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ORIGINAL ARTICLE

Genetic parameters in subtropical pine F_1 hybrids: heritabilities, between-trait correlations and genotype-by-environment interactions

Pomerayi Mutete[1] · **Ruramai Murepa**[1] · **Washington J Gapare**[2]

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Abstract Growth and stem straightness traits of 29 *Pinus caribaea* var. *hondurensis* × *Pinus tecunumanii* (PCH × PTEC) and 26 *P. caribaea* var. *hondurensis* × *Pinus oocarpa* (PCH × POOC) hybrid pair-crosses plus a total of 16 intraspecific families were assessed at ages 5, 8 and 15 years from planting at two sites. The PCH × PTEC hybrid was the most productive, yielding 37 % more than a *Pinus elliottii* local control and was 21 % superior to either parental species in DBH growth. PCH × POOC hybrid was, on average, 16 % superior to either parental species for DBH. Narrow-sense heritability estimates were low to moderate for growth traits (average of 0.27) and stem straightness (0.16). The estimated additive genetic correlations between growth traits and ages within traits were high (>0.8) and positive, providing confidence in early selection based on diameter at breast height. The high proportion of estimated additive genetic variance compared to dominance variance in the F_1 pine hybrids suggests that breeding strategies that maximize the use of additive genetic variance may be effective. The ranking of the 11 PCH parents based on general hybridizing ability predictions (estimated breeding values as hybrids) was somewhat inconsistent between PTEC and POOC hybrid crosses for all traits ($r_{9\ \text{d.f.}}$=0.38–0.45; p ~0.15–0.25). There was no evidence of practically important G × E interaction for the hybrids except for PCH × PTEC height growth. This study suggests that a single, multi-hybrid breeding population seems appropriate in Zimbabwe if the trial sites are representative of the planting target zone.

Keywords Tree breeding · Heritability · Pines · F_1 hybrids · Genetic correlation · Genotype by environment interaction · General hybridizing ability (GHA)

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✉ Washington J Gapare
Washington.Gapare@csiro.au

[1] Forest Research Centre, Forestry Commission, P. O. Box HG 595, Highlands, Harare, Zimbabwe

[2] Commonwealth Scientific and Industrial Research Organisation, GPO Box 1600, Canberra ACT 2601, Australia

Introduction

Zimbabwe is divided into five Provisional Silvicultural Zones (PSZ) (Fig. 1) (Barrett and Mullin 1968). Commercial pine and eucalypt forestry are concentrated in PSZ I to III which experience a subtropical to temperate climate due to the modifying effect of altitude with pronounced dry and wet seasons. Predominant pine species include *Pinus patula* Schiede ex Schlechtendal Chamisso, *Pinus taeda* L., *Pinus elliottii* Engelm. and *P. kesiya* Royle ex Gordon, in total covering 88,000 ha (Timber Producers Federation 2011). Predictions are that, by 2030, the total planted area will reach approximately 120, 000 ha (Arnold and White 1994; Timber Producers Federation 2014). Of this area, 80 % or 96,000 ha will be planted to pines (Timber Producers Federation 2014). This area is predicted to span across PSZ III to IV. Species trials established on PSZ III and IV indicated that the current commercial pine species were not sufficiently productive (Barnes 1981; Crockford 1995). For example, mean annual increments for *P. elliottii* in PSZ III and IV are usually around 16 m^3 ha^{-1} $year^{-1}$ compared to 26 m^3 ha^{-1} $year^{-1}$ in PSZ I and II (Crockford 1995; Timber Producers Federation 1999; Gotore et al. 2014). *P. patula* and *P. taeda* are not tolerant of moisture deficits that typify PSZ III and IV while *P. elliottii*, though tolerant, is slow in capturing site and invariably low in volume production

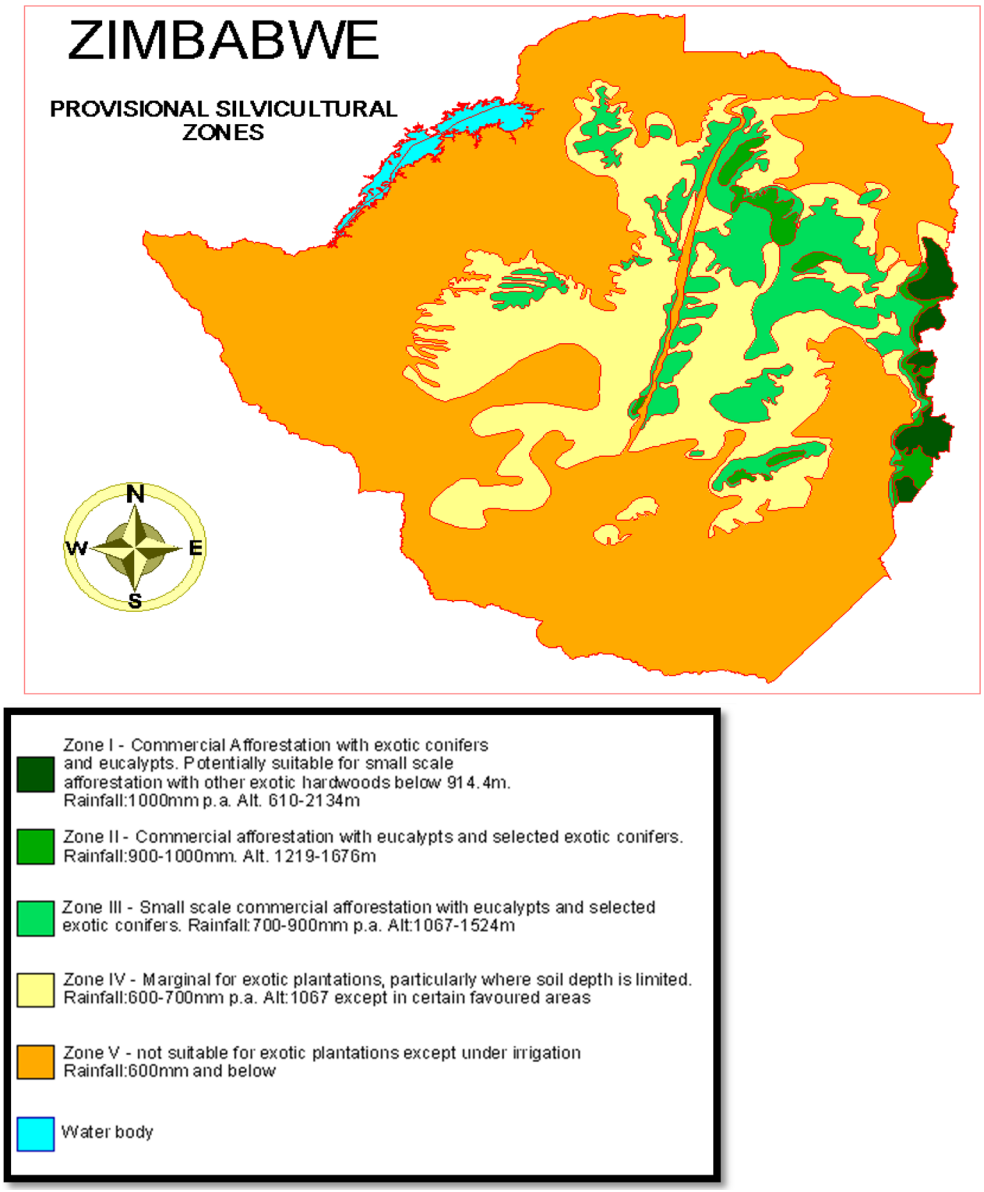

Fig 1 Map of Zimbabwe showing Provisional Silvicultural Zones. Modified from Barrett and Mullin (1968)

compared to other species (Barnes 1989; Mullin 1992). The major limiting factors in PSZ III and IV include low rainfall and high temperature which increases evapotranspiration. It was perceived that some of the limitations of the currently planted pure pine species in Zimbabwe could be overcome by more species introduction and breeding and also through their inter-specific hybridization (Barnes 1989; Barnes et al. 1997; Nyoka 2000).

