Estimates of genetic parameters for growth and wood properties in Eucalyptus pellita F. Muell. to support tree breeding in Vietnam

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ORIGINAL PAPER

Estimates of genetic parameters for growth and wood properties in *Eucalyptus pellita* F. Muell. to support tree breeding in Vietnam

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Abstract

• ***Key message*** ***Eucalyptus pellita*** **demonstrated good growth and wood quality traits in this study, with young plantation grown timber being suitable for both solid and pulp wood products. All traits examined were under moderate levels of genetic control with little genotype by environment interaction when grown on two contrasting sites in Vietnam.**

• ***Context*** *Eucalyptus pellita* currently has a significant role in reforestation in the tropics. Research to support expanded of use of this species is needed: particularly, research to better understand the genetic control of key traits will facilitate the development of genetically improved planting stock.

• ***Aims*** This study aimed to provide estimates of the heritability of diameter at breast height over bark, wood basic density, Kraft pulp yield, modulus of elasticity and microfibril angle, and the genetic correlations among these traits, and understand the importance of genotype by environment interactions in Vietnam.

• ***Methods*** Data for diameter and wood properties were collected from two 10-year-old, open-pollinated progeny trials of

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E. pellita in Vietnam that evaluated 104 families from six native range and three orchard sources. Wood properties were estimated from wood samples using near-infrared (NIR) spectroscopy. Data were analysed using mixed linear models to estimate genetic parameters (heritability, proportion of variance between seed sources and genetic correlations).

• ***Results*** Variation among the nine sources was small compared to additive variance. Narrow-sense heritability and genetic correlation estimates indicated that simultaneous improvements in most traits could be achieved from selection among and within families as the genetic correlations among traits were either favourable or close to zero. Type B genetic correlations approached one for all traits suggesting that genotype by environment interactions were of little importance. These results support a breeding strategy utilizing a single breeding population advanced by selecting the best individuals across all seed sources.

• ***Conclusion*** Both growth and wood properties have been evaluated. Multi-trait selection for growth and wood property traits will lead to more productive populations of *E. pellita* both with improved productivity and improved timber and pulp properties.

Keywords *Eucalyptus pellita* · Wood properties · Heritability · Genetic correlation

1 Introduction

Eucalyptus pellita F. Muell, or red mahogany, is a medium to large tree that can grow up to 40 m in height and over 1 m in diameter (Harwood 1998; Dombro 2010). Timber of this species from natural stands is easily sawn and suitable for poles, flooring, panelling and general construction (Hillis and Brown 1978; Harwood 1998). There are two disjunct areas of natural forest where *E. pellita* occurs: southern New Guinea (across both Papua New Guinea and Irian Jaya, lowlands with elevation below 100 m above sea level (asl)) and northern Queensland, Australia (elevation up to 600 m asl). *E. pellita* has good growth and high survival when grown in plantations located both within its natural distribution and as an exotic in the regions with mean annual rainfall from 1,080 to 3,550 mm and mean annual temperature from 19 to 27 °C (Clarke et al. 2009). The species currently plays an important role in reforestation in countries such as Brazil, Cuba, Indonesia, Malaysia and the Philippines and has been identified as suitable for plantation establishment on coastal sites of northern Queensland (Clarke et al. 2009).

Eucalyptus species are grown widely for pulp production in many countries (Eldridge et al. 1993; Poke and Raymond 2006) and are an important source of short fibre cellulosic pulp, which is used for high-quality writing and printing paper or tissue products (Raymond 2002; Raymond and Schimleck 2002; Schimleck et al. 2006). As with many other eucalypts, *E. pellita* is used for a variety of products. Sawn timber of red mahogany is used to make fine furniture and in construction, as well as for many other purposes (Clarke et al. 2009). In addition, *E. pellita* is also one of the preferred raw materials for the pulp and paper industry (Dombro 2010); its Kraft pulping and paper-making properties are acceptable, being very similar to those of plantation-grown *Eucalyptus urophylla* of the same age and slightly inferior to those of plantation-grown *Eucalyptus globulus* (Clarke et al. 2009).

