




Genetic parameters for growth and wood chemical properties in *Eucalyptus urophylla* × *E. tereticornis* hybrids

Shengkan Chen^{1,2} · Qijie Weng² · Fagen Li² · Mei Li² · Changpin Zhou^{1,2} · Siming Gan^{1,2} 

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Abstract

• **Key message** Growth and wood chemical properties are important pulpwood traits. Their narrow-sense heritability ranged from 0.03 to 0.49 in *Eucalyptus urophylla* × *E. tereticornis* hybrids, indicating low to moderate levels of genetic control. Genetic correlations were mostly favorable for simultaneous improvement on growth and wood traits. Additive and non-additive genetic effects should be considered in making a hybrid breeding strategy.

• **Context** Eucalypt hybrids are widely planted for pulpwood production purposes. Genetic variations and correlations for growth and wood chemical traits remain to be explored in *Eucalyptus* interspecific hybrids.

• **Aims** Our objectives were to clarify the heritability of growth and wood chemical traits and determine the genetic correlations between traits and between trials in *E. urophylla* × *E. tereticornis* hybrids.

• **Methods** Two trials of 59 *E. urophylla* × *E. tereticornis* hybrids derived from an incomplete factorial mating design were investigated at age 10 for growth (height and diameter) and wood chemical properties (basic density, cellulose content, hemicellulose content, lignin content, and syringyl-to-guaiacyl ratio). Mixed linear models were used to estimate genetic parameters.

• **Results** Narrow-sense heritability estimates were 0.13–0.22 in growth and 0.03–0.49 in wood traits, indicating low to moderate levels of additive genetic control. Genetic correlations were mostly positively significant for growth with basic density and cellulose content but negatively significant with hemicellulose and lignin contents, being favourable for pulpwood breeding purpose. Type-B correlations between sites were significant for all the traits except diameter and lignin content.

• **Conclusion** Hybrid superiority warrants the breeding efforts. An appropriate breeding strategy should be able to capture both additive and non-additive genetic effects.

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Contribution of the co-authors Shengkan Chen performed the data analysis, drafted the paper, and participated in the collection of growth data in the field. Qijie Weng coordinated the fieldwork and participated in the measurement of growth and wood chemical properties. Fagen Li participated in the maintenance of field trials and the collection of growth data. Mei Li participated in the data analysis and the paper revision. Changpin Zhou coordinated the research project and participated in the measurement of growth and wood chemical properties. Siming Gan designed the study, supervised the work, and finalized the paper.

✉ Changpin Zhou
zhouchangpin@126.com

✉ Siming Gan
siming_gan@126.com; Siming.Gan@ritf.ac.cn

Shengkan Chen
chenshengkan@126.com

Qijie Weng
qjw65@126.com

Fagen Li
lifagen2002@126.com

Mei Li
limei3043@126.com

¹ State Key Laboratory of Tree Genetics and Breeding, Chinese Academy of Forestry, Xiangshan Road, Beijing 100091, China

² Key Laboratory of State Forestry Administration on Tropical Forestry, Research Institute of Tropical Forestry, Chinese Academy of Forestry, 682 Guangshan 1 Road, Guangzhou 510520, China

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1 Introduction

Trees of the genus *Eucalyptus* L'Her. are widely planted in tropical and subtropical regions, with global plantation area estimated to be more than 21 million ha (Midgley 2013). Eucalypt tree plantations are valuable for timber, biomass, honey, and oil production (Eldridge et al. 1993) and provide the largest source of short fiber for pulp and paper industry worldwide (Kien et al. 2009). The vast majority of eucalypt planting stock is of interspecific hybrids, particularly hybrid clones. In China, for instance, hybrids of *E. grandis* Maiden, *E. urophylla* S. T. Blake, *E. camaldulensis* Dehnh., and/or *E. tereticornis* Smith predominate the eucalypt pulpwood plantations (Wei 2005) and a few of clonal hybrids account for as much as 90% of the eucalypt plantation area established (Turnbull 2007; Luo et al. 2012). Thus, breeding and deployment of hybrids play a pivotal role in eucalypt plantation forestry.

E. urophylla occurs naturally on some islands of East Timor and Indonesia spreading between about 7° 23' S and 10° S in latitude, while *E. tereticornis* has a very wide natural distribution along a long strip (latitudinal range 6–38° S) from southern Papua New Guinea to southern Victoria, Australia (FAO 1979; Eldridge et al. 1993). Both species are economically important for eucalypt growers in many countries, including Brazil (Gonçalves et al. 2013), India (Balasaravanan et al. 2005), and China (Wang 2010) that rank the top three of the list of eucalypt plantation areas in the world. Moreover, interspecific hybrids between the two species have great potential for heterosis exploitation and genetic gain achievement in plantation forestry. In southern China, *E. urophylla* × *E. tereticornis* clones have been widely cultivated in coastal regions due to their features in fast growth, high productivity, and resistance to moderate typhoon (Peng et al. 2013).

Growth and wood properties are considered as major economic traits affecting the plantation productivity and subsequently the management profitability. For pulp and paper making purposes, the important wood traits include basic density, cellulose content, hemi-cellulose content, lignin content, and lignin syringyl-to-guaiacyl (S/G) ratio, which are strongly related with pulp yield and delignifying chemical consumption (Wallis et al. 1996; Rencoret et al. 2007). In addition, pulpwood traits are likely to have implications for solid wood production, e.g., higher basic density being favourable for increased strength and stiffness (Dickson et al. 2003). To date, genetic variations have been reported for growth and wood traits in a number of *Eucalyptus* populations, such as diameter, wood basic density, lignin content, and S/G ratio

in *E. globulus* Labill. (Stackpole et al. 2011) and *E. urophylla* (Hein et al. 2012; Denis et al. 2013) provenances/families. These traits are generally under low to moderate levels of additive genetic control (Raymond 2002; Hein et al. 2012; Denis et al. 2013), highlighting the potential of genetic improvement through selection. Also, published genetic correlations between growth and wood properties are variable among traits and populations, showing no conclusive evidence for a strong negative relationship and indicating the possibility of simultaneous improvement on some of the traits (Raymond 2002; Stackpole et al. 2011; Hein et al. 2012; Denis et al. 2013). However, genetic variations and correlations available for such pulping traits as cellulose, hemi-cellulose, and/or lignin contents in *Eucalyptus* are limited to *E. globulus* (Poke et al. 2006; Stackpole et al. 2011) and *E. urophylla* (Kien et al. 2009; Hein et al. 2012; Denis et al. 2013), and other taxa, especially interspecific hybrids, remain to be explored. Moreover, such pulping traits were analyzed mostly with only single-site trials in previous reports, and their across-site variation patterns (e.g., genotype by environment interaction) were poorly understood.

