INTERSPECIFIC PINE HYBRIDS II. GENOTYPE BY ENVIRONMENT INTERACTIONS ACROSS AUSTRALIA, SWAZILAND AND ZIMBABWE

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ABSTRACT

Collaborative research trials of Queensland-bred pine hybrids have been established in many sites outside Australia. These trials enable the estimation of genotype × environment effects, which are important in determining the level of regionalisation needed in any breeding program. Correlations across sites testing hybrids between *Pinus caribaea* var. *hondurensis* and both *P. oocarpa* and *P. tecunumanii* established in Australia, Swaziland, and Zimbabwe are reported. Diameter at breast height and height were measured in all trials, straightness in Australia and Zimbabwe, and wind firmness and lean in Australia, all at five years of age. For each pair of tests, additive genetic correlations and the correlation between full-sib family means were estimated for growth traits across sites. Genetic correlations between test-pairs located within the same country were all strong (0.65 to 0.95); however for pairs of tests in different countries the genetic correlations averaged 0.41 and 0.38 for *P. oocarpa* and *P. tecunumanii* hybrids, respectively. Family mean correlations were not as strong as genetic correlations, although they followed a similar pattern. A hybrid-production strategy, involving a two-staged approach of (a) reproducing proven superior families for local deployment and (b), crossing parents with high (hybrid) breeding values to produce additional families for testing across a broad range of sites for future deployment, is proposed.

Key words: *Pinus caribaea, Pinus tecunumanii, Pinus oocarpa,* genotype × environment interaction, genetic correlation, hybrids.

INTRODUCTION

Genotype × environment interaction (GEI) causes changes in ranking of the genetic worth of genotypes across different environmental regimes (HODGE 1996). If GEI exists, it presents a number of different options to the tree breeder. Rather than the more general approach of selecting for general adaptation across a broad range of sites, breeding programs may be 'regionalised' (JOHNSON & BURDON 1990), to provide further gains by selecting for specific adaptation (MATHESON & COTTERILL 1990). In Queensland, Australia, the success of inter-specific tropical pine hybrids (*e.g.* NIKLES 1996, POWELL & NIKLES 1996), stimulated the production and testing of other hybrid combinations, to enable GEI and performance testing both at a national and international level (*eg.* BARRETT *et al.* 1991, NIKLES 1987, NIKLES 1991). Two such hybrid combinations were those between *Pinus caribaea* var *hondurensis* Barr & Golf. (PCH) crossed with either *Pinus tecunumanii* (Schw.) Eguiluz et Perry (PTEC) or *Pinus oocarpa* (Schiede) (POOC). Previous reports from collaborative trials established in Zimbabwe have suggested that gains predicted from the deployment of PCH × PTEC or PCH × POOC hybrids could be more than double that of pure species commercial controls (GWAZE *in review*). However, while hybrid genotypes rank consistently across sites within Australia (DIETERS *et al.* 1997), and genetic variance estimates from the same sites have shown that the importance of additive and dominance was largely site dependant (GWAZE *et al.* 2000), little is known regarding the stability of the hybrids between countries.

Genotype × Environment interaction has been shown to be important for families of the pure species *Pinus tecunumanii*, particularly for straightness (DVORAK & SHAW 1992). However, in a smaller experiment across 2 sites in Malawi, no significant GEI was found

for growth traits of this species (MUNTHALI & STEWART 1998). Studies with PCH within Australia have generally shown that family and population performance is highly consistent across sites (GIBSON *et al.* 1983, WOOLASTON *et al.* 1991a, b). The strength of additive genetic correlations across sites for pine hybrids in Queensland, Australia, suggested that, at least within Queensland, the GEI effects are detectable in some hybrid combinations (PCH × PTEC hybrids, DIETERS *et al.* 1997), although this was not the case for all hybrids tested (PCH × POOC, r_g 0.89–0.95, DIETERS *et al.* 1997). Hybrid performance has been shown to vary relative to pure parental performance in *Eucalyptus* (*E. grandis* × *E. tereticornis*, *E. grandis* × *E. camaldulensis* and *E. grandis* × *E. urophylla*), depending on bioclimatic conditions (VERRYN *et al.* 1996). Similarly, a large family × environment interaction was found for *Populus tremuloides* × *P. tremula* hybrids planted on two sites, which differed primarily in their soil fertility and uniformity (LI & WU 1997).

