# MID-ROTATION PERFORMANCE OF *PINUS CARIBAEA VAR. HONDURENSIS* HYBRIDS WITH BOTH *P. OOCARPA* AND *P. TECUNUMANII*: HYBRID SUPERIORITY, STABILITY OF PARENTAL PERFORMANCE AND POTENTIAL FOR A MULTI-SPECIES SYNTHETIC BREED

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## ABSTRACT

$F_1$ hybrid progeny between *Pinus caribaea* var. *hondurensis* (PCH) and both *P. oocarpa* (POOC) and *P. tecunumanii* (PTEC) established in field tests at two locations in Queensland were used to evaluate growth relative to PCH controls, and to estimate genetic parameters for the hybrid populations. These two PCH hybrids showed significantly greater growth (diameter and height) than the PCH controls in three of the four field tests, growing at the two locations. The PCH × PTEC hybrids showed greater productivity than the PCH × POOC hybrids when compared to the PCH controls. Heritability estimates for growth were low to moderate for both hybrid combinations with the amount of additive variance increasing with time, as did the proportion of additive to non-additive variance. The performance of PCH parents was maintained across-sites for growth, wind-firmness and straightness regardless of the species (PCH, PTEC or POOC) to which they were mated. PCH parents performed similarly across-sites with high additive and dominance genetic correlations between sites for growth traits, and the genetic correlations were high between diameter at 5 years and both diameter and height at 10 years of age. Additionally, strong correlations were found for the common PCH parents when crossed with PCH, POCC or PTEC. Evaluation of growth and the associated genetic parameter estimates support the inclusion of these taxa in a multi-species synthetic breed for site-specific deployment in central and southeast Queensland.

**Keywords:** Breeding strategy, interspecific hybridisation, genetic parameters, heritability, genotype by environment interaction, age-age correlation

## INTRODUCTION

Over the past 50 years the breeding program previously managed by the Queensland Forestry Research Institute (QFRI, now Department of Primarily Industries and Fisheries – Forestry) in Australia has tested various exotic pine species and their hybrids for solid wood production (NIKLES 1996, DIETERS 2000). The major emphasis has been on *Pinus caribaea* var. *hondurensis* Barr. & Golf. (PCH) and *Pinus elliottii* var. *elliottii* Engelm. (PEE), and now the $F_1$ hybrid between these two species has become the taxon of choice for plantation establishment on coastal lowland sites in southeast Queensland and well-drained sites of the central Queensland coast. The PEE × PCH $F_1$ hybrid is now being deployed on all suitable sites in Queensland in monoclonal blocks of tested clones. Clonal testing and mass propagation of the best clones via rooted cuttings is expected to yield large genetic gains (WALKER *et al.* 1996) in growth, stem quality and wood properties. The development of a hybrid breeding strategy to underpin the clonal program is a short-term goal for plantation forestry in Queensland (KERR *et al.* 2004a).

Simulation studies designed to elucidate the benefits of various hybrid breeding strategies have identified the creation of a synthetic breed as generating the most genetic gain per year over a large range of genetic structures, with a modified form of reciprocal recurrent selection being the next best option (KERR *et al.* 2004b). The development of a stable synthetic breed, by recurrent selection from an initial (genetically diverse) $F_1$ hybrid base population, potentially has many biological and economic advantages for many forest tree species. It is planned to adopt a synthetic breeding strategy in Queensland for the continued genetic improvement of the PEE × PCH hybrid. However, many other hybrid combinations have been developed and tested in Queensland and have considerable potential for deployment on some sites or for particular end-uses (Dieters 2000, Nikles 1996).

When considering plans for the development of a synthetic hybrid from PEE and PCH, it became apparent that selected $F_1$ individuals from other hybrid combinations (i.e. other than PEE × PCH) could be used advantageously as parents in the development of a multi-species synthetic. Inclusion of multiple species in a synthetic would allow for the inclusion of desirable traits found in other pines; such as better growth in tropical climates, reduced branch size/angle, enhanced stem form, greater resistance to wind-damage and superior wood quality. Creation of a synthetic breed would be facilitated if parents for advanced generation crosses could be selected without testing the parent in each hybrid combination. If a given parent performs relatively well regardless of the species with which it is combined, the selection of parents for a synthetic breed would be simplified.

This paper reports on 10-year data from four tests of $F_1$ hybrid progeny resulting from crosses between PCH and both *P. oocarpa* Schiede (POOC) and *P. tecunumanii* (Schw.) Eguiluz & J.P. Perry (PTEC), that were established in tests at two near-coastal locations in Queensland. Results of five-year data collected in these hybrid tests were reported by Dieters *et al.* (1997), Dungey *et al.* (2000), and Gwaze *et al.* (2000). This paper examines the data from a different perspective and presents additional 10-year data. Although hybrids between PCH and either POOC or PTEC are known to have faster early growth when compared to pure PCH (Francis *et al.* 1984, Nikles 1989), their poor wind-firmness (i.e. resistance to wind-damage in comparison to pure PCH) may limit the commercial deployment of these hybrids in locations, such as Queensland, which are affected by strong winds. Nevertheless, it has been recognised that a superior $F_1$ individual, selected in hybrid families of either PCH × POOC or × PTEC, may have considerable value if used as a parent for further hybridisation with PEE × PCH ($F_1$ or $F_2$), PEE (for deployment in the sub-tropics) or PCH and *Pinus caribaea* var. *caribaea* (for deployment in the tropics). Such hybrid parents could provide genes for wood quality traits, coppicing ability, or disease resistance, as well as additional volume production. In this paper we therefore examine the stability of performance of the common (PCH) parents across genetic backgrounds, the performance of the hybrid taxa compared to pure PCH controls, and the stability of hybrid performance across-sites and ages.