Traditional wet chemistry methods for assessing wood pulping properties are time consuming and expensive, restricting the ability to process large populations that are always adopted for genetic variation analysis. Moreover, a relatively large amount of wood (e.g., more than 500 g) is usually sampled for laboratory pulping, which needs to damage trees. More recently, rapid, inexpensive, and non-destructive methods such as near infrared reflectance spectroscopy (NIRS) have been developed to assess wood physical and chemical properties of large populations (Tsuchikawa 2007; Colin et al. 2015). In the case of *Eucalyptus*, NIRS technology has been successfully applied to genetic analysis of wood traits of several species, e.g., *E. globulus* (Stackpole et al. 2011), *E. urophylla* (Hein et al. 2012; Denis et al. 2013), and *E. cloeziana* F. Muell. (Li et al. 2017), but has not been extended to interspecific hybrids, including *E. urophylla* × *E. tereticornis*.

In the present study, we used two field trials of 59 *E. urophylla* × *E. tereticornis* hybrids derived from an incomplete factorial mating design to investigate genetic parameters for growth and wood chemical properties. We applied NIRS calibrations to predict wood properties including basic density, cellulose content, hemi-cellulose content, lignin content, and S/G ratio. Our objectives were to determine the heritability of growth and wood chemical traits as well as the genetic correlations between traits and between trials.

2 Materials and methods

2.1 Plant materials and field trials

An incomplete factorial mating of 10 *E. urophylla* females with 10 *E. tereticornis* males resulted in 62 crosses (He et al. 2012), of which 59 were maintained finally in the field trials (Weng et al. 2014). The 10 maternal open-pollinated half-sib families were also tested. The field trials were established at Yong'an (117° 23' E, 25° 53' N) and Changtai (117° 52' E, 24° 46' N) counties in Fujian Province, China, in July 2003 as described earlier (Weng et al. 2014). Both trials followed a randomized complete block design with four replicates of four-tree row plots at a spacing of 2 × 3 m between trees.

2.2 Trait measurement

Growth traits were measured for height (H , m) at around 0.5, 1.5, 2.5, 4, 7.5, and 10 years of age ($H_{0.5}$, $H_{1.5}$, $H_{2.5}$, H_4 , $H_{7.5}$, and H_{10} , respectively) as well as diameter at breast height (D , cm) at around 1.5, 2.5, 4, 7.5, and 10 years ($D_{1.5}$, $D_{2.5}$, D_4 , $D_{7.5}$, and D_{10} , respectively). Wood chemical properties at 10 years, including basic density (BD_{10} , g cm⁻³), cellulose content (CC_{10} , %), hemicellulose content (HC_{10} , %), Klason lignin content (LC_{10} , %), and lignin S/G ratio (S/G_{10}), were predicted based on NIRS calibrations developed previously (patents pending). Briefly, about 10 g of wood swarf sample was collected per living tree by drilling the peeled stem (around 5 cm in depth at 1.3 m height) and then air dried, ground, and scanned on a MPA spectrometer (Bruker Optik, Ettlingen, Germany; resolution at 8 cm⁻¹ within 800–2778 nm). Each sample was scanned for five times, and value of each wood trait was the average of the five predictions.

2.3 Statistical analyses

The data were statistically analyzed with the software ASReml (Gilmour et al. 2009). Growth traits at age 7.5 and earlier were described earlier (Weng et al. 2014), and analysis of variance (ANOVA) was carried out here for each trait at age 10 for each trial and pooled trials using univariate single-tree mixed linear models as simplified below:

$$y = Xb + Za + e \quad (1)$$

where y is the vector of individual observations, X is the known design matrix for fixed effects b (i.e., replicate for single site analysis but site and replicates within site for site-pooled analysis), Z is the known design matrix for random effects a (i.e., female, male, female × male

interaction, and, if applicable, their interactions with site), and e is the vector of random residuals. The significance level of a random effect was determined using the one-tailed likelihood ratio test in ASReml (Gilmour et al. 2009).

The variance components estimated above were used to estimate single-site biased heritability (h^2_b) and dominance effect (d^2_b) as well as pooled site unbiased heritability (h^2) and dominance effect (d^2):

$$h^2_b = \frac{2(\sigma_f^2 + \sigma_m^2)}{\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_e^2} \quad (2)$$

$$d^2_b = \frac{4\sigma_{fm}^2}{\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_e^2} \quad (3)$$

$$h^2 = \frac{2(\sigma_f^2 + \sigma_m^2)}{\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_{fs}^2 + \sigma_{ms}^2 + \sigma_{fms}^2 + \sigma_e^2} \quad (4)$$

$$d^2 = \frac{4\sigma_{fm}^2}{\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_{fs}^2 + \sigma_{ms}^2 + \sigma_{fms}^2 + \sigma_e^2} \quad (5)$$

where σ_f^2 , σ_m^2 , σ_{fm}^2 , σ_{fs}^2 , σ_{ms}^2 , σ_{fms}^2 , and σ_e^2 are variance components of female, male, female × male, female × site, male × site, female × male × site, and random residuals, respectively, in corresponding univariate models aforementioned. Standard errors of the heritability and dominance effect estimates were derived from Taylor series approximation of the R pin function in ASReml (Gilmour et al. 2009).

