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CORRELATIONS BETWEEN PURE AND HYBRID COMBINING ABILITIES OF SLASH PINE PARENTS

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ABSTRACT

Four trials were analysed to provide taxa comparisons for growth and stem quality as well as genetic parameters for Queensland bred *Pinus elliottii* (PEE) and *P.elliottii* × *P.caribaea* var. *hondurensis* (PCH) F_1 hybrids. Of particular interest was the genetic correlation between related progenies in pure species and hybrid combination (r_{ph}), or equivalently the correlation between the general combining ability (GCA) and general hybridising ability (GHA). PEE families produced less volume than either the PCH controls or the F_1 hybrid families and exhibited slightly more crown defects than either of the other two taxa. The heritability estimates were very high for the F_1 hybrid trials but moderate to low in the pure PEE trials. Type-B genetic correlations were high within the same taxa giving further evidence of the low levels of genotype by environment interaction found within southeast Queensland for these two taxa. Pearson correlations between univariate GCA and GHA estimates provided similar r_{ph} estimates to those obtained directly from multivariate analyses. There was no correlation between the GHA and GCA estimates for the 56 PEE parents represented in this study for growth traits; however, a high and positive correlation was found for straightness. While straightness in hybrids may be selected for using pure PEE progeny trial data, growth traits in pure and hybrid progeny of PEE appear to be uncorrelated. Field testing of F_1 hybrid families or poly-crossed PEE parents prior to operational deployment or inclusion in more intensive clonal screening programs will continue to be necessary if resources are to be focused on the very best hybrid families.

Keywords: *Pinus elliottii*, *P.elliottii* × *P.caribaea* var. *hondurensis*, genetic correlations.

INTRODUCTION

The present paper describes experiment 671, which was established primarily to estimate the correlation between General Combining Ability (GCA) and General Hybridising Ability (GHA see NIKLES and NEWTON 1991)) (r_{ph}) using field trials established with open-pollinated *Pinus elliottii* var. *elliottii* Engelmannii (PEE) seedlings and hybrid seedling progeny. Hybrid seedlings were produced by poly-crossing the same PEE parents as those from which open pollinated seed was collected with a mixture of pollens from selected *P. caribaea* var. *hondurensis* Morelet (PCH) parents. Simulation studies designed to evaluate a range of hybrid breeding strategies have identified r_{ph} as a decisive variable in the selection of an appropriate breeding strategy as changes in this statistic have a large impact on the genetic gains produced per unit cost (KERR *et al.* 2004). Significant expenditures in breeding hybrid trees for the selection of hybrid parents used in operational tree improvement programs can be avoided if superior parents can be selected on the basis of the performance of their pure bred offspring. The work reported here was undertaken to provide reliable estimates of r_{ph} to assist in the design of an optimal hybrid pine breeding strategy for *Pinus elliottii* var. *elliottii* (PEE) and *P.caribaea* var. *hondurensis* (PCH) in Queensland.

The clear superiority of PEE×PCH hybrids over the pure (parental) species in many field trials convinced tree breeders in southeast Queensland that the use of hybrids was the best way forward. Trials of F_1 hybrids planted as early as 1958 showed the promise of this hybrid, but commercial deployment of hybrids was delayed due to the low number of viable F_1 hybrid seeds per cone generated from controlled crossing. When the field trials of experiment 671 were established, pure species reforestation utilised open pollinated (OP) seed from orchards while hybrid seed was created using mass pollination in mono-clonal orchards. Large amounts of hybrid seed were created after pollen catkins were removed from all PEE clones within monoclonal orchards and unbagged female flowers were pollinated in large numbers (*ie.* hand-pollination). This method provided much of the relatively scarce F_1 seed needed for operational reforestation (approximately 180 kilograms between 1985 and 1992); however, hand-pollination was abandoned in the early 1990s due to heterogeneity in some stands thought to be caused by self-pollination and/or contaminant pollen. Subsequently, relatively small amounts of hybrid seeds have been produced by controlled-pollination (*ie.* pollination of bagged PEE flowers) and then multiplied using vegetative propagation by cuttings. Refinements in propagation strategies that allow for the reforestation of large areas from very few seeds requires great certainty that the parents selected for hybrid seed production are the best available. QFRI has utilised advanced analytical techniques such as best linear unbiased prediction (BLUP) to rank all parents tested in PEE, PCH and F_1 hybrid progeny tests separately, but more comprehensive approaches have been proposed to combine data from pure species and hybrid trials in a single analysis (KERR *et al.* 2004). The accuracy of hybrid breeding value predictions would increase if r_{ph} is significant and both pure and hybrid progeny test data could be used simultaneously in a multivariate BLUP application (GROENEVELD 1990, MRODE 1996). On the other hand, if r_{ph} for the traits of interest is not significantly different from zero, the increase in both the complexity of the prediction process and the computing resources required to generate the simultaneous breeding value predictions would not provide any benefit to hybrid parent selection.