This study examines the stability of PCH × POOC and PCH × PTEC hybrids across several sites within Queensland, Australia, and between countries (Australia, Zimbabwe, Swaziland) using genetic correlations (BURDON 1977). Heritabilities and the extent of both additive and dominance variation within the different hybrid populations were also explored. The implications of results obtained were then discussed in the context of selection efficiency for hybrid production and hybrid breeding strategies.

MATERIALS AND METHODS

Genetic material

The Australian material, described by GWAZE *et al.* (2000), was from four factorial matings between PCH and both PTEC and POOC (two 11 × 6 [Exp. 690] and two 5 × 4 [Exp. 700] factorials, with linking families). Both experiments were planted at two locations, Cardwell and Wongi (Table 1). Hybrid families tested in all other countries were a subset of these factorial mating designs produced in Australia and were planted at one site in Swaziland (Usutu Pulp) and two sites in Zimbabwe, John Meikle and Cashel (Table 1). Unfortunately, very few families are common to Experiments 690 and 700, and to the Zimbabwe and Swaziland trials (Tables 2 & 8).

The trial at John Meikle consisted of 6 replicates of 16 incomplete blocks and 5 tree line plots; at Cashel, 6 randomised complete blocks and 5 tree line plots and; in Swaziland, 5 replicates with 10 trees per line plot were planted in randomised complete blocks. In Australia, the hybrid families were planted in 36 randomised complete blocks, with each family represented by a single tree in each block and the PCH × PTEC and PCH × POOC hybrids were kept in separate but adjacent blocks within each site. At all other sites the two hybrids were randomly mixed within each block.

Assessments

Assessments of height (HT), diameter at breast height (DBH), straightness (STR) and wind firmness (WF) are described in detail by GWAZE *et al.* (2000) in Queensland, and GWAZE (in review) in Zimbabwe. Straightness in Zimbabwe was assessed as described by GWAZE (in review), on a 1 (crooked) to 7 (straight) scale. In Swaziland (Usutu), DBH was assessed for all trees, and HT for the first two trees of every plot.

Statistical analysis

All analyses for genetic correlations were undertaken using an individual tree model in the package ASREML (GILMOUR *et al.* 1998, see also GWAZE *et al.* 2000). Analysis between sites or countries was undertaken using model [1].

$$y_l = X_1 s + X_2 r + Z_1 f + Z_2 a + e \qquad [1]$$

where y is a vector of observations, s is a vector of site effects (fixed), r is a vector of replicate effects (fixed),

Table 1. Site details of experimental hybrid field trials.

	Australia		Swaziland	Zimbabwe	
	Cardwell (Cr)	Wongi (W)	Usutu (U)	John Meikle (JM)	Cashel (Cs)
Longtitude	146°E	152°E	32°E	33°E	33°E
Latitude	18°S	25°S	27°S	19°S	20°S
Altitude (m)	30	30	1025	1300	1525
Annual rainfall (mm)	2130	1060	900	1711	745

Table 2. Number of trees, number of parents, number of families and overall means (± standard deviation) for height, diameter, volume and straightness at 5 years of age at 2 sites in Zimbabwe and 1 site in Swaziland.

	PCH × POOC			PCH × PTEC		
	Cashel	John Meikle	Usuru	Cashel	John Meikle	Usuru
No. of trees	801	773	1400	854	866	1350
No. of parents (PCH, PTEC, POOC)	19.10	18.10	18.8	23.8	23.8	21.8
No. of families	27	26	28	29	29	27
Height (m)	6.9±1.4	9.5±1.4	7.3±1.1	7.7±1.4	10.0±1.5	8.0±1.2
Diameter (cm)	11.4±2.6	15.4±2.4	10.5±2.4	13.0±2.3	16.7±2.1	11.7±2.3
Straightness	3.5±0.9	4.1±0.7	–	3.3±0.8	4.1±0.7	–

f is a vector of random family effects (ie. specific combining ability), a is a vector of additive genetic effect of the individual trees (random) and e is a vector of residuals, which includes three quarters of the dominance variance and environmental error. X_1 and X_2 are the design matrix for the fixed effects site and replicate, and Z_1, and Z_2 are design matrices for the random effects, relating observations to the effects in the model.