## MATERIALS AND METHODS

### Genetic material

Eleven unrelated first- and second-generation PCH parents were crossed with pollen from six POOC and six PTEC parents to produce two 11 × 6 factorial arrays. Sixty-one out of the possible sixty-six hybrid crosses (in each factorial) produced sufficient seed for establishment in at least one test (Dieters *et al.* 1997). The PCH parents were plus-trees intensively selected in Queensland plantations that had been established using unimproved seed imported from the Mountain Pine Ridge (MPR) provenance of Belize. The POOC and PTEC parents were, in both cases, local selections from two separate native provenances: El Zapotillo and Valle de Angeles (both from Honduras), and MPR (Belize) and Yucul (Nicaragua), for POOC and PTEC respectively.

### Hybrid and pure species evaluation

The hybrid families were established in field tests at two coastal lowland locations, one in subtropical south Queensland (Wongi – lat. 25 °S long. 152 °E, mean annual rainfall 1155 mm/yr, mean daily maximum and minimum temperatures 26.9 °C and 15.2 °C – rainfall and temperature data from Maryborough) and the other in tropical north Queensland (Cardwell – lat. 18 °S, long. 146 °E, mean annual rainfall 2118 mm/yr, mean daily maximum and minimum temperatures 28.2 °C and 18.8 °C). The PCH × PTEC and PCH × POOC hybrids were planted in separate but adjacent tests at the two locations. Each test was established in a randomised complete block design with six replications of six-tree non-contiguous plots for a total of thirty-six trees per site per family in each test. Three controls of pure PCH were included in the field tests to allow a direct assessment of the performance of the hybrids relative to the taxon (PCH) that was being deployed operationally on these sites. The three controls included in each test were: 1) unimproved PCH — a mixture of seed from many roadside PCH trees within plantations established with unimproved MPR seed; 2) PCH clonal seed orchard mix (PCH CSO) — a sample of plants raised from seeds collected in clonal seed orchards (derived from the MPR provenance) that was used operationally at the time these trials were established; and, 3) individual control-pollinated families of PCH — a small number of full-sib families derived from some of the PCH parents used to produce the hybrid progeny.

Since publication of earlier results from these trials (Dieters *et al.* 1997, Gwaze *et al.* 2000, and Dungey *et al.* 2000), a major review has been completed of all the PCH progeny trials planted in eastern Queensland since 1970. This review included data from over 335,000 individual trees, growing in 179 trials that were established by the QFRI and it antecedents. The results (unpublished) from this analysis were then used to predict breeding values for all the parents and their offspring represented in these field trials (Dieters, 2002 – QFRI internal report). Breeding values are now available for the following traits: height (HT) and over bark diameter (DBH) at 6 and 10 years of age (HT6, HT10, DBH6 and DBH10), stem straightness (STR6), foxtailing (FOX) and wind-firmness (WF). FOX and WF were analysed as binomial scores – *e.g.* presence/absence of foxtails, and windfirm/non-windfirm trees. Breeding values (BVs) were predicted for over 1400 parent trees and their progeny using an individual tree model that incorporated a fixed effect for site and block within-site, a fixed effect for pollen source and a random genetic effect for each tree. BVs of the PCH parents used to produce the PCH × PTEC and PCH × POOC hybrid progeny reported here were compared to the PCH BVs from the comprehensive review of pure PCH progeny trials to investigate the stability of parental performance across different genetic backgrounds.

## Field assessments

Five years after planting, all trees were assessed for over bark diameter at breast height (DBH5), stem straightness (ST5), wind firmness (WF5) and longest internode (LI5). Stem straightness was assessed on a six-point scale with a score of six assigned to the straightest trees (Cotterill & Dean 1990). Windfirmness was scored on a four-point scale that categorized the amount of lean from vertical with a score of four assigned to trees with little or no discernible wind-damage, and a score of one assigned to severely damaged trees. The length of the longest internode, assessed visually, placed trees into one of four classes: trees with a maximum internode length greater than 3 metres were classified as 1, while those with a maximum less than 1 metre were classified as 4. This assessment provides a measure of a tree's propensity to produce foxtails, which is generally regarded as an undesirable trait since long-internode length is frequently linked to top breakage. The current paper focuses on measurements taken ten years after planting, ie. diameter at breast height (DBH10) and height (HT10). Portions of the analysis of the five-year data are presented here for clarity, but readers should refer to the results of the fifth year measure (DBH5, ST5 and WF5) reported previously (Dieters *et al.* 1997; Gwaze *et al.* 2000) for full details.

## Statistical analysis

Proc MIXED (SAS Institute 1994) was used to evaluate the significance of effects and provide least square means for estimates of taxa within-site effects for comparisons to PCH controls. Restricted maximum likelihood (REML) estimates of variance components were obtained using PROC MIXED. The statistical model used for the single site analyses was:

$$Y_{jklm} = \mu + B_j + F_k + M_l + FM_{kl} + FB_{jk} + MB_{jl} + P_{jkl} + E_{jklm}$$

where: $Y_{jklm}$ is the $m^{th}$ tree of the $kl^{th}$ family in the $j^{th}$ block; $\mu$ is the overall mean; $B_j$ is fixed effect of the $j^{th}$ block, $F_k$ is the random effect of the $k^{th}$ female parent, ~ $N(0, \sigma^2_f)$; $M_l$ is the random effect of the $l^{th}$ male parent, ~ $N(0, \sigma^2_m)$; $FM_{kl}$ is the random interaction between the $k^{th}$ female parent and the $l^{th}$ male parent, ~ $N(0, \sigma^2_{fm})$; $FB_{jk}$ is the random effect of the interaction between the $j^{th}$ block and the $k^{th}$ female parent, ~ $N(0, \sigma^2_{bf})$; $MB_{jl}$ is the random effect of the interaction between the $j^{th}$ block and the $l^{th}$ male parent, ~ $N(0, \sigma^2_{bm})$; $P_{jkl}$ is the random effect of variation between plots, ~ $N(0, \sigma^2_p)$; and $E_{jklm}$ is the random error associated with the $m^{th}$ observation of the $kl^{th}$ family in the $j^{th}$ block ~ $N(0, \sigma^2_e)$.

