Journal of Genetics (2021)100:46
https://doi.org/10.1007/s12041-021-01299-x

RESEARCH ARTICLE

Quantitative genetic analysis of wood property traits in biparental population of *Eucalyptus camaldulensis* x *E. tereticornis*

ABDUL BARI MUNEERA PARVEEN[1], MUTHUSAMY MUTHUPANDI[1], NAVEEN KUMAR[2], SHAKTI SINGH CHAUHAN[2], P. VELLAICHAMY[1], S. SENTHAMILSELVAM[1], D. RAJASUGUNASEKAR[1], BINAI NAGARAJAN[1], A. MAYAVEL[1], VIJAYA KUMAR WAMAN BACHPAI[1], VEERASAMY SIVAKUMAR[1] and MODHUMITA GHOSH DASGUPTA[1]*

[1]*Institute of Forest Genetics and Tree Breeding, R.S. Puram, Coimbatore 641 002, India*
[2]*Institute of Wood Science and Technology, 18th Cross Malleshwaram, Bengaluru 560 003, India*
*For correspondence. E-mail: gmodhumita@gmail.com, ghoshm@icfre.org.

Received 17 October 2020; revised 2 March 2021; accepted 8 March 2021

Abstract. *Eucalyptus* breeding programme mainly aims at increasing productivity associated with wood property traits which are suitable for different end uses. The principal challenge in this endeavor is to combine productivity with industrially relevant wood traits. In the present study, 23 hybrid clones derived from a biparental mapping population of *Eucalyptus camaldulensis* x *E. tereticornis* was assessed for six wood property traits across two sites in Tamil Nadu, India. The mean of most of the traits evaluated was consistently higher in Muthupettai, indicating significant site effect. Combined and location-wise analysis indicated additive genetic control of assessed traits. The stability of acoustic velocity in study sites, negligible G x E interaction and significant correlation with dynamic modulus of elasticity (DMoE) implies its use in selecting trees/logs for solid wood properties. Combined analysis of locations revealed low to moderate heritability (0.294–0.439) for all the traits with H^2 being highest for cellulose per cent (0.439) followed by acoustic velocity (0.416). Genetic advance was calculated and was the highest for diameter (10.47%) followed by DMoE (9.19%). The two major chemical constituents of wood, namely total lignin and cellulose per cent showed 7.13% and 7.53% advancement in the hybrids. The out-performance of several hybrid clones when compared to the parents for different wood traits reiterates the use of *Eucalyptus* hybrids in plantation programmes to improve quality of raw material suitable for industrial application.

Keywords. eucalyptus hybrids; correlation; genetic gain; heritability; wood properties.

Introduction

Wood properties have major impact on the processing cost and product quality. Minor changes in the quality traits contribute to significant economic gains in the pulp industry (Assis 2000). *Eucalyptus* wood is the raw material for energy sector, paper pulp, charcoal, sawn timber and wood panel industries (Marco de Lima *et al*. 2019) and are the largest source for short fibre (Kien *et al*. 2009). They are planted in over 90 countries and contribute towards 17.5% of world's paper pulp (Hart and Santos 2015; Torres-Dini *et al*. 2016). The focus of *Eucalyptus* breeding programmes is increasing productivity associated with wood properties suitable for industrial application through selection of species/genotypes for hybrid combination and clonal multiplication of selected hybrids (Griffin *et al*. 2000; Fonseca *et al*. 2010; Assis 2011).

The major wood property traits influencing pulp yield include basic density, cellulose, hemicellulose and lignin content, and lignin syringyl-to-guaiacyl (S/G) ratio (Rencoret *et al*. 2007). Extensive variation in these properties are documented in several species including *E. globulus* (Stackpole *et al*. 2011), *E. urophylla* (Kien *et al*. 2009; Hein *et al*. 2012; Kullan *et al*. 2012; Denis *et al*. 2013; Prasetyo *et al*. 2017; Pupin *et al*. 2018), *E. pellita* (Prasetyo *et al*. 2017), *E. grandis* (Osorio *et al*. 2001; Prasetyo *et al*. 2017), *E. nitens* (Kube *et al*. 2001; Raymond 2002; Hamilton *et al*. 2009; Kullan *et al*. 2012), *E. bosistoana* (Davies *et al*. 2017), *E. camaldulensis* and *E. tereticornis* (Varghese *et al*. 2008), *Eucalyptus* hybrids (Bison *et al*. 2007), *E. urophylla*

× *E. tereticornis* (Weng *et al*. 2014; Chen *et al*. 2018), *E. grandis* x *E. globulus* (Torres-Dini *et al*. 2016), *E. urophylla* x *E. grandis* (Wu *et al*. 2011; Chaix *et al*. 2011; Makouanzi *et al*. 2017; Tan *et al*. 2018), *E. urophylla* x *E. pellita* (Chaix *et al*. 2011), *E. grandis* × *E. urophylla* (Resende 2002) and *E. grandis* × *E. camaldulensis* (Marco de Lima *et al*. 2019).

Requirement of mature trees, destructive sampling methods, large sample size and high cost limits the routine use of wood property traits as selection criteria in breeding programmes (Marco de Lima *et al*. 2019). Hence, trait analysis is restricted to a subset of genotypes short-listed for deployment. Use of nondestructive and indirect method for evaluation of wood traits is a promising strategy for large-scale analysis in breeding programmes. Nondestructive evaluation (NDE) of standing trees and logs using sound wave propagation is considered as a reliable indicator of timber quality and acoustic tools are used to assess intrinsic wood properties (Wang *et al*. 2007). The application of acoustic velocity in determining the log stiffness is reported in *Eucalyptus* (Tsehaye *et al*. 2000; Dickson *et al*. 2003; Chauhan and Aggarwal 2011).

The inheritance pattern of wood related traits is documented in several tree species including *Eucalyptus* and are reported to be under low to moderate levels of additive genetic control, highlighting the potential for genetic improvement through selection (Costa *et al*. 2004; Hein *et al*. 2012; Araújo *et al*. 2012; Denis *et al*. 2013; Rezende *et al*. 2014; Tan *et al*. 2018). The knowledge on heritability, intertrait correlation and variance components is vital for maximizing the genetic gain and sustain long-term genetic progress of progenies (Marco de Lima *et al*. 2019).

The Institute of Forest Genetics and Tree Breeding, Coimbatore, India initiated the genetic improvement programme of *E. tereticornis* and *E. camaldulensis* in 1995 in collaboration with Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia with introductions of natural provenances with broad genetic base (Doran *et al*. 1996; Varghese *et al*. 2008). Seed orchards were established and outstanding families and provenances were selected and propagated as clones (Varghese *et al*. 2002). The clonal performance was evaluated under multiple environments and high yielding clones were released for deployment in plantation programmes. Concurrently, clones were also selected for hybridization programmes to increase the wood productivity for paper and pulp industries.

To the best of our knowledge, genetic assessment of interspecific hybrids of *Eucalyptus* in Indian conditions remains to be explored. Hence, the study was undertaken in a biparental mapping population of *E. camaldulensis* (Ec111) x *E. tereticornis* (Et86) with the aim to (i) assess the feasibility of using acoustic tools for indirect estimation of wood property traits, (ii) document the variance component, heritability and intertrait correlation of different wood property traits for simultaneous selection of multiple trait, (iii) record the genotype by environment interaction for individual wood related traits, and (iv) identify traits with maximum genetic gain to facilitate testing, selection and deployment of hybrid clones in future.