The corresponding expected values and variance/covariance matrices were:

$$\begin{bmatrix} y \\ f \\ a \\ e \end{bmatrix} \sim N \left(\begin{bmatrix} X_{1s} + X_{2r} \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & Z_f F & Z_a G & R \\ FZ_f & F & 0 & 0 \\ GZ_a & 0 & G & 0 \\ R & 0 & 0 & R \end{bmatrix} \right)$$

Where the phenotypic variance $V = Z_f F Z_f' + Z_a G Z_a' + R$, and where R is the residual (co)variance matrix, $F = I \otimes G_{fo}$ where I is the identity matrix, G_{fo} 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 (σ_f^2) was interpreted as one quarter of the dominance variance (σ_D^2). Epistasis was assumed to be negligible. Details on individual tree models have been outlined further in GWAZE *et al.* (2000).

Individual test analysis of the John Meikle trial also included a fixed effect term for block. Standard errors of all genetic correlations were estimated using a Taylor series approximation (GILMOUR *et al.* 1998, STUART & OLD 1987). Genetic correlations were not calculated for site pairs with low numbers of parents in common, including the comparison between Swaziland and Zimbabwe, and between 690 and 700 in Queensland. Spearman's rank correlations were obtained for each test pair using the procedure CORR (SAS 1990) amongst least-squares family means at each site. Least squares means were estimated using the procedure GLM (SAS 1990) and Spearman's correlations were chosen because it was the changes in the ranks of the families that were of interest across sites.

RESULTS

Means

Mean height, diameter and straightness for the trials outside Australia, were greatest at the John Meikle site in Zimbabwe (Table 2). The Cashel site had the lowest mean growth of the three trials. Cashel also had the lowest annual rainfall of all the trial sites (Table 1). Straightness was the best at the John Meikle site, both within Zimbabwe and across all sites (see also GWAZE *et al.* 2000), although the slight differences in scale may account for this (1 to 6 within Australia, 1 to 7 within Zimbabwe).

Heritability

Individual narrow sense heritabilities for growth traits (DBH and HT) in the PCH × POOC hybrid combination were moderate for both the Zimbabwe sites (Table 3), and low for the site in Swaziland (Table 3) and were comparable to estimates obtained for the Australian sites (GWAZE *et al.* 2000). All heritability estimates for the PCH × PTEC hybrids were low, with the exception of DBH at Cashel (Table 3). Straightness heritability estimates were low to moderate (0.11 to 0.24, Table 3). *Pinus caribaea* var. *hondurensis* × *Pinus oocarpa* generally had higher estimates than PCH × PTEC hybrids at the same site, although this was not the case for HT (Usutu) and STR (Cashel and John Meikle).

Importance of dominance variance

Dominance variance was consistently low for growth

Table 3. Estimates of heritability ± standard error in *P. caribea* var. *hondurensis* (PCH) by *P. oocarpa* (POOC) and *P. tecunumanii* (PTEC) hybrids at the Cashel and John Meikle sites in Zimbabwe, pooled estimates for Zimbabwe (Cashel + John Meikle) and one site in Swaziland (Usutu).

Hybrid	Site	HT	DBH	STR
PCH × POOC	Cashel	0.47±0.16	0.42±0.14	0.24±0.23
	John Meikle	0.38±0.15	0.32±0.13	0.16±0.12
	Cashel + John Meikle	0.38±0.12	0.35±0.11	0.12±0.19
	Usutu	0.09±0.12	0.13±0.09	–
PCH × PTEC	Cashel	0.10±0.18	0.26±0.24	0.11±0.12
	John Meikle	0.16±0.11	0.00±0.11	0.14±0.14
	Cashel + John Meikle	0.07±0.09	0.00±0.10	0.14±0.11
	Usutu	0.11±0.18	0.02±0.11	–

Table 4. Ratio of dominance to additive variance (D_A) and the reatio of dominance to phenotypic variance (D_P) in PSH × POOC and PCH × PTEC hybrids in two tests in Zimbabwe (Cashel and John Meikle) and one site in Swaziland (Usutu) and from the two Zimbabwe sites combined (Cashel + John Meikle) (NE = not estimable).