The across-site model is the same as that given above, but with the inclusion of fixed terms for test and block nested within test, as well as random terms for test-by-female-parent interaction, test-by-male-parent interaction, and female-parent-by-male-parent-by-test interaction. Across-site analysis used standardized data, which was transformed by dividing each observation by the square root of the within test error variance (previously estimated from the single-site analyses for each trait). The PCH controls were dropped from the analyses when estimating variance components and genetic correlations between taxa and sites; however, they were included for the purposes of estimating least squares means with SAS.

The variance among the female and male parents was regarded as an estimate of ¼ of the variance among the parental BVs in hybrid combination, i.e.

an estimate of ¼ of the additive variance (¼$\sigma_A^2$). This in turn was used to estimate the proportion of phenotypic variance transmitted to the hybrid progeny (i.e. heritability) with no additional reference to the hybrid nature of the genotypes that were progeny tested. Similarly, the interaction between female and male parents was assumed to provide an estimate of ¼ of the dominance variance (¼$\sigma_D^2$). Likewise, the breeding value predictions of the parental superiority or inferiority relative to the tested population are not explicitly referred to as either general hybridising ability, *sensu* Nikles & Newton (1991), or general combining ability. Heritability estimates were calculated for female and male parents as:

$$h^2 = 4(\sigma_f^2/\sigma_P^2) \text{ or } h^2 = 4(\sigma_m^2/\sigma_P^2)$$

where: $\sigma_f^2$ = variance among female parents, $\sigma_m^2$ is the variance among male parents, and $\sigma_P^2$ = is the total phenotypic variance calculated as the sum of all variance components. Heritability estimates obtained from the analysis of single-site data are biased upwards due to an inclusion of genotype-by-environment interaction in the genetic variance, and are denoted with a subscript 'b'.

The ratio of additive to dominance variance was then calculated using the average additive variance of the male and female parents, divided by the variance component for families (*i.e.* interaction of male and female parents), as follows:

$$\sigma_a^2/\sigma_d^2 = \tfrac{1}{2}(\sigma_f^2 + \sigma_m^2)/\sigma_{fm}^2$$

Alternatively, these parameters ($h^2$ and $\sigma_A^2/\sigma_D^2$) can be viewed as: (1) 4× ratio of variance between female (or male) parents to the total variance, and (2) ratio of the average variance between parents and the variance between families, requiring no genetic interpretation of the observed variance components.

ASREML (Gilmour *et al.* 1999) was used to predict BVs for each tree in the four hybrid tests. The statistical model used in ASREML allowed site to interact at the tree and family level, which generated predictions for all trees and families at each site, site-specific variance components and site-trait correlations. The genetic correlation is defined as the correlation between BVs (Falconer & Mackay 1996). Given that BLUP provides the best available approximation of the true BVs, Pearson's product moment correlations between the BLUPs were used to provide suitable estimates of the genetic correlations. The method is similar to that of the family mean correlations of Dungey *et al.* (2000), differing only in that random BLUPs were correlated rather than fixed least square means. There will be some shrinking of the correlation between the BVs compared to the 'true' genetic correlation, particularly for BVs predicted with low precision as in low heritability traits with few observations (Lambeth & Huber, 1997). However, given the low level of imbalance in these tests, all BVs are predicted with approximately the same level of precision, therefore simple correlations among the BVs are expected to provide good (though probably slightly conservative) estimates with no need for an adjustment using the accuracy of the predictions (Lu *et al.* 1999).

Type B genetic correlations (Yamada 1962) of the same trait at different sites were calculated as:

$$r_B = \sigma_f^2/(\sigma_f^2 + \sigma_{fe}^2)$$

where: $\sigma_f^2$ = female variance, and $\sigma_{fe}^2$ = female by test interaction estimated from across site analyses using standardized data. Similar calculations were preformed with the variance between male parents ($\sigma_m^2$) and the interaction of male parents with sites ($\sigma_{me}^2$). In addition to Yamada's correlation, a multivariate approach was used within ASREML treating the same trait (*e.g.* height) observed in the four tests, as four separate traits. This allowed for the estimation of the genetic correlations between the additive and dominance effects at each test location.

## RESULTS AND DISCUSSION

### Growth and yield of hybrids compared to PCH controls

In particular, the PCH × PTEC hybrids showed evidence of hybrid superiority for growth at both locations. Individual tree diameter and height were greater at Cardwell, at both five and ten years of age, than at the Wongi location (Table 1), as might be expected due to the higher annual temperatures and rainfall at the Cardwell location. Both hybrids grew well compared to the controls at both locations with an average increase in diameter of 14 % and 6 % over the unimproved and clonal seed orchard material respectively. The same was true for height improvement with an across site superiority of 11 % and 5 % over the unimproved and clonal seed orchard material, respectively. Additionally, improvement within the pure species for growth was apparent when comparing the unimproved material with the clonal seed orchard material and the mean of the control pollinated families. Significant improvement over the PCH controls for growth traits was evident ($p < 0.1$) for both DBH and HT at three of the four tests across the two locations, with the exception being the POOC test at Cardwell.