Phenotypic (r_p) and additive genetic (r_g) correlation coefficients between traits or between ages of the same growth trait were estimated based on phenotypic and additive covariances and variance components from bivariate analyses of pooled trials:

$$r_p = \frac{\sigma_{p_x p_y}}{\sqrt{\sigma_{p_x}^2 \sigma_{p_y}^2}} \quad (6)$$

$$r_g = \frac{\sigma_{a_x a_y}}{\sqrt{\sigma_{a_x}^2 \sigma_{a_y}^2}} \quad (7)$$

where $\sigma_{p_x p_y}$ and $\sigma_{a_x a_y}$ are the phenotypic and additive covariances, respectively, between traits x and y or between ages x and y of the same growth trait; $\sigma_{p_x}^2$ and $\sigma_{p_y}^2$ are phenotypic variance components for x and y , respectively; and $\sigma_{a_x}^2$ and $\sigma_{a_y}^2$ are genetic variance components for x and y , respectively. Two-tailed likelihood ratio tests were used to determine whether a correlation was significant with difference from zero (Gilmour et al. 2009). In addition, type-B genetic correlations (r_B) were also calculated to detect genotype × environment interaction for each trait at age 10, using likelihood ratio test (LRT) of the departure of r_B from one in ASReml (Gilmour et al. 2009).

Data availability The data that support the findings of this study are available from the corresponding authors upon reasonable request.

3 Results

3.1 Trait means

Means and coefficients of variation (*CV*) for all traits observed at age of 10 years are presented in Table 1. As compared to maternal open-pollinated (OP) families, hybrids had consistently higher means in H_{10} , D_{10} , BD_{10} , HC_{10} , and LC_{10} but smaller means in CC_{10} and S/G_{10} for both single and across sites.

For growth traits H_{10} and D_{10} in hybrids, the Yong'an trial had consistently higher mean values than Changtai, with H_{10}

Table 1 Means of 10-year-old height (H_{10}), diameter at breast height (D_{10}), basic density (BD_{10}), cellulose content (CC_{10}), hemi-cellulose content (HC_{10}), Klason lignin content (LC_{10}), and lignin syringyl-to-guaiacyl (S/G_{10}) for *E. urophylla* × *E. tereticornis* hybrids and maternal open-pollinated (OP) families grown at two sites

Trait	Site	Hybrid		OP family	
		Mean	CV (%)	Mean	CV (%)
H_{10} (m)	Yong'an	17.5***	23.6	16.5*	21.7
	Changtai	15.6	30.8	14.6	32.1
	Across sites	16.5	27.9	15.4**	32.5
D_{10} (cm)	Yong'an	14.6	30.6	13.1*	32.1
	Changtai	14.0	43.8	13.2	41.5
	Across sites	14.3	38.0	13.2*	34.7
BD_{10} (g cm ⁻³)	Yong'an	0.48	8.4	0.46*	6.5
	Changtai	0.47	7.8	0.46**	8.7
	Across sites	0.47	8.1	0.46***	8.7
CC_{10} (%)	Yong'an	43.9***	4.6	44.7*	4.7
	Changtai	48.2	5.6	48.7	7.2
	Across sites	46.0	6.9	46.9**	7.6
HC_{10} (%)	Yong'an	20.5***	8.0	20.3	7.9
	Changtai	16.5	18.7	16.2	16.8
	Across sites	18.5	17.2	18.1	17.0
LC_{10} (%)	Yong'an	28.4***	3.7	28.3	4.5
	Changtai	27.4	3.1	27.0	8.4
	Across sites	27.9	3.9	27.6	7.1
S/G_{10}	Yong'an	2.13***	16.0	2.26**	13.7
	Changtai	2.44	17.6	2.48	17.3
	Across sites	2.28	18.4	2.38	16.8

Asterisks in columns of "Hybrid" and "OP family" indicate significance levels of difference between the two sites (for hybrids only) and between hybrid and the maternal OP family, respectively, based on the *t* test

CV coefficient of variation

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

and D_{10} means differing significantly ($P \leq 0.001$) and non-significantly ($P > 0.05$), respectively, between the two trials (Table 1). As Changtai showed a slower growth in spite of higher mean annual temperature, the better growth at Yong'an may be due to higher annual rainfall (1564 mm at Yong'an vs. 1466 mm at Changtai; Weng et al. 2014).

For wood property traits in hybrids, Yong'an had greater means in BD_{10} , HC_{10} , and LC_{10} but smaller means in CC_{10} and S/G_{10} as compared with Changtai, with between-site differences being non-significant in BD_{10} ($P > 0.05$) but significant in other wood traits ($P \leq 0.001$; Table 1). Wood properties displayed generally smaller phenotypic variations than growth, such that their *CV* values ranged between 3.1% (LC_{10} at Changtai) and 18.7% (HC_{10} at Changtai).

3.2 Variance components and heritability

Variance components of female, male, and female × male interaction varied somewhat for the traits and sites analyzed (Table 2). For single site analysis, both female and male variances were significant ($P \leq 0.05$, 0.01, or 0.001) for majority of the traits at Yong'an and Changtai, while female × male interactions were not significant ($P > 0.05$) for all traits except for H_{10} at Changtai ($P \leq 0.05$). For across site analysis, however, female, male, and female × male interaction variances were all non-significant ($P > 0.05$) except for σ_f^2 in H_{10} ($P \leq 0.01$) and σ_m^2 in BD_{10} and S/G_{10} ($P \leq 0.05$).