Materials and methods

Eucalyptus pedigree and field trial description

Interspecific cross between *E. camaldulensis* (Ec111) x *E. tereticornis* (Et86) was conducted to develop the biparental mapping population (Rajasugunasekar *et al*. 2015). Et86 is a selection from Seed Production Area established by the Institute at Pudukottai, Tamil Nadu, India while Ec111 belongs to the Kennedy River provenance from Queensland, Australia (CSIRO seed lot no. 17864) selected from Provenance Resource Stand at Pudukottai, Tamil Nadu, India. A total of 160 progenies were planted in two locations at Karur and Muthupettai, Tamil Nadu in 2011 in an area of 1 ha. Two tree plots with spacing of 3 m x 1.5 m in four replications was established in completely randomized block design (table 1). However, due to severe drought conditions, the survivability of the hybrid clones was significantly affected in Karur. Hence, the study was restricted to 23 hybrid clones common across both locations and three replications per

Table 1. Location and description of field sites.

	Karur, Tamil Nadu	Muthupettai, Tamil Nadu
Latitude	10°57′27.41″N	10°23′44.52″N
Longitude	78°04′38.75″E	79°29′41.96″E
Altitude (m)	137	9
Annual rainfall (mm)	595	1196
Soil	Sandy loam	Coastal alluvial soil
Mean annual temperature (°C)	28.7	30.8
Absolute minimum temperature (°C)	17	26.39
Absolute maximum temperature (°C)	39	35.19
Spacing (m)	3 × 1.5	3 × 1.5
Trees/plot	2	2
Replications	4	4

clone were harvested at an approximate age of 2 years and six months. The wood logs were air dried for six months and wood discs were processed for proximate analysis and acoustic studies.

Assessments of wood property traits in Eucalyptus pedigree

***Ultrasonic velocity and modulus of elasticity*:** Wood samples were weighed (with and without bark) and measured for bark thickness and wood volume (without bark). The samples were subsequently air-dried at room temperature until they reached to a constant weight. The air-dried samples were weighted, and volume and ultrasonic pulse velocity were measured. UltraSonic timer at 90 KHz frequency (Fakopp, Enterprise BT, Agfalva, Hungary) with spiked probe was used to measure the pulse transit time along the length of the sample. Ultrasonic pulse velocity (V) was calculated using the following equation:

$$\mathrm{V} = \text{sample length}/(\text{pulse transit time} - 15).$$

Where, 15 is the time correction factor. The dynamic modulus of elasticity (DMoE) was calculated using the μs following equation:

$$\mathrm{DMoE} = \text{air}-\text{dry density} \times \mathrm{V}^2.$$

Air dry density was determined from air dried weight and volume.

Estimation of total lignin and cellulose content

Approximately 100 g of wood discs were chipped, powdered and sieved through 240-micron sieve. The wood sample (200 mg) was extracted with 7 mL of dichloromethane for 15 min. Subsequently, an extract free sample was obtained by washing and extracting the wood powder with toluene: ethanol (1:1 v/v), water (twice) and acetone. The samples were then dried overnight at 60°C and the extractive free samples were used for the estimation of cellulose and lignin.

Cellulose content was estimated using the protocol described by Updegraff (1969) and the micro protocol was optimized based on the process described by Kumar and Turner (2015) with a few modifications. Approximately 10 mg of dried extractive free sample was mixed with 1 mL of Updegraff solution (acetic acid: nitric acid: distilled water in the ratio 8:1:2 v/v/v) and boiled at room temperature for 10 min. Subsequent to cooling, the solution was washed with distilled water followed by acetone wash and allowed to dry. To the dried pellet, 67% sulphuric acid was added and incubated at room temperature for 1 h and the solution was later made up to 20 mL with distilled water. One mL of the sample was mixed with 9 mL anthrone reagent and boiled for 10 min. Absorbance was measured at 630 nm after cooling the samples. The total cellulose content was calculated as glucose equivalent from the calibration curves of a glucose standard solution using the following equation and expressed as % cellulose. All tests were conducted in triplicate.

$$\%\text{Cellulose} = \frac{\text{sample OD} \times \text{sample concentration} \times \text{total volume of sample used} \times \text{total made up volume}}{\text{standard OD} \times \text{volume taken} \times \text{sample weight}}$$

Total lignin content was estimated using acetyl bromide method with minor modification (Rodrigues *et al.* 1999; Moreira-Vilar *et al.* 2014). About 5 mg of dried extractive free sample was mixed with 0.5 mL of 25% (v/v) acetyl bromide, 20 μL of 70% perchloric acid and incubated at 70^0C for 30 min. Subsequent to cooling, 2 M NaOH, 5 M hydroxylamine-HCl and 9 mL of glacial acetic acid was added and centrifuged at 8000 rpm for 15 min at room temperature. Six hundred μL of the solution was mixed with 2.4 mL of glacial acetic acid and absorbance was measured at 280 nm with a molar extinction coefficient of 22.9 $\mathrm{g}^{-1}\mathrm{Lcm}^{-1}$ for lignin determination (Moreira-Vilar *et al.* 2014). Total lignin was calculated using the following equation and expressed as % lignin.

$$\%\text{lignin} = 100(\mathrm{A_s} - \mathrm{A_b})\mathrm{V}/\mathrm{aw}.$$

Where A_s is the sample OD; A_b, blank OD; V, volume of sample (mL); a, molar extinction coefficient of total lignin; w, sample weight (gm).

Estimation of phenotypic variance and heritability

Phenotypic data recorded for the wood properties were individually subjected to analysis of variance and for combined locations, through Univariate General Linear Model using SPSS 19 (SPSS, Chicago, USA) to determine the significance of the main effects and interactions. The phenotypic and genotypic variance was determined using the following equation:

$$\sigma^2\mathrm{p} = \sigma^2\mathrm{g} + \sigma^2\mathrm{e}$$
$$\sigma^2\mathrm{g} = \frac{\mathrm{Mg} - \mathrm{Me}}{\mathrm{r}}.$$

Where σ^2p is phenotypic variance, σ^2g is genotypic variance, σ^2e is error variance (error mean square), M_g is mean square of genotypes, M_e is mean square of error and r is number of replications.

Broad sense heritability (H^2) for each wood property trait for individual location was estimated using the formula given below (Allard 1960; Falconer 1990):

$$\mathrm{H}^2 = \frac{\sigma^2\mathrm{g}}{\sigma^2\mathrm{p}}.$$

In combined location, heritability analysis was conducted following the method described by

Table 2. Diameter, density, ultra sonic velocity, dynamic modulus of elasticity, cellulose and total lignin content in *E. camaldulensis* x *E. tereticornis* across the locations (KR, Karur; MP, Muthupettai).

