEC hybrid tests, and three PCH × POOC tests) were analysed using the individual tree model and ASREML. Individual narrow-sense heritability, ratio of dominance to additive variance, ratio of dominance to phenotypic variance, and phenotypic and genetic correlations were estimated from data collected at five years of age for height, diameter, stem straightness and angle of stem lean and for wind-firmness assessed at one to two years of age. Heritability estimates for all traits ranged from 0.06 to 0.63. There were no large differences in heritability estimates between sites for growth traits, but there were large differences between estimates from different tests for straightness, lean and wind-firmness, with these traits being more strongly inherited in tests at the location with the lowest rainfall. Generally, dominance variance was less important than additive variance for the traits studied. Genetic correlations between height and diameter were high (0.80–0.82) for the PCH × POOC hybrid and low to moderate (0.47–0.61) for the PCH × PTEC hybrid. Genetic correlations between growth traits and straightness, wind-firmness and stem lean were low, yet high between stem straightness, stem lean and wind-firmness. Genetic correlations between the parental performance of PCH in separate genetic tests of the pure PCH and its performance in hybrid tests tended to be high and positive for growth traits but low and negative for straightness. In contrast, genetic correlations between the performance of PCH × PTEC and PCH × POOC were high and positive for stem straightness, stem lean and wind-firmness, but low to moderate for growth traits.

**Keywords:** *Pinus caribaea* var. *hondurensis*, *P. tecunumanii*, *P. oocarpa*, hybrids, heritability, genetic correlation.

### INTRODUCTION

Hybrids play a major role in improving the productivity of commercial plantations in many parts of the world, particularly Brazil, Congo and South Africa (MARTIN 1989, NIKLES 1992) and lately, Australia (NIKLES 1991, 1996), and have the potential for commercial application in many countries given their performance relative to the commonly planted pure species (eg. Argentina, Brazil, China and South Africa, NIKLES 1995; Zimbabwe, GWAZE 1999; Venezuela, BLANCO & LAMBETH 1991).

One of the biggest challenges in forestry is the development of tree breeding strategies for continued genetic improvement of hybrids. An effective hybrid breeding program depends on reliable genetic parameter estimates which are essential for predicting hybrid

breeding values, combining different traits in selection, predicting genetic response to selection and determining the optimum breeding strategy. To date, genetic improvement of hybrids has been constrained by lack of genetic parameters for hybrids (LI & WYCKOFF 1994). These genetic parameters include additive and dominance variances, heritability and genetic correlations. For example, estimates of additive variance in hybrid populations are important for estimating the hybrid breeding values, and heritability estimates are required to predict genetic gain in  $F_2$  populations (eg. NIKLES 1996, for the *Pinus elliottii* × *P. caribaea* var. *hondurensis* hybrid). The choice of broad breeding strategy for improvement of hybrids depends on the level of additive and dominance variances, and the correlation between performance in the pure-species with that in hybrid combination. A breeding strategy based on

within pure species selection and crossing (PSS) utilises additive genetic variance only, while reciprocal recurrent selection (RRS) as proposed by COMSTOCK *et al.* (1949), utilises both additive and non-additive genetic variance. Effectiveness of the RRS versus the PSS is determined not only by additive and non-additive variances, but also by the genetic correlation between pure species and hybrid performance with the former strategy being favoured in the case of high non-additive genetic variance, low heritability, and low correlation (WEI & VAN DER STEEN 1991). Therefore, estimates of genetic parameters are necessary not only for the pure species but also for the hybrid populations if an effective breeding strategy for improving hybrid performance is to be identified.

There are relatively few studies which have reported genetic parameters for hybrids (eg. DIETERS *et al.* 1997, BLADA 1992, and POWELL & NIKLES 1996 for pine hybrids; VOLKER 1995, and BOUVET & VIGNERON 1996 for eucalypt hybrids). Additive genetic variance was found to be more important than dominance variance in pine hybrids (DIETERS *et al.* 1997, BLADA 1992, POWELL & NIKLES 1996). In the eucalypt hybrids, BOUVET & VIGNERON (1996) found additive variance to be more important in *Eucalyptus urophylla* × *E. grandis* hybrids, but not in hybrids between *Eucalyptus urophylla* and *E. pellita*. Heritability estimates in these eucalypt hybrids varied from low to moderate.