At the beginning of the period in the late 1980's when hybrid pines were selected for deployment in Queensland plantations, seed production methods were rather expensive and significant resources were devoted to producing F_1 seed. Identification of the best parents for hybrid production was essential to ensure resources were focused on the correct genotypes. It was recognised early on in the hybrid program that selecting parents for F_1 seed production based on pure species breeding values might not be achieving optimal gains. For example, if r_{ph} values were negative, selection for hybrid production based on the pure species breeding values would produce relatively inferior hybrid trees. On the other hand, r_{ph} values close to one would make the expensive testing of hybrid progeny an unnecessary step in the improvement process. The necessity of an objective determination of the correlation between pure species and hybrid combining abilities was recognised by QFRI staff and this led to the establishment of experiment 671, which was designed to provide empirical estimates of r_{ph}.

METHODS

Genetic MaterialGenetic Material

Open-pollinated seeds from 46 PEE parents and F_1 hybrid poly-cross families (PEE x PCH) from the same PEE parents provided the planting stock for this experiment. Open-pollinated seed collected from grafted ramets in seed orchards was the source for the PEE seedlots, while control pollination with a mix of 18 PCH pollens was used to create the hybrid seeds. Although the pollen mix represented a large number of PCH clones, the number of effective pollen parents for each PEE parent was probably much lower than 18, with poly-cross families representing a subset of compatible pollen parents. Interrelated second-generation PEE parents were used in the experiment, which necessitated the use of pedigree information for breeding value prediction and allowed for the prediction of breeding values for an additional 10 PEE parents.

Progeny Trials

The four progeny tests representing Experiment 671 were planted at three sites (Table 1) allowing for the estimation of r_{ph} within and across sites. The field trials at Beerburum and Byfield contained only the PEE or F_1 material respectively, which reflects the operational planting program at the time: PEE or F_1 families were planted in south east Queensland while PCH or F_1 progeny were planted in central Queensland (*ie.* Byfield). Both PEE and F_1 progeny trials were planted at the Tuan site giving a total of four trials (Table 1). These progeny trials provided direct estimates of GCA and GHA for these families at the sites where they were commonly being deployed.

The experimental design consisted of 36 replicates of single-tree plots in each progeny test. At Tuan, the PEE and hybrid progeny were planted in separate but adjacent tests. At all sites, the tests were surrounded by at least two isolation rows of the same species planted within the tests. Although comparing the PEE and F_1 hybrids was not the primary objective of these experiments, a common control of PCH was included in all tests for this purpose. Results for growth (height, diameter and volume) at eleven years of age and straightness at six years of age are presented (Table 2). Growth at six years of age is not shown due to a lack of data after fire damaged 24 of the 36 blocks in the PCH experiment planted at Beerburrum, these blocks were not assessed at six years. Re-assessment at eleven years of age showed no significant difference between the

Table 1. Experimental material: Open pollinated PEE seedlings and F_1 polycross seed included in the analysis. Open pollinated seed collected from ortets in plantations and operational polycross seedlots were removed for the genetic analysis.