**Table 1. Least square means for PCH × POOC and PCH × PTEC hybrids and PCH controls at Cardwell and Wongi.**

| Site | Material | DBH 5 (cm) | DBH 10 (cm) | HT 10 (m) | St 5 (1–6) | LI 5 (1–4) | WF 5 (1–4) |
|---|---|---|---|---|---|---|---|
| Cardwell | PCH × POOC | 17.2 | 25.2 | 21.9 | 3.7 | 3.9 | 3.4 |
| | PCH Unimproved | 16.5 | 23.4* | 21.3 | 2.5* | 3.4* | 3.5 |
| | PCH CSO | 17.0 | 24.1# | 21.8 | 3.6 | 3.7* | 3.7* |
| Cardwell | PCH × PTEC | 18.1 | 25.2 | 23.4 | 3.0 | 3.7 | 3.1 |
| | PCH Unimproved | 14.8* | 20.1* | 20.8* | 2.2* | 3.3* | 3.1 |
| | PCH CSO | 15.8* | 21.7* | 21.9* | 3.1 | 3.5* | 3.6* |
| | PCH CP families | 16.6* | 23.3* | 22.4* | 3.8# | 3.6 | 3.5* |
| Wongi | PCH × POOC | 12.7 | 18.9 | 15.0 | 3.9 | 3.9 | 3.7 |
| | PCH Unimproved | 12.9 | 18.0* | 14.1* | 3.3* | 3.2* | 3.5* |
| | PCH CSO | 13.6* | 19.4 | 15.0 | 4.4* | 3.2* | 3.8 |
| Wongi | PCH × PTEC | 13.1 | 19.0 | 15.6 | 3.7 | 3.6 | 3.6 |
| | PCH Unimproved | 11.8* | 16.1* | 13.5* | 3.4 | 3.2* | 3.7* |
| | PCH CP families | 12.8 | 18.4 | 14.7* | 4.5* | 3.4* | 3.9* |

* Significantly different ($\alpha = 0.10$) from hybrid families, # Significantly different ($\alpha = 0.05$) from hybrid families.

PCH × PTEC hybrids were taller than either the PCH × POOC hybrids or the PCH controls at both locations; however, direct statistical tests were not possible due to the physical separation of the hybrid tests at each location. Although the tests (of the two hybrids) were planted adjacent to one another at each location, rather than being completely randomised with one another, common PCH controls were established for direct comparison with the hybrid progeny. The PCH growth of the same control material in the PCH × PTEC tests was much slower than the PCH growth in the adjacent PCH × POOC tests. For example, the mean heights of the unimproved control at 10 years of age, were 21.3m and 20.8m at Cardwell and 14.1m and 13.5m at Wongi for the PCH × POOC and PCH × PTEC hybrids respectively at these two locations (Table 1). Therefore, by chance it appears that the PCH × POOC hybrids have been established on slightly better sites than the PCH × PTEC hybrids. Of greater importance is the differential between the hybrids and the unimproved control (planted in all four tests): the hybrids involving PTEC are clearly superior to the POOC hybrids. For example, percentage advantage in height at 10 years of age over the unimproved control were 11.5 % and 15.6 % for the PCH × PTEC hybrids at Cardwell and Wongi respectively, compared to only 2.8 % and 6.4 % for the PCH × POOC hybrids at Cardwell and Wongi. Hence the PCH × PTEC hybrids yielded around 9 % additional gain in height compared to unimproved PCH. The same trend is observed for diameter (Table 1), but the additional gain in diameter associated with the PCH × PTEC hybrids is much higher, at approximately 15 % for diameter compared to 9 % for height. There is also some evidence that PTEC has thinner bark than either PCH or POOC (Bill Dvorak, *pers. comm.*), and unpublished data from separate Queensland tests indicate that the PCH × PTEC hybrid generally has thinner bark than PCH; however, the difference in bark thickness was only significant at one site of the four sites (Paul Toon, *pers. comm.*). Hence the differences observed here in over-bark diameters (PCH × PTEC hybrid cf. pure PCH) may have been larger if we had compared the under-bark diameters.

In addition to absolute diameter, the diameter increment from age 5 to 10 of each hybrid was greater than that of the unimproved PCH control. While the POOC hybrids were not different from the PCH control at age 5, they were significantly larger at age 10. Other organizations working with these Central American species, have also observed increasing growth rates with age in POOC on some sites (DVORAK *et al.* 2000a), and for PCH across-sites in Brazil, Colombia and Venezuela (HODGE & DVORAK 2001).

The hybrids were straighter and had longer internode lengths than the unimproved PCH control at both sites, but usually their straightness was poorer than the improved PCH control (Table 1). The clonal seed orchard material and control pollinated families of PCH showed significantly greater windfirmness compared than the hybrids at both sites, with the exception of the PCH × POOC hybrid at

Wongi where the difference was not significant (Table 1).

### Genetic parameters

The genetic parameters estimated from paired-site analysis of the 61 PCH × POOC and 57 PCH × PTEC families planted at both the Cardwell and Wongi locations are given in Table 2. Parameters obtained from the analysis of data from each of the four tests are presented separately in Table 3. Heritability estimates were obtained for the female (PCH) and male (PTEC or POOC) parents, while the ratio of additive to dominance variance used an average additive effect from the maternal and paternal estimates. Type B genetic correlations between hybrid performance at Cardwell and Wongi were estimated for each set of hybrids from the across-sites analysis using Yamada's method. Parameter estimates for diameter at five years of age, and assessments of stem straightness and wind-firmness have been reported previously (DIETERS *et al.* 1997, and GWAZE *et al.* 2000), therefore genetic parameters for these traits are not reported again here.