Attributes that make this species attractive for plantation establishment are its fast growth, good stem straightness, good coppicing ability, broad adaptation to a range of environmental conditions, good resistance to pests and diseases and suitability for a variety of wood products (Clarke et al. 2009). Consequently, *E. pellita* is currently one of the main species used in afforestation in several countries (Harwood 1998; Leksono et al. 2008; Clarke et al. 2009; Brawner et al. 2010). In Vietnam, eucalypts are one of the most important groups of plantation species, supplying both solid wood and pulpwood for industrial applications. Several progeny trials and seed orchards of *E. pellita* have been established in Vietnam since 2002 (Kha et al. 2003). A better understanding of the genetic control of growth and wood properties in *E. pellita* is required to support genetic improvement efforts and its use in industrial plantations.

The present study used two progeny trials of *E. pellita* established in Vietnam to investigate the genetic control of growth and wood properties in 104 open-pollinated families derived from nine seed sources (three first-generation seed orchards in Australia and six provenance collections from the native stands). The objectives were to compare diameter at breast height (diameter), Kraft pulp yield, basic density, modulus of elasticity and microfibril angle among the seed sources; partition variation for all traits into genetic and environmental components and estimate the heritability of the traits; and estimate the genetic correlations among traits and trials. These parameters are important to estimate the direct and indirect responses from selection and to guide the development of an *E. pellita* breeding program in Vietnam.

2 Materials and methods

2.1 Study trials, genetic materials and assessment

This study evaluated two open-pollinated progeny trials of *E. pellita* at 10 years of age that were established in Vietnam in 2002 (Table 1). Trials were derived from open-pollinated seed

Table 1 Location and design details of the *E. pellita* open-pollinated progeny trials established in Vietnam

Description	Trial	
	1	2
Location	Pleiku-Gia Lai	Bau Bang-Binh Duong
Latitude	13° 58′ N	11° 16′ N
Longitude	108° 01′ E	106° 37′ E
Elevation (m asl)	780	45
Mean annual precipitation (mm)	1,900	2,200
Genetic material[a]	9 (94)	9 (98)
Number of replicates	6	8
Number of trees per plot[b]	4	4
Initial spacing	4×1.5 m	4×1.5 m
No. of trees at establishment[b]	2,496	4,200
No. of trees after thinning[c]	657	470
Planted date	Sep 2002	Oct 2002

[a] Genetic material included in trials with number of seed sources followed by the total number of families in parentheses

[b] Number of trees at establishment. Each four-tree row plot consists of a single open-pollinated family

[c] Number of trees at the time of assessment in 2012 after the second thinning that retained the one best tree per plot

that had been collected from either selections within seedling seed orchards (SSOs) of range-wide collections (three seed orchards) or natural stands of *E. pellita* (six provenances). The three SSOs were developed in Australia, following a thinning protocol similar to that described below for the trials assessed for this study (refer to Harwood et al. (1997) for a full description). Based upon the results of Harwood et al. (1997), which showed that the Queensland populations were less productive than New Guinea populations, all selections from SSOs included in the Vietnam trials were derived from New Guinea families and all native range populations included were also of New Guinea origin (Table 2). There were 94 and 98 families in the Vietnamese trials established near Pleiku and Bau Bang, respectively, with a total of 104 families represented across the two trials. The number of families in common within each seed source ranged from 4 to 32 between the two trials with the composition of the two trials relatively balanced with respect to families within seed sources.

The two trial sites differed in growing conditions, with a strong contrast in elevation, temperature and rainfall (Table 1). Trial 1 (Pleiku) was established in the central highland plateau of Vietnam at an elevation of 780 m asl, in a cooler and lower rainfall environment. Trial 2 (Bau Bang) was located in southern Vietnam at a low elevation of 45 m asl. Both trials were established using row-column designs that were generated using the CycDesign (Williams et al. 2002). These trials were managed for conversion into SSOs by progressively removing inferior individual trees within family plots, in order to provide a source of improved seed for use in further plantation development. Both trials were thinned twice, with trial 1 thinned in 2007 and 2009 and trial 2 thinned in 2005 and 2007. After the first thinning of the four-tree row plots, the best two trees were retained in each plot, with the subsequent thinning leaving the single best tree in each plot.