The narrow-sense heritability estimates for growth traits H_{10} and D_{10} ranged between 0.13 and 0.22 in single and across site analyses (Table 2), implying a generally low level of additive genetic control of the growth. Also, h^2 across sites fluctuated slightly for height and diameter at breast height after age 4 (Fig. 1), which indicated relatively stable heritability with advancing age. Meanwhile, narrow-sense heritability of wood properties varied notably from 0.03 (HC_{10} across sites) to 0.49 (S/G_{10} at Changtai), suggesting low to moderate levels of additive genetic effect. The across-site h^2 values were consistently less than those of single sites for all the traits. In addition, the dominance estimates for all growth and wood property traits were generally small at single and across sites, suggesting a weak dominance effect on these traits.

3.3 Trait-trait, age-age, and type-B correlations

The coefficients of r_p and r_g between 10-year-old traits are given in Table 3. Values of r_p and r_g were significantly positive between growth traits H_{10} and D_{10} ($P \leq 0.001$), but significantly negative or non-significant between most wood properties except for positively significant r_p between CC_{10} and S/G_{10} and between HC_{10} and LC_{10} ($P \leq 0.001$). Growth traits generally showed significantly positive r_g with BD_{10} and

Table 2 Variance components of female (σ_f^2), male (σ_m^2), and female \times male interaction (σ_{fm}^2) as well as narrow-sense heritability (h_b^2 and h^2 for single and across sites, respectively) and dominance as a ratio of phenotypicvariance (d_b^2 and d^2 for single and across sites, respectively) for each trait measured at age of 10 years in *E. urophylla* \times *E. tereticornis* hybrids grown at two sites. Trait abbreviations were as shown in Table 1

Trait	Site	σ_f^2 (\pm SE)	σ_m^2 (\pm SE)	σ_{fm}^2 (\pm SE)	h_b^2 or h^2 (\pm SE)	d_b^2 or d^2 (\pm SE)
H_{10}	Yong'an	0.56 (\pm 0.48)*	0.59 (\pm 0.52)*	0.58 (\pm 0.57)	0.14 (\pm 0.08)	0.14 (\pm 0.14)
	Changtai	1.55 (\pm 1.02)***	$1.83 (\pm 0.12) \times 10^{-6}$	1.27 (\pm 0.67)*	0.15 (\pm 0.09)	0.24 (\pm 0.13)
	Across sites	1.14 (\pm 0.69)**	0.14 (\pm 0.23)	0.32 (\pm 0.46)	0.13 (\pm 0.07)	0.07 (\pm 0.10)
D_{10}	Yong'an	0.72 (\pm 0.55)*	1.45 (\pm 0.89)***	$8.72 (\pm 0.59) \times 10^{-6}$	0.22 (\pm 0.09)	$1.75 (\pm 0.09) \times 10^{-6}$
	Changtai	2.56 (\pm 1.59)***	0.31 (\pm 0.56)	0.95 (\pm 1.01)	0.16 (\pm 0.09)	0.11 (\pm 0.11)
	Across sites	1.28 (\pm 0.93)	0.70 (\pm 0.54)	0.37 (\pm 0.43)	0.14 (\pm 0.07)	0.05 (\pm 0.06)
BD_{10}	Yong'an	$5.26 (\pm 4.89) \times 10^{-5}$	$1.27 (\pm 0.82) \times 10^{-4}$ **	$4.74 (\pm 5.23) \times 10^{-5}$	0.22 (\pm 0.11)	0.12 (\pm 0.13)
	Changtai	$8.57 (\pm 5.80) \times 10^{-5}$ ***	$5.39 (\pm 4.32) \times 10^{-5}$ *	$4.24 (\pm 4.41) \times 10^{-5}$	0.21 (\pm 0.10)	0.13 (\pm 0.13)
	Across sites	$1.27 (\pm 0.06) \times 10^{-10}$	$8.56 (\pm 5.22) \times 10^{-5}$ *	$4.44 (\pm 2.84) \times 10^{-5}$	0.12 (\pm 0.07)	0.12 (\pm 0.08)
CC_{10}	Yong'an	0.12 (\pm 0.10)*	0.20 (\pm 0.14)**	$5.50 (\pm 0.38) \times 10^{-7}$	0.16 (\pm 0.08)	$5.53 (\pm 0.24) \times 10^{-7}$
	Changtai	0.88 (\pm 0.52)***	0.46 (\pm 0.29)***	$1.36 (\pm 0.09) \times 10^{-6}$	0.36 (\pm 0.13)	$7.26 (\pm 0.59) \times 10^{-7}$
	Across sites	0.15 (\pm 0.22)	0.12 (\pm 0.16)	$5.07 (\pm 0.25) \times 10^{-7}$	0.09 (\pm 0.09)	$4.49 (\pm 0.16) \times 10^{-7}$
HC_{10}	Yong'an	0.14 (\pm 0.10)*	0.19 (\pm 0.12)**	0.02 (\pm 0.07)	0.24 (\pm 0.10)	0.03 (\pm 0.11)
	Changtai	0.27 (\pm 0.31)	0.02 (\pm 0.15)	0.48 (\pm 0.37)	0.06 (\pm 0.08)	0.21 (\pm 0.16)
	Across sites	$5.54 (\pm 0.28) \times 10^{-7}$	0.08 (\pm 0.08)	$5.54 (\pm 0.28) \times 10^{-7}$	0.03 (\pm 0.03)	$3.70 (\pm 0.12) \times 10^{-7}$
LC_{10}	Yong'an	$2.41 (\pm 2.54) \times 10^{-2}$	$6.59 (\pm 4.48) \times 10^{-2}$ **	$0.92 (\pm 3.15) \times 10^{-2}$	0.16 (\pm 0.09)	0.03 (\pm 0.11)
	Changtai	$2.92 (\pm 2.39) \times 10^{-2}$ *	$1.87 (\pm 2.00) \times 10^{-2}$	$2.71 (\pm 2.56) \times 10^{-2}$	0.13 (\pm 0.08)	0.15 (\pm 0.14)
	Across sites	$1.48 (\pm 1.94) \times 10^{-2}$	$3.31 (\pm 2.61) \times 10^{-2}$	$1.88 (\pm 1.67) \times 10^{-2}$	0.10 (\pm 0.07)	0.08 (\pm 0.07)
S/G_{10}	Yong'an	$0.79 (\pm 0.61) \times 10^{-2}$ *	$1.73 (\pm 1.00) \times 10^{-2}$ ***	$0.73 (\pm 0.46) \times 10^{-2}$	0.41 (\pm 0.16)	0.24 (\pm 0.15)
	Changtai	$2.50 (\pm 1.46) \times 10^{-2}$ ***	$1.94 (\pm 1.11) \times 10^{-2}$ ***	$0.37 (\pm 0.50) \times 10^{-2}$	0.49 (\pm 0.16)	0.08 (\pm 0.11)
	Across sites	$0.05 (\pm 0.77) \times 10^{-2}$	$1.71 (\pm 0.94) \times 10^{-2}$ *	$0.28 (\pm 0.35) \times 10^{-2}$	0.23 (\pm 0.15)	0.07 (\pm 0.09)