The breeding programs of *P. patula*, *P. taeda* L. and *P. elliottii* are almost three generations advanced from their wild base populations, and much has been learnt about their genetics (Crockford et al. 1988; Barnes et al. 1992a, b; Nyoka and Barnes 1995; Pswarayi et al. 1996; Gapare and Musokonyi 2002; Nyoka et al. 2010). In the early 1990s, new germplasm including several provenances of *P. patula* that had not been previously included in the breeding program and also some hitherto untested species (*Pinus maximinoi* H.E., *Pinus tecunumanii* Eguiluz & Perry and *P. greggii* Engelm. ex Parl.) were included in the testing program (Barnes 1981; 1989; 1993). The motivation was to reduce the monoculture of *P. patula* in high-altitude areas as well as reduce the dependence on *P. elliottii* in the low-altitude areas. Introduction of *P. maximinoi*, *P. tecunumanii* and *Pinus greggii* was also perceived to be a long-term solution to finding suitable species for marginal environments (Barnes 1989). For example, *P. tecunumanii* has demonstrated high growth rates and is tolerant to drought (Nyoka and Barnes 1995; Nyoka et al. 2010). The planting of seed from the top 10 families of the low-elevation *P. tecunumanii* gave gains in 8-year volume of respectively 13 and 23 % over *P. patula* at Stapleford and Cashel sites, though some issues of susceptibility to wind damage were also noted (Nyoka et al. 2010).

In order to meet future wood requirements, there has been a steady expansion of commercial pine forestry into marginal areas for most of the tested species. This has led to the development of options for sustainable improvement of forest plantation productivity including research into performance of hybrids. Earlier work on pine hybrids in the 1970s involved *P. elliottii* and *P. taeda* (Barnes and Mullin 1978). The hybrid was developed because the two species had complementary traits and were likely to cross easily given that they were closely related (Barnes and Mullin 1978). Results from the hybrid trials were not encouraging and no investment in hybrid testing was made until 1993 when interspecific hybrids involving *Pinus caribaea* var. *hondurensis*, *P. elliottii*, *Pinus oocarpa* and *P. tecunumanii* were tested on two sites. Gwaze (1999) reported that hybrid vigour (heterosis) in all the traits was exhibited in all the hybrids at the two sites, being more clearly expressed at the low-elevation drier site. The volume production of the hybrid between *P. caribaea* and *P. tecunumanii* was more than four times that of the commonly grown *P. elliottii* and 52 % more than the best performing pure species (*P. tecunumanii*) at the wetter site (Gwaze 1999).

By way of precedent, experience with the *P. elliottii*×*P. caribaea* hybrid in Queensland, Australia, where it was planted on almost 70,000 ha, demonstrated that it exceeded the productivity of *P. elliottii* (Dieters 1999; Dieters and Brawner 2007). The hybrid appears to inherit the high growth rate from *P. caribaea* and stem straightness, wind firmness, high wood density and adaptability to wet sites from *P. elliottii* (Nikles 2000; Dieters and Brawner 2007). There is also experience of *P. elliottii*×*P. caribaea* hybrid in Argentina where it has shown superior performance compared to the pure species in field trials (Cappa et al. 2013). The *P. elliottii*×*P. caribaea* hybrid is planted commercially in Argentina, Australia and South Africa. The use of *P. caribaea* var. *hondurensis* in combination with other species such as *P. tecunumanii*, *P. elliottii* and *P. oocarpa* is therefore predicted to give hybrids combining high productivity, adaptation and stem strength (e.g. Dieters et al. 1997).

However, several reviews have noted some of the challenges associated with hybrids. As highlighted in a review by Dungey (2001), some challenges include selection of parental species, early crossing and multiplication options. Other notable challenges include hybrid invariability, high development costs when compared with pure species strategies (for fixed resources and hybrids requiring more complex breeding strategies; e.g. Dungey 2001; Kerr et al. 2004a, b). Obtaining hybrid seed in sufficient quantities for commercial forestry can be extremely difficult and expensive (Gwaze 1999).

The high cost of hybrid breeding relative to pure species breeding creates an imperative to identify the most efficient breeding strategy. Proposed and commercially used strategies for breeding pine hybrids have been reviewed in detail (Dungey et al. 1999; Shelbourne 2000; Kerr et al. 2004a, b). For example, Dungey et al. (1999) concluded that most strategies are either an adaptation of the original reciprocal recurrent selection (RRS) strategy outlined by Comstock et al. (1949) or use recurrent selection for general combining ability (GCA) in the parent species. Kerr et al. (2004a, b) developed and simulated synthetic species (SYN) and pure species selection (PSS) strategies. Their conclusion was that SYN strategy was the most cost-effective across a wider range of genetic structures, in particular where there is less dominance variance and the pure hybrid correlations in both species are positive (Kerr et al. 2004b).

This paper combines age-5 data reported by Gwaze (1999) with growth and stem straightness measures at ages 8 and 15 years from planting to compare the productivity trends of hybrids against their pure parental species for completeness. The specific objectives of this study were to (1) estimate genetic parameters, additive and dominance variances and heritability for height, diameter at breast height (DBH) and stem straightness, (2) estimate genetic correlations between studied traits and (3) examine genotype by environment (G×E) interaction of the same traits. We also used the data to study how well the breeding values of *P. caribaea* var. *hondurensis* parents corresponded between the two interspecific hybrid combinations (e.g. Dieters et al. 1997). Additionally, we use this information to discuss the implications and selection strategies for genetic improvement of pine hybrids in Zimbabwe in order to increase the profitability of future softwood plantations in Zimbabwe.

Materials and methods

Genetic material and genetic tests

The control-pollinated hybrid families were provided to the Zimbabwe Forestry Commission by the then Queensland Forest Research Institute, Australia, through the then Oxford Forestry Institute, UK in 1992. The families originated from an incomplete factorial design of unrelated first- and second-generation parents (Dieters et al. 1997). Eleven unrelated first- and second-generation *P. caribaea* var. *hondurensis* (PCH) parents were crossed with six first-generation *P. oocarpa* (POOC) parents and six first-generation *P. tecunumanii* (PTEC) parents to form two 11×6 factorial arrays. The PCH parents were used as the female parents in all factorial crosses, and there were three POOC parents from each of Zapotillo and Angeles provenances and three PTEC parents from each of Mountain Pine Ridge and Yucul provenances (Dieters et al. 1997). The parents represented in the genetic crosses were both very few in number and were generally not represented in interspecific crosses precludes any firm conclusions about heterosis.

The two factorials were almost complete, with 61 of the possible 66 F_1 families produced in each factorial. However, not all pair-crosses were made available for the Zimbabwe tests. The actual number of hybrid families included in the tests in Zimbabwe is provided in Table 1. These included several controls (Table 1). Controls of the pure species were included in the tests, but they were generally unrelated to the hybrids. The *P. elliottii* control from Zimbabwe was a full-sib cross between parents of outstanding growth. Five families of *P. caribaea* var. *hondurensis* (PCH)×*P. elliottii* hybrid crosses were also included in the tests as part of the controls. Seedlings were raised at John Meikle Forest Research Station, and the tests were established at two contrasting sites, Cashel and Mukandi in 1993 (Table 2).

Field design at Mukandi was an incomplete block design with 6 replicates and 16 blocks. Each family was planted in five-tree row plots and the spacing between trees was 3×3 m. At Cashel, the design was randomised complete block with six replicates. Spacing and plot size were as at Mukandi.

For this set of trials, survival was assessed at 5, 8 and 15 years and expressed as a percentage of the total number of planted trees for each taxon. Productivity traits were assessed at the same ages: Height was measured on all live trees, denoted as HT5, and HT8 and HT15; tree diameter was measured at breast height (1.3 m above ground level) over bark, denoted as DBH5, DBH8 and DBH15; and stem straightness was assessed using a 7-point absolute visual scale (1=crooked to 7=very straight), denoted as STR5, STR8 and STR15. Both trials were thinned to 50 % of initial stocking prior to the age 15 years assessments, leaving too few trees for precise genetic parameter estimation: We therefore only estimated trait means for each taxon at each site at age 15 years. Age-5 data were the subject of an earlier publication (Gwaze 1999), and we include these data in our analysis in order to get a comprehensive overview of the performance from juvenile to later ages.

Table 2 Details of hybrid field test sites (adapted from Gwaze 1999)

	Mukandi	Cashel
Longitude	32° 51′ E	32^0 50′ E
Latitude	18^0 41′S	19^0 37′S
Altitude (m)	1300	1525
Mean annual rainfall (mm)	1711	745
Soil parental material	Granite	Shale

Statistical models and analyses

Comparison of taxa

Taxa differences were tested against family-within taxon variation, the latter being a pooled variance of family means using ANOVA in ASReml R (Butler et al. 2009; R Development Core Team 2011). The significance of differences between taxa at $p<0.05$ was tested using the Bonferroni and Newman-Keuls adjusted *t* tests (Armitage et al. 2001).