	Diameter (cm)		Density (kg/m^3)		Acoustic velocity (km/s)		DMoE (GPa)		Cellulose (%)		Total lignin (%)	
Clone ID	MP	KR	MP	KR	MP	KR	MP	KR	MP	KR	MP	KR
C8	37.48 ± 7.81	39.70 ± 17.71	610 ± 0.01	620 ± 0.09	3.74 ± 0.08	3.52 ± 0.35	8.59 ± 0.26	7.59 ± 0.35	42.99 ± 1.76	37.76 ± 2.85	17.38 ± 0.59	15.45 ± 1.08
C43	45.57 ± 3.30	42.02 ± 2.13	680 ± 0.003	640 ± 0.04	3.65 ± 0.16	3.39 ± 0.10	9.15 ± 0.84	7.30 ± 0.01	39.12 ± 7.35	31.55 ± 2.24	15.66 ± 0.24	19.86 ± 0.16
C46	65.65 ± 0.07	44.90 ± 5.94	640 ± 0.001	670 ± 0.02	3.53 ± 0.21	4.02 ± 0.26	7.98 ± 0.92	10.84 ± 1.06	39.55 ± 1.16	35.41 ± 0.79	14.80 ± 0.50	17.56 ± 1.34
C62	52.65 ± 8.22	31.71 ± 1.89	630 ± 0.01	690 ± 0.06	3.81 ± 0.05	3.31 ± 0.16	9.14 ± 0.36	7.61 ± 1.36	39.70 ± 2.0	31.14 ± 5.83	13.97 ± 1.21	16.12 ± 1.64
C85	42.51 ± 5.98	42.35 ± 3.63	580 ± 0.01	680 ± 0.04	3.47 ± 0.14	3.08 ± 0.03	6.96 ± 0.41	6.46 ± 0.55	40.96 ± 1.47	41.17 ± 3.71	15.58 ± 0.07	16.78 ± 0.85
C88	62.01 ± 4.60	62.74 ± 14.24	620 ± 0.02	710 ± 0.01	3.39 ± 0.14	3.57 ± 0.28	7.18 ± 0.38	9.09 ± 1.60	41.3 ± 4.84	38.39 ± 7.16	15.87 ± 0.45	19.06 ± 1.78
C89	36.82 ± 1.84	31.55 ± 8.59	630 ± 0.02	630 ± 0.02	3.62 ± 0.03	3.15 ± 0.01	8.27 ± 0.36	6.23 ± 0.11	36.66 ± 2.34	39.30 ± 5.08	15.42 ± 1.03	14.88 ± 2.11
C104	77.99 ± 13.45	32.29 ± 6.24	650 ± 0.01	710 ± 0.02	3.40 ± 0.30	3.30 ± 0.41	7.50 ± 1.46	7.82 ± 1.75	31.74 ± 2.14	33.31 ± 0.71	18.04 ± 0.46	15.75 ± 1.51
C133	50.49 ± 1.29	30.32 ± 0.09	580 ± 0.02	640 ± 0.01	3.80 ± 0.19	3.55 ± 0.29	8.38 ± 0.50	8.05 ± 1.16	42.65 ± 1.97	38.17 ± 2.53	14.17 ± 1.16	18.80 ± 0.52
C137	43.29 ± 5.68	40.14 ± 3.78	610 ± 0.03	680 ± 0.01	3.52 ± 0.04	3.27 ± 0.23	7.57 ± 0.58	7.31 ± 1.15	42.08 ± 0.68	38.49 ± 1.71	15.24 ± 1.22	17.10 ± 0.56
C150	48.85 ± 7.86	43.82 ± 4.09	630 ± 0.01	680 ± 0.05	3.67 ± 0.05	3.09 ± 0.23	8.43 ± 0.10	6.51 ± 1.44	40.14 ± 1.63	30.02 ± 1.14	17.52 ± 0.27	16.94 ± 0.50
C161	40.82 ± 5.15	50.78 ± 4.90	630 ± 0.001	650 ± 0.01	3.66 ± 0.27	3.74 ± 0.10	8.47 ± 1.27	9.15 ± 0.39	43.47 ± 0.76	37.31 ± 0.32	15.70 ± 0.25	16.11 ± 2.75
C166	39.68 ± 6.34	47.70 ± 13.63	620 ± 0.04	690 ± 0.07	3.90 ± 0.22	3.10 ± 0.19	9.44 ± 1.60	6.69 ± 1.50	36.33 ± 1.13	36.31 ± 1.11	16.20 ± 0.03	14.34 ± 0.69
C198	54.93 ± 18.35	30.37 ± 0.83	620 ± 0.003	620 ± 0.03	3.76 ± 0.11	2.94 ± 0.06	8.75 ± 0.58	5.38 ± 0.04	37.01 ± 1.26	42.41 ± 4.31	16.89 ± 0.04	18.90 ± 3.93
C199	48.53 ± 1.39	42.59 ± 10.48	610 ± 0.03d	700 ± 0.01	3.43 ± 0.15	3.43 ± 0.39	7.13 ± 0.34	8.31 ± 2.02	39.75 ± 1.03	34.81 ± 1.06	15.91 ± 1.33	16.43 ± 0.94
C234	32.41 ± 3.61	35.48 ± 8.49	590 ± 0.004	660 ± 0.01	4.30 ± 0.59	3.62 ± 0.08	10.98 ± 3.04	8.71 ± 0.28	33.77 ± 3.06	31.42 ± 1.74	17.29 ± 0.22	15.02 ± 0.67
C246	39.20 ± 4.32	29.93 ± 7.76	670 ± 0.004	600 ± 0.03	4.13 ± 0.08	4.27 ± 0.02	11.4 ± 0.49	10.95 ± 0.59	44.64 ± 1.58 b	33.88 ± 3.11	13.41 ± 0.52	16.07 ± 1.90
C312	38.62 ± 7.81	46.61 ± 8.56	600 ± 0.02	640 ± 0.05	4.07 ± 0.33	3.55 ± 0.13	9.93 ± 1.23	8.05 ± 1.21	35.34 ± 0.32	36.21 ± 3.19	16.55 ± 0.61	19.49 ± 0.64
C313	43.89 ± 3.32	43.79 ± 5.07	630 ± 0.01	690 ± 0.01	3.47 ± 0.09	3.20 ± 0.10	7.61 ± 0.30	7.04 ± 0.54	33.14 ± 5.22	35.6 ± 5.01	16.94 ± 0.59	15.77 ± 1.09
C327	53.74 ± 35.65	31.80 ± 5.04	640 ± 0.01	710 ± 0.01	3.35 ± 0.13	3.99 ± 0.87	7.24 ± 0.71	11.53 ± 4.77	39.17 ± 1.32	39.02 ± 5.0	13.88 ± 1.07	17.88 ± 3.89
C339	43.65 ± 7.09	35.25 ± 1.40	600 ± 0.02	660 ± 0.05	3.76 ± 0.48	3.99 ± 0.90	8.50 ± 1.95	11.00 ± 5.52	39.38 ± 4.45	42.15 ± 2.79	14.64 ± 0.39	15.41 ± 0.74
C343	42.28 ± 6.94	38.10 ± 9.60	680 ± 0.02	720 ± 0.01	3.87 ± 0.04	3.37 ± 0.31	10.10 ± 0.14	8.25 ± 1.47	36.81 ± 0.61	33.23 ± 4.04	13.13 ± 0.02	12.89 ± 0.52
C344	53.52 ± 2.35	38.65 ± 13.29	630 ± 0.01	660 ± 0.03	4.09 ± 0.45	3.65 ± 0.67	10.62 ± 2.17	9.01 ± 3.62	34.68 ± 7.09	36.62 ± 9.88	16.18 ± 1.57	19.21 ± 2.81
Ec111	40.57 ± 8.67	54.58 ± 1.75	600 ± 0.0003	680 ± 0.04	3.61 ± 0.37	3.54 ± 0.30	7.89 ± 1.62	8.61 ± 1.90	42.34 ± 2.10	43.01 ± 2.21	14.4 ± 0.13	17.76 ± 1.09
Et86	47.38 ± 2.23	57.40 ± 10.47	580 ± 0.01	690 ± 0.04	4.00 ± 0.15	3.90 ± 0.22	9.29 ± 0.50	10.57 ± 1.78	38.67 ± 0.03	39.86 ± 0.34	15.48 ± 0.04	18.25 ± 3.32
Significance												
Genotype (G)	*		**		*		*		**		***	
Location (E)	**		***		***		NS		**		***	
G x E	**		**		NS		NS		NS		**	

Data presented are mean of triplicate values ± SD (standard deviation). Two-way ANOVA was performed for linear model, on raw data. Significance: $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ and NS indicates not significant.

Table 3. Location-wise and combined location mean values of wood property traits assessed in parents and hybrids of *E. camaldulensis* (Ec111) x *E. tereticornis* (Et86).