Hybrid	Site		HT	DBH	STR
PCH × POOC	Cashel	D_A	0.11±0.36	0.02±0.33	2.21±3.57
		D_P	0.05±0.16	0.01±0.13	0.53±0.38
	John Meikle	D_A	0.00±0.00	0.15±0.40	1.13±1.90
		D_P	0.00±0.12	0.05±0.12	0.18±0.18
	Cashel + John Meikle	D_A	0.00±0.16	0.09±0.23	4.42±9.87
		D_P	0.00±0.06	0.03±0.08	0.52±0.34
	Usutu	D_A	1.54±3.80	1.93±2.28	–
		D_P	0.15±0.22	0.24±0.15	–
PCH × PTEC	Cashel	D_A	3.24±8.28	0.88±2.05	0.88±2.41
		D_P	0.34±0.31	0.23±0.34	0.10±0.18
	John Meikle	D_A	0.40±1.10	NE	1.89±3.20
		D_P	0.06±0.14	0.41±0.24	0.26±0.22
	Cashel + John Meikle	D_A	2.99±5.87	NE	1.03±1.75
		D_P	0.21±0.16	0.45±0.22	0.15±0.15
	Usutu	D_A	3.16±7.65	0.00±7.84	–
		D_P	0.35±0.33	0.00±0.16	–

traits (DBH and HT) for PCH × POOC hybrids in Zimbabwe, but not at Usutu (Table 4). All other dominance estimates showed considerable variation, both for straightness in the PCH × POOC and PCH × PTEC hybrids and growth in the PCH × PTEC hybrids. The highest dominance estimates were detected for HT at Cashel, and the pooled tests at Cashel and John Meikle, and Usutu in the PCH × PTEC hybrids and for STR for the combined Cashel and John Meikle estimates, in the PCH × POOC hybrids (Table 4). All dominance estimates, like heritability estimates, had high standard errors, most probably related to the relatively small sample sizes (Table 2).

Correlations among traits

Genetic and phenotypic correlations for John Meikle, Cashel and the two sites combined are given in Tables 5, 6, and 7 respectively. All genetic correlations between HT and DBH were moderate to high. At John Meikle, correlations were also strong between height and straightness (Table 5), however at Cashel, the relationship was only poor to moderate, the PCH × POOC providing a higher estimate than PCH × PTEC. Straightness and DBH were moderately correlated, except for PCH × POOC at John Meikle (Table 5).

Trait-trait genetic correlations obtained from the analysis of the pooled data from the Zimbabwe sites (John Meikle and Cashel, Table 7), ranged from 0.41 to 0.85, with moderate to high estimates obtained between HT and DBH, HT and STR and moderate correlations for DBH and STR. Combining the two data sets for estimates of additive genetic trait-trait correlations generally gave estimates between those obtained for

Table 5. Genetic (r_A) and phenotypic (r_P) correlations ± standard errors at the John Meikle site, for PCH × POOC and PCH × PTEC hybrids. r_A below diagonal and r_P above diagonal.

Trait	Hybrid	HT	DBH	STR
HT	PCH × POOC		0.69±0.10	0.50±0.04
	PCH × PTEC		0.49±0.03	0.54±0.03
DBH	PCH × POOC	0.72±0.13		0.44±0.05
	PCH × PTEC	0.68±0.18		0.33±0.04
STR	PCH × POOC	0.63±0.17	0.26±0.26	
	PCH × PTEC	0.78±0.13	0.61±0.19	

Table 6. Genetic (r_A) and phenotypic (r_P) correlations ± standard errors at the Cashel site, for PCH × POOC and PCH × PTEC hybrids. r_A below diagonal and r_P above diagonal.