### Heritability and the ratio of additive and dominance variances

Estimates of biased (single-site) and unbiased (paired-site) heritability for growth (Tables 2 and 3) are generally low to moderate (0.1 to 0.3), but similar to many other published estimates for pine species. The unbiased heritability estimates from the paired site analyses (Table 2) are generally intermediate

**Table 2. Genetic parameter estimates across two planting sites for heritability of female (PCH, female $h^2$) and male (PTEC or POOC, male $h^2$) parents, ratio of additive to dominance variance ($\sigma_A^2/\sigma_D^2$) and Type B genetic correlations for female (PCH, female $r_{gB}$) and male (PTEC or POOC, male $r_{gB}$) parents with standard error in parentheses.**

| Trait | Hybrid | Heritability (female $h^2$) | Heritability (male $h^2$) | $\sigma_A^2/\sigma_D^2$ | Type B (female $r_{gB}$) | Type B (male $r_{gB}$) |
|---|---|---|---|---|---|---|
| DBH 10 | PCH × POOC | 0.21 (0.11) | 0.33 (0.24) | 2.40 (1.99) | 0.85 (0.15) | 0.75 (0.16) |
| | PCH × PTEC | 0.25 (0.14) | 0.23 (0.21) | 6.82 (7.60) | 0.71 (0.10) | 0.56 (0.14) |
| HT 10 | PCH × POOC | 0.11 (0.07) | 0.19 (0.13) | 4.01 (3.70) | 0.61 (0.16) | 0.79 (0.12) |
| | PCH × PTEC | 0.12 (0.08) | 0.11 (0.10) | 3.86 (4.51) | 0.66 (0.16) | 0.55 (0.22) |
| LI | PCH × POOC | 0.01 (0.02) | 0.01 (0.01) | 2.57 (7.17) | 0.28 (0.51) | 0.79 (0.58) |
| | PCH × PTEC | 0.03 (0.03) | 0.11 (0.08) | 0.96 (0.94) | 0.55 (0.23) | 0.89 (0.20) |

Note: Ratio of additive to dominance variance calculated with the average male and female additive variance.

**Table 3. Genetic parameter estimates by site for biased heritability of female (PCH, female $h_b^2$) and male (PTEC or POOC, male $h_b^2$) parents, and ratio of additive to dominance variance ($\sigma_A^2/\sigma_D^2$) with standard error in parentheses.**

| Trait | Hybrid | Site | Heritability (female $h_b^2$) | Heritability (male $h_b^2$) | $\sigma_A^2/\sigma_D^2$ |
|---|---|---|---|---|---|
| DBH 10 | PCH × POOC | Cardwell | 0.29 (0.15) | 0.49 (0.31) | 3.18 (2.40) |
| | | Wongi | 0.16 (0.09) | 0.37 (0.24) | 1.80 (1.49) |
| | PCH × PTEC | Cardwell | 0.42 (0.19) | 0.55 (0.35) | 7.38 (5.86) |
| | | Wongi | 0.20 (0.11) | 0.14 (0.10) | 1.23 (0.94) |
| HT 10 | PCH × POOC | Cardwell | 0.18 (0.09) | 0.24 (0.16) | 5.27 (5.31) |
| | | Wongi | 0.19 (0.10) | 0.22 (0.15) | 4.39 (4.13) |
| | PCH × PTEC | Cardwell | 0.17 (0.09) | 0.22 (0.15) | 4.96 (5.19) |
| | | Wongi | 0.24 (0.12) | 0.09 (0.07) | 1.26 (0.94) |
| LI | PCH × POOC | Cardwell | 0.06 (0.04) | 0.03 (0.02) | NE |
| | | Wongi | 0.07 (0.04) | 0.00 (0.01) | 15.5 (17.0) |
| | PCH × PTEC | Cardwell | 0.05 (0.03) | 0.06 (0.05) | 1.41 (1.70) |
| | | Wongi | 0.06 (0.04) | 0.19 (0.13) | 1.50 (1.39) |

between the two biased heritability estimates (Table 3) from the respective single site analyses.

The heritability of the female parents (PCH) might be expected to be higher than that of the male parents, due to the larger number of female (11) than male (6) parents. However, there is no consistent pattern evident in the results of the either the biased or unbiased results (Tables 2 & 3). The PTEC unbiased heritability estimates were generally lower than companion estimates for POOC; however, differences were not consistent, and certainly well within the limits of the standard errors on the heritability estimates. The biased heritability estimates for diameter and height (Table 3) were often higher at Cardwell where growth was better. An increase in heritability in hybrid pine progeny tests from improvement of site quality through silvicultural practices that increase growth has been noted in tests planted in the southeast USA (LOPEZ-UPTON *et al.* 1999). In contrast to the heritability of diameter and height, the heritability estimates of internode length were generally very low (Tables 2 & 3), and probably not significantly different from zero (i.e. the estimate was less than two standard deviations from zero).

When heritability estimates for diameter at 10 years of age are compared to those for diameter at 5 years of age (DIETERS *et al.* 1997), the heritability increased for all single-site and paired-site estimates. An increase in heritability has also been shown to occur in various other species (e.g. WEI & BORRALHO 1996). This increase is no doubt partially a result of the increase in scale as the trees grow, which is evident in the fact that increases in single-site estimates were usually much greater than the related paired-site estimates. Analysis of the paired-sites used standardised data to remove effects of differences in scale between sites, but it also has the effect of removing differences in scale between the two ages. Therefore, any scale effects are absent from the estimates presented for the paired-site analyses.

The increase in heritability with time was associated with an increase in the $\sigma^2_a/\sigma^2_d$ ratio (cf. Tables 2 & 3 with DIETERS *et al.* 1997), suggesting that the amount of additive variance is increasing with age, while the amount of non-additive variance is remaining relatively constant. In the paired-site analyses, the ratio of additive to dominance variance, increased from under 2.0 in diameter at 5 years of age (DIETERS *et al.* 1997) to 2.4 and 6.8 for diameter at 10 years in the POOC and PTEC hybrids respectively (Table 2), and suggests additive gene effects increasingly regulate the genetic control of growth in these pine hybrids as they mature. This is similar to results found with growth traits in eucalypt hybrids (VOLKER 1995, BOUVET & VIGNERON 1996) where additive effects were found to predominate. Similar age trends have also been reported in *Pinus taeda* (BALOCCHI *et al.* 1993, LI *et al.* 1996) and *Pinus elliottii* (DIETERS *et al.* 1995) progeny tests in the southeast USA.