This study was undertaken to estimate genetic parameters, additive and dominance variances, and heritability for height, diameter at breast height (1.3m above ground level), stem lean, wind-firmness and stem straightness, and correlations for *Pinus caribaea* var. *hondurensis* Barr. & Golf. (hereafter referred to as PCH) × *P. tecunumanii* (Schw.) Eguluz et Perry (PTEC) and *P. caribaea* var. *hondurensis* × *P. oocarpa* Schiede (POOC) hybrids at five years of age in Australia using an individual tree model. This study reports the analysis of two experiments (Exps. 690 and 700): some results from Exp. 690 have been previously reported by DIETERS *et al.* (1997), however, this study includes a broader array of genetic material, makes efficient use of all information in the pedigree by using the individual tree model, and provides estimates of the standard errors on the genetic correlations. Also, genetic correlations between PCH in the pure-species and hybrid combinations and across hybrid combinations were estimated to determine the consistency of PCH as a parent on different genetic backgrounds.

## MATERIALS AND METHODS

### Genetic material

In the first set of tests (Exp. 690) eleven PCH female parents were crossed with six POOC and six PTEC male parents. In the second set of tests (Exp. 700) five PCH female parents were crossed with four POOC parents and four PTEC parents. In addition, four families (of each hybrid) were included in Exp. 700 to provide genetic links with Exp. 690 and earlier tests of these hybrids. Only three families (in each hybrid), and one PTEC and three PCH parents were common to Exps. 690 and 700. Pure PCH tests were also established to compare the performance of parents in the pure species combinations with those in the hybrid tests. This experiment (Exp. 699) included full and half-sib families from 48 female PCH parents and 9 PCH male parents. However, there were only eight common parents in Exps. 699 and 700, and a negligible number common to Exps. 699 and 690.

### Genetic field tests

Field tests of Exps. 690 and 700 were established at two locations, Cardwell in north Queensland (longitude: 146° 02' E, latitude: 18° 16' S, altitude: 30 m, MAR: 2130 mm, soils: red and yellow earths) and Wongi in south Queensland (longitude: 152° 33' E, latitude: 25° 26' S, altitude: 100 m, MAR: 1060 mm, soils: grey and yellow podzols). Although field tests of Exp. 699 were also planted at two locations, only the test planted in north Queensland at Cardwell survived to five years of age. The field tests of Exp. 690 were planted in 1989, while those of Exps. 699 and 700 were planted in 1991. All field tests used a randomised complete block design with 36 replicates of single tree plots of each family. In Exps. 690 and 700 the PCH × POOC and PCH × PTEC hybrids were planted in separate, but adjacent, blocks. *Pinus caribaea* var. *hondurensis* × *Pinus tecunumannii* hybrids were included in four genetic tests (ie. two experiments × two locations), but the PCH × POOC hybrids were not tested at Cardwell in Exp. 700 due to concerns about this hybrid's susceptibility to wind damage (ie. a total of only three genetic tests).

### Assessments

Height (HT), diameter (DBH) and stem-straightness (STR) were assessed at 5 years. Height was not assessed at Wongi site in Exp. 690, and wind-firmness and stem lean were not assessed in Exps. 699 and 700 since these tests were not damaged by wind. Stem straightness was visually assessed using a 6-point scale (1 = crooked, 6 = very straight: COTTERILL & DEAN 1990). Wind-firmness was visually assessed immediately following wind damage on a four-point scale: 1 =

>45°, 2 = 20–45°, 3 = 5–20°, and 4 = 0–5° lean from vertical at one year of age at Cardwell and at two years of age at Wongi in Exp. 690. Stem lean was measured in degrees from vertical for all trees in Exp. 690 at 5 years of age, at which stage some trees may have recovered from wind damage suffered at one and two years of age. Individual tree assessments were made by different teams at the two sites.

**Statistical analysis**

Genetic parameters and their standard errors were estimated using an individual tree model ASREML (GILMOUR *et al.* 1998). ASREML estimates variance components under a general mixed model by restricted maximum likelihood (REML). It uses the average information algorithm (GILMOUR *et al.* 1995), and sparse matrix techniques to efficiently solve large mixed models (GILMOUR *et al.* 1998). The model includes a random effect to the breeding value of each tree, both for trees with records and those that are represented as parents or grandparents in the analysis. ASREML also has advantage over other REML programs, due to its faster computational speeds. The following individual tree model was used in the analysis of individual site data:

$$y = Xr + Z_1f + Z_2a + e \quad [1]$$

where  $y$  is a vector of observations,  $r$  is a vector of replicate effects (fixed),  $f$  is a vector of random family effects (ie. specific combining ability),  $a$  is a vector of additive genetic effects of the individual trees (random) and  $e$  is a vector of residuals.  $X$  is the design matrix for fixed effects, and  $Z_1$  and  $Z_2$  are design matrices for random effects. The corresponding expected values and variance/covariance matrices were:

$$\begin{bmatrix} y \\ f \\ a \\ e \end{bmatrix} \sim N \left( \begin{bmatrix} X_r \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & Z_1F & Z_2G & R \\ FZ_1' & F & 0 & 0 \\ GZ_2' & 0 & G & 0 \\ R & 0 & 0 & R \end{bmatrix} \right) \quad [2]$$