Assumptions of analysis based on conventional quantitative genetic model

Some simplifying assumptions are necessary in order to model genetic architecture of hybrid populations. For example, the genetic loci controlling the traits examined may be assumed to be common to PCH, PTEC, POOC and PCH×PTEC and PCH×POOC hybrids populations, and alleles and genotypes segregate freely and randomly within and between populations. We may also assume epistasis to be negligible. Although the assumption of no epistasis is probably unrealistic, this assumption is necessary in most studies using quantitative genetic approaches due to statistical difficulty of measuring interactions among numerous loci (Kerr et al. 2000). However, simulation studies have demonstrated that when analysis of

Table 1 Details of the genetic material used (adapted from Gwaze 1999)

Taxon	Supplier	Families	
		Type	Number
P. elliottii (PEE 1)	Zimbabwe, FRC	Full-sib	1
P. elliottii (PEE 2)	Australia, QFRI	OP (Orchard)	3
P caribaea var. *hondurensis* (PCH)	Australia, QFRI	OP (Orchard)	5
P. tecunumanii (PTEC)	UK, OFI	OP (wild)	2
P. oocarpa (POOC)	Zimbabwe, FRC	OP (Orchard)	5
PCH×PTEC	Australia, QFRI	Full-sib	29[a]
PCH×POOC	Australia, QFRI	Full-sib	27[a]
PCH×PEE	Australia, QFRI	Full-sib	5[a]

FRC Forest Research Centre, *QFRI* Queensland Forest Research Institute, *OFI* Oxford Forest Institute (seed from Honduras and Nicaragua), *OP* open pollinated (approximate half-sib)

[a] Number of pair-crosses provided for the tests in Zimbabwe

variance is applied, even where epistatic (additive×additive, additive×dominance, dominance×dominance), effects are present, and fitted into the model, much of the variance due to epistatic effects is in fact partitioned into the main effects (e.g. Cheverud and Routman 1995). For the purpose of breeding strategy design, the main distinction is that between additive-related and dominance-related gene effects, and so the formal assumption of no epistasis in our models is considered unlikely to result in erroneous conclusions.

Data analyses

The PCH×PTEC (29) and PCH×POOC (27) hybrid crosses at each site were analysed separately. All pure species and PCH×PELL hybrids were excluded from genetic parameter estimation due to the smaller numbers of families (Table 1), except for taxon performance comparisons. A series of genetic analyses were conducted using ASReml R (Butler et al. 2009; R Development Core Team 2011). Diagnostic plots were used to verify normal distribution of residuals and identify outliers. Univariate models were first fitted to HT, DBH and STR for 5 and 8 years data from each trial. Survival was reported to be above 95 % for all taxa in Gwaze (1999), and we did not reanalyse any survival data.

For single-site analyses, we followed the parental model [1] similar to one used by Brawner et al. (2005):

$$Y_{jklm} = \mu + B_j + F_k + M_l + FM_{kl} + FB_{jk} + MB_{jl} + P_{jkl} + E_{jklm} \quad (1)$$

where $Y_{jklm}$is the mth tree of the klth family in the jth block, μ is the overall mean, B_j is the fixed effect of the jth block, F_k is the random effect of the kth female parent, $\sim N(0, \sigma^2_f)$, M_l is the random effect of the lth male parent, $\sim N(0, \sigma^2_m)$, FM_{kl} is the random effect of the interaction between the kth female parent and the lth male parent, $\sim N(0, \sigma^2_{fm})$, FB_{jk} is the random effect the interaction between the jth block and the kth female parent, $\sim N(0, \sigma^2_{bf})$, MB_{jl} is the random effect of the interaction between the jth block and the lth male parent, $\sim N(0, \sigma^2_{bm})$, P_{jkl} is the random effect of variation between plots, $\sim N(0, \sigma^2_p)$ and E_{jklm} is the random error associated with the mth observation of the klth family in the jth block$\sim N(0, \sigma^2_e)$.

The pooled 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×female-parent interaction, test×male-parent interaction and female-parent×male-parent×test interaction (Brawner et al. 2005). Across-sites analysis used standardized data, which were 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) (Brawner et al. 2005). Results from single-site analyses were used to obtain starting values for the pooled-site analyses. Both heterogeneous dominance and error variances were included in the model (e.g. Costa e Silva et al. 2005).

In order to determine how well the breeding values of PCH parents corresponded between the two interspecific hybrid combinations (e.g. Dieters et al. 1997), best linear unbiased predictions (BLUPs) were obtained for each of the 11 (female) PCH parents, from the pooled-site analyses, separately for PCH×PTEC and PCH×POOC hybrid crosses using the software ASReml R (Butler et al. 2009; R Development Core Team 2011). Dieters et al. (1997) noted that such predictions of the average effects of the female parents are estimates of their general hybridizing abilities (GHA), as defined by Nikles and Newton (1991), in contrast with the conventional general combining abilities (GCA).

For noninbred parents, these variance components can be interpreted in the following manner (Cockerham 1963; Becker 1984): σ^2_f, and σ^2_m are estimates of one-quarter of the additive genetic variance, σ^2_A; σ^2_{fm} is an estimate of one-quarter of the dominance variance, σ^2_D, σ^2_{fs} and σ^2_{ms} are estimates of one-quarter of the additive–site interaction variance, σ^2_{AE} and σ^2_{fms} is an estimate of one-quarter of the dominance–site interaction variance, σ^2_{DS}. The corresponding estimates of σ^2_f, σ^2_m, and σ^2_{fm}, from the single-site analyses are upwardly biased due to the confounded effects of genotype–environment interactions (Comstock and Moll 1963). Therefore, σ^2_f, (or σ^2_m) and σ^2_{fm} are biased estimates of one-quarter of the additive and dominance variances, respectively.

We repeated the analysis of these data using an individual-tree model. Such a model assumes that the additive variances in the population are the same for the female and male parents. Given that the present-day geographic ranges of these species are often found growing alongside PCH, POOC and PTEC on sites from Belize to Nicaragua (Dvorak et al. 2000a, b), it may be a reasonable assumption that these species are closely related and therefore their variances in the segregating population are the same for female and male parents. For example, a phylogenetic study by Dvorak et al. (2000b) suggested PCH, PTEC and POOC are closely related. We also assumed that it may not be possible to disentangle their likely differences in the additive variance between the male and female parents due to sampling error.

The model assigns a random effect to the breeding value of each tree, both for trees with records and those that are represented as parents or grandparents in the analysis. Each model incorporated the full pedigree including parents and grandparents by inclusion in the additive genetic relationship matrix for the trees (Gilmour et al. 2009). However, the female and male parents of the 11 first- and second-generation selections were assumed unknown and coded zero in the pedigree table. The incorporation of this pedigree is critical as it considers dependences (i.e. genetic relationships) that occur in these reduced hybrid populations, hence improving the estimation of genetic parameters.

The statistical model [2] used in the analysis of individual-site data was as follows:

$$y_{ijklm} = \mu + B_i + tree_j + fam_k + plot_l + e_{ijklm} \quad (2)$$

where y_{ijklm} is the individual-tree measurement, μ is the overall mean, B_i is the fixed effect of block, $tree_j$ is the random additive genetic effect of individual tree ~ $N(0, \sigma_A^2)$, fam_k is the random effect of full-sib family ~ $N(0, \sigma_{fam}^2)$, $plot_l$ is the random effect of plot ~ $N(0, \sigma_{\text{plot}}^2)$ and e_{ijklm} is the random residual effect ~ $N(0, \sigma_E^2)$.

The pooled-site model is the same as that given in [2] except that trial is an additional fixed effect, and $\mathbf{y}_i$ is now defined as the vector of observations for a single trait indexed (i) by trial.