SE standard error

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

CC_{10} (except that between H_{10} and CC_{10}) but non-significant with S/G_{10} and negatively significant with HC_{10} and LC_{10} .

In terms of age-age correlations, r_p and r_g in growth (H and D) between the final age 10 and earlier years were all significantly positive and increased generally with age (Fig. 2). In particular, the r_g coefficients of age 10 with ages after 1.5 years remained stably high for H and D , indicating the possible time of age 1.5 for early prediction of mature growth.

The coefficients of r_B between Yong'an and Changtai were significantly departed from one in H_{10} , BD_{10} , CC_{10} , HC_{10} , and S/G_{10} ($P \leq 0.05$, 0.01, or 0.001; Table 3), indicating strong genotype \times environment interaction effects on these traits. However, non-significant r_B were found in D_{10} and LC_{10} ($P > 0.05$; Table 3), suggesting possibly weak genotype \times environment interactions.

4 Discussion

This study presents quantitative genetics analysis on growth and wood chemical traits in a factorial mating population of *E. urophylla* \times *E. tereticornis* hybrids. Information on genotype \times environment interactions in such pulping traits as

cellulose, hemi-cellulose, and lignin contents is described firstly in *Eucalyptus*. The results will improve our understanding on the genetic control of growth and wood properties and have implications for defining eucalypt hybrid breeding strategy.

4.1 Performance of *E. urophylla* \times *E. tereticornis* hybrids vs. maternal species

Coupled with superior growth of *E. urophylla* \times *E. tereticornis* hybrids mentioned earlier (Peng et al. 2013; Weng et al. 2014) and also above, the wood properties of the hybrid trees demonstrate their suitability for plantation establishment for producing pulp and paper. For instance, the basic density is within the range of some popularly cultivated hybrid clones of *E. urophylla* \times *E. grandis* and *E. urophylla* \times *E. tereticornis* (431–497 and 449–506 kg m⁻³ at 5.5 years, respectively; Luo et al. 2012), and the cellulose and lignin contents are similar to several pulp-oriented plantation species like *E. globulus* (42.2% in cellulose content at 11 years; Apiolaza et al. 2005) and *E. urophylla* (28.0% in Klason lignin content at 14 years; Hein et al. 2012). Moreover, as indicated, genetic variation exists at both within and between hybrids and it is

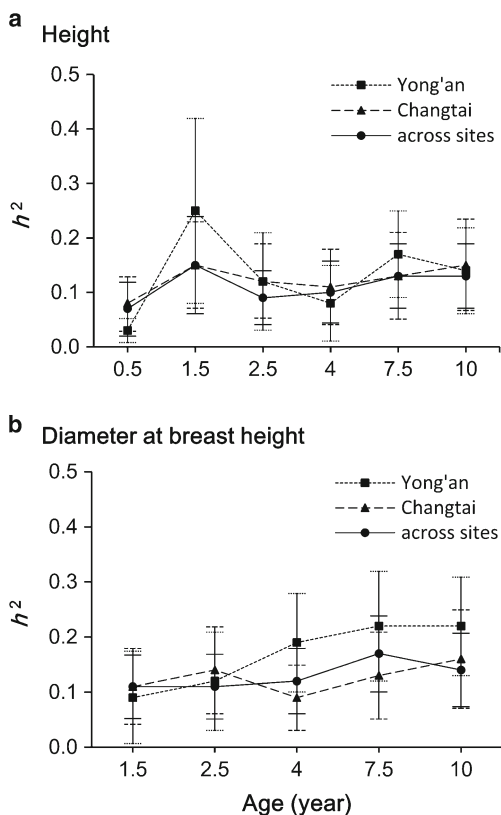


Fig. 1 Trend in narrow-sense heritability (h^2) of growth with age for *E. urophylla* × *E. tereticornis* hybrids tested at two sites. **a** Height. **b** Diameter at breast height. The h^2 values at Yong'an for age 4 and earlier were as estimated in He et al. (2012), while those of age 7.5 and earlier across sites were as estimated in Weng et al. (2014). Bars indicate standard errors

therefore likely to select elite genotypes with improved phenotypic performance for deployment.