Where the phenotypic variance  $V = Z_1FZ_1' + Z_2GZ_2' + R$ , and where  $R$  is the residual (co)variance matrix,  $F = I \otimes G_f$  where  $I$  is the identity matrix,  $G_f$  is the family (co)variance matrix,  $G = A \otimes G_o$ , where  $A$  is the numerator relationship matrix and  $G_o$  = the additive (co)variance matrix and  $\otimes$  is the direct or Kronecker product. The relationship matrix  $A$  is used in the definition of  $G$  and is derived from the relationships between the parents and the progeny. The full-sib family variance

component ( $\sigma_f^2$ ) was interpreted as one quarter of dominance genetic variance ( $\sigma_D^2$ ). Epistasis was assumed to be negligible. The PCH × POOC and PCH × PTEC hybrids were analysed separately.

Individual tree models originate from linear models used in breeding values by animal breeders, and are based on the estimation of the breeding value of ( $\hat{a}_i$ ), for individual ‘animal’  $i$  that can be calculated as:

$$a_i = b(y_i - \mu)$$

where  $b$  is the regression of the true breeding value on phenotypic performance and  $\mu$  is the mean performance of trees, and is assumed to be known (MRODE 1996). Full details for multivariate models is given by MRODE (1996). Individual tree models such as this have been used in a number of genetic parameter estimates for tree species, and more details of this type of approach are given in BORRALHO & POTTS (1996), VAILLANCOURT *et al.* (1996) and VOLKER *et al.* (1994). For analyses of data across sites, site was fitted as an additional fixed effect. Individual narrow sense heritabilities were calculated as the additive genetic variation divided by the phenotypic variation ( $\sigma_P^2$ ):

$$h^2 = \sigma_A^2 / (\sigma_A^2 + \sigma_f^2 + \sigma_e^2)$$

The importance of the dominance variance was evaluated in two ways (GWAZE *et al.* 1997), dominance as a proportion of additive variance  $D_A = \sigma_D^2 / \sigma_A^2$ , and dominance as a proportion of phenotypic variance  $D_P = \sigma_D^2 / \sigma_P^2$ ; where the full-sib family variance ( $\sigma_{FM}^2$ ) was interpreted as  $1/4 \sigma_D^2$  (assuming no epistasis).

Genetic correlations between pure PCH and PCH in the PCH × PTEC hybrids, and between PCH in the PCH × PTEC and in PCH × POOC hybrids (with more than six common parents) were estimated using a bivariate, individual tree model ASREML (GILMOUR *et al.* 1998). Standard errors of all genetic correlations were estimated using a Taylor series approximation (GILMOUR *et al.* 1998, STUART & OLD 1987).

**RESULTS**

**Individual site analyses**

**Means**

The number of trees, number of parents, number of families, overall means and their standard deviations are presented in Table 1. For growth, the mean values differed between Cardwell and Wongi with the former site having faster growth, probably due to higher rainfall, warmer climate, and better soils at this location

**Table 1.** Number of trees, number of parents, number of families and overall means ( $\pm$  standard deviation) for height, diameter, stem straightness, and stem lean at 5 years of age, and wind-firmness assessed at 1-2 years of age in seven hybrid tests in Australia.

	PCH $\times$ POOC			PCH $\times$ PTEC			
	690C*	690W	700W	690C	690W	700C	700W
No. of trees	2142	2148	847	2058	2115	839	856
No. of parents (Fem. $\times$ Male)	11 $\times$ 6	11 $\times$ 6	5 $\times$ 4**	11 $\times$ 6	11 $\times$ 6	5 $\times$ 4	5 $\times$ 4
No. of families	61	61	22	61	57	24	24
Height (m)	11.5 $\pm$ 1.6	NA	10.4 $\pm$ 1.3	12.7 $\pm$ 1.5	NA	12.8 $\pm$ 1.5	11.0 $\pm$ 1.4
Diameter (cm)	17.0 $\pm$ 3.0	12.6 $\pm$ 2.2	15.3 $\pm$ 2.6	18.0 $\pm$ 2.4	13.0 $\pm$ 1.8	17.6 $\pm$ 2.6	15.2 $\pm$ 2.3
Straightness (1-6)	3.7 $\pm$ 1.7	3.9 $\pm$ 1.2	3.6 $\pm$ 1.2	3.0 $\pm$ 1.5	3.7 $\pm$ 1.1	3.5 $\pm$ 1.1	3.3 $\pm$ 1.1
Lean ( $^{\circ}$ )	7.1 $\pm$ 6.0	5.1 $\pm$ 6.2	NA	10.2 $\pm$ 7.8	5.9 $\pm$ 6.5	NA	NA
WF (1-4)	3.4 $\pm$ 0.88	3.7 $\pm$ 0.53	NA	3.1 $\pm$ 1.0	3.6 $\pm$ 0.59	NA	NA