Site	Genetic material	Experiment number	Families tested	Date planted	Latitude
Byfield	F_1	6711	36	January 1989	22° 50′
Tuan	P_{EE}	6712	46	April 1989	25° 38′
Tuan	F_1	6714	38	April 1989	25° 38′
Beerburum	P_{EE}	6713	41	August 1990	27° 05′

burnt and non-burnt sections of the Beerburrum test and all data was then used for the analysis reported here.

Data Analysis

Data sets from the four progeny tests were compiled, cleaned of outliers more than 3 standard deviations from the mean, and then standardised (mean = 0, variance = 1) for across site analysis by first removing the average effect and then dividing by the phenotypic variance. Least square means were estimated for each taxon at each site and across sites with Proc Mixed in SAS (SAS Institute 1990) using non-standardized data. Across site analyses for genetic parameters and breeding value predictions were completed using ASREML (Gilmour *et al.* 2000). The mixed model for across site analysis included test and replicate within test as fixed effects and a random tree by experiment interaction. This generated a GCA or GHA prediction for all individuals at each test and allowed for the specification of site-specific error and genetic variances as well as genetic correlations between the taxa planted at each site.

A univariate approach was also used to generate estimates of r_{ph} and other genetic parameters. A paired site analysis within taxa was used to produce variance components for estimates of genetic control h^2 [1], and genotype by environment interaction r_b [2]. The model used in ASREML, which was also used to generate the paired site GCA and GHA breeding values, included factors for test, replicate within test, tree and tree by site interaction. The BLUP solutions for all trees used as both pure and hybrid parents were predicted in separate analyses rather than a single multivariate analysis and parental predictions were then paired to approximate r_{ph}. Pearson correlation coefficients between the GCA and GHA breeding values of the same PEE parents were then estimated with Proc Corr in SAS to approximate the true r_{ph}. Although r_{ph} estimates Correlating BLUP solutions rather than least square means (Dungey *et al.* 2000) was used to avoid bias in parameter estimates due to the inclusion of fractions of the within-family variance (Li & Wu 1997).

Heritability:

$$h^2 = 4(\sigma_a^2/\sigma_p^2) \qquad [1]$$

Yamada's Type B correlation:

$$r_b = \sigma_a^2/(\sigma_a^2 + \sigma_{ae}^2) \qquad [2]$$

where: σ_a^2 = additive variance, σ_p^2 = phenotypic variance and σ_{ae}^2 = additive by environment interaction

RESULTS AND DISCUSSION

The two experiments planted at Tuan (6712 and 6714) provided a comparison between PEE and F_1 families at the same site as well as comparisons with three commercial PCH controls (Table 2). The OP PEE families grew significantly slower and were much straighter than the OP PCH controls that were planted within the PEE experiment. Faster early growth of the PCH controls within the PEE experiment would have increased growth differentials due to competition effects (the controls were planted as single tree plots randomised within the PEE OP families). Differences between the F_1 hybrids and the PCH controls were not as great as those observed between PEE and the F_1; however, the F_1 hybrids were generally smaller than PCH. The percentage of trees with basket whorls or double leaders was relatively low at the Tuan site and differences were small with a slight trend toward the PCH controls showing fewer crown defects. The F_1 hybrid grew much faster in trial 6711 at Byfield where the site index is generally higher than plantations in southeast Queensland and the tropical climate is more similar to the native range of PCH than what is found in southeast Queensland.

Of the six correlations (r_b) between different experiments, the four estimates classified as r_{ph} are presented in bold in Table 3. Type b correlations between the same species planted at different sites were

Table 2. Growth and Yield. Least square means and standard errors for PEE open pollinated progeny or F_1 hybrid progeny and three PCH seed orchard controls (R5240, T5030 & T5050).