## Stability – Genetic correlations

The stability of a genotype, when defined as the ability of that genotype to maintain it's ranking for a given trait within a population across-sites or ages, was assessed using correlations between predicted BVs and direct estimates of genetic correlations from multivariate analyses. Stability has been used in the literature primarily to describe the consistency of genotype ranking between sites, and will be used as such here in addition to the connotation of stability across genetic backgrounds (crossed with the same or another species) and stability between ages. These well balanced experiments with excellent survival and family representation permitted straightforward estimations of the correlation between BVs. The breeding values generated from this set of tests and the broader Queensland PCH progeny test series (DIETERS 2002 – unpublished report) allowed for the estimation of several measures of stability: (1) Stability of the PCH parents against different genetic backgrounds, i.e. PCH, POOC and PTEC; (2) Stability of PCH, POOC and PTEC parents across two contrasting sites; and, (3) Stability of the PCH, POOC and PTEC parents from the 5 year to 10 year assessment.

The correlation between predicted BVs of PCH parents estimated from progeny with a genetic background of either pure PCH or that from another species, was used as one indicator of stability. The first two sections of Table 4 present genetic correlations (correlations between BVs) predicted using data from the 4 hybrid tests that form the basis of this paper and BVs from another 179 pure-species PCH tests established throughout the coastal regions of Queensland (DIETERS 2002 – unpublished report). The third section of Table 4 presents correlations between the BVs of the PCH parents estimated using either data from the PCH × PCH or the PCH × PTEC hybrid tests.

### 1) Correlations across different genetic backgrounds

Correlations between BVs for the same trait predicted from pure PCH tests and the hybrid tests were consistently high (>0.75) with the exception of internode length in Table 4, sections 1 and 2, on the diagonals. The expression of long internode length (i.e. foxtailing) is known to be reasonably site specific. From the mean values in Table 1, it can be seen that the average internode is quite short in the four

**Table 4. Correlations between 11 PCH parental breeding values predicted using 174 pure PCH progeny trials and PCH breeding values from paired site analysis the same parents tested at Cardwell and Wongi as PCH × PTEC or PCH × POOC hybrids.**

| | | PCH Bvs predicted from PCH × PTEC hybrid trials | | | | |
|---|---|---|---|---|---|---|
| | | HT 10 | DBH 10 | ST | LI | WF |
| 1. Pure PCH Bvs from 174 trials | HT 10 | 0.85** | 0.62** | 0.07 | –0.25 | 0.20 |
| | DBH 10 | 0.64** | 0.83** | -0.36 | 0.04 | -0.30 |
| | St 6 | 0.32 | –0.12 | 0.87** | –0.09 | 0.86** |
| | Fox | 0.07 | –0.12 | 0.07 | 0.54* | 0.15 |
| | WF | 0.11 | –0.33 | 0.78** | –0.47 | 0.83** |
| | | PCH Bvs predicted from PCH × POOC hybrid trials | | | | |
| | | HT 10 | DBH 10 | ST | LI | WF |
| 2. Pure PCH Bvs from 174 trials | HT 10 | 0.83** | 0.80** | 0.07 | –0.34 | 0.12 |
| | DBH 10 | 0.42 | 0.88** | –0.33 | –0.28 | –0.32 |
| | St 6 | 0.46 | -0.04 | 0.87** | 0.15 | 0.82** |
| | Fox | 0.30 | 0.03 | 0.12 | 0.62** | 0.26 |
| | WF | -0.27 | -0.27 | 0.71** | -0.10 | 0.75** |
| | | PCH Bvs predicted from PCH × POOC hybrid trials | | | | |
| | | HT 10 | DBH 10 | ST | LI | WF |
| 3. PCH Bvs predicted from PCH × PTEC hybrid trials | HT 10 | 0.78** | 0.75** | 0.33 | –0.11 | 0.29 |
| | DBH 10 | 0.36 | 0.78** | -0.02 | -0.01 | -0.07 |
| | ST | 0.31 | –0.18 | 0.94** | 0.15 | 0.89** |
| | LI | -0.04 | -0.07 | -0.03 | 0.87** | -0.23 |
| | WF | 0.43 | -0.09 | 0.93** | 0.03 | 0.93** |

* Significant correlation at $p < 0.10$, ** Significant correlation at $p < 0.05$.

hybrid tests. By contrast, in the tests for which the pure PCH BVs for foxtailing were derived, internode length was usually only assessed if there was a fairly high incidence of foxtailing in the trial. Hence, the trait assessed in the hybrid tests (i.e. foxtailing on sites which had not produced a significant incidence of this trait) may not be exactly the same as that assessed in the pure PCH tests (i.e. foxtailing on sites which had a relatively high incidence of foxtails).

Wind-firmness is a problem in both PTEC and POOC when planted where strong winds are common, with whole stands occasionally blown over during strong winds associated with cyclones or severe thunderstorms. The moderate to high correlations of 0.83 and 0.73 for PTEC and POOC respectively, provide promise that selection of more wind-firm PCH parents will produce more wind-firm hybrid progeny (Table 4). Improvement in wind-firmness within PCH (NIKLES *et al.* 1983) has been successful in the Queensland breeding program, as evidenced in these four tests, with the unimproved PCH control showing less wind-firmness compared to either improved control (Table 1).