\* C = Cardwell; W = Wongi; NA = not assessed.

\*\* Four additional families were included of each hybrid to provide links with Exp. 690, and increased the total number of parents tested to nine PCH and six of both POOC and PTEC.

compared to Wongi. At Wongi, mean values for growth were higher for the 700 tests than the 690 tests, but at Cardwell means were similar. Mean stem lean and wind-firmness scores indicate that trees were more affected by wind at Cardwell than at Wongi. Mean height and diameter were similar for the two different hybrids in the same test and location (Table 1). The PCH  $\times$  POOC hybrids tended to be straighter than the PCH  $\times$  PTEC hybrids, while both had similar lean and wind firmness.

### Heritability

Heritability for height and diameter ranged from 0.06 to 0.29, and that for stem straightness ranged from 0.08 to 0.63 (Table 2). Heritability estimates for stem lean and wind-firmness ranged from 0.13 to 0.44, and were similar at each site (Table 2). Differences in heritability seem to be related more to site than to the hybrid combination. In tests of Exp. 690 there were moderate differences in heritability estimates between locations

for growth traits, and large differences between locations for stem straightness, stem lean and wind-firmness, with these traits being strongly inherited at Wongi. However, the Exp. 700 tests had slightly lower heritability estimates than the tests in Exp. 690 but were more consistent across locations, and the standard errors were a larger proportion of the heritability estimates, possibly a consequence of the fewer number of parents and families in these tests.

### Importance of dominance variance

The ratio of the dominance to additive variance ( $D_A$ ) was less than one for all traits in the tests of Exp. 690, indicating that additive variance was generally more important than the dominance variance (Table 3).  $D_A$  for growth traits was higher (0.48 – 0.97) than that for straightness, lean and wind-firmness (0.01–0.41; Table 3). Consequently, the ratio between dominance and phenotypic variance was higher for growth traits than the other traits. For the Exp. 700 tests, dominance

**Table 2.** Estimates of individual narrow-sense heritability ( $\pm$  standard errors) in PCH  $\times$  POOC and PCH  $\times$  PTEC hybrids in seven tests in Australia from individual site analyses.

Hybrid	Site	HT	DBH	STR	LN	WF
PCH $\times$ POOC	690C	0.27 $\pm$ 0.10	0.29 $\pm$ 0.11	0.22 $\pm$ 0.08	0.14 $\pm$ 0.06	0.17 $\pm$ 0.06
	690W	–	0.24 $\pm$ 0.09	0.60 $\pm$ 0.16	0.35 $\pm$ 0.11	0.31 $\pm$ 0.10
	700W	0.06 $\pm$ 0.13	0.17 $\pm$ 0.14	0.36 $\pm$ 0.15	–	–
PCH $\times$ PTEC	690C	0.27 $\pm$ 0.10	0.24 $\pm$ 0.09	0.21 $\pm$ 0.08	0.13 $\pm$ 0.05	0.24 $\pm$ 0.08
	690W	–	0.09 $\pm$ 0.04	0.63 $\pm$ 0.17	0.35 $\pm$ 0.12	0.44 $\pm$ 0.13
	700C	0.12 $\pm$ 0.10	0.20 $\pm$ 0.12	0.12 $\pm$ 0.09	–	–
	700W	0.13 $\pm$ 0.09	0.21 $\pm$ 0.11	0.08 $\pm$ 0.07	–	–

**Table 3. Ratio of dominance to additive variance ( $D_A$ ) in PCH × POOC and PCH × PTEC hybrids in seven tests in Australia from individual site analyses. Ratio to phenotypic variance ( $D_p$ ) is in parentheses.**