Test	Taxa	Db 11$^+$	Ht 11	V 11	St 6	Bw 6	DL 6
6711	F_1	22.0±0.16	14.8±0.07	25.8±0.42	3.5±0.04	0.17±0.01	0.09±0.01
6712	P_{EE}	19.3±0.06	12.6±0.03	16.0±0.13	3.7±0.03	0.06±0.01	0.15±0.01
	R 5240	24.7±0.43*	14.7±0.19*	29.5±1.02*	3.1±0.21*	0.00±0.04	0.06±0.06
	T 5030	23.3±0.42*	14.5±0.19*	26.0±0.90*	2.9±0.21*	0.03±0.04	0.09±0.06
	T 5050	23.7±0.42*	14.8±0.18*	27.0±0.89*	2.8±0.20*	0.09±0.04	0.00±0.06*
6713	P_{EE}	17.2±0.07	13.8±0.03	13.9±0.13	3.26±0.07	0.09±0.01	0.12±0.02
6714	F_1	20.8±0.09	13.5±0.04	20.9±0.23	3.6±0.03	0.02±0.00	0.10±0.01
	R 5240	21.1±0.80	14.8±0.36*	21.7±1.93	3.1±0.24*	0.00±0.03	0.03±0.06
	T 5030	20.5±0.74	14.6±0.33*	20.7±1.77	3.9±0.22	0.00±0.03	0.06±0.05
	T 5050	22.3±0.71*	15.3±0.32*	27.1±1.74*	3.6±0.21	0.00±0.03	0.00±0.05*

Db 11 = Diameter at 11 years (cm), Ht 11 = Height at 11 years (m), V 11 = Volume at 11 years (m^3 x 100), St 6 = straightness at 6 years (1–4), Bw 6 = Basket whorls at 6 years (%) and DL 6 = Double leaders at 6 years (%)
* = significantly different than progeny at $p = 0.05$

very high and support observations by WOOLASTON *et al.* (1991) for PCH and DIETERS (1998) for PEE (1996) that there appears to be little GxE interaction across sites in these pine populations. In contrast to the high within species additive genetic correlations, the r_{ph} varied from positive to negative with large standard errors associated with the estimates. The average of all r_{ph} estimates for growth traits was 0.02, which is rather low compared to estimates of r_{ph} taken from QFRI experiment 674 (r_{ph} between PEE and F_1 (0.76±0.13) and r_{ph} between PCH and F_1 (0.71±0.16)) (POWELL & NIKLES 1996). On the other hand, r_{ph} estimates for straightness were very high and positive compared to growth estimates of r_{ph}. The same pattern was observed at ten years of age in a similar study completed by DIETERS and NIKLES (1998) that used a much larger dataset including all data available at that time from F_1 and PEE progeny tests established in southeast and central Queensland: the correlations between pure and hybrid breeding values of slash pine parents were estimated to be negligible for growth traits and positive for straightness across all tests. Nikles and Newton (1991) observed the same trend in hoop pine (*Araucaria cunninghamii*) and PEExPCH tests: r_{ph} is inconsistent and unpredictable for growth and consistently high for straightness. Dieters and Dungey (2000) concluded that r_{ph} may be reduced if the ratio of dominance to additive genetic variance is high; given the lack of dominance found for straightness in other PEE trials, straightness r_{ph} values greater than volume r_{ph} should be expected.

Due to the very low r_{ph} estimates compared to the genetic correlations of the same taxa at different sites (r_b) we decided to check the simple correlation between the GCA and GHA estimates from separate analyses of the hybrid and PEE data. Estimates of r_{ph} from this subsequent analysis (Table 4) obtained from Pearson correlation coefficients between the GCA and GHA predictions across two tests (6712 and 6713 for GCA, and 6711 and 6714 for GHA predictions) were similar to the estimates previously obtained from the multivariate approach (Table 3). This analysis produced a graphical demonstration of the lack of correspondence between GCA and GHA for growth and the reverse for straightness, as shown in Figure 1. The paired site analysis produced very high heritability estimates for the F_1 hybrid trials and low to moderate heritability estimates for PEE trials. The high type b correlations between tests of the same taxa again demonstrate the low levels of genotype by environment interaction within each taxon. None of the r_{ph} estimates were significantly different than zero except for straightness.