Due to the absence of paternal OP progeny, it is not possible to evaluate the magnitude of hybrid superiority over both parental pure species. Nevertheless, the generally higher values of *E. urophylla* × *E. tereticornis* hybrids than maternal OP families in certain traits, especially such adaptive traits as

H_{10} and D_{10} , may provide evidence for existence of hybrid superiority. Possible explanations for hybrid superiority include heterosis, complementarity, and greater allelic diversity (as reviewed by Madhibha et al. (2013)). In our case, the maternal species *E. urophylla* grew usually faster than the paternal *E. tereticornis* (Liang 2000), and the better growth of their hybrids than *E. urophylla* OP families may indicate the effect of heterosis. On the other hand, while the paternal *E. tereticornis* exhibited generally higher wood basic density (e.g., 0.50–0.62 g cm⁻³ at 8 years depending on site and provenance; Lu et al. 2000) than the maternal *E. urophylla*, it seems that their hybrid mean of wood density was intermediate between the parental species. Thus, complementarity could play a role in hybrid superiority for certain wood properties. This may imply different genetic mechanisms underlying hybrid superiority of multiple trait types. Nevertheless, the wood properties other than basic density analyzed here are unavailable for the paternal species, and their hybrid superiority, at least from an economic viewpoint, remains to be explored. Moreover, in order to detect possible effect of greater allelic diversity, the parental allelic recombination along with its relationship to hybrid performance needs further investigation using molecular markers.

The significant differences between sites for most traits are similar to previous observation on earlier growth and wood density (Weng et al. 2014). This may reflect the hybrid feature of phenotypic plasticity across environments. As noted, interspecific hybrids of *Eucalyptus* are sensitive to environmental variation in growth (Lee et al. 2001) and wood property traits (Malan and Verryn 1996). Also, the expression of hybrid superiority is often environment dependent (Potts and Dungey 2004). Three models have been proposed to account for the genetic basis of phenotypic plasticity, including overdominance, pleiotropy, and epistasis (Scheiner 1993). Of these, pleiotropy and epistasis are of characteristic effects on plastic response (Pigliucci 2005), especially for hybrids of outcrossing tree species (e.g., *Populus trichocarpa* Torr. & Gray × *P. deltoides* Bart. ex Marsh.; Wu

Table 3 Phenotypic and genetic correlations (r_p and r_g , below and above the diagonal, respectively) as well as type-B genetic correlation (r_B , on the diagonal and in italic) for growth and wood property traits at age 10 in *E. urophylla* × *E. tereticornis* hybrids. Trait abbreviations were as shown in Table 1

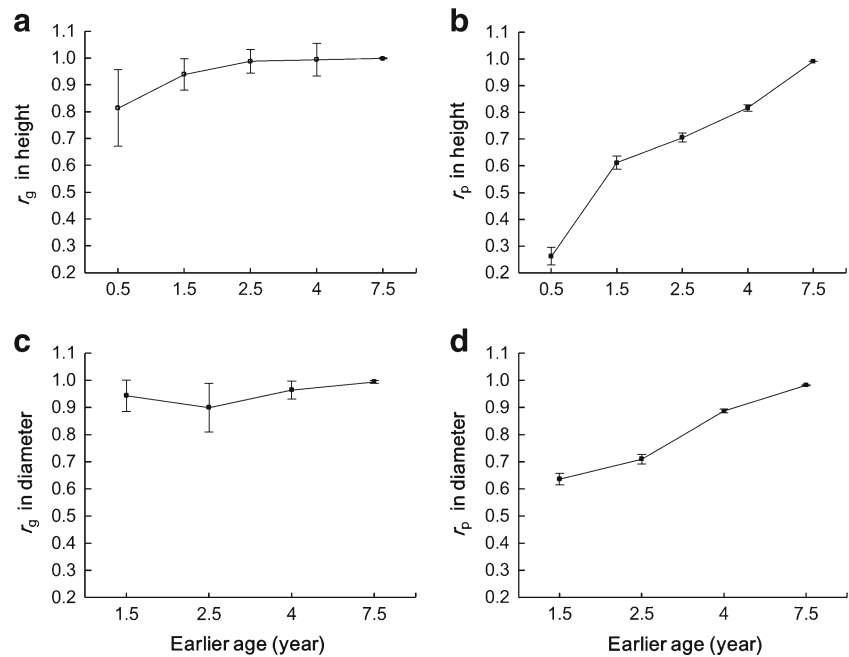
Trait	H_{10} (±SE)	D_{10} (±SE)	BD_{10} (±SE)	CC_{10} (±SE)	HC_{10} (±SE)	LC_{10} (±SE)	S/G_{10} (±SE)
H_{10}	0.72 (±0.20)*	0.97 (±0.03)***	0.55(±0.19)**	0.32 (±0.31)	-0.68 (±0.30)*	-0.57 (±0.27)*	0.12 (±0.27)
D_{10}	0.86 (±0.01)***	0.83 (±0.20)	0.62 (±0.17)***	0.41 (±0.27)*	-0.86 (±0.22)***	-0.55 (±0.27)*	0.11 (±0.28)
BD_{10}	0.62 (±0.02)***	0.67 (±0.02)***	0.64 (±0.21)*	-0.15 (±0.29)	-0.25 (±0.34)	-0.34 (±0.28)	-0.53 (±0.21)**
CC_{10}	-0.01 (±0.04)	0.08 (±0.04)*	-0.13 (±0.04)***	0.25 (±0.28)**	-0.67 (±0.23)**	0.05 (±0.36)	0.23 (±0.27)
HC_{10}	-0.01 (±0.04)	-0.18 (±0.04)***	-0.06 (±0.04)	-0.66 (±0.02)***	0.01 (±0.55)***	0.46 (±0.33)	-0.56 (±0.23)**
LC_{10}	0.01 (±0.04)	-0.15 (±0.04)***	0.02 (±0.04)	-0.05 (±0.04)	0.46 (±0.03)***	0.82 (±0.29)	-0.37 (±0.26)
S/G_{10}	-0.30 (±0.04)***	-0.27 (±0.05)***	-0.48 (±0.03)***	0.51 (±0.04)***	-0.57 (±0.03)***	-0.20 (±0.04)***	0.61 (±0.15)***

The significance of r_B on the diagonal represents the likelihood of difference between the two trial sites (departure from one)

SE standard error

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Fig. 2 Age-age genetic (r_g) and phenotypic (r_p) correlations between the final age 10 and earlier years in growth traits. **a** r_g in height. **b** r_p in height. **c** r_g in diameter at breast height. **d** r_p in diameter at breast height. Bars indicate standard errors