Correlations between PCH parents used in combination with either PTEC or POOC were positive and high for growth (0.78 for both HT10 and DBH10, Table 4 – Section 3). The correlation between the PCH BVs from PCH × PTEC trials and the PCH BVs from PCH × POOC trials were slightly lower than those estimated between hybrid and pure species BVs (i.e. 0.78 vs. 0.85 and 0.83 for HT10). This may be due to better precision of the pure PCH BVs, an increase in the total variation in the hybrids due to heterosis or a bias caused by genotype by environment interaction. However, the absolute differences are small and probably well within the accuracy of these correlations.

The correlations between traits were mostly weak, with the exception of the correlation between straightness and wind-firmness (Table 4). This could be an artefact of the assessment – trees affected by wind-damage have as a consequence bent stems. However, during the assessment attempts were made to separate effects of wind-damage on stem straightness from true sinuosity of the stem. Further, there is some evidence from the PCH breeding program that intensive selection for stem-straightness is associated with wind-firmness. Repeatedly, when plus-trees (that have been selected prior to wind-damage) are inspected following wind-damage to the stand, most of the trees intensively selected for stem straightness have shown good wind-firmness. This combined with the known improvement in wind-firmness from the PCH breeding program (cf. Table 1) suggests that the favourable correlation between stem straightness and wind-firmness is probably real, and not simply due to the assessment method.

Overall, the correlations between PCH parental BVs (regardless of genetic background) were very high suggesting that PCH parents can be reliably selected for these traits based on either hybrid or pure species progeny performance with confidence. This contrasts with previous estimates of the genetic correlations between the performance in hybrid and pure species combination, using data from another test of PCH × PTEC (grown at Cardwell and Wongi) and only one PCH trial planted at Cardwell with just eight parents in common (GWAZE *et al.* 2000), where the correlations were lower for growth traits (particularly across-sites) but similar for stem quality. The increased correlation between parental BVs reported here is probably due to two factors: (1) more precise BV predictions due to using the complete set of 179 tests versus data from a single test, and (2) the larger number of parents in common.

### 2) Correlations across-sites: Genotype-by-environment interactions

Yamada's Type B genetic correlations at ten (Table 2) and five years (DIETERS *et al.* 1997) were generally high reflecting the stability of parental performance across the two locations. PCH × POOC was more stable for growth traits than PCH × PTEC; however, differences in estimates of the Type B correlations were much less than the respective standard errors associated with these estimates. Therefore, the observed differences in stability across-sites associated with the PTEC parents (male $r_b$) may not be real. PTEC was found to have important family × site interactions for growth traits in a large series of CAMCORE trials across countries but considerably less interaction within countries (HODGE & DVORAK 1999). DUNGEY *et al.* (2000) also report a similar pattern for trials of hybrids between PCH and both POOC and PTEC, where the genetic correlations within country (Australia or Zimbabwe) were generally much better than the correlations between countries. The Type B estimates for non-growth traits were all high with the exception of internode length in PCH. The low incidence of long internodes and low heritability for this trait could be reasons for the apparent poor stability of this trait across sites.

The multivariate approach used to predict the parental breeding value permitted estimation of each tree's breeding value at each location, but also estimates of additive and dominance genetic correlations between taxa and locations (Tables 5 & 6). The additive genetics correlations for the same taxa across-sites (eg DBH10 for PCH × PTEC hybrids = 0.86, Table 5) were higher than would be expected based on the female and male type B genetic correlations (0.71 and 0.51 respectively, Table 2). Inflation of the additive covariance may result from the larger number of parents (17 vs. 11 female or 6 male parents), or may be a consequence of the hybrid nature of the progeny involved (ie. violation of assumptions for estimation of additive variance). Dominance correlations are presented in Table 5 for traits measured at 5 (DBH, ST5, and WF5) and 10 (DBH10 and HT10) years of age. The additive (Tables 2 & 5) and dominance (Table 6) genetic correlations between locations were positive and high for growth traits, indicating material selected at one location would produce progeny that would perform well in other locations. The Type B correlations were above SHELBOURNE'S (1972) suggested threshold of 0.67 for the PCH × POOC hybrids but below this limit for growth traits in the PCH × PTEC hybrids. Similarly the dominance correlations between sites (Table 6) were also consistently lower for the PCH × PTEC hybrids. This suggests that hybrids of PCH × PTEC may be less stable across-sites than PCH × POOC hybrids at both the parental and family levels.

### 3) Age-age correlations

The additive correlations between diameter measured at age 5 years and diameter at 10 years were simply estimated by correlating the breeding values of the parents (estimated separately for each trait, location and age in ASREML). Given the high level of balance in these experiments, this is approximately equal to the age-age genetic correlation as previously described. In all cases the age-age correlations between the DBH breeding values were very high, and significant at the 0.05 level – all age-age correlations of age 5 and 10 year DBH breeding values exceeded 0.95. This suggests that 5 year growth is a very good predictor of the mid-rotation performance of these two interspecific hybrids.

**Table 5. Additive genetic correlation trials above diagonal (standard errors in parenthesis) and Yamada 's type B genetic correlation below diagonal for DBH at 5 years, DBH at 10 years, height at 10 years, straightness at 5 years and wind firmness at 5 years.**

| | | Cardwell PCH × POOC | Cardwell PCH × PTEC | Wongi PCH × POOC | Wongi PCH × PTEC |
|---|---|---|---|---|---|
| DBH 10 | C. PCH × POOC | 0,83 | 0.86 (0.10) | 0.87 (0.08) | 0.52 (0.22) |
| | C. PCH × PTEC | | | 0.96 (0.08) | 0.86 (0.09) |
| | W. PCH × POOC | | | | 0.87 (0.13) |
| | W. PCH × PTEC | | 0.41 | | |
| HT 10 | C. PCH × POOC | 0,73 | 0.85 (0.12) | 0.83 (0.10) | 0.51 (0.21) |
| | C. PCH × PTEC | | | 0.98 (0.06) | 0.80 (0.12) |
| | W. PCH × POOC | | | | 1.00 (0.07) |
| | W. PCH × PTEC | | 0.62 | | |
| LI | C. PCH × POOC | 0,62 | 0.98 (0.05) | 0.87 (0.07) | 0.74 (0.13) |
| | C. PCH × PTEC | | | 0.79 (0.11) | 0.79 (0.10) |
| | W. PCH × POOC | | | | 0.99 (0.03) |
| | W. PCH × PTEC | | 0.59 | | |