Hybrid	Site	HT	DBH	STR	LN	WF
PCH × POOC	690C	0.85 (0.23)	0.85 (0.25)	0.16 (0.03)	0.31 (0.04)	0.41 (0.07)
	690W	–	0.68 (0.17)	0.22 (0.13)	0.16 (0.06)	0.09 (0.03)
	700W	6.54 (0.40)	1.72 (0.29)	0.16 (0.06)	–	–
PCH × PTEC	690 C	0.53 (0.14)	0.48 (0.12)	0.16 (0.03)	0 (0)	0.08 (0.02)
	690W	–	0.97 (0.08)	0.14 (0.09)	0.30 (0.11)	0.01 (0.01)
	700C	2.25 (0.27)	1.06 (0.22)	0.77 (0.09)	–	–
	700W	0.85 (0.11)	0.34 (0.07)	1.73 (0.13)	–	–

**Table 4. Genetic ( $r_A$ ) and phenotypic ( $r_p$ ) correlations for the Exp. 690 tests at Cardwell for PCH × POOC and PCH × PTEC hybrids.  $r_A$  below diagonal and  $r_p$  above diagonal. Plus/minus standard errors of genetic correlation.**

Trait	Hybrid	HT	DBH	STR	LN	WF
HT	PCH × POOC		0.79	0.14	–0.07	0.02
	PCH × PTEC		0.65	0.11	–0.11	0.15
DBH	PCH × POOC	0.80±0.10		0.06	0.02	–0.03
	PCH × PTEC	0.47±0.21		0.08	–0.08	0.13
STR	PCH × POOC	0.28±0.25	–0.06±0.27		–0.49	0.30
	PCH × PTEC	0.34±0.25	0.24±0.26		–0.50	0.34
LN	PCH × POOC	–0.35±0.25	0.14±0.27	–0.89±0.07		–0.31
	PCH × PTEC	–0.26±0.27	–0.20±0.28	–0.96±0.04		–0.32
WF	PCH × POOC	0.25±0.26	–0.07±0.28	0.92±0.06	–0.91±0.06	
	PCH × PTEC	0.28±0.25	0.24±0.26	0.92±0.06	–1.00±0.03	

**Table 5. Genetic ( $r_A$ ) and phenotypic ( $r_p$ ) correlations for the Exp. 690 tests at Wongi.  $r_A$  ( $\pm$  standard errors) below diagonal and  $r_p$  above diagonal.**

Trait	Hybrid	DBH	STR	LN	WF
DBH	PCH × POOC		0.12	0.08	–0.09
	PCH × PTEC		0.12	–0.07	0.01
STR	PCH × POOC	–0.03±0.27		–0.49	0.52
	PCH × PTEC	0.12±0.28		–0.53	0.58
LN	PCH × POOC	0.34±0.24	–0.80±0.10		–0.52
	PCH × PTEC	–0.19±0.28	–0.97±0.02		–0.55
WF	PCH × POOC	–0.16±0.27	0.90±0.05	–0.76±0.12	
	PCH × PTEC	0.05±0.28	0.95±0.03	–0.97±0.02	

variance was more important than additive variance for growth traits for PCH × POOC at Wongi, and PCH × PTEC at Cardwell but not for PCH × PTEC at Wongi (Table 3). The ratio of dominance to additive variance

was larger for growth than stem straightness in Exp. 700 ; however, the relative importance of dominance variance for stem straightness of PCH × PTEC was larger in the Exp. 700 tests than in Exp. 690 tests (Table 3).

**Table 6. Genetic ( $r_A$ ) and phenotypic ( $r_P$ ) correlations for the Exp. 700 tests at Cardwell.  $r_A$  ( $\pm$  standard errors) below diagonal and  $r_P$  above diagonal.**

Trait	Hybrid	HT	DBH	STR
HT	PCH $\times$ PTEC		0.67	0.15
DBH	PCH $\times$ PTEC	0.61 $\pm$ 0.22		0.05
ST	PCH $\times$ PTEC	0.05 $\pm$ 0.36	0.21 $\pm$ 0.35	

**Table 7. Genetic ( $r_A$ ) and phenotypic ( $r_P$ ) correlations for the Exp. 700 tests at Wongi.  $r_A$  ( $\pm$  standard errors) below diagonal and  $r_P$  above diagonal.**

Trait	Hybrid	HT	DBH	STR
HT	PCH $\times$ POOC		0.81	0.14
	PCH $\times$ PTEC		0.73	0.02
DBH	PCH $\times$ POOC	0.82 $\pm$ 0.11		0.15
	PCH $\times$ PTEC	0.60 $\pm$ 0.22		0.10
ST	PCH $\times$ POOC	0.19 $\pm$ 0.33	0.37 $\pm$ 0.29	
	PCH $\times$ PTEC	-0.73 $\pm$ 0.20	-0.19 $\pm$ 0.35	