1997). The pleiotropy model assumes that phenotypic plasticity is a function of the differential expression of the same gene in different environments (Via and Lande 1985), while the epistasis model assumes that plasticity is due to genes which determine the magnitude of response to environmental effects and interact with other genes that determine the average expression of the trait (Lynch and Gabriel 1987). In the present study, in addition to significant phenotypic difference between sites, H_{10} , LC_{10} , and S/G_{10} showed positively significant r_B coefficients ($P \leq 0.01$ or 0.001 ; Table 3), demonstrating the important effect of the pleiotropy model. However, CC_{10} and HC_{10} showed significant phenotypic difference but non-significant r_B between sites, which may be interpreted by the epistasis model. In particular, the epistasis model can explain exclusively the plasticity of HC_{10} because of the negative r_B value (-0.36 ± 0.30).

4.2 Parental genetic effects, heritability, and dominance estimates for growth and wood properties

Female and male genetic effects, as denoted by their variance components, were significant for majority of the traits in single site analysis, demonstrating the importance of parental additive contribution to the hybrid performance at either of Yong'an and Changtai sites. Similarly, significant female and male genetic effects were found in height and breast-high diameter of single-site trials of *E. urophylla* \times *E. pellita* F. Muell. (mating design R90-10; Bouvet and Vigneron 1995) and *E. urophylla* \times *E. camaldulensis* (Gan et al. 2004). Nonetheless, there were still a few of cases in which female and/or male effects were not significant (e.g., HC_{10} at Changtai; Table 2). This may indicate that the magnitude of

parental genetic effects could vary with trait and site, especially when the number of parents was small (Paul et al. 1997). Further, when analyzed across sites, both female and male effects shifted to be non-significant with three exceptions (σ_f^2 in H_{10} and σ_m^2 in BD_{10} and S/G_{10} ; Table 2), which was also a contrasting comparison to the significant female and male effects on earlier growth (at 7.5 years and earlier) and wood density (at 7.5 years) of the same trials (Weng et al. 2014). Such a shift of parental effects could be due to declining variability among families and to increasing error variance with age (Paul et al. 1997). In addition, the non-significant female \times male variance components for single- and across-site analyses of all traits, except for H_{10} at Changtai ($P \leq 0.05$; Table 2), may indicate the relatively weak effect of parental interaction (dominance) in our population. Non-significant female \times male interactions were also observed in other hybrid populations, such as *E. urophylla* \times *E. grandis* (mating design R89-20) and *E. urophylla* \times *E. pellita* (mating design R89-21) for height and breast-high diameter at age 4 and earlier (Bouvet and Vigneron 1995).

The generally low estimates of narrow-sense heritability and dominance for growth and wood property traits are comparable to those reported previously with *Eucalyptus* pure species. For example, Volker et al. (2008) reported narrow-sense heritability of 0.10–0.19 and 0.29 and dominance of 0.05–0.12 and 0.04 for breast-high diameter (ages 2–10) and Pilodyn-based wood density (age 6), respectively, in an *E. globulus* factorial mating population. This may imply similar hereditary pattern of interspecific hybrids to pure species populations, particularly when the parental species are taxonomically closely related. This could be the case for *E. urophylla* and *E. tereticornis* that belong to the same

section *Exsertaria* L.D. Pryor & L.A.S. Johnson ex Brooker of subgenus *Symphyomyrtus* (Schauer) Brooker (Pryor and Johnson 1971). However, extremely high narrow-sense heritability values were described elsewhere, especially for wood properties, such as 0.61–0.76 for wood density, S/G ratio, and Klason lignin content at age 14 in *E. urophylla* (a factorial mating population of 33 full-sib families; Hein et al. 2012) and 0.84 for cellulose content at age 11 in *E. globulus* (35 open-pollinated families; Apiolaza et al. 2005). As narrow-sense heritability may vary with trait, age, species, population, and/or site (He et al. 2012), the discrepancy between studies is not unexpected. In the present study, the parents had been selected for their superior growth, so their additive genetic variation and in turn the narrow-sense heritability estimates in phenotypic traits could decrease to some extent. In addition, the generally small dominance estimates may suggest the less importance of dominance effects on expression of growth and wood property traits in the *E. urophylla* × *E. tereticornis* hybrids. Meanwhile, heterosis is hypothetically explained by dominance, overdominance, and epistasis genetic effects (Shen et al. 2014), and the weak dominance effect may thus imply the relative importance of overdominance and/or epistasis in heterosis formation.

The single-site narrow-sense heritability estimates of each trait were larger than their across-site counterpart. This is expected, because the interaction between additive genetic and environmental effects cannot be separated from additive variance in single-site analysis and, consequently, the heritability will be biased upwards (Dieters et al. 1995). Thus, narrow-sense heritability estimates of single- and across-sites were called biased and unbiased heritability, respectively, in the forestry literature (as reviewed by Dieters et al. (1995)). Nevertheless, across-site heritability could be intermediate between those from individual sites, e.g., for growth and wood traits in *E. pellita* (Hung et al. 2015) and for growth in *Pinus caribaea* Morelet var. *hondurensis* (Sénéclauze) W.H. Barrett & Golfari × *Pinus tecunumanii* Eguliz & Perry and *P. caribaea* var. *hondurensis* × *Pinus oocarpa* Schiede ex Schltdl. (Mutete et al. 2015).

4.3 Genetic correlations between traits

High genetic correlations between growth traits height and diameter have been widely described in *Eucalyptus* and other tree species, e.g., 0.87 in 9-year-old *E. urophylla* (Kien et al. 2009) and 0.71–0.96 at ages 5 and 8 in *P. caribaea* var. *hondurensis* × *P. tecunumanii* and *P. caribaea* var. *hondurensis* × *P. oocarpa* (Mutete et al. 2015). High genetic correlations indicate that the expression of both traits is most likely controlled by the same class of genes in an organism. These correlations also indicate that taller trees should be expected to exhibit bigger diameter. Thus, genetic improvement of diameter, a readily measurable trait, will result in the

improvement of height, which is always difficult to measure for tall trees.