Trait	Hybrid	HT	DBH	STR
HT	PCH × POOC		0.81±0.02	0.49±0.06
	PCH × PTEC		0.71±0.03	0.41±0.04
DBH	PCH × POOC	0.94±0.04		0.47±0.06
	PCH × PTEC	0.93±0.05		0.36±0.05
STR	PCH × POOC	0.56±0.18	0.48±0.21	
	PCH × PTEC	0.17±0.33	0.43±0.27	

Table 7. Genetic (r_A) and phenotypic (r_P) correlations ± standard errors for the pooled Zimbabwe sites (Cashel and John Meikle) for PCH × POOC and PCH × PTEC hybrids. r_A below diagonal and r_P above diagonal.

Trait	Hybrid	HT	DBH	STR
HT	PCH × POOC		0.75±0.02	0.51±0.04
	PCH × PTEC		0.60±0.02	0.49±0.03
DBH	PCH × POOC	0.65±0.14		0.45±0.05
	PCH × PTEC	0.85±0.08		0.35±0.04
STR	PCH × POOC	0.84±0.07	0.41±0.21	
	PCH × PTEC	0.61±0.17	0.59±0.17	

individual sites. However, this was not the case in two instances (HT and DBH for PCH × POOC, HT and STR for PCH × PTEC).

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 to 14).

Genetic correlations were generally positive, and although general trends were unclear, correlations for PCH × PTEC hybrids (DBH), between Swaziland and Australia and the John Meikle site in Zimbabwe and Australia (experiment 690), were strong, with an average of 0.74 and 0.70 respectively (Table 8). However, correlations between the two Zimbabwe sites and the Australian sites for DBH, were not always strong, with Cashel having the lowest genetic correlation between sites in PCH × PTEC hybrids. In particular, correlations were essentially zero between Cashel and Swaziland, and between Cashel and 700W and John Meikle and 700W (Table 8). Between site genetic correlations in the PCH × POOC hybrids gave a stronger relationship between Cashel and the majority of sites in Australia and Swaziland (0.50 to 0.54, Table 9), although correlations for DBH were poor for 700W. Correlations were generally higher for within country PCH × POOC paired comparisons (0.45–0.95, Table 9) when compared with between country comparisons (average 0.39) and were generally lower than correla-

Table 8. PCH × PTEC estimates of within and across country family mean correlations (above diagonal) and genetic correlations ± standard error (below diagonal) for DBH for 4 tests in Australia, 1 test in Swaziland (U) and 2 tests in Zimbabwe (Cs and JM). Number of families in common is given in parentheses. (Cr Cardwell; W Wongi; U Usutu; Cs Cashel; JM John Meikle). *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

	690Cr	690W	700Cr	700W	U	Cs	JM
690Cr		0.63*** (57)	0.50 ns (3)	0.50 ns (3)	0.57 ns (9)	0.45 ns (13)	0 .33 ns (13)
690W	0.95±0.04		0.50 ns (3)	0.50 ns (3)	0.43 ns (9)	0.48 ns (13)	0.58* (13)
700Cr	0.58±0.42	0.24±0.53		0.73*** (24)	0.40 ns (8)	−0.31 ns (8)	0.50 ns (8)
700W		0.79±0.32	0.83±0.13		−0.02 ns (8)	−0.52 ns (8)	0.52 ns (8)
U	0.62±0.25	0.86±0.16	0.59±0.30	0.54±0.34		– (1)	– (1)
Cs	0.38±0.31	0.32±0.34	0.33±0.40	−0.53±0.31	−0.14±0.32		0.38* (29)
JM	0.69±0.23	0.70±0.24	0.33±0.46	−0.07±0.43	0.43±0.30	0.65±0.19	

Table 9. PCH × POOC estimates of within and across country family mean correlations (above diagonal) and genetic correlations ± standard error (below diagonal) for DBH for 2 tests in Australia (690 Cr, 690 W), 1 test in Swaziland (U) and 2 tests in Zimbabwe (Cs and JM). Number of families in common are given in parentheses. (Cr Cardwell; W Wongi; U Usutu; Cs Cashel; JM John Meikle). *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