**Table 8. Individual narrow-sense heritability estimates ( $h^2$ ), genetic ( $r_A$ ) and phenotypic ( $r_P$ ) correlations for pooled analyses across two sites for the Exp. 690 tests.  $h^2$  ( $\pm$  standard error) below diagonal and  $r_P$  above diagonal.**

Trait	Hybrid	DBH	STR	LN	WF
DBH	PCH $\times$ POOC	<b>0.26<math>\pm</math>0.10</b>	0.09	0.04	-0.05
	PCH $\times$ PTEC	<b>0.15<math>\pm</math>0.06</b>	0.10	-0.07	0.09
STR	PCH $\times$ POOC	-0.04 $\pm$ 0.26	<b>0.34<math>\pm</math>0.11</b>	-0.48	0.37
	PCH $\times$ PTEC	0.17 $\pm$ 0.26	<b>0.29<math>\pm</math>0.10</b>	-0.51	0.41
LN	PCH $\times$ POOC	0.25 $\pm$ 0.25	-0.88 $\pm$ 0.06	<b>0.23<math>\pm</math>0.08</b>	-0.38
	PCH $\times$ PTEC	-0.20 $\pm$ 0.26	-0.98 $\pm$ 0.02	<b>0.21<math>\pm</math>0.07</b>	-0.40
WF	PCH $\times$ POOC	-0.10 $\pm$ 0.26	0.95 $\pm$ 0.03	-0.86 $\pm$ 0.07	<b>0.19<math>\pm</math>0.07</b>
	PCH $\times$ PTEC	0.11 $\pm$ 0.27	0.94 $\pm$ 0.03	-0.97 $\pm$ 0.02	<b>0.29<math>\pm</math>0.09</b>

### Correlations among traits

Genetic correlations at an individual tree level, between height and diameter were positive and high (0.80 – 0.82) for PCH  $\times$  POOC hybrid and moderate (0.47–0.61) for PCH  $\times$  PTEC (Tables 4, 6 and 7). Genetic correlations between growth traits and the other traits were either low positive or low negative, with large standard errors, except for an exceptionally high negative correlation (-0.73) between height and straightness in PCH  $\times$  PTEC hybrid for tests in Exp. 700 tests at Wongi (Tables 4–7).

High and favourable genetic correlations were found between stem straightness and lean, and wind-firmness with small standard errors (Tables 4–7). A negative correlation is expected between stem lean and

wind-firmness since the traits are inversely related, i.e. a severely leaning tree (large angle from vertical) was scored low for wind-firmness. Phenotypic correlations were generally lower than the equivalent genetic correlations for the same trait-trait comparisons, and followed the same trend as genetic correlations.

### Pooled analyses

Results from pooled analyses across sites, show that heritability estimates ranged from 0.11 to 0.34 (Tables 8 & 9). Estimates from tests in Exp. 690 (Table 8) were equivalent to those from Exp. 700 (Table 9) for DBH but higher for stem straightness. Generally, the heritability estimates from the data pooled across two sites were intermediate between those from individual sites.

**Table 9.** Individual narrow-sense heritability estimates ( $h^2$ ), genetic ( $r_A$ ) and phenotypic ( $r_p$ ) correlations for pooled analyses across two sites for the 700 tests for PCH × PTEC hybrids:  $h^2$  on diagonal,  $r_A$  below diagonal and  $r_p$  above diagonal ( $\pm$  standard errors of heritability and genetic correlations).

Trait	Hybrid	HT	DBH	STR
HT	PCH × PTEC	0.11±0.08	0.70	0.08
DBH	PCH × PTEC	0.61±0.21	0.18±0.10	0.06
ST	PCH × PTEC	-0.40±0.29	-0.12±0.33	0.12±0.08

**Table 10.** Ratio dominance to additive variance ( $D_A$ ) in PCH × POOC and PCH × PTEC hybrids from pooled analyses. Ratio of dominance to phenotypic variance ( $D_p$ ) is in parentheses.

Hybrid	Tests	HT	DBH	STR	LN	WF
PCH × POOC	690	–	0.77 (0.20)	0.22 (0.08)	0.23 (0.05)	0.16 (0.03)
PCH × PTEC	690	–	0.60 (0.09)	0.14 (0.04)	0.11 (0.02)	0.06 (0.02)
	700	1.80 (0.20)	0.89 (0.16)	0.67 (0.08)	–	–

**Table 11.** Genetic correlation ( $\pm$  standard errors) between pure PCH (Exp. 699) and the PCH × POOC and PCH × PTEC hybrids in Exp. 690 ( $r_{across}$ ).