Estimation of genetic parameters

Parental model

The REML variance component estimates from the parental model were used to estimate heritability (biased $h^2{}_b$, and unbiased, h^2 from single- and pooled-site analyses, respectively. Single-site analyses yield an estimate of heritability which is upwardly biased due to the confounded effects of genotype-by-environment interactions (Comstock and Moll 1963; Hodge and White 1992). Two separate estimates of the heritability can be obtained—one from the female parents and one from the male parents (Dieters et al. 1997). Additional formulae can be obtained by substituting the appropriate male and male × site variance components into the equations below. The formulae used to estimate these genetic parameters are listed below:

$$\hat{h}^2 b = \frac{4\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_m^2 + \hat{\sigma}_{fm}^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2} \quad (3)$$

$$\hat{h}^2 = \frac{4\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_m^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_{ms}^2 + \hat{\sigma}_{fm}^2 + \hat{\sigma}_{fms}^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2} \quad (4)$$

Biased dominance as a proportion of phenotypic variance ($d^2{}_b$) was only estimated from single-site estimates as follows:

$$\hat{d}^2{}_b = \frac{4\hat{\sigma}_{fm}^2}{\hat{\sigma}_f^2 + \hat{\sigma}_m^2 + \hat{\sigma}_{fm}^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2} \quad (5)$$

Individual-tree model

Observed variance components were used to estimate the causal variance components for each trait and interpreted as follows: $\hat{\sigma}_A^2$ is estimate of additive genetic variance, $\hat{\sigma}_D^2 = 4\hat{\sigma}_{fam}^2$ is the estimate of dominance genetic variance, $\hat{\sigma}_G^2 = \hat{\sigma}_A^2 + \hat{\sigma}_D^2$ is the estimate of total genetic variance assuming no epistasis. Individual narrow-sense heritabilities (denoted $\hat{h}^2 bi$ to indicate it is from individual tree model) from the single-site analyses (upwardly biased due to the confounded effects of genotype × environment interactions (Comstock and Moll 1963)) were estimated as the additive genetic variation divided by the phenotypic variation ($\sigma^2{}_P$):

$$\hat{h}^2{}_{bi} = \hat{\sigma}_A^2 / \hat{\sigma}_P^2 \quad (6)$$

where phenotypic variance is estimated as:

$$\hat{\sigma}_P^2 = \hat{\sigma}_A^2 + \hat{\sigma}_{fam}^2 + \hat{\sigma}_{plot}^2 + \hat{\sigma}_E^2 \quad (7)$$

Pooled-site analysis was conducted for each trait in order to calculate unbiased heritability estimates. In that case, an unbiased estimate of narrow-sense heritability was estimated as:

$$\hat{h}^2{}_i = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} \quad (8)$$

where phenotypic variance from pooled-site analyses is estimated as:

$$\hat{\sigma}_P^2 = \hat{\sigma}_A^2 + \hat{\sigma}_{S_A}^2 + \hat{\sigma}_{Sfam}^2 + \hat{\sigma}_{plot}^2 + \hat{\sigma}_E^2 \quad (9)$$

σ_A^2, σ_{plot}^2 and σ_E^2 are as defined in Eq 2, σ_{SA}^2 and σ_{Sfam}^2 are the interaction variances between site and additive genetic effects and site × full-sib family effects, respectively.

Approximate standard errors of the heritability estimates were derived based on Taylor series approximation using the R pin function (White 2013).

The additive genetic correlation estimates between traits 1 and 2 were obtained from the estimated additive covariance and variance components from the individual-tree model as:

$$r_A = \frac{\hat{\sigma}_{A_1A_2}}{\sqrt{\hat{\sigma}_{A_1}^2 \hat{\sigma}_{A_2}^2}} \quad (10)$$

where:

$\sigma_{A_1A_2}$ = additive genetic covariance component between trait 1 and trait 2

$\sigma_{A_1}^2$ = additive genetic variance for trait 1 at each site

$\sigma_{A_2}^2$ = additive genetic variance for trait 2 at each site

For female, male, dominance (from model 1) and additive genetic effects (model 2), the first indication of their significance was given by the ratio of the variance components to their corresponding standard error. Terms for which this ratio was >2 were regarded as significant. Terms for which the ratio was <1 were regarded as not significant. For ratios between 1

and 2, the likelihood ratio (LR) test was applied (−2×(difference between log likelihoods including and excluding the term)~χ^2; Gilmour et al. 2009; Stram and Lee 1994).

In order to determine the extent of genotype×environment interaction for each of the traits, univariate, paired-pooled analysis was conducted. Heterogeneous error terms were fitted for each site for each trait. Type B additive genetic correlation estimates (r_B) were then made following Burdon (1977) and higher values (>~0.8) indicate little genotype×environment interaction, and lower values indicate that practically important genotype-×-environment interactions exist (Robertson 1959). One-tailed LR tests were used to test an estimated type B additive genetic correlation against +1. This was done by using a parameterisation of (co)variance matrix based on a correlation form and constraining the correlation parameter to be +1 under the null hypothesis to be tested. If $\log L_1$ and $\log L_2$ are the REML log-likelihoods from the unrestricted and the restricted (r_B=1) models, respectively, the test statistic (D) is given by:

$$D = 2(\log L_1 - \log L_2) \quad (11)$$

which is distributed approximately as χ^2 under H_0, with degrees of freedom given by the difference between the number of parameters estimated under the non-restricted and the restricted models (Costa e Silva et al. 2005; Gilmour et al. 2009).

Results

Estimates of trait means by taxon

Phenotypic means and standard errors for all traits observed at each site are presented in Table 3. At both sites, the hybrids outperformed the pure species, with the hybrids between *P. caribaea* var. *hondurensis* and *P. tecunumanii* (PCH×PTEC) being the most productive in terms of height and DBH at all ages. Generally, the hybrids were significantly different from the pure species (p<0.05) for growth traits at all ages (Table 3). Growth (height and DBH) was better at Mukandi than at Cashel for all taxa at age 5 years, but reversed at ages 8 and 15 years. The PCH×PTEC hybrid was the most productive for height and DBH at age 8 years at both sites. The PCH×PTEC hybrid continued to be the most productive taxon, being on average 10 % better than either parental species. The hybrids had better stem straightness than pure species at Mukandi, whereas at Cashel, the pure species had as straight stems as the hybrids. Similar trends were evident at ages 8 and 15 years.

Growth performance of pure species and hybrids

Percent superiority of the hybrids over *P. elliottii* local control (PEE1) at 8 and 15 years at Cashel and Mukandi are shown in Table 4. Generally, the hybrids were superior to the local control at age 8 and 15 years from planting, except for PCH×POOC (*P. caribaea* var. *hondurensis*×*P. oocarpa*) which was inferior for height by almost 14 % at Cashel and Mukandi at age 8 years. Likewise, stem straightness for the hybrids at age 8 years were inferior to the *P. elliottii* local control. All three hybrids were superior to parental species and mid parent values for all traits at both ages and sites (Tables 5, 6 and 7). For example, PCH×PTEC (*P. caribaea* var. *hondurensis*×*P. tecunumanii*) hybrid was on average, 21 % superior to either parental species in DBH growth. PCH×POOC hybrid was on average, 16 % superior to either parental species and mid parent values for DBH. The PEE×PCH (*P. elliottii*×*P. caribaea* var. *hondurensis*) hybrid was on average, 30 % superior to either

Table 3 Means for growth and form traits for various taxa

Taxon	Cashel	Mukandi	Cashel	Mukandi	Cashel	Mukandi
	HT5 (m)		DBH5 (cm)		STR5 (1–7)	
PEE1	5.2f	6.5e	8.9d	9.7d	3.5ab	3.5cd
PEE2	5.5ef	7.2e	9.8cd	10.7d	3.8a	3.8bc
POOC	6.6cd	8.7d	10.5c	13.7c	3.0c	3.4d
PCH	5.9e	8.8cd	10.0c	13.8c	2.9c	3.6cd
PTEC	6.5d	8.9cd	10.2c	13.7c	3.0c	3.6cd
PCH×PTEC	7.7a	10.0a	12.9a	16.7a	3.4b	4.1b
PCH×POOC	6.9bc	9.5b	11.3b	15.4b	3.4b	4.1b
PEE×PCH	7.2b	9.3bc	13.3a	15.7b	3.7a	4.2a
	HT8 (m)		DBH8 (cm)		STR8 (1–7)	
PEE1	13.3d	10.4c	19.2d	13.6d	3.7ab	4.6abc
PEE2	14.6cd	11.5c	21.4cd	14.9d	3.9a	4.8ab
POOC	15.2c	13.2b	22.6c	19.5c	2.8c	3.4d
PCH	15.7c	13.9b	22.3c	19.4c	3.2bc	4.2d
PTEC	15.2c	13.6b	22.1c	19.7c	2.9c	3.5d
PCH×PTEC	18.0 a	15.6a	27.5a	23.8a	3.4b	4.1c
PCH×POOC	17.3b	15.4a	25.5b	22.5b	3.8a	4.5bc
PEE×PCH	17.0b	14.9a	26.8ab	22.8b	4.1a	5.2a
	HT15 (m)		DBH15 (cm)		STR15 (1–7)	
PEE1	19.7d	17.4e	23.5e	18.8d	4.3bc	4.6ab
PEE2	21.6cd	19.2e	26.8de	22.6d	5.0a	6.2a
POOC	22.8c	21.5d	28.5cde	30.6c	3.5c	4.8d
PCH	22.9c	21.9cd	29.4cd	31.0c	4.0bc	5.3bc
PTEC	23.7bc	22.0bcd	33.5bc	33.1bc	3.7c	4.8cd
PCH×PTEC	25.8a	23.6a	37.3a	37.1a	4.3b	5.7b
PCH×POOC	25.4a	23.3ab	35.6b	34.7b	4.8a	6.2a
PEE×PCH	24.8ab	22.8abc	34.8b	34.6b	5.1a	6.6a