	Parents		Hybrids		
Trait	*E. camaldulensis* (EC111)	*E. tereticornis* (Et86)	Min	Max	Mean ± SD
Muthupettai					
Diameter (cm)	40.57 ± 8.67	47.38 ± 2.23	32.41	77.99	47.59 ± 10.52
Density (kg/m^3)	600 ± 0.0003	580 ± 0.01	580	680	620 ± 0.03
Acoustic velocity (km/s)	3.61 ± 0.37	4.00 ± 0.15	3.35	4.30	3.71 ± 0.26
DMoE (GPa)	7.89 ± 1.62	9.29 ± 0.50	6.96	11.40	8.67 ± 1.27
Cellulose (%)	42.34 ± 2.10	38.67 ± 0.03	31.74	44.64	38.71 ± 3.49
Total lignin (%)	14.4 ± 0.13	15.48 ± 0.04	13.13	18.04	15.67 ± 1.37
Karur					
Diameter (cm)	54.58 ± 1.75	57.40 ± 10.47	29.93	62.74	39.68 ± 8
Density (kg/m3)	680 ± 0.04	690 ± 0.04	600	720	670 ± 0.03
Acoustic velocity (km/s)	3.54 ± 0.30	3.90 ± 0.22	2.94	4.27	3.48 ± 0.35
DMoE (GPa)	8.61 ± 1.90	10.57 ± 1.78	5.38	11.53	8.21 ± 1.65
Cellulose (%)	43.01 ± 2.21	39.86 ± 0.34	30.02	42.41	36.25 ± 3.49
Total lignin (%)	17.76 ± 1.09	18.25 ± 3.32	12.89	19.86	16.78 ± 1.83
Combined location					
Diameter (cm)	47.58 ± 9.91	52.39 ± 7.09	29.93	77.99	43.63 ± 10.07
Density (kg/m^3)	640 ± 0.05	640 ± 0.08	580	720	650 ± 0.04
Acoustic velocity (km/s)	3.58 ± 0.04	3.95 ± 0.07	2.94	4.30	3.6 ± 0.32
DMoE (GPa)	8.25 ± 0.51	9.93 ± 0.91	5.38	11.53	8.44 ± 1.47
Cellulose (%)	42.67 ± 0.47	39.27 ± 0.84	30.02	44.64	37.48 ± 3.67
Total lignin (%)	16.08 ± 2.38	16.87 ± 1.96	12.89	19.86	16.22 ± 1.69

Zhang *et al*. (2017) using the equation:

$$H^2 = \frac{\sigma^2 g}{\sigma^2 g + \frac{\sigma^2 ge}{e} + \frac{\sigma^2 e}{er}},$$

where σ^2g, σ^2ge, and σ^2e are the genotypic, genotype-by-environment interaction and error variance components, respectively and e and r are the number of environments and replicates within each environment included in the corresponding analysis, respectively.

Genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) was estimated according to the method described by Singh and Chaudhary (1979) as follows:

$$\mathrm{GCV}(\%) = \frac{\sqrt{\sigma 2g}}{\overline{\mathrm{X}}} \times 100,$$

$$\mathrm{PCV}\,(\%) = \frac{\sqrt{\sigma 2p}}{\overline{\mathrm{X}}} \times 100,$$

where $\overline{\mathrm{X}}$ is the grand mean.

Expected genetic advance (GA) was calculated by the method described by Awas *et al*. (2015) using the following equation:

$$\mathrm{GA} = (K)\sigma AH2,$$

where K is selection differential (2.06 at 5% selection intensity) and σA is phenotypic standard deviation.

Genetic advance as a percentage of mean (GAM) was also estimated using the following formula:

$$\mathrm{GAM} = \frac{\mathrm{GA}}{\overline{\mathrm{X}}} \times 100.$$

Further, correlation between the documented phenotypic data was determined by Pearson's correlation coefficient (r) using SPSS 19 (SPSS, Chicago, USA). The Pearson correlation was considered significant when the P value was less than 0.5.

Results

Phenotypic variation of wood property traits

The variation recorded in the parents (*E. tereticornis* and *E. camaldulensis*) and 23 hybrids for all wood properties across both locations is presented in table 2. In parents, a significant difference between the locations was documented for diameter, DMoE and total lignin per cent. The mean of all traits evaluated is presented in table 3 and was consistently higher in Muthupettai, except for density and lignin which were marginally high in Karur.

Combined and location-wise analysis revealed that mean of all independent traits excluding diameter were

Table 4. Estimated intertrait Pearson correlations among the wood property traits across the study locations.

Trait	Diameter (cm)	Density (kg/m^3)	Acoustic velocity (km/s)	DMoE (GPa)	Cellulose (%)
Karur					
Density (kg/m^3)	0.25				
Acoustic velocity (km/s)	−0.01	−0.68***			
DMoE (GPa)	−0.04	−0.58***	1.00***		
Cellulose (%)	0.17	−0.18	−0.02	0.03	
Total lignin (%)	0.49*	−0.97***	0.35	0.29	0.77***
Muthupettai					
Density (kg/m^3)	0.38*				
Acoustic velocity (km/s)	−0.71***	−0.12			
DMoE (GPa)	−0.56**	0.28	0.92***		
Cellulose (%)	−0.38	−0.16	−0.41*	−0.47*	
Total lignin (%)	0.12	−0.30	−0.10	−0.23	−0.74***

Significance: $^*P \le 0.05$, $^{**}P \le 0.01$, $^{***}P \le 0.001$.

intermediate between the parents suggesting additive genetic control. Extremely stunted growth of a few hybrid clones like C246, C327 and C344 in Karur resulted in reduced mean for diameter (table 2). In hybrids, diameter was consistent across locations in C85, C88 and C313 while C8, C89, C198 and C256 showed no significant difference for density across locations. However, DMoE varied in both parents and hybrids across both locations. A few hybrid clones exhibited stable expression in studied locations for traits like diameter (C85, C88 and C313) and cellulose (C85, C116, C312, C327). The stable expression of density and acoustic velocity was exhibited by 65% and 78% of hybrid clones, respectively. The stability of acoustic velocity in both study sites was also recorded with negligible G x E interaction (table 2). Further, G x E interaction was not significant for DMoE and cellulose, while it was significant ($P \le 0.01$) for diameter, density and lignin content (table 2).

Intertrait correlation, heritability and genetic advancement

The estimated intertrait correlations among the different wood property traits evaluated in the present study is presented in table 4. Strong and positive correlation between acoustic velocity and dynamic modulus of elasticity ($P \le 0.001$**)** was observed in both locations. Significant moderate negative correlation was recorded between wood diameter and acoustic velocity (−0.71; $P \le 0.001$) and DMoE (−0.56; $P \le 0.01$) at Muthupettai. Similarly, significant negative correlations between the total lignin and cellulose (−0.74, $P \le 0.001$) was observed at Muthupettai.

Broad sense heritability (H^2) of wood properties was estimated for individual site and for combined locations. H^2 was higher for all evaluated traits in Muthupettai when compared to Karur except for diameter. Lignin per cent documented highest H^2 in Muthupettai and diameter registering highest in Karur at 0.40 (table 5). The combined analysis of both the locations revealed low to moderate heritability (0.294–0.439) for all traits with H^2 being highest for cellulose per cent (0.439) followed by acoustic velocity (0.416) (table 6).

Discussion

Wood related traits are highly plastic with significant natural variations at intraspecific and interspecific levels and are governed by metabolic and hormone fluxes (Mizrachi and Myburg 2016). Additionally, wood phenotypes are confounded by significant influence of environmental factors like temperature, precipitation, photoperiod, nutrient availability and edaphic conditions (Groover *et al.* 2010). Bioprocessing of pulp production and other wood products depends on aggregate wood properties (Mizrachi *et al.* 2017) and hence multi-trait selection of genotypes for breeding and deployment is an effective strategy to maximize and sustain wood productivity.