Locations of test pair	Trait	$r_{pure}$	$r_{across}$
Cardwell – Cardwell	DBH – DBH	0.82±0.22	0.39±0.28
	HT – HT	0.75±0.34	0.69±0.18
	LN – LN	–	0.96±0.08
	ST – ST	-0.36±0.50	0.93±0.08
	WF – WF	–	0.99±0.05
Cardwell – Wongi	DBH – DBH	0.15±0.57	0.41±0.30
	HT – HT	0.56±0.46	–
	LN – LN	–	0.92±0.06
	ST – ST	-0.34±0.48	0.97±0.03
	WF – WF	–	0.99±0.03

Dominance variance was less than additive variance in all traits ( $D_A$  less than 1), except height in Exp. 700 (Table 10), and the relative importance of dominance variance was greater for growth traits than the other traits.

As was found in individual site analyses, genetic correlations between growth traits and other traits were low, and those between straightness, lean and wind firmness were high (Tables 8 and 9).

**Correlations between PCH in pure species and PCH in the hybrid combination, and PCH across hybrids**

Genetic correlations between parental performance of pure PCH (Exp. 699) planted at Cardwell and the hybrid PCH × PTEC in Exp. 700 (eight PCH parents in common) at Cardwell were high and positive (Table 11). However these same correlations were only low to moderate

for the Cardwell-Wongi pair of tests (Table 11). Genetic correlations for stem straightness were consistently low and negative.

Genetic correlations of parental PCH performance across PCH × POOC and PCH × PTEC hybrids within Exp. 690 (eleven PCH parents in common) were high and positive for stem straightness, stem lean and wind firmness (>0.92), but low to moderate for growth traits (0.39–0.69) (Table 11).

**DISCUSSION**

Heritability estimates for stem straightness, stem lean and wind-firmness were higher at Wongi than at Cardwell. Tests of Exp. 690 at Cardwell had about double the phenotypic variance in straightness and wind-firmness than that at Wongi (Table 1), and this could have contributed to a reduced heritability in tests

located at Cardwell. Cardwell tests of Exp. 690 also suffered more wind damage than those tests planted at Wongi. For example, the tests at Cardwell had 20–30% of trees with greater than 20° lean while less than 5% of trees at Wongi were severely affected by wind-damage. Hence, the higher phenotypic variances at Cardwell were probably due to the higher proportion of the more extreme values. (Note: Severely wind damaged trees tended to have very poor stem straightness).

Heritability estimates from the data pooled across the two locations were intermediate between those from individual tests. Heritability estimates are usually inflated from single site analyses because they confound the GEI with the additive variance. The fact that the pooled  $h^2$  estimates were intermediate suggests that, the importance of GEI may vary between sites, and that some individual sites probably had very little GEI, whereas others seemed to be greatly affected. The GEI was also trait dependant, for example straightness at 690 Wongi (Table 2), had highly inflated heritabilities, but DBH estimates were low. However, genetic correlations across sites were greater than 0.80 for all traits (DUNGEY *et al.* 2000) indicating that in general, genotype  $\times$  environment interactions were negligible, and hence pooling data from the different sites was considered appropriate for this study.

The heritability estimates for both PCH  $\times$  POOC and PCH  $\times$  PTEC hybrids were low to moderate for growth traits (0.11 – 0.26) using pooled data. These estimates are consistent with those reported by DIETERS *et al.* (1997) using a parental model, and by POWELL & NIKLES (1996) for *P. elliottii*  $\times$  PCH  $F_1$  hybrids in Australia (0.12–0.24). In contrast, the heritability estimates for stem straightness reported in this study are much higher than that reported by POWELL & NIKLES (1996) using an 8-point relative scale. This may be partly attributed to the fact that some tests in this study were more affected by wind damage than those reported by POWELL & NIKLES (1996), as well as inherent differences between the different hybrid populations.

The results showed that all traits in the hybrid populations were under moderate to strong additive genetic control, and dominance variance was less important than additive variance (except for height in the Exp. 700 tests). The predominance of additive genetic variance in hybrids is consistent with reports by DIETERS *et al.* (1997) and POWELL & NIKLES (1996) in pine hybrids, and BOUVET & VIGNERON (1996) in eucalypt hybrids. The results suggest that breeding strategies which maximise the use of additive genetic variance will be effective. Experience in Congo, however, indicated that the correlation of the performance of parents in the pure species and in hybrid

combination may be low even though dominance variance is low relative to additive variance (PH. VIGNERON personal comm.) This indicates that the predominance of additive genetic variance alone (in either pure species or hybrid populations), may not be a good indicator of the most effective breeding strategy.