**Table 6. Site-site correlation between dominance effects for hybrid pine progeny.**

| | | Cardwell PCH × POOC | Cardwell PCH × PTEC |
|---|---|---|---|
| DBH 5 | W. PCH × POOC | 0.88 (0.14) | |
| | W. PCH × PTEC | | 0.59 (0.36) |
| DBH 10 | W. PCH × POOC | 0.78 (0.16) | |
| | W. PCH × PTEC | | 0.63 (0.28) |
| HT 10 | W. PCH × POOC | 0.73 (0.45) | |
| | W. PCH × PTEC | | 0.56 (0.37) |
| ST 5 | W. PCH × POOC | 1.00 (0.61) | |
| | W. PCH × PTEC | | 1.00 (0.37) |
| WF 5 | W. PCH × POOC | 0.26 (0.48) | |
| | W. PCH × PTEC | | 1.00 (1.21) |

## IMPLICATIONS FOR A SYNTHETIC BREED

These tests have produced evidence of the stability of PCH parental performance against different genetic backgrounds, in different environments, and at different ages. Genetic correlations between species, sites and ages were high, which suggest that good (i.e. high breeding value) PCH parents can be used to produce sound hybrid families for operational deployment when combined with either PTEC or POOC.

Simulation studies designed to elucidate the benefits of various hybrid breeding strategy options have identified the creation of a synthetic breed as superior under most genetic architectures (KERR *et al.* 2004b). The creation of a synthetic breed by intermating advanced generation hybrids was found to provide the most genetic gain per breeding cycle when there is less dominance variance than additive variance and the correlation between pure and hybrid species BV's is greater than zero. Although results from studies differ, this is the structure found in the PCH, PEE and $F_1$ hybrid populations managed by QFRI (DIETERS & DUNGEY 2000, POWELL 2001). Using outstanding $F_1$ and subsequent hybrid generations to advance a breeding program is expected to stabilise a synthetic population after two or three generations of mating, due to the exponential reduction in linkage disequilibrium between unlinked genes (FALCONER & MACKAY 1996). However, if the dominance theory of heterosis is assumed the original superiority found in the $F_1$ cross will diminish unless other taxa are included in the breed; as shown by GREGORY *et al.* (1991) the retention of gain due to heterosis will decrease from 75 % to 50 % when two taxa are used compared to using four taxa. However, levels of dominance variance were found to be low in PEE × PCH hybrids (DIETERS & DUNGEY 2000). In either case, retention of any heterotic effects caused by dominant gene action favours the inclusion of multiple species in a synthetic breed.

Inclusion of multiple species in a synthetic breed would allow the incorporation of desirable traits found in other species. For example, the fast growth in tropical climates, fine branching and low resin content of PTEC or the high wood density, pitch canker resistance, drought resistance and sprouting ability of POOC (DVORAK et al. 2000 a & b) might be infused into a PEE × PCH synthetic. South African studies of PTEC and POOC wood have shown both these species can produce solid wood products of high quality (DVORAK *et al.* 2000a & b). Production of large quantities of improved hybrid seed has been difficult for large reforestation programs based on hybrid germplasm, but seed production problems have been overcome by using vegetative plant production systems and innovations in control pollinated seed production. Enhanced seed set in advanced generation hybrid crosses (NIKLES 1992) will allow for the production of large numbers of seed needed for the deployment of families or clones in propagation systems that require many seed.

Creation of a synthetic breed would be facilitated if parents for advanced generation crosses could be selected without testing the candidate parents in a specific hybrid combination. If a parent consistently ranks well regardless of the species with which it is combined, it would be considered stable against different genetic backgrounds and the correlation between pure and hybrid species performance would be high. The extensive network of PCH progeny trials established by the QFRI could then be used to select parents for inclusion in the synthetic breed without creating hundreds of new crosses. This network of trials has shown that the very best parents could be used to generate propagules for plantation establishment across the entire estate given the low amount of genotype by environment interaction (GEI) found in the parent species (WOOLASTON *et al.* 1991 a & b). Utilization of GEI is still possible (VERRYN *et al.* 1996) by directing the various synthetic genotypes to specific sites based on non-PCH species contained within the composite. For example, planting a synthetic line containing POOC to drought-prone sites, or avoiding planting PTEC or POOC lines to sites subject to severe wind damage, could be used to increase yield or minimize risks. Increasing the diversity of a principally PEE × PCH synthetic breed by including other species has the potential to increase the range of sites over which the material is currently planted and incorporate additional complementary traits into the hybrids that are currently deployed to operational plantations.

## CONCLUSION

Results reported here support the concept of including additional taxa in the development of a PEE × PCH-based synthetic breed. The high genetic correlations between PCH parental predictions when crossed with PCH, PTEC or POOC suggest good PCH parents will produce well-adapted progeny if crossed with these similar taxa. Additive effects are more important than dominance effects and both are well correlated across-sites and genetic backgrounds, indicating that hybrid superiority should be maintained in advanced generations. Parents and families are also expected to perform similarly across very distinct sites. In addition, selection at early ages will be effective at capturing the majority of the available genetic gain. Inter-mating with POOC and/or PTEC to modify traits found in the PEE × PCH $F_1$ hybrid (currently used for most of the reforestation efforts of the Department of Primary Industries in Queensland) is expected to consistently increase yield and has the potential to improve various quality traits.

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