Relatively few estimates of r_{ph} for hybrid pines are found in the literature, and the only estimates of r_{ph} that are directly comparable, considering species and environment, come from QFRI experiment 674 (Powell and Nikles 1996). Estimates of r_{ph} from 674 were derived from progeny tests planted on a similar range of sites using 12 PEE parents and 12 PCH parents to create pure and hybrid families. These trials produced generally positive estimates of r_{ph}, but inspection of GCA to GHA plots show correlations primarily driven by a few very good or very poor combinations rather than a general trend. The results of the present study contrast to the positive correlations found in experiment 674. POWELL (2001) reports that with the exception of

Table 3. Additive genetic correlation estimates from a single multivariate analysis of each trait with respective standard error estimates, r_{ph} in bold.

			PEE	PEE – 6713	F_a – 6714 F_1 –
Db 11	F_1	6711	**-0.03±0.22**	**0.22±0.25**	0.89±0.07
	PEE	6712		0.95±0.19	**-0.39±0.19**
	PEE	6713			**-0.13±0.25**
Ht 11	F_1	6711	**0.02±0.22**	**0.37±0.29**	0.86±0.07
	PEE	6712		0.77±0.23	**-0.02±0.21**
	PEE	6713			**0.34±0.28**
V 11	F_1	6711	**0.10±0.22**	**0.24±0.30**	0.89±0.07
	PEE	6712		1.08±0.25	**-0.22±0.21**
	PEE	6713			**-0.32±0.29**
St 6	F_1	6711	**0.89±0.11**	**0.59±0.19**	0.84±0.10
	PEE	6712		0.83±0.14	**0.90±0.09**
	PEE	6713			**0.85±0.13**

Table 4. Estimates of heritability h^2 and type-b genetic correlation (r_b) within a taxon and the Pearson correlation between pure and hybrid breeding value predictions (r_{ph}) from paired site analyses of hybrid and pure species families planted in experiment 671 (± standard error).

Trait	Taxa	Test Pair	h^2	r_b	r_{ph}
Db 11	F_1	6711–6714	0.60±0.15	0.87±0.09	-0.09±0.17
	PEE	6712–6713	0.15±0.05	0.92±0.17	
Ht 11	F_1	6711–6714	0.67±0.27	0.80±0.24	0.06±0.19
	PEE	6712–6713	0.16±0.06	0.62±0.18	
V 11	F_1	6711–6714	0.61±0.16	0.84±0.10	-0.05±0.17
	PEE	6712–6713	0.13±0.04	0.88±0.19	
St 6	F_1	6711–6714	0.34±0.10	0.84±0.12	0.71±0.13
	PEE	6712–6713	0.27±0.08	0.71±0.17	

straightness, the correlation of the hybrid with either parental species was positive and moderate to high. Similar estimates of r_{ph} to those reported at 10 years of age in experiment 674 were recently found for growth traits using the methods reported above at 15-years, confirming the positive r_{ph} found by POWELL (2001) at a later age.

Estimates of r_{ph} from QFRI experiment 690 involving PCH x *P. oocarpa* (POOC) and PCH x *P. tecunumanii* (PTEC) (FRANCIS *et al.* 1984) were much higher than those found in experiment 671 (DIETERS *et al.* 2003, GWAZE 2000). For example, the r_{ph} estimates averaged nearly 0.80 between pure PCH breeding values and either PCHxPTEC or PCHxPOOC hybrid breeding values for growth traits. A slightly different approach that produced correlations between PCH parental breeding values derived from the PCHxPTEC and PCHxPOOC hybrids also showed correlations for growth traits between PCH breeding values were very high. The complex interrelationship of these three Mesoamerican pines compared to the distinct separation between PCH and PEE could account for the differences in r_{ph}. POOC from Central America is thought to be a relatively recent progenitor of PTEC (DVORAK *et al.* 2000b), which would imply significant genomic similarities. In addition, natural hybridisation between PCH, PTEC and POOC has long been suspected within the natural range of these species (DVORAK *et al.* 2000a) and the resultant similarity may have amplified these r_{ph} estimates relative to the r_{ph} estimates from the more geographically and genetically distant PEE and PCH (FURMAN *et al.* 1997, DVORAK *et al.* 2000c).