The same letter within a subcolumn for each trait indicates significant difference between means at p<0.05 using the Bonferroni and Newman-Keuls adjusted t tests

PEE1 Pinus elliottii control – Zimbabwe select, *PEE2 P. elliottii* – Australia select, *POOC P. oocarpa*, *PCH P. caribaea* var. *hondurensis, PTEC P. tecunumanii*, *PCH*× *PTEC P. caribaea* var. *hondurensis*× *P. tecunumanii*, *PCH*× *POOC P. caribaea* var. *hondurensis*×*P. oocarpa*, *PEE*× *PCH P. elliottii*×*P. caribaea* var. *hondurensis*

Table 4 Superiority (%) of the hybrids over the local control PEE1 at 8 and 15 years

Taxon	Cashel	Mukandi	Cashel	Mukandi	Cashel	Mukandi
	HT8		DBH8		STR8	
PCH×PTEC	26.1	33.3	30.2	42.9	−8.8	−12.2
PCH×POOC	−13.9	−13.0	7.8	16.4	−13.6	−2.2
PEE×PCH	21.8	30.2	28.4	40.3	9.8	11.5
	HT15		DBH15		STR15	
PCH×PTEC	23.6	26.3	37.0	49.3	0.0	19.3
PCH×POOC	22.4	25.3	34.0	45.8	10.4	25.8
PEE×PCH	20.6	23.7	32.5	45.7	15.7	30.3

POOC P. oocarpa, *PCH P. caribaea* var. *hondurensis*, *PTEC P. tecunumanii*; *PCH× PTEC P. caribaea* var. *hondurensis*×*P. tecunumanii*, *PCH× POOC P. caribaea* var. *hondurensis*×*P. oocarpa*, *PEE× PCH P. elliottii*×*P. caribaea* var. *hondurensis*

parental species and mid parent values for DBH at age 8 years and maintained that superiority to age 15 years.

Heritabilities and genetic correlations between traits, ages and sites

Biased narrow-sense heritability estimates for each of the traits at ages 5 and 8 years from both parental and individual tree models are presented in Table 8. Female heritability estimates for growth traits among hybrids were generally significant ($p<0.05$), with a few exceptions. For example, significant $\hat{h}^2b$ was observed for HT5 and HT8 for both hybrids at Cashel but PCH×PTEC hybrid was not significant for HT5 and HT8 at Mukandi. Male heritability estimates for all traits were generally insignificant ($p>0.05$), and in some cases, the estimates were 0 and where heritability estimate was greater than 0, the standard errors were larger than the estimate (Table 8). Estimates of female and male heritability for stem straightness (STR5 and STR8) for both hybrids were insignificant ($p>0.05$). Generally, $\hat{h}^2bi$ for height and DBH were low to moderate, and significant

Table 5 Superiority (%) of the PCH x PTEC (*P. caribaea* var. *hondurensis*×*P. tecunumanii*) over pure parent species and mid-parent at 8 and 15 years

Taxon	Cashel	Mukandi	Cashel	Mukandi	Cashel	Mukandi
	HT8		DBH8		STR8	
PCH	14.6	12.2	23.3	22.7	6.2	2.4
PTEC	18.4	14.7	24.4	20.8	17.2	17.1
Mid-parent	16.1	13.0	23.9	21.7	9.7	5.1
	HT15		DBH15		STR15	
PCH	12.7	7.8	26.9	19.7	7.5	7.5
PTEC	8.9	7.3	11.3	12.1	16.2	18.8
Mid-parent	10.7	7.3	18.4	15.6	10.3	11.8

PCH P. caribaea var. *hondurensis*, *PTEC* P. *tecunumanii*

Table 6 Superiority (%) of the PCH x POOC (*P. caribaea* var. *hondurensis*×*P. oocarpa*) over pure parent species and mid-parent at 8 and 15 years

Baseline	Cashel	Mukandi	Cashel	Mukandi	Cashel	Mukandi
	HT8		DBH8		STR8	
PCH	10.2	10.8	14.3	16.0	18.8	7.1
POOC	13.8	16.7	12.8	15.4	35.7	32.4
Mid-parent	11.6	13.2	13.3	15.4	26.7	18.4
	HT15		DBH15		STR15	
PCH	10.9	6.4	21.1	11.9	20.0	17.0
POOC	11.4	8.4	24.9	13.4	37.1	29.2
Mid-parent	10.9	7.4	22.8	12.7	26.3	21.6

POOC P. oocarpa, *PCH P. caribaea* var. *hondurensis*

$\hat{h}^2bi$ was observed for these traits at both sites, except for stem straightness (STR5 and STR8) and HT5 for PCH×PTEC hybrid. For example, $\hat{h}^2bi$ for PCH×PTEC hybrid for STR5 were not significant. Significant values of $\hat{h}^2bi$ for height (HT5 and HT8) ranged from 0.14 to 0.51. $\hat{h}^2bi$ for diameter at breast height (DBH5, DBH8) ranged from 0.15 to 0.48, with higher estimates observed at Cashel than Mukandi. For example, significant $\hat{h}^2bi$ for DBH5 at Cashel was almost double that at Mukandi for PCH×PTEC hybrid. In cases where female heritability was significant for a trait, so was the estimate from the individual tree model. For example, ($\hat{h}^2bi$) from the individual-tree model for growth traits were significant ($p<0.05$) in most cases where $\hat{h}^2b$ were also significant.

Pooled-site estimates of narrow-sense heritabilities for each of the traits at ages 5 and 8 years from the two models are shown in Table 9. Pooled-site heritability estimates were generally intermediate between the two heritability estimates from the respective single-site analyses. For example, significant pooled-site $\hat{h}^2$ was observed for HT5 and HT8 for PCH× POOC (Table 9). Pooled-site analyses showed narrow-sense heritability estimates that ranged from 0.02 to 0.40, with the

Table 7 Superiority (%) of the PEE x PCH (*P. elliottii*×*P. caribaea* var. *hondurensis*) over pure parent species and mid-parent at 8 and 15 years

Baseline	Cashel	Mukandi	Cashel	Mukandi	Cashel	Mukandi
	HT8		DBH8		STR8	
PEE	16.4	29.6	25.2	53.0	5.1	8.3
PTEC	8.3	7.2	20.2	17.5	28.1	23.8
Mid-parent	11.8	17.3	22.9	33.3	17.1	15.6
	HT15		DBH15		STR15	
PEE	14.8	18.8	29.9	53.1	2.0	6.5
PTEC	8.3	4.1	18.4	11.6	27.5	24.5
Mid-parent	11.7	10.7	24.3	29.1	13.3	15.8

PCH P. caribaea var. *hondurensis*, *PTEC P. tecunumanii*

Table 8 Estimates of narrow-sense heritabilities±approximate standard errors for single-site ($\hat{h}^2b$) analyses for female and male and from individual tree model ($\hat{h}^2bi$), and dominance as a proportion of phenotypic variance ($\hat{d}^2b$) of *P. caribaea* var. *hondurensis* (PCH) by *P. oocarpa* (POOC) and *P. tecunumanii* (PTEC) F_1 hybrids