The genetic correlations indicate that if selection is made on growth alone there will be a weak or no genetic response in straightness. DIETERS (1996) also found a weak correlation using the same relative scale on *Pinus elliottii*, and GWAZE *et al.* (1997) and PSWARAYI *et al.* (1996) both found a similar result using an absolute scale on *P. taeda* and *P. elliottii*, respectively. The assertion that genetic correlations between growth and straightness are positive in more wind-firm taxon (POWELL & NIKLES 1996) is weakly supported in this study. For example, genetic correlations between diameter and straightness in this study were low and negative in PCH  $\times$  POOC, and low and positive in PCH  $\times$  PTEC. *Pinus caribaea* var. *hondurensis*  $\times$  *Pinus oocarpa* is known to be more sensitive to wind damage than PCH  $\times$  PTEC in Australia (DIETERS *et al.* 1997), hence supporting the assertion. In contrast, there was no discernible trend in the genetic correlations between height and straightness in both hybrids – ranged from a high negative (–0.73) to a low positive (0.34) in both hybrids (Tables 7 and 4).

Straightness and wind damage assessments were highly correlated, probably indicating that straightness was confounded with wind damage – wind damaged trees were not straight. This may be expected since stem straightness was assessed 3–4 years after the occurrence of wind damage, and many of the crooked trees may have resulted from leaning trees that had corrected themselves. If stem straightness had been assessed soon after the trials were damaged by wind, then it may have been possible to more clearly separate these two traits. However, this is generally not possible since wind damage most frequently occurs in young trees, when it is very difficult to accurately assess the stem straightness due to the mass of foliage retained on the lower stem of these trees.

Wind damage was assessed using a visual score of wind-firmness immediately following wind damage and 3–4 years later by measuring the angle of lean. Heritability estimates for stem lean and wind-firmness were similar, and genetic correlations between the two traits were very strong, indicating that the visual assessment, which is less time consuming, was just as effective. Therefore, both traits need not be assessed, and the visual assessment of wind-firmness is preferable due to the lower cost of this method. These results also indicate that *ad hoc* assessments of genetic tests may not be required to capture information on wind damage, since



assessments a number of years after the event provided essentially the same information.

Genetic correlations between parental performance in pure PCH and in the PCH × PTEC F<sub>1</sub> hybrids in Exp. 700 were high for growth traits when both genetic tests were planted at Cardwell; however the correlations were low between the PCH test at Cardwell and the PCH × PTEC test at Wongi. Therefore, it appears that location or genotype × environment effects may be influencing the genetic correlation between pure and hybrid performance, and the correlations may have been higher if the pure PCH and hybrids were grown in the same experiment under common environmental conditions rather than in separate genetic tests. The high genetic correlations indicate that performance in the pure species is a good indicator of performance in the hybrid combination for height and diameter, if planted at the same location. This result is consistent with that of POWELL & NIKLES (1996) with *Pinus elliottii* var. *elliottii* (PEE) × PCH hybrid and its pure species, and may explain the apparent contradiction between the results of POWELL & NIKLES (1996) and DIETERS & NIKLES (1998). Nevertheless, the correlations between the pure PCH and the hybrid are difficult to reconcile with the genetic correlations between the PCH × POOC and PCH × PTEC hybrids (Table 11) where the correlations are weak for growth traits both within and between locations but correlations for stem straightness, lean and wind-damage are all strong. DIETERS & NIKLES (1998) also report very weak correlations for growth traits between *P. elliottii* and its hybrid with PCH, while the same correlations for stem straightness were stronger.

The implications of these results for the development of breeding strategies are not clear. Data presented indicate that for these sites, additive variance was usually more important than dominance in the hybrids investigated but depended on trait and site. This would suggest that breeding strategies, involving reciprocal recurrent selection (RRS) are not required for deployment across the sites tested. However, correlations between pure species and hybrid performance and between two different (but closely related hybrids) gave conflicting results. Under certain situations and for some traits a strong correlation was found across different genetic backgrounds. However, these correlations seem to be diminished when data was pooled across tests, and locations. Although good correlations may exist between performance in these pure species and hybrid populations tested (required for the implementation of pure species selection and crossing [PSS] breeding methods), it is unknown if they persist across the entire breeding population, or across untested locations. Therefore, breeding strate-

gies for deployment across the tested locations would ideally involve the evaluation of both pure and hybrid populations. This strategy, although not always the most economically attractive, will always provide genetic gain from selection and breeding.

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