Acoustic tools for estimation of wood property traits in Eucalyptus

Nondestructive evaluation (NDE) of standing trees and logs using sound wave propagation is considered as a reliable indicator of timber quality and acoustic tools are routinely used to assess intrinsic wood properties (Wang *et al.* 2007). Reports have confirmed that acoustic velocity can partially predict wood characters like tracheid length and chemical composition of cell walls (Evans 2000; Albert *et al.* 2002). It is also a surrogate measure of microfibril angle and lower acoustic values are characterized with low microfibril angle (Chauhan and Walker 2006; Apiolaza 2009).

The mean acoustic velocity of air-dried logs determined in the parents and hybrids of *E. camaldulensis* x *E. tereticornis* was comparable at 3.71 ± 0.26 km/s and 3.48 ± 0.35 km/s in Muthupettai and Karur, respectively and combined location was 3.6 ± 0.32 km/s indicating the additive genetic control of the trait. It was comparable to earlier studies

Table 5. Estimates of minimum, maximum, mean value, standard deviation and standard error, variances at genotypic, phenotypic and residual level and coefficient of variation at genotypic, phenotypic level, individual broad sense heritability (H^2) and genetic advance in absolute and per cent of mean for the wood property traits in mapping population of *E. camaldulensis* x *E. tereticornis* at each location.

Trait	Min.	Max.	Mean	SD	SE	σ^2g	σ^2p	σ^2e	CV_G (%)	CV_P (%)	H^2	GA	GAM (%)
Muthupettai													
Diameter (cm)	32.41	77.99	47.30	10.17	2.03	54.64	152.24	97.60	15.63	26.09	0.36	6.41	13.54
Density (kg/m^3)	580	680	620	0.03	0.006	0.001	0.001	0.0003	4.096	4.861	0.71	0.03	5.60
Acoustic velocity (km/s)	3.35	4.30	3.72	0.26	0.05	0.04	0.10	0.06	5.11	8.30	0.38	0.17	4.59
DMoE (GPa)	6.96	11.40	8.66	1.23	0.25	0.86	2.16	1.30	10.73	16.99	0.40	0.86	9.95
Cellulose (%)	31.74	44.64	38.86	3.42	0.68	7.21	16.23	9.02	6.91	10.37	0.44	2.67	6.87
Total lignin (%)	13.13	18.04	15.61	1.33	0.27	1.52	2.04	0.53	7.89	9.16	0.74	1.74	11.14
Karur													
Diameter (cm)	29.93	62.74	40.98	8.898	1.78	45.64	112.72	67.08	16.49	25.91	0.40	6.32	15.43
Density (kg/m^3)	600	720	670	0.033	0.01	0.0004	0.0018	0.0014	2.90	6.29	0.21	0.01	1.83
Acoustic velocity (km/s)	2.94	4.27	3.50	0.342	0.07	0.054	0.18	0.13	6.61	12.10	0.30	0.18	5.11
DMoE (GPa)	5.38	11.53	8.32	1.650	0.33	0.767	4.68	3.91	10.52	25.98	0.16	0.47	5.71
Cellulose (%)	30.02	43.01	36.66	3.664	0.73	6.014	20.84	14.82	6.69	12.45	0.29	1.86	5.06
Total lignin (%)	12.89	19.86	16.87	1.783	0.36	1.517	4.84	3.33	7.30	13.04	0.31	0.98	5.81

σ^2p, Phenotypic variance; σ^2g, genotypic variance; σ^2e, error variance; CV_G, coefficient of genotypic variation; CV_P, coefficient of phenotypic variation; H^2, broad sense heritability; GA, expected genetic advance; GAM (%), genetic advance as a percentage of mean.

reported in *E. nitens* (Blackburn *et al.* 2010), *E. tereticornis* (Chauhan and Aggarwal 2011), *E. camaldulensis* (Ishiguri *et al.* 2013), *E. alba* (Wahyudi *et al.* 2015), *E. grandis* (Chauhan and Sethy 2016) and *E. urophylla*, *E. grandis* and *E. pellita* (Prasetyo *et al.* 2017). Stability of acoustic velocity across locations was also reported in *E. nitens* (Blackburn *et al.* 2014) and *E. globulus* (Hamilton *et al.* 2017).

Another inference from the trait correlation analysis was the strong positive correlation ($P \leq 0.001$) between acoustic velocity and DMoE in both locations. Modulus of elasticity is an important parameter indicating mechanical strength of wood and is critical for engineered structures (Chauhan and Aggarwal 2011). It is a composite function of microfibril angle and basic density (Lindström *et al.* 2002) with moderate heritability (Santos *et al.* 2004). Earlier reports have documented moderate to strong correlation of acoustic velocity with DMoE (Lindström *et al.* 2002; Dickson *et al.* 2003; Chauhan and Aggarwal 2011) in agreement with the present study. This information becomes relevant in the present scenario, since *Eucalyptus* wood is increasingly being used for high value saw logs and engineered wood products in addition to its use in pulp industries (Sharma *et al.* 2005; Pelletier *et al.* 2008; Chauhan and Aggarwal 2011). The study implies that acoustic tool can be used as a selection parameter to predict the solid wood properties in *Eucalyptus* hybrids as it was least influenced by location.

Inconsistency in correlation with wood related traits in both locations was documented in the present study (table 4). The probable reason for this incongruity could be attributed to relatively small sample size adversely affecting the precision of estimations, variation in trait expression due to site heterogeneity and distinct difference in growth rate of hybrids in both locations. The site effect on trait correlation is attributed to complex manifestation of G x E (Li *et al.* 2017) affected by factors like altitude, rainfall, pH and soil nutrients as reported in *Eucalyptus* hybrids (Souza *et al.* 2017; Chen *et al.* 2018). Variation in phenotypic expression of wood related traits across locations is affected by difference in growth rates (Zobel and Van Buijtenen 1989). Enhanced or retarded growth rates are known to modify the physicochemical attributes of trees influencing wood characters (Savidge 1996). In the present study, the two sites selected had contrasting climatic and edaphic conditions with Karur receiving an annual rainfall of 595 mm while Muthupettai received 1196 mm rainfall (table 1). Further, due to severe drought conditions in Karur during the assessment period, the growth and survivability of the hybrid clones were severely affected, indicating negative effect on the wood property traits and explaining the consistently lower values for most of the assessed traits. The same reasons can be attributed to the inconsistent trait correlations documented in the study. However, the possibility of simultaneous independent selection for traits with different end uses cannot be ruled out if the study can be extended to larger sample size in multiple environments to minimize the pseudo-relationship between traits.

Heritability and genetic advancement of wood property traits

Effective tree breeding relies on the understanding of heritability of different wood properties to maximize the genetic

Table 6. Estimates of variances at genotypic, phenotypic and environment and coefficient of variation at genotypic, phenotypic and residual level, heritability in broad sense (H^2), standard error, genetic advance in absolute and percent of mean for the wood property traits in mapping population of *E. camaldulensis* x *E. tereticornis* from location combined analysis.