Trait	Taxon	No. of pair-crosses	Test	Heritability (female $\hat{h}^2b$)[a]	Heritability (male $\hat{h}^2b$)[a]	Tree model ($\hat{h}^2bi$)[b]	Proportion of dominance ($\hat{d}^2b$)[c]
HT5	PCH×PTEC	29	Cashel	0.40±0.18*	0.01±0.05	0.25±0.08*	0.02±0.12
			Mukandi	NE	0.15±0.13	0.10±0.08	NE
HT5	PCH×POOC	27	Cashel	0.45±0.18*	0.62±0.31*	0.51±0.08*	NE
			Mukandi	0.49±0.19*	0.17±0.14	0.36±0.09*	NE
HT8	PCH×PTEC	29	Cashel	0.53±0.23*	0.13±0.16	0.36±0.10*	NE
			Mukandi	0.08±0.07	0.22±0.14	0.14±0.05*	NE
HT8	PCH×POOC	27	Cashel	0.75±0.27*	NE	0.40±0.10*	NE
			Mukandi	0.35±0.16*	0.03±0.10	0.23±0.13*	0.12±0.16
DBH5	PCH×PTEC	29	Cashel	0.59±0.18*	NE	0.36±0.08*	
			Mukandi	NE	0.26±0.20	0.15±0.10	0.21±0.20
DBH5	PCH×POOC	27	Cashel	0.43±0.18*	0.36±0.29	0.48±0.09*	NE
			Mukandi	0.47±0.19*	0.14±0.14	0.35±0.10*	0.03±0.10
DBH8	PCH×PTEC	29	Cashel	0.21±0.14	0.49±0.35	0.34±0.10*	
			Mukandi	0.14±0.08*	0.29±0.19	0.19±0.06*	NE
DBH8	PCH×POOC	27	Cashel	0.49±0.40	0.42±0.41	0.46±0.20*	0.47±0.40
			Mukandi	0.25±0.14*	NE	0.14±0.10	0.07±0.09
STR5	PCH×PTEC	29	Cashel	0.15±0.18	0.08±0.11	0.09±0.11	0.18±0.20
			Mukandi	0.11±0.17	0.20±0.17	0.06±0.09	0.16±0.17
STR5	PCH×POOC	27	Cashel	0.16±0.34	0.21±0.26	0.19±0.18	0.62±0.40
			Mukandi	0.16±0.16	0.07±0.13	0.39±0.07*	0.21±0.17
STR8	PCH×PTEC	29	Cashel	0.12±0.28	NE	NE	0.26±0.29
			Mukandi	0.09±0.12	0.13±0.12	0.11±0.07	0.10±0.13
STR8	PCH×POOC	27	Cashel	0.27±0.17	0.52±0.31	0.37±0.10*	NE
			Mukandi	0.25±0.19	0.22±0.21	0.24±0.18	0.11±0.17

Significance levels based on one-tailed LR tests that were used to test the departure of female, male and dominance variance from zero. Statistical significance for estimated heritability is same as for additive genetic variance

NE not estimable and assumed to be zero

*Significant ($p<0.05$), otherwise not significant ($p>0.05$)

[a] Estimated from Eq 3

[b] Estimated from Eq 6

[c] Estimated from Eq 5

lowest value for HT5 for PCH×PTEC hybrid and the largest for HT5 and DBH5 for PCH×POOC hybrid (Table 9). $\hat{d}^2_b$ was non-significant ($p>0.05$), and in some cases, the estimates were 0 and where heritability estimate was greater than 0, the standard errors were larger than the estimate (Table 8).

Age-age and trait-trait genetic correlation estimates (r_A) from single-site analyses are presented in Table 10. Generally, r_A were statistically significant and followed expectations for all hybrids and traits at both sites. For example, r_A between HT5 and HT8 were significant and averaged 0.96, and r_A between HT5 and DBH5 averaged 0.87. For DBH and STR, r_A was generally significant and ranged from 0.18 to 0.74. This correlation is favourable, indicating that selection for larger diameter would improve stem straightness.

The importance of G×E interaction was assessed for all traits for the two hybrids through the magnitude of a common estimate of the genetic correlation between the performances of the same trait measured in different trials. The results showing estimated type B additive genetic correlation that are significantly different from +1 based on LR tests are presented in Table 9. We also used Robertson's (1959) threshold of 0.8 to indicate practical significance of G×E interaction, i.e. values below 0.8 are deemed to indicate presence of practically important G×E interaction. For PCH×PTEC hybrid, r_B between sites for height averaged 0.62, suggesting G×E interaction. For height, r_B between sites averaged 0.90 for PTEC×POOC hybrid. For DBH, r_B between sites for all hybrids were >0.83. Similar trends were also observed for stem straightness, $r_B>0.83$.

Table 9 Estimates of narrow-sense heritabilities±approximate standard errors for pooled-site ($\hat{h}^2$) analyses for female and male, and from individual-tree model ($\hat{h}^2_i$) and type B genetic correlations (r_B) of *P. caribaea* var. *hondurensis* (PCH) by *P. oocarpa* (POOC) and *P. tecunumanii* (PTEC) F_1 hybrids

Trait	Taxon	Heritability (female $\hat{h}^2$)[a]	Heritability (male $\hat{h}^2$)[a]	Tree model ($\hat{h}^2 i$)[b]	r_B
HT5	PCH×PTEC	0.16±0.14	0.02±0.05	0.02±0.05	0.68*
HT5	PCH×POOC	0.43±0.16*	0.34±0.20	0.40±0.11*	0.85
HT8	PCH×PTEC	NE	0.16±0.11	0.15±0.06*	0.56*
HT8	PCH×POOC	0.50±0.17*	0.07±0.08	0.35±0.10*	0.95
DBH5	PCH×PTEC	0.21±0.18	NE	0.28±0.09*	0.83
DBH5	PCH×POOC	0.39±0.16*	0.32±0.20	0.40±0.10*	0.86
DBH8	PCH×PTEC	0.17±0.10	0.38±0.22	0.22±0.09*	0.96
DBH8	PCH×POOC	0.31±0.17*	0.04±0.12	0.23±0.12*	0.96
STR5	PCH×PTEC	0.13±0.14	0.10±0.10	0.07±0.10	0.83
STR5	PCH×POOC	0.29±0.27	0.10±0.17	0.15±0.18	0.90
STR8	PCH×PTEC	0.05±0.14	0.07±0.09	0.08±0.08	0.96
STR8	PCH×POOC	0.27±0.20	0.25±0.22	0.27±0.18	0.93

Significance levels based on one-tailed LR tests that were used to test the departure of female, male and dominance variance from zero and r_B from +1. Statistical significance for estimated heritability is same as for additive genetic variance

NE not estimable and assumed to be zero

* significant ($p<0.05$), otherwise not significant ($p>0.05$)

[a] Estimated from Eq 4

[b] Estimated from Eq 8

Table 10 Trait-trait genetic correlations (r_A) for PCH×PTEC and PCH×POOC hybrids

Test	PCH×PTEC	HT8	DBH5	DBH8	STR5	STR8
Cashel	HT5	0.95***	0.96***	0.81**	0.77*	0.49**
	HT8		0.82**	0.82**	0.48***	0.63*
	DBH5			0.91***	0.72*	0.39**
	DBH8				0.35**	0.47**
	STR5					0.98***
	PCH×POOC					
	HT5	0.97**	0.96***	0.93***	0.70*	0.50**
	HT8		0.95***	0.92***	0.43*	0.63**
	DBH5			0.98***	0.63*	0.30*
	DBH8				0.38*	0.18^{ns}
	STR5					0.94***
Mukandi	PCH×PTEC					
	HT5	0.99**	0.92***	0.93***	0.73**	0.46*
	HT8		0.88**	0.71**	0.53*	0.62*
	DBH5			0.91***	0.69*	0.42*
	DBH8				0.42*	0.38*
	STR5					0.95***
	PCH×POOC					
	HT5	0.98***	0.90***	0.94***	0.88***	0.81***
	HT8		0.83**	0.90***	0.93***	0.92***
	DBH5			0.99***	0.78**	0.54*
	DBH8				0.85**	0.74*
	STR5					0.98***

Significance levels were based on two-tailed LR tests to test the departure of r_A from zero

ns not significant

*$p<0.05$; **$p<0.01$; ***$P<0.001$

Relationships between the general hybridizing abilities (GHA) of 11 PCH parents used in the two sets of hybrids at ages 5 and 8 years from planting were of similar magnitude. Figure 2a–c shows the relationships for traits at age 8 years. There was no consistent pattern in the rankings of the parents used in the two sets of hybrids for all traits. The correlation coefficients between the two sets of breeding value predictions (breeding value=2×GHA) were 0.45, 0.38 and 0.40 for HT8, DBH8 and STR8, respectively (Fig. 2a–c). Although the correlations between the GHAs for all traits were positive, they were not significant at the p=0.05 level (Steel and Torrie 1980, p. 597). However, there were four parents that consistently ranked above average for HT8 and DBH8 when crossed with *P. oocarpa*. Only three of those parents ranked above average for STR8. The four PCH parents were among the second-generation parents (Dominic Kain – personal communication, 2014).