	690Cr	690W	700W	U	Cs	JM
690Cr		0.79*** (62)	0.40 ns (4)	0.19 ns (15)	0.52* (15)	0.52 ns (14)
690W	0.95±0.04			0.43 ns (15)	0.64* (15)	0.51 ns (14)
700W	0.62±0.27	0.43±0.32		0.36 ns (11)	0.64 ns (7)	0.46 ns (7)
U	0.34±0.28	0.50±0.25	0.18±0.41		– (0)	– (0)
Cs	0.50±0.24	0.52±0.24	0.26±0.35	0.54±0.26		0.74*** (26)
JM	0.43±0.25	0.41±0.25	0.39±0.30	0.46±0.28	0.86±0.11	

Table 10. PCH × PTEC estimates of within and across country family mean correlations (above diagonal) and genetic correlations ± standard error (below diagonal) for HT for 4 tests in Australia (690Cr, 690W, 700Cr, 700W), 1 test in Swaziland (U) and 2 tests in Zimbabwe (Cs and JM). Number of families in common are given in parentheses. (Cr Cardwell; W Wongi; U Usutu; Cs Cashel; JM John Meikle). *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

	690Cr	700Cr	700W	U	Cs	JM
690Cr		−1.0*** (3)	−1.0*** (3)	0.42 ns (13)	0.32 ns (13)	0.42 ns (13)
700Cr			0.57** (24)	0.50 ns (8)	0.48 ns (8)	0.02 ns (8)
700W		0.86±0.13		0.10 ns (8)	0.43 ns (8)	−0.07 ns (8)
U	0.57±0.35	0.87±0.27	0.57±0.38		– (1)	– (1)
Cs	−0.40±0.32	0.92±0.16	0.44±0.40			0.43* (29)
JM	0.65±0.30	−0.31±0.45	0.24±0.45			

tions found in the PCH × PTEC hybrids (Table 8 cf. Table 9).

No clear trend was discernible for paired correlations using height. While Swaziland estimates were positively correlated with the Australian sites (PCH × PTEC), they were not consistently or well correlated for the PCH × POOC combination (Tables 10, 11). Similarly, at the two Zimbabwean sites, correlations were positive but poor with Australian sites, in the PCH × POOC combination. It was of interest, the Cashel and Cardwell sites were highly genetically correlated for height (Table 10).

Straightness provided a much clearer picture, especially within the PCH × PTEC combination (Table 12), where correlations were generally high between Australian and Zimbabwean tests. In contrast, correlations between the individual tests Cardwell and Cashel were low for both hybrid combinations (Tables 12, 13).

The ranking of individual families seemed to be more influenced by environment, as family correlations

Table 11. PCH × POOC estimates of within and across country family mean correlations (above diagonal) and genetic correlations ± standard error (below diagonal) for HT for 2 tests in Australia (690Cr, 700W), 1 test in Swaziland (U) and 2 tests in Zimbabwe (Cs and JM). Number of families in common are given in parentheses. (Cr Cardwell; W Wongi; U Usutu; Cs Cashel; JM John Meikle). *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

	690Cr	700W	U	Cs	JM
690Cr		0.40 ns (4)	–0.67** (15)	0.23 ns (15)	0.34 ns (14)
700W			0.05 ns (11)	0.39 ns (7)	0.46 ns (7)
U	–0.88±0.36	0.39±0.31		– (0)	– (0)
Cs	0.34±0.28	0.39±0.31			0.77*** (26)
JM	0.44±0.27	0.54±0.29			

Table 12. PCH × PTEC estimates of within and across country family mean correlations (above diagonal) and genetic correlations ± standard error (below diagonal) for straightness for 4 tests in Australia (690Cr, 690W, 700Cr, 700W) and 2 tests in Zimbabwe (Cs and JM). Number of families in common is given in parentheses. (Cr Cardwell; W Wongi; U Usutu; Cs Cashel; JM John Meikle). *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