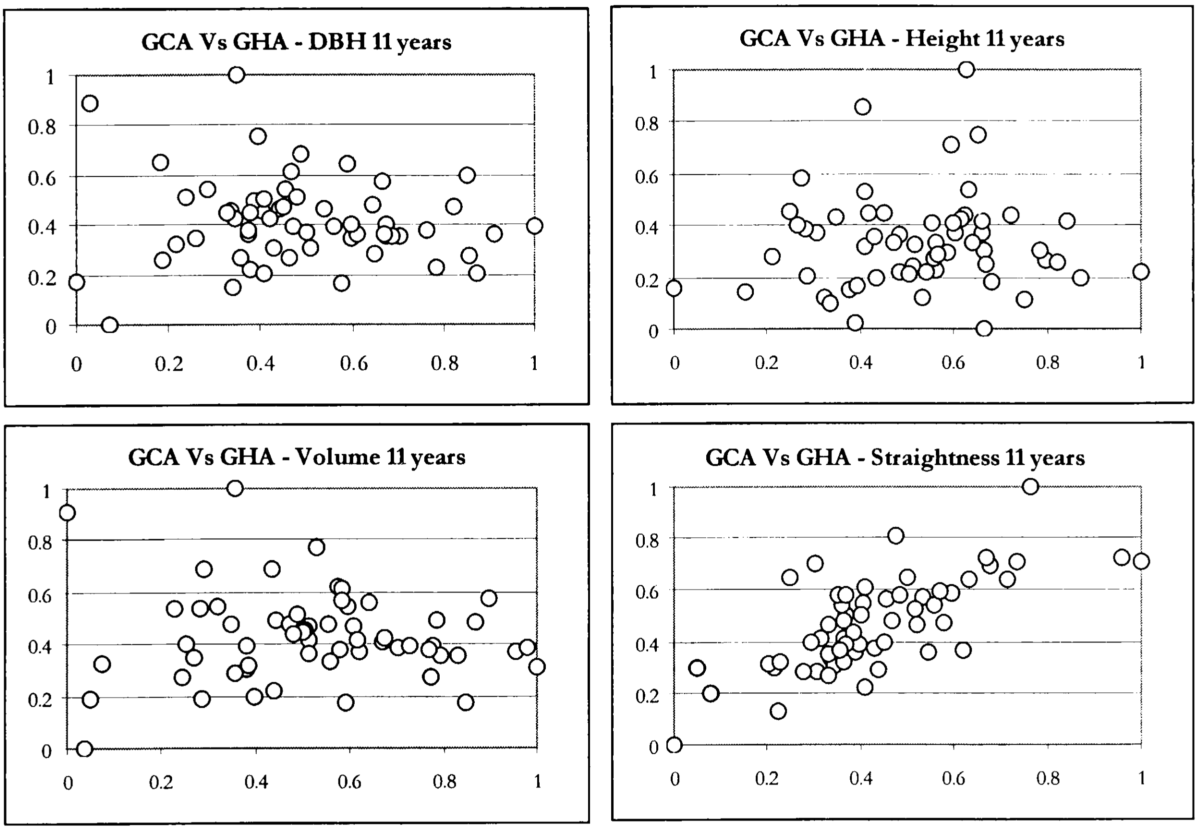

Figure 1. General combining ability versus general hybridising ability for 59 slash pine parents represented by open pollinated (GCA) and polymix (GHA) seed lots scaled to percentage values.

CONCLUSIONS AND RECOMMENDATIONS

Estimates of r_{ph} derived from experiment 671 between pure PEE and hybrid breeding value predictions are low for growth and high for straightness. This would suggest that pure PEE breeding values could be used to identify parents that produce straight hybrid progeny but pure PEE breeding values for growth are not useful for identifying parents that produce fast growing hybrid progeny. Other hybrid trials involving PCH indicate that r_{ph} values for growth between PCH parents and hybrid offspring are greater than r_{ph} values between PEE and hybrid offspring Kain *et al.* (2003). There is a possibility of directing hybrid production by selecting PCH parents for growth and PEE parents for straightness; however, the predictive capacity of pure species breeding values for hybrid production is rather low and progeny trials of the hybrid offspring will be required prior to making operational recommendations.