Discussion

The results from this study explore several aspects of the genetic architecture of the tested pine hybrids that are relevant to

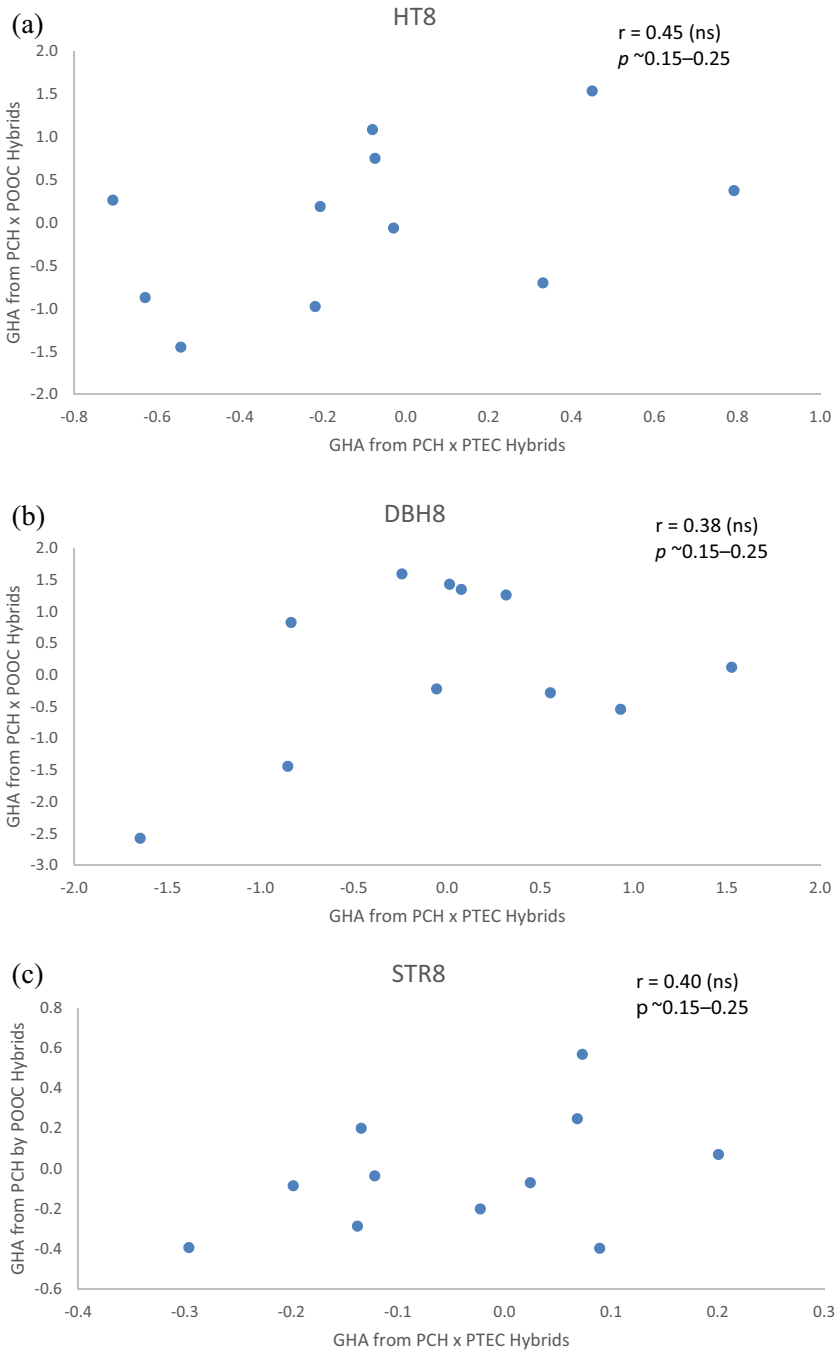

Fig. 2 **a–c** Relationships between the general hybridizing abilities (GHA) of 11 *P. caribaea* var. *hondurensis* (PCH) parents that were predicted from age-8 data of F_1 hybrid crosses with six *P. oocarpa* (POOC) and six *P. tecunumanii* (PTEC) across two sites for height (HT8), diameter at breast height (DBH8), and straightness (STR8), respectively. The significance of the r value (correlation between the two sets of GHA predictions) was not significant at p=0.05 (Steel and Torrie 1980, page 597)

define breeding strategies. *P. elliottii* and *P. tecunumanii* are some of the currently recommended commercial species for areas represented by Cashel site (Silvicultural Zones III and IV) while *P. elliottii* is also one of the recommended species for areas represented by Mukandi site. This study has shown that the hybrids had better growth performance than the pure species at both sites, with pure species being more productive at Mukandi than Cashel due to better site conditions (higher rainfall, more fertile soils that are deep and acidic) at Mukandi. Soils at Cashel are derived from sedimentary rocks with varying proportions of other minerals, mainly shale and have moderately shallow soils compared to Mukandi. PCH×PTEC (*P. caribaea* var. *hondurensis*×*P. tecunumanii*) hybrid was the most productive hybrid. For example, PCH×PTEC hybrid was 37 % better than *P. elliottii* local control, the currently recommended species at Cashel and Mukandi sites. Likewise, PEE×PCH (*P. elliottii*×*P. caribaea* var. *hondurensis*) hybrid was almost 35 % superior to *P. elliottii* control. Barnes and Mullin (1978) found that the hybrid between *P. elliottii* and *P. taeda* outperformed the pure species on sites marginal for the pure species, but not on sites optimal for the pure species. *P. elliottii* is known to struggle at low elevation, drier sites like Cashel (Table 2), and therefore, PCH×PTEC and PEE×PCH hybrids are obvious candidates for such areas covering Silvicultural Zones III and IV. These hybrids could also replace *P. patula* and *P. taeda* in these zones because they are not tolerant of moisture deficits that typify these two zones.

P. tecunumanii has demonstrated high growth rates and tolerance to drought and could be developed into a major commercial species in Zimbabwe (Nyoka et al. 1996; Tembani et al. 2014). Its drawback is susceptibility to stem breakage, even in light winds (Dvorak et al. 1993; Nyoka and Barnes 1995; Nyoka et al. 2010). Growth rates for PCH in Zimbabwe are unimpressive when compared to other unimproved pine species like *P oocarpa* or *P. tecunumanii* (Gapare and Musokonyi 2002). *P. tecunumanii* used in combination with *P. elliottii*, *P. oocarpa* and *P. caribaea* var. *hondurensis* has shown that it could provide hybrids combining high productivity, adaptation and strong stems (Tables 5, 6 and 7). For example, PCH×PTEC hybrid was 21 % superior to either parental species and mid parent values for DBH and showed same superiority at age 15 years. *P. caribaea* var. *hondurensis* provides resistance to stem breakage (Gwaze 1999). One obstacle to commercial development of this hybrid is that *P. caribaea* var. *hondurensis* does not flower at high altitudes in Zimbabwe (Gapare and Musokonyi 2002). Gwaze (1999) suggested that importing seed from Australia or improving flowering of the species by planting at low altitudes are potential solutions.

The results of the comparison of pure species and hybrids should be treated as indicative only. In this study, the presumed heterosis was present in all hybrids at both sites and was expressed more at Cashel (marginal site) than the wetter site (Mukandi), where strong dominance effects were exhibited at both ages (Gwaze 1999). The growth results at ages 8 and 15 years confirm to some extent the results of Gwaze (1999) that there is potential gain for hybrid species. Heterosis reported here may be inflated, particularly that of the hybrid between PCH×PTEC, because one of the pure parental species, *P. tecunumanii*, was from natural stands. Brawner et al. (2005) reported that PCH×PTEC hybrids showed evidence of hybrid superiority for growth at two locations in Queensland, Australia. For example, PCH×PTEC grew well at the both locations with an average increase in diameter at age 10 years of 14 and 11.5 % over PCH and PTEC, respectively.