Trait	*P* value of location effect	σ^2g	σ^2p	σ^2e	CV$_G$ (%)	CV$_P$ (%)	CV$_E$ (%)	H^2	SE	GA	GAM (%)
Diameter (cm)	< 0.01**	47.78	162.03	82.33	14.05	25.87	18.44	0.294	1.09	5.15	10.47
Density(kg/m^3)	<0.001***	0.0005	0.0017	0.001	3.49	6.44	4.94	0.315	0.01	0.02	3.30
Acoustic velocity (km/s)	<0.001***	0.066	0.16	0.093	7.06	10.99	8.38	0.416	0.03	0.23	6.39
DMoE (GPa)	Not significant	1.12	3.59	2.605	12.21	21.85	18.62	0.313	0.14	0.80	9.19
Cellulose (%)	< 0.01**	9.73	22.16	11.92	8.28	12.50	9.17	0.439	0.38	2.84	7.53
Total lignin (%)	<0.001***	1.68	4.48	1.927	8.31	13.58	8.90	0.376	0.15	1.11	7.13

***$P < 0.001$; **$0.001 < P < 0.01$ - level of significance of effects.

σ^2p, Phenotypic variance; σ^2g, genotypic variance; σ^2e, error variance; CV$_{G,}$ coefficient of genotypic variation; CV$_{P,}$ coefficient of phenotypic variation; H^2, broad sense heritability; GA, expected genetic advance; GAM (%), genetic advance as a percentage of mean.

gain and sustain the long-term genetic progress of the progenies (Marco de Lima *et al*. 2019). The combined location analysis in the present study revealed moderate H^2 for acoustic velocity which is similar to earlier studies in *E. nitens* (Blackburn *et al*. 2014), *E. pilularis* and *E. dunnii* (Raymond *et al*. 2008). Cellulose per cent showed the maximum heritability at 0.439 as reported in *E. globulus*, *E. urophylla* and *E. nitens* and its significant correlation with pulp yield was earlier established (Kube *et al*. 2001; Raymond and Schimleck 2002; Schimleck *et al*. 2004; Kien *et al*. 2009).

Interspecific hybrids of *Eucalyptus* are reported to be sensitive to environmental heterogeneity for wood property traits and the expression of hybrid superiority is predominantly site specific (Potts and Dungey 2004). This probably explains the significant variation in heritability estimates between locations specifically for density and total lignin content (table 5). The single site heritability estimates were predominantly higher and biased than combined locations since interaction with additive genetic and environment effect cannot be separated from additive variance (Dieters *et al*. 1995; Li *et al*. 2017). In a study conducted in families of *E. urophylla* x *E. pellita* and *E. urophylla* x *E. grandis*, it was reported that heritability of wood traits depended on the hybrid genotype and density of plantation (Chaix *et al*. 2011). Even though the present study indicates that cellulose can be used as selection criteria with no significant G x E interaction, the analysis should be interpreted with caution since it showed inconsistent phenotypic correlation and estimates were made from low sample size and was limited to two locations.

Genetic advancement has critical influence in tree breeding programmes as it indicates the average improvement of the trait in the progenies which is governed by genetic variability, heritability and selection intensity. High genetic advance with high heritability estimates indicates additive gene effect and is considered as the ideal condition for selection (Larik *et al*. 2000). In earlier studies, the genetic advance in *Eucalyptus* clones for diameter was high at 22.75% (Huse *et al*. 2018) and 21% in *E. urophylla* x *E. grandis* at 2% selection intensity (Makouanzi *et al*. 2017). The present study in *E. camaldulensis* x *E. tereticornis* showed highest genetic advance for diameter in individual and combined location analysis (10.47% at 5% selection intensity) indicating its potential for improvement in future hybridization programmes since it will directly impact wood volume. However, the estimates presented in this study may be less precise due to limited sample size and trial sites.

In conclusion, the hybrid superiority is well documented in *Eucalyptus* and has been effectively harnessed in the plantation programmes to enhance productivity per unit area (reviewed by Potts and Dungey 2004; Madhibha *et al*. 2013). The genetic control of wood property traits in *Eucalyptus* is well documented and these traits are under low to moderate level of additive genetic control. The present study in *E. camaldulensis* x *E. tereticornis* documented the phenotypic variation, heritability, trait correlation and genetic gain in six wood related traits which have significant impact on its industrial use. The effect of location was predominant in most of the assessed traits. Acoustic velocity was one of the most stable traits with minimum G x E interaction. The significant correlation of this trait with DMoE in both locations implies that it can be used as a tool for selecting wood with mechanical strength for engineered wood products. The genetic gain in diameter in the hybrid combination indicates possibilities of further improvement of this trait in hybrid breeding programmes.

Acknowledgements

The authors acknowledge Department of Biotechnology, Government of India for funding the research work (project no. BT/PR10539/PBD/16/1064/2013). The funding support as research fellowship was provided to ABMP, MM, NK, VP and SS by Department of Biotechnology, Government of India. The support extended by Tamil Nadu Newsprint and Papers Limited, Kagithapuram, Karur, Tamil Nadu in establishing and maintaining the hybrid trials is gratefully acknowledged.

References

Albert D. J., Clark T. A., Dickson R. L. and Walker J. C. F. 2002 Using acoustic to sort radiata pine pulp logs according to fibre characteristics and paper properties. *Int. For. Rev.* **4**, 12–19.

Allard R. W. 1960 *Principles of plant breeding*, John Wiley, New York.

Apiolaza L. 2009 Very early selection for wood quality: screening for early winners. *Ann. For. Sci.* **66**, 601.

Araújo J. A., Borralho N. M. G. and Dehon G. 2012 The importance and type of non-additive genetic effects for growth in *Eucalyptus globulus*. *Tree Genet. Genomes* **8**, 327–337.

Assis T. F. 2000 Production and use of eucalyptus hybrids for industrial purposes. In Proceedings of Hybrid Breeding and Genetics of Forest Trees Proceedings of QFRI/CRC-SPF Symposium, 9–14 April 2000, Noosa, Queensland, Australia.

Assis T. F. 2011 Hybrids and mini-cutting: a powerful combination that has revolutionized the Eucalyptus clonal forestry. *BMC Proc.* **5**, I18.

Awas G., Mekbib F. and Ayana A. 2015 Variability, heritability and genetic advance for some yield and yield related traits and oil content in Ethiopian coriander (*Coriandrum sativum* L.) genotypes. *Int. J. Plant Breed. Genet.* **9**, 10.

Bison O., Ramalho M. A. P., Peçanha Rezende G. D. S., Aguiar A. M. and de Resende M. D. V. 2007 Combining ability of elite clones of *Eucalyptus grandis* and *Eucalyptus urophylla* with *Eucalyptus globulus*. *Genet. Mol. Biol.* **30**, 417–422.

Blackburn D., Hamilton M., Harwood C., Innes T., Potts B. and Williams D. 2010 Stiffness and checking of *Eucalyptus nitens* sawn boards: genetic variation and potential for genetic improvement. *Tree Genet. Genomes* **6**, 757–765.

Blackburn D. P., Hamilton M. G., Williams D. R., Harwood C. E. and Potts B. M. 2014 Acoustic wave velocity as a selection trait in *Eucalyptus nitens*. *Forests* **5**, 744–762.

Chaix G., Denis M., Polidori J., Vigneron P., Makouanzi G., Diombokho A. *et al.* 2011 Genotype × environment interactions for growth and wood traits for eucalyptus hybrids. In Proceedings, IUFRO Working Group 2.08.03: improvement and culture of eucalypts, pp. 175–176, 14–18 November 2011, Porto Seguro, Brazil.

Chauhan S. S. and Walker J. C. F. 2006 Variations in acoustic velocity and density with age, and their interrelationships in radiata pine. *For. Ecol. Manag.* **229**, 388–394.

Chauhan S. and Aggarwal P. 2011 Segregation of *Eucalyptus tereticornis* Sm. clones for properties relevant to solid wood products. *Ann. For. Sci.* **68**, 511–521.

Chauhan S. and Sethy A. 2016 Differences in dynamic modulus of elasticity determined by three vibration methods and their relationship with static modulus of elasticity. *Maderas-Cienc Tecnol.* **18**, 373–382.

Chen S., Weng Q., Li F., Li M., Zhou C. and Gan S. 2018 Genetic parameters for growth and wood chemical properties in *Eucalyptus urophylla* × *E. tereticornis* hybrids. *Ann. For. Sci.* **75**, 16.