Diameters were measured, and wood samples were collected from all remaining trees across the two trials in March 2012. Diameter over bark at breast height (1.3 m) was measured for all stems using a diameter tape. Wood swarf samples were taken at approximately 1.3 m above ground using a 16-mm spade bit and a handheld electric drill. Samples were free of bark and collected to a depth of approximately 40 mm under bark. After sampling, the hole in each tree was sterilised with methylated spirits and sealed to minimise the risk of pathogen damage. The swarf samples were placed in labelled paper bags and air-dried. The dried samples were sifted to separate out wood fines (<1 mm), which were then transferred into glass vials (45×20 mm in size) for near-infrared (NIR) analysis. All samples were scanned to obtain NIR spectra on a Bruker MPA FT-NIR instrument (Bruker Optik, Ettlingen, Germany, www.bruker.com) with spectra between 4,000 and 15,000 cm^{-1} (~700–2,500 nm) obtained at 8 cm^{-1} resolution. Wood traits were estimated using data from the NIR spectra recorded for each sample in a manner similar to that described by Brawner et al. (2012). The spectral data were imported into *The Unscrambler* software (Camo Software, Oslo, Norway, www.camo.com, version 10.1) to predict the four wood traits using NIR calibration models (Appendix 1) developed previously by Meder et al. (2011). These are partial least square (PLS) regression models that were prepared using spectra transformed to their second derivatives following the Savitzky-Golay method (Savitzky and Golay 1964) with an integration window of 15 points and a second-order polynomial fit, to relate the NIR spectra to reference values previously determined using standard laboratory protocols for each wood property trait (Meder et al. 2011).

2.2 Statistical analyses

Statistical analyses were conducted using Genstat version 16.0 (www.vsni.co.uk). All across-trial analyses were indexed by trial, and data was standardised by trial and replicate within trial to have a zero mean and a phenotypic variance of one in order to eliminate scale effects (White et al. 2007). Mixed linear models were used to estimate genetic parameters using restricted maximum likelihood (REML, Patterson and Thompson 1971) and to generate best linear unbiased prediction (BLUPs, White and Hodge 1989) of the parental breeding values. *Z* tests were conducted to determine if random effects were significantly different from zero, and Wald statistics were used to test the significance of fixed effects. All models

Table 2 Genetic materials included in the two *E. pellita* progeny trials in Vietnam

Seed source	Location	State/province	Country	Number of families within trials		Latitude (°N)	Longitude (°E)	Elevation (m)
				1	2			
17854	Bupul Muting	Irian Jaya	Indonesia	10	12	7.21	140.36	40
18197	South of Kiriwo	WP	PNG	4	4	8.25	141.30	45
18199	Serisa Village	WP	PNG	31	32	8.36	141.26	45
18955	Serisa	WP	PNG	7	7	8.33	141.26	45
19206	Kiriwo	WP	PNG	4	6	8.25	141.30	45
19207	Goe	WP	PNG	7	7	8.20	141.32	50
19616	Kairi SSO	QLD	Australia	6	6	17.12	145.34	715
19673	Cardwell SSO	QLD	Australia	11	11	18.24	146.06	20
19718	Melville SSO	NT	Australia	14	13	11.34	130.34	20

Seed source numbers are as allocated by CSIRO

WP Western Province, *PNG* Papua New Guinea, *NT* Northern Territory, *QLD* Queensland, *SSO* seed seedling orchard

assumed that the random effects were normally distributed with expectations of zero and corresponding variances. Estimates of genetic parameters were approximated using the observed components of variance estimated from the general linear model in similar manner to Brawner et