	690Cr	690W	700Cr	700W	Cs	JM
690Cr		0.79*** (57)	0.50 ns (3)	1.00*** (3)	0.78** (13)	0.81*** (13)
690W	0.95±0.04		0.50 ns (3)	1.00*** (3)	0.77** (13)	0.81*** (13)
700Cr				0.60** (24)	–0.28 ns (8)	–0.02 ns (8)
700W			0.95±0.08		–0.21 ns (8)	–0.26 ns (8)
Cs	0.83±0.17	0.75±0.18	0.81±0.17	0.82±0.18		0.65*** (29)
JM	1.11±0.13	0.92±0.09	0.64±0.25	0.74±0.21		

Table 13. PCH × POOC estimates of within and across country family mean correlations (above diagonal) and genetic correlations ± standard error (below diagonal) for straightness for 3 tests in Australia (690Cr, 690W, 700W) and 2 tests in Zimbabwe (Cs and JM). Number of families in common are given in parentheses. (Cr Cardwell; W Wongi; Cs Cashel; JM John Meikle). *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

	690Cr	690W	700W	Cs	JM
690Cr		0.83*** (62)	–0.20 ns (4)	0.61* (15)	0.48 ns (14)
690W	0.94±0.04		0.80 ns (4)	0.88*** (15)	0.76** (14)
700W				0.04 ns (7)	0.57 ns (7)
Cs	0.44±0.25	0.77±0.12	0.62±0.22		0.71*** (26)
JM	0.16±0.33	0.53±0.25	0.72±0.25		

Table 14. Family mean rank correlations of lean and wind firmness for both PCH × PTEC and PCH × POOC hybrids between two sites (690 at Cardwell and Wongi), in Australia. Number of families in common between sites are given in parentheses. *, **, * indicate significance levels of 0.001, 0.05 and 0.01 respectively.**

		PCH × PTEC 690W	PCH × POOC 690W	PCH × PTEC 690W family	PCH × POOC 690W family
lean	690Cr	0.91±0.06	0.95±0.04	0.68*** (57)	0.77*** (62)
Wind firmness	690Cr	0.80±0.11	0.86±0.09	0.71*** (57)	0.66*** (62)

were generally lower than genetic correlations between the same sites. Family correlations were high within a country for DBH and height (Tables 8, 9) but were generally non-significant between countries. However, John Meikle was significantly correlated with 690 at Wongi for both growth traits (DBH and height), and

Cashel in Zimbabwe was also significantly correlated with both Australian 690 tests (Wongi and Cardwell, Tables 8–11). Straightness, however, was strongly correlated between most sites (Tables 12 and 13), as were lean and wind firmness in the Australian tests where these traits were assessed (Table 14).

DISCUSSION

Heritability estimates were comparable with estimates obtained for tests in Queensland (GWAZE *et al.* 2000), although estimates for DBH were higher at Cashel in Zimbabwe. Estimates for growth traits were generally higher in the PCH × POOC hybrid than in the PCH × PTEC hybrid, and were higher at Cashel than either of the other two African tests. The PCH × PTEC hybrid had very low heritability estimates in all tests except Cashel. Cashel was the driest and the highest elevation site included in this study and these extreme factors may have contributed to greater genetic differentiation and higher heritabilities at this site. The site with slower growth, Usutu, also had some of the lowest heritabilities. Differences in estimates between sites may well be attributable to some genotype × environment effects.

Heritability estimates were also comparable with those of PCH × *Pinus elliottii* var. *elliottii* hybrids (POWELL & NIKLES 1996) and with pure species estimates for PCH (for HT: 0.09–0.37), and PTEC (for HT: 0.09–0.42; VÁSQUEZ & DVORAK 1996). However, PCH × PTEC heritabilities estimated from the tests examined in this paper were consistently lower than estimates calculated elsewhere. Certainly, the majority of estimates calculated here also had relatively high standard errors, probably a reflection of the small sample sizes (773 to 1350 individual trees, Table 2) and differences in heritability estimates may reflect the smaller overall population size represented in these tests.