Costa E. S. J., Borralho N. M. and Potts B. M. 2004 Additive and non-additive genetic parameters from clonally replicated and seedling progenies of *Eucalyptus globulus*. *Theor. Appl. Genet.* **108**, 1113–1119.

Davies N. T., Apiolaza L. A. and Sharma M. 2017 Heritability of growth strain in *Eucalyptus bosistoana*: a Bayesian approach with left-censored data. *N.Z.J. For. Sci.* **47**, 5.

Denis M., Favreau B., Ueno S., Camus-Kulandaivelu L., Chaix G., Gion J. M. *et al.* 2013 Genetic variation of wood chemical traits and association with underlying genes in *Eucalyptus urophylla*. *Tree Genet. Genomes* **9**, 927–942.

Dickson R. L., Raymond C. A., Joe W. and Wilkinson C. A. 2003 Segregation of *Eucalyptus dunnii* logs using acoustics. *For. Ecol. and Manag.* **179**, 243–251.

Dieters M. J., White T. L., Littell R. C. and Hodge G. R. 1995 Application of approximate variances of variance components and their ratios in genetic tests. *Theor. Appl Genet.* **91**, 15–24.

Doran J. C. K., Pinyopusarerk K., Arnold R. and Harwood C. E. 1996 Breeding Plan for *Eucalyptus camaldulensis* in Tamil Nadu. UNDP/FAO Regional Project on Improved Productivity of Man-Made Forests through Application of Technological Advances in Tree Breeding and Propagation. (RAS/91/004-FORTIP), 40p. FAO, Rome.

Evans R. 2000 Measuring wood and fibre properties. In *WTRC workshop 2000*, pp.15–20 Wood Technology Research Centre, University of Canterbury.

Falconer D. S. 1990 *Introduction to quantitative genetics*, John Wiley, New York.

Fonseca S. M., Resende M. D. V., Alfenas A. C., Guimarães L. M. S., Teotônio A. and Dario G. 2010 Manual prático de melhoramento genético do eucalipto, pp. 200. UFV, Viçosa.

Griffin A., Harbard J., Centurion C. and Santini P. 2000 Breeding *Eucalyptus grandis x globulus* and other inter-specific hybrids with high inviability – problem analysis and experience with Shell Forestry projects in Uruguay and Chile (ed. H. S. InL Dungey, M. J. Dieters and D. G. Nikles). Hybrid Breed Genet For Trees Proc QFRI/CRC-SPF Symp 9–14th April 2000 Aust Dep Prim Ind Brisbane 1–13, Noosa, Queensland.

Groover A., Nieminen K., Helariutta Y. and Mansfield S. D. 2010 Wood formation in *Populus*. In: Genetics and genomics of *Populus* (ed. Jansson, Bhalerao and Groover), Springer, Dordrecht.

Hamilton M.G., Freeman J.S., Blackburn D.P., Downes G.M., Pilbeam D.J. and Potts B.M. 2009 Genetic variation in *Eucalyptus nitens* pulpwood and wood shrinkage traits. *Tree Genet. Genomes* **5**, 307–316.

Hamilton M.G., Freeman J.S., Blackburn D.P., Downes G.M., Pilbeam D.J. and Potts B.M. 2017 Independent lines of evidence of a genetic relationship between acoustic wave velocity and kraft pulp yield in *Eucalyptus globulus*. *Ann. For. Sci.* **74**, 17.

Hart P. W. and Santos R. B. 2015 Changing the face of short fiber - a review of the *Eucalyptus* revolution. *Tappi J.* **14**, 353–359.

Hein P. R. G., Bouvet J.-M., Mandrou E., Vigneron P., Clair B. and Chaix G. 2012 Age trends of microfibril angle inheritance and their genetic and environmental correlations with growth, density and chemical properties in *Eucalyptus urophylla* S. T. Blake wood. *Ann. For. Sci.* **69**, 681–691.

Huse S. A., Gunaga R. P. and Sinha S. K. 2018 Genetic Estimates of Growth and Wood Anatomical Properties in Eucalypts Clones. *Int. J. Genet.* **10**, 495–497.

Ishiguri F., Diloksumpun S., Tanabe J., Iizuka K. and Yokota S. 2013 Stress-wave velocity of tree and dynamic Youngš modulus of logs of 4-year-old *Eucalyptus camaldulensis* trees selected for pulpwood production in Thailand. *J. Wood Sci.* **59**, 506–511.

Kien N. D., Quang T. H., Jansson G., Harwood C. E., Clapham D. and von Arnold S. 2009 Cellulose content as a selection trait in breeding for kraft pulp yield in *Eucalyptus urophylla*. *Ann. For. Sci.* **66**, 711.

Kube P. D., Raymond C. A. and Banham P. W. 2001 Genetic parameters for diameter, basic density, cellulose content and fibre properties for *Eucalyptus nitens*. *For. Gen.* **8**, 285–294.

Kullan A. R. K., van Dyk M. M., Hefer C. A., Jones N., Kanzler A. and Myburg A. A. 2012 Genetic dissection of growth, wood basic density and gene expression in interspecific backcrosses of *Eucalyptus grandis* and *E. urophylla*. *BMC Genet.* **13**, 60.

Kumar M. and Turner S. 2015 Protocol: a medium-throughput method for determination of cellulose content from single stem pieces of *Arabidopsis thaliana*. *Plant Methods* **11**, 46.

Larik A. S., Malik S. I., Kakar A. A. and Naz M. A. 2000 Assessment of heritability and genetic advance for yield and yield components in *Gossypium hirsutum* L. *J. Med. Sci.* **13**, 39–44.

Li Y., Suontama M., Burdon R. D. and Dungey H. S. 2017 Genotype by environment interactions in forest tree breeding: review of methodology and perspectives on research and application. *Tree Genet. Genomes* **13**, 60.

Lindström H., Harris P. and Nakada R. 2002 Methods for measuring stiffness of young trees. *Holz Roh Werkst.* **60**, 165–174.

Madhibha T., Murepa R., Musokonyi C. and Gapare W. 2013 Genetic parameter estimates for interspecific *Eucalyptus* hybrids and implications for hybrid breeding strategy. *New For.* **44**, 63–84.

Makouanzi G., Chaix G., Nourissier S. and Vigneron P. 2017 Genetic variability of growth and wood chemical properties in a clonal population of *Eucalyptus urophylla* × *Eucalyptus grandis* in the Congo. *Sout. for J. For. Sci.* **80**, 151–158.

Marco de Lima B., Cappa E. P., Silva-Junior O. B., Garcia C., Mansfield S. D. and Grattapaglia D. 2019 Quantitative genetic parameters for growth and wood properties in *Eucalyptus* "*urograndis*" hybrid using near-infrared phenotyping and genome-wide SNP-based relationships. *PLoS One* **14**, e0218747.

Mizrachi E. and Myburg A. A. 2016 Systems genetics of wood formation. *Curr. Opin. Plant Biol.* **30**, 94–100.

Mizrachi E., Verbeke L., Christie N., Fierro A. C., Mansfield S. D., Davis M. F. *et al*. 2017 Network-based integration of systems genetics data reveals pathways associated with lignocellulosic biomass accumulation and processing. *Proc. Natl. Acad. Sci. USA* **114**, 1195–1200.

Moreira-Vilar F. C., Siqueira-Soares Rde C., Finger-Teixeira A. *et al*. 2014 The acetyl bromide method is faster, simpler and presents best recovery of lignin in different herbaceous tissues than Klason and thioglycolic acid methods. *PLoS One* **9**, e110000.