At present, it is recommended to produce a synthetic breed that is open for the inclusion of genes from the wide variety of the pines tested by DPI. A synthetic breeding strategy using PEE and PCH as the base has been shown to be the most robust hybrid breeding strategy of those reviewed in terms of the effect on genetic gains per dollar caused by changes in r_{ph}, even where r_{ph} is close to zero as reported here. As long as r_{ph} is not negative, a synthetic breed will produce more genetic gain per unit cost than various other hybrid breeding strategies under a wide range of genetic architectures (KERR *et al.* 2004). Although estimates of r_{ph} from experiment 671 do not agree with estimates from other hybrid pine trials planted in Queensland, this experiment contains the largest number of PEE parents tested in both pure species and hybrid combination [46 parents] within a single replicated experiment. This suggests that estimates of r_{ph} obtained from experiment 671 are likely to be more reliable than estimates obtained other experiments such as experiment 674 (12 PEE and 12 PCH parents) and experiment 690 (11 PCH, 6 PTEC and 6 POOC parents) which contain progeny of a relatively small number of parents.

Although the results from experiment 671 reported here indicate very low pure-hybrid correlations between PEE and the PEExPCH hybrid for growth there were no negative estimates of r_{ph}, which would imply difficulties in producing a superior synthetic breed, and suggest that a modified form or reciprocal recurrent selection is likely to optimise genetic gain (KERR *et al.* 2003). However, it should be noted that low r_{ph} estimates reflect the difficulty in selecting the founding parents for a synthetic breed and do not imply difficulties in selection of hybrid parents for the production of superior F_2 or F_3 progeny. Given the substantial amount of work that has already taken place to produce superior F_1 progeny and the move into F_2 or F_3 parents for seed production implied in the adoption of a synthetic breeding strategy, estimates of parent-offspring correlations between F_1 selections and their F_2 offspring will be more indicative of future gains than currently available r_{ph} estimates.

The low r_{ph} values reported here for growth traits suggest that assortative mating of PEE and PCH parents (based on GCA information) to produce the expanded hybrid base population, may not be effective. Therefore, it is likely that each parent will need to be mated a number of times to ensure advantageous matings among the PEE and PCH parents. Alternatively, results reported by Kain *et al.* (2003) suggest that GCA estimates from PCH progeny tests, may be more strongly correlated with growth of the hybrid than that of GCA from PEE tests. Hence an alternative approach may be to rank PEE parents based on GCA for straightness, and rank PCH parents on GCA for growth, and then assortatively hybridise the PEE and PCH parents based on their relative rankings for straightness and growth within the pure species (if GHA information is not available).

The results indicate that testing of PEE parents for GHA of growth traits will be necessary to identify superior families for intensive clonal testing if F_1 hybrid cuttings are the desired deployment population. Other trials established by QFRI indicate this may not be the case for traits under a strong degree of genetic control such as wood density (KAIN *et al.* 2003) where r_{ph} is generally higher or SCA effects are low (DIETERS & DUNGEY 2000). Currently breeding values based on hybrid progeny are available for 97 PEE, 162 PCH and 58 F_1/F_2 parents, with a further 100 unrelated PEE parents scheduled to be established in GHA tests in 2004. In the short-term it would not appear necessary to implement large-scale testing of additional PEE or PCH parents for GHA, rather the most outstanding parents can be used to produce elite hybrid families for inclusion in clonal tests. Movement of the breeding strategy towards the adoption of a synthetic hybrid, will entail the production of an expanded hybrid base population from which a hybrid breeding population will be selected. This in turn will generate supplementary information on the GHA of the additional PEE and PCH parents, and the most outstanding parents can then be used as the founding population for the synthetic population.

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