Results indicated that all traits were predominantly under additive genetic control. However, while dominance estimates were all relatively low, estimation of dominance variance is less precise, especially with low numbers of parents and small sample sizes (NAMKOONG & ROBERDS 1974). Trends, however, indicated that dominance was greater for straightness than for the other growth traits, and greatest in the Zimbabwean tests (Table 4).

Although it was difficult to identify any clear patterns, the additive genetic correlations (ie. type B genetic correlations *in sensu* BURDON 1977) were generally positive, and where pairs of tests were reasonably well linked (ie. had a number of parents and families in common), the genetic correlations were at least moderate. Correlations reported here are also very similar to averages quoted by HODGE (1996) for PTEC (tested in Brazil, Colombia, South Africa, and Venezuela, 87 tests in total) of 0.76 within country, and 0.39 between countries. Further, WOOLASTON *et al.* (1991b) reported type B genetic correlations for PCH on sites within Queensland ranging between zero and one, averaging 0.59 for tests of Queensland open-pollinated families tested on eight sites. Therefore, it appears that these hybrids are subject to a similar level of genotype × environment interaction (GEI) as that reported for open-pollinated families of either PCH or PTEC. These results therefore provide no indication that hybrids are more (or less) stable in their performance across different sites than are the pure species.

These findings are consistent with variation in hybrid versus pure species performance in *Eucalyptus*, where hybrid performance varied in comparison to pure species depending on rainfall and soil characteristics (VERRYN *et al.* 1996). Similarly, there was a large family × environment interaction for hybrids between *Populus tremuloides* × *P. tremula* planted on two sites, which differed primarily in their soil fertility and uniformity. Even within the pure species, PTEC was found to have important family × site interactions, particularly for straightness (DVORAK & SHAW 1992). However, in an experiment across two sites in Malawi, no significant interactions were found in the growth traits of this species (MUNTHALI & STEWART 1998). Studies with PCH within Australia have generally shown that family and population performance is highly consistent across sites (GIBSON *et al.* 1983, WOOLASTON *et al.* 1991a, b).

In this study of PCH × PTEC and PCH × POOC hybrids, it should be noted that the reduced genetic correlations found between tests located in different countries will be partially related to differences in the accuracy of the breeding values, caused by low number of parents in common between tests. This will have the effect of reducing the value of the genetic correlations. Therefore, some of the apparent additive × environment interaction observed here between sites in different countries may be caused by imbalance in the family structure, rather than true GEI. Nevertheless, it appears as if some genotype × environment interaction was present across the sites and/or hybrids examined.

The PCH × POOC hybrids demonstrate fairly consistent correlations between test sites: genetic correlations are mostly between 0.35 and 0.5, while most family rank correlations are between 0.4 and 0.6 (Table 8–14). However, the across site performance of the PCH × PTEC hybrids seems to be more variable. For example: the Swaziland site shows strong genetic correlations with sites in Queensland; genetic correlations involving the Cashel site in Zimbabwe are lower than average,

and many of the estimates are not significantly different from zero; the John Meikle site had quite variable correlations with the other sites; and correlations between sites in southern Africa and Queensland were often higher than correlations between sites within southern Africa.

The general trend of moderate and positive correlations between tests with good linkage suggests that the breeding values of the parents involved in the production of these hybrids are reasonably consistent across the sites and countries where these tests were located. Nevertheless, the performance of individual families at one particular site (Cashel) seems to be more strongly influenced by GEI. Therefore, a testing and deployment strategy involving the production of hybrid families by crossing parents with high (hybrid) breeding values, and the testing of these families across multiple sites, may prove optimal. Superior families identified in these trials could then be reproduced and vegetatively multiplied for commercial deployment in specific locations. Further, clonal testing of individuals from superior families may identify clones with low GEI, that are stable across multiple environments and these could be used for future commercial deployment. If family trials were clonally replicated across sites, the best clones could then be selected for immediate deployment without further testing (SELBOURNE 1972, 1992). This strategy would capture gains from using parents with high breeding values and any GEI at the family and clonal level and would be optimal for species such as POOC, due to its coppicing ability.

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