Osorio L. F., White T. L. and Huber D. A. 2001 Age trends of heritabilities and genotype-by environment Inter actions for growth traits and wood density form clonal trials of *Eucalyptus grandis* Hill ex Maiden and their implications for optimal selection age and design of clonal trials. *Theor. Appl. Genet.* **106**, 735–743.

Pelletier M. C., Henson M., Boyton S., Thomas D. and Vancaly J. K. 2008 Genetic variation in dimensional stability of *Eucalyptus pilularis* (Smith) assessed using increment cores and test blocks. *N. Z. J. for Sci.* **38**, 194–210.

Potts B. M. and Dungey H. S. 2004 Interspecific hybridization of *Eucalyptus*: key issues for breeders and geneticists. *New For.* **27**, 115–138.

Prasetyo A., Aiso H., Ishiguri F., Wahyudi I., Wijaya I. P. G., Ohshima J. and Yokota S. 2017 Variations on growth characteristics and wood properties of three *Eucalyptus* species planted for pulpwood in Indonesia. *Tropics* **26**, 59–69.

Pupin S., Silva P. H. M., Piotto F. A., Miranda A. C., Zaruma D. U. G., Sebbenn A. M. and Moraes M. L. T. 2018 Genotype x Environment interaction, stability, and adaptability in progenies of *Eucalyptus urophylla* S.T. BLAKE using the AMMI model. *Silvae Genet.* **67**, 51–56.

Rajasugunasekar D., Vellaichamy P., Mayavel A., Sivakumar V., Modhumitha D., Bachpai V. K. W. *et al.* 2015 Interfacing classical and molecular breeding in red gums in India: Observed and expected gains: In: Book of abstracts IUFRO Eucalypt Conference 2015, held on 21- 24 October 2015, Zhanjiang, Guangdong, China.

Raymond C. A. 2002 Genetics of Eucalyptus wood properties. *Ann. Forest Sci.* **59**, 525–531.

Raymond C. A. and Schimleck L. R. 2002 Development of near infrared reflectance analysis calibrations for estimating genetic parameters for cellulose content in *Eucalyptus globulus*. *Can. J. For. Res.* **32**, 170–176.

Raymond C. A., Henson M., Pelletier M.-C., Boyton S., Joe B., Thomas D., Smith H. and Vanclay J. 2008 Improving dimensional stability in plantation-grown *Eucalyptus pilularis* and *E. dunnii*. pp 1–65, Forest and wood products Australia, Melbourne, Australia.

Rencoret J., Gutierrez A. and del Rio J. 2007 Lipid and lignin composition of woods from different eucalypt species. *Holzforschung* **61**, 165–174.

Resende M. D. V. 2002 Genética biométrica e estatística no melhoramento de plantas perenes. *Brasilia: Embrapa Informação Tecnológica.* 975.

Rezende G. D. S. P., Resende M. D. V. and Assis T. F. 2014 *Eucalyptus breeding for clonal forestry In Challenges and opportunities for the World's forests in the 21st Century* (ed. T. Fenning), pp 393–424, Dordrecht, Springer Netherlands.

Rodrigues J., Faix O. and Pereira H. 1999 Improvement of the acetylbromide method for lignin determination within large scale screening programmes. *Holz Als Roh- Und Werkstoff* **57**, 341–345.

Santos P., Geraldi I. and Garcia J. 2004 Estimates of genetic parameters of wood traits for sawn timber production in Eucalyptus grandis. *Genet. Mol. Biol.* **27**, 567–573.

Savidge R. A. 1996 Xylogenesis, genetic and environmental regulation, a review. *IAWA J.* **17**, 269–310.

Schimleck L. R., Jones P. D., Peter G. F., Daniels R. F. and Clark A. III. 2004 Nondestructive estimation of tracheid length from sections of radial wood strips by near infrared spectroscopy. *Holzforschung* **58**, 375–381.

Sharma S. K., Rao R. V., Shukla S. R., Kumar P., Sudheendra R., Sujatha M. and Dubey Y. M. 2005 Wood quality of coppiced Eucalyptus tereticornis for value addition. *IAWA J.* **26**, 137–147.

Singh R. K., Chaudhary B. D. 1979 *Biometrical methods in quantitative genetic analysis*, Kalyani publication, New Delhi.

Souza T., Ramalho M., Marco B., Gabriel D. and Sampaio D. 2017 Performance of Eucalyptus clones according to environmental conditions Desempenho de clones de eucalipto em função de condições ambientais. *Sci. For.* **45**, 601–610.

Stackpole D. J., Vaillancourt R. E., Rodrigues J. and Potts B. M. 2011 Genetic variation in the chemical components of *Eucalyptus globulus* wood. *G3* **1**, 151–159.

Tan B., Grattapaglia D., Wu H. X. and Ingvarsson P. K. 2018 Genomic relationships reveal significant dominance effects for growth in hybrid *Eucalyptus*. *Plant Sci. J.* **267**, 84–93.

Torres-Dini D., Nunes A. C. P., Aguiar A., Nikichuk N., Centurión C., Cabrera M., Moraes M. L. T., Resende M. D. V. and Sebbenn A. M. 2016 Clonal selection of *Eucalyptus grandis x Eucalyptus globulus* for productivity, adaptability, and stability, using SNP markers. *Silvae Genet.* **65**, 30–38.

Tsehaye A., Buchanan A. H. and Walker J. C. F. 2000 Sorting of logs using acoustics. *Wood Sci. Technol.* **34**, 337–344.

Updegraff D. M. 1969 Semi micro determination of cellulose in biological materials. *Anal. Biochem.* **32**, 420–424.

Varghese M., Nicodemus A., Nagarajan B., Ravi N. and Hegde R. 2002 A breeding program for improving productivity of *Eucalyptus camaldulensis* and *E. tereticornis* in India. In Recent eucalypt research in India (ed. S. K Bagchi, M. Varghese and Siddappa), pp 19-28, IFGTB, Coimbatore.

Varghese M., Harwood C. E., Hegde R. and Ravi N. 2008 Evaluation of provenances of Eucalyptus camaldulensis and clones of *E. camaldulensis* and *E. tereticornis* at contrasting sites in southern India. *Silvae Genet.* **57**, 170–179.

Wahyudi I., Ishiguri F., Makino K., Tanabe J., Tan L., Tuhumury A., Iizuka K. and Yokota S. 2015 Growth characteristics and wood properties of 26-year-old *Eucalyptus alba* planted in Indonesia. *Int. Wood Prod. J.* **6**, 84–88.

Wang X., Carter P., Ross R. J. and Brashaw B. K. 2007 Acoustic assessment of wood quality of raw forest materials –a path to increased profitability. *For. Prod. J.* **57**, 6–14.

Weng Q., He X., Li F., Li M., Yu X., Shi J. and Gan S. 2014 Hybridizing ability and heterosis between *Eucalyptus urophylla* and *E. tereticornis* for growth and wood density over two environments. *Silvae Genet.* **63**, 15–24.

Wu S. J., Xu J. M., Li G. Y., Risto V., Lu Z. H., Li B. Q. and Wang W. 2011 Estimation of basic density and modulus of elasticity of eucalypt clones in southern china using nondestructive methods. *J. Trop. For. Sci.* **23**, 51–56.

Zhang A. O., Wang H., Beyene Y., Semagn K., Liu Y., Cao S., Cui Z., Ruan Y., Burgueño J., San Vicente F., Olsen M., Prasanna B., Crossa J., Yu H. and Zhang X. 2017 Effect of trait heritability, training population size and marker density on genomic prediction accuracy estimation in 22 bi-parental tropical maize populations. *Front. Plant Sci.* **8**, 1916.

Zobel B. J. and Van Buijtenen J. P. 1989 *Wood variation: its causes and control*, Springer-Verlag, Berlin.

Corresponding editor: MANOJ PRASAD