For growth traits H_{10} and D_{10} , the significantly positive r_g coefficients between the final age of 10 and earlier ages indicate the possibility of early prediction, and the generally increasing trend with age suggests the advancing reliability with age. Similar magnitude and trend in age-age genetic correlations were observed in other tree species. Wei and Borralho (1998) found r_g of 0.70–1.00 for height and diameter at age 5 with earlier ages in *E. urophylla*. Weng et al. (2015) reported r_g of 0.88–0.99 for height at age 20 with ages 5, 10 and 15 in *Pinus banksiana* Lamb. Considering the increasingly high r_g of age 10 with ages after 1.5 in H_{10} and D_{10} , it would be feasible to predict mature growth as early as 1.5 years old.

Three pairs of wood property traits showed negatively significant r_g , namely, CC_{10} vs. HC_{10} , BD_{10} vs. S/G_{10} , and HC_{10} vs. S/G_{10} , while the remaining genetic correlations were non-significant (Table 3). The magnitude of r_g for wood properties can vary more or less with population in *Eucalyptus*. For instance, genetic correlation between wood density and cellulose content was positively significant in *E. nitens* (0.36; Hamilton et al. 2009), very low in *E. urophylla* (0.09; Denis et al. 2013), but negatively significant in *E. globulus* (−0.31; Stackpole et al. 2011). In our *E. urophylla* × *E. tereticornis* hybrids, those negatively significantly correlated traits may be controlled by pleiotropic genes that function contrarily in different traits. This would be meaningful for simultaneous improvement of certain wood traits related with pulp yielding, such as reduction of hemi-cellulose and increase of cellulose and/or S/G ratio, despite of the unfavorable correlation between BD_{10} and S/G_{10} . In particular, hemi-cellulose is one of the useless polymers that have to be removed during pulping process, but it has drawn large interest in the possible utilization as barrier films (Salmén 2015). So far to our knowledge, few studies have analyzed its correlation with other wood traits. Only Denis et al. (2013) reported relatively high genetic correlations (0.26–0.63) with wood traits such as basic density, cellulose, Klason lignin, and S/G in *Eucalyptus*, with which our results disagreed basically. Thus, the correlation pattern depicted here would add a new dimension to the comprehensive understanding of relationship of hemi-cellulose with other wood properties.

Growth traits generally showed significant, positive r_g with BD_{10} and CC_{10} (except non-significant r_g between H_{10} and CC_{10}) but non-significant with S/G_{10} and negatively significant with HC_{10} and LC_{10} . Such correlations are favorable for improving growth, wood density, and cellulose content and reducing hemi-cellulose and lignin contents for pulpwood breeding purpose (Greaves et al. 1997). Similarly, Stackpole et al. (2011) found significantly positive and negative genetic correlations for diameter with cellulose and lignin contents, respectively, in *E. globulus*, and Hein et al. (2012) revealed a highly negative correlation between height and lignin content

(-0.60 ± 0.25) in *E. urophylla*. However, contrasting genetic correlations were published in the literature, e.g., 0.11 (non-significant) and -0.36 ($P \leq 0.05$) for two separate sites between diameter and basic density in *E. nitens* (Apiolaza et al. 2005). Thus, the genetic correlations between growth and wood property traits may vary with population and trial site.

4.4 Implications for defining hybrid breeding strategy

The objective for pulpwood breeding in *Eucalyptus* aims to save the total pulp cost by improving wood density, growth, and pulp yield (Greaves et al. 1997). Cellulose content can be an alternative trait to pulp yield given their strong correlation (Raymond 2002). Meanwhile, low lignin content and high S/G are linked to more efficient chemical pulping (Stackpole et al. 2011) and could be added to the list of pulpwood breeding traits. The *E. urophylla* \times *E. tereticornis* hybrid superiority detected here for such traits as growth (height and diameter) and wood basic density demonstrates the value of hybrid breeding.

Hybrid superiority has been long recognized in *Eucalyptus* (as reviewed by Potts and Dungey 2004; Madhibha et al. 2013). In the present case, the possible mechanisms underlying hybrid superiority include heterosis and complementarity. Heterosis is the expression of non-additive genetic effects, while complementarity is only the result of additive gene action (Retif and Stanger 2009). Therefore, a strategy that can capture both additive and non-additive genetic effects seems most appropriate for breeding *E. urophylla* \times *E. tereticornis* F₁ hybrids. In this regard, the reciprocal recurrent selection strategy with forward selection (RRS-SF; Nikles 1992) is preferred. RRS-SF focuses on forward selection based on an index integrating parental general combining ability for both pure species, hybrid performance, and individual tree data (Kerr et al. 2004), in which pure species progeny and hybrids are bred simultaneously (Madhibha et al. 2013). The genetic gains can be realized through clonal testing and deployment, enabling the capture of both additive and non-additive genetic effects (Libby and Rauter 1984). However, Kerr et al. (2004) simulated the efficiency of four hybrid breeding strategies and found that the genetic gain per year was highly dependent upon such estimates as additive/dominance variance ratio, heritability, and pure-hybrid correlations. These estimates vary usually with trait, and a single strategy may not be the most efficient for all of the economic traits interested.

Vegetative propagation provides an efficient way for reproduction of elite genotypes for operational planting. *E. urophylla* \times *E. tereticornis* hybrids can be readily vegetatively propagated, especially with tissue culture (Liu and Wang 2005). This would warrant the efforts of hybrid breeding in term of genetic gain realization. Also, vegetative propagation will allow for clonal test across multiple sites so that

hybrid clones matching to a target environment could be selected out.

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Compliance with ethical standards

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

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