Reports on genetic parameter estimates for pine interspecific hybrid populations remain scarce (Powell and Nikles 1996; Dieters et al. 1997; Gwaze et al. 2000), and in cases where they are available, the sample size is small and there is a general lack of pure species controls. This means that there is little information on whether hybrid populations behave similarly to pure species populations and conform to current quantitative genetic models (e.g. Kain 2003). Generally, the estimates of female and male heritability were non-significant and had large standard errors, perhaps due to the limited sample size. $\hat{h}^2b$ for the female parents (PCH) might be expected to be significant compared to male heritability due to the higher number of female (11) than male (6) parents. However, no consistent pattern emerged in the results. The pooled-site heritability estimates for PCH×POOC hybrids for DBH were generally higher than the companion estimates for PCH×PTEC hybrids. Brawner et al. (2005) observed similar patterns for these hybrids grown at two sites in Queensland, Australia. The lack of significant female $\hat{h}^2b$ for stem straightness for the hybrids is in contrast with results reported by Dieters et al. (1997) for the same material but grown in Queensland, Australia. They reported female $\hat{h}^2b$ of 0.41±0.20 and 0.48±0.23 for PCH×POOC and PCH×PTEC, respectively. However, we note that heritability estimates are specific to sites and also that the hybrids were developed in Queensland, Australia.

The estimates of female and male heritability need to be interpreted with caution, given the small number of female and male parents and families in the tests. The parents of each species also represented a mix of provenances—three POOC parents from each of Zapotillo and Angeles provenances and three PTEC parents from each of Mountain Pine Ridge and Yucul provenances (Dieters et al. 1997). Such a mix and the small number of female and male parents would make it difficult to meaningfully detangle their likely differences in the additive variance between the male and female parents. The observed differences in female and male heritability estimates may have been inflated by difference provenance origin. The limitation in these data also makes it impossible to definitively recommend using the parental or individual-tree model. Generally, use of a parental model which provides heritability estimates for both female and male parents would provide

the breeder with details in terms of breeding strategy to adopt—either focus on female or make parent selections depending on heritability.

Estimates of genetic parameters of the hybrids show individual-tree, narrow-sense heritabilities for height, DBH and stem straightness to be low to moderate (Powell and Nikles 1996; Dieters et al. 1997; Gwaze et al. 2000). For example, Dieters et al. (1995; 1997) reported narrow-sense heritability estimates for PEE×PCH and PCH×POOC hybrids for DBH, height and straightness in the same range as observed in our study. Dominance variance was negligible and less precisely estimated, an expected result given the very low numbers of parents and small sample sizes (White and Hodge 1989). Trends, however, indicated that dominance was greater for stem straightness at age 5 years (STR5) than for the other growth traits and greatest at Mukandi (Table 8). In the pooled-site analyses, dominance was relatively unimportant compared with additive variance (details not shown). We would expect dominance to be relatively low due to increased heterozygosity and absence from inbreeding in the population (e.g. Wu 1997). The predominance of additive genetic variance in hybrids is consistent with reports by Dieters et al. (1997) and Powell and Nikles (1996) in pine hybrids and Madhibha et al. (2013) in eucalypt hybrids. These results suggest that breeding strategies which maximize the use of additive genetic variance may be effective.

Genetic correlation estimates between height and DBH at both ages were large and positive, above 0.80 (Table 9). These correlations indicate both traits at the two ages are likely controlled by the same set of genes: The result gives confidence in early selection. Genetic correlations between DBH and STR at both sites were low but significant, indicating larger diameter associated with straight stems. This is a favourable correlation, suggesting that selection for DBH may also give candidates with straighter stems. Similar patterns have been observed in parental species and also the hybrids (Dieters et al. 1997; Gwaze et al. 2000; Gapare and Musokonyi 2002).

Heritability estimates from the data pooled across the two sites were generally intermediate between those from individual sites. There was no evidence of practically important G×E interaction for the hybrids except for height growth for PCH×PTEC hybrid. This suggests that PCH×PTEC and PCH×POOC hybrids appear to be stable across the two sites. It is not clear what is driving G×E for height growth in PCH×PTEC hybrid. Our results suggest that the importance of G×E interaction was trait and hybrid taxon dependent, for example, height for PCH×PTEC hybrid. While G×E interaction in hybrid populations is not well understood, the developmental stability of hybrids has been defined from two different models, epistasis and pleiotropy (Wu 1997). Wu (1997) postulated that low developmental stability may result from reactions to the new environment and from a breakdown of co-adapted gene complexes. However, we note that *P. tecunumanii* parents for the PCH×PTEC hybrid originated from low-elevation provenances (Yucul and Mountain Pine Ridge (MPR)). Nyoka et al. (2010) reported the MPR provenance to be interactive for growth at Cashel. For example, the provenance showed exceptional height growth at two years, where it was ranked among the best but its growth rate subsequently declined with increasing age, to be ranked lowest for both growth and stem straightness at age five and eight years (Nyoka et al. 2010). *P. caribaea* var. *hondurensis*, in particular the MPR provenance is also known to exhibit G×E interaction (e.g., Woolaston et al. 1991) and also between Mukandi and Cashel (Gapare and Musokonyi, 2002).

Implications for hybrid breeding strategy

The hybrids studied here appear to be robust and well adapted to the target areas, expressing favorable genes from both parents. In this study, we recommend that synthetic (SYN) hybrid strategy would be the most cost-effective strategy, given that there is less dominance variance and the pure–hybrid correlations in both species are greater than zero (e.g. 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 (Brawner et al. 2005). Using outstanding material in 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 and Mackay 1996). The ultimate effect of continued selection within a synthetic would be to increase the most favourable double homozygote and decrease the frequency of all others.

We envisage that the 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. For example, if a parent consistently ranks above average 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. In this study, there were non-significant correlations between the GHAs of the two interspecific combinations for all traits at ages 5 and 8 years. This may be due to imprecise estimates of the GHA of the respective hybrids because of a smaller sample size. For example, the correlation between the true and predicted breeding values were very low ranging from 0.11 to 0.33 for HT8 and DBH8. Our results differ from those of Dieters et al. (1997) who reported identical rankings of the parents for stem straightness, but not so for DBH at age 5 years. Dieters et al. (1997) also attributed their correlations to the level of dominance variance which was small relative to additive variance. Brawner et al. (2005) reported positive and high correlations

(>0.75) between PCH parents used in combination with either PTEC or POOC for growth traits. They attributed the increased correlations compared to those reported by Dieters et al. (1997) to more precise breeding value predictions from a larger number of tests and parents. However, we identified four second-generation PCH parents that consistently ranked above average for HT8 and DBH8 when crossed with *P. oocarpa*. The statistical significance of the correlations between GHAs of the two interspecific combinations could be expected to be increased by increasing the sample size. However, the 'true' genetic correlations between parental performances in hybrid combinations between the two species would be higher than our estimates because of independence of errors of estimating breeding values in the respective species combinations.

As a follow-up to the proposed strategy, several species and interspecific hybrids using locally bred parents are being tested by the Research and Development Division of the Zimbabwe Forestry Commission in Zimbabwe. The focus is on interspecific hybrids of the central American and Mexican closed cone pines as well as hybrids based on *P. caribaea*. The central American and Mexican closed-cone pines included *P. patula*, *P. tecunumanii*, *P. oocarpa*, *P. greggii* and *P. pringlei*. For *P. patula*, *P. tecunumanii* and *P. oocarpa*, three outstanding parents in progeny and also in provenance/progeny tests were selected, while those of *P. greggii* and *P. pringlei* were the available parents that have not been field-tested as there is no proper breeding programme for these two species in Zimbabwe (Barnes et al. 1997; Nyoka 2000).

However, the adoption of the hybrids as commercial tree species has its limitations and careful consideration is needed before it is implemented. For example, breeding of PCH and subsequent hybrids may be a challenge in Zimbabwe because PCH does not flower at high altitudes. A notable option suggested by Barnes (1993) was for Zimbabwe to run a joint program with Mozambique to establish breeding seedling orchards of PCH in low-elevation areas of Mozambique to produce seeds for both Zimbabwe and Mozambique. The vegetative propagation facility at Mukandi Nursery may be used for vegetative multiplication of very juvenile material in order to extend the small amount of control-crossed seed (e.g. Madhibha et al. 2013). Another option could be by importing seed from other countries as mentioned by Gwaze (1999), but this option is likely to be even more expensive and may not be sustainable for the local industry. While growth traits will remain important, other hybrid programs elsewhere have started focusing on wood properties and are generally inherited in an additive manner (Kain 2003). This is particularly important given the trend towards shorter rotations in pines which often result in larger amounts of corewood (Gapare et al. 2006). This will need to be taken into account in future breeding strategies.

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Conflict of interest The authors declare that they have no conflict of interest.

Data archiving statement Height, diameter and stem straightness data used in this manuscript will be made available as an electronic supplement to this publication upon acceptance of the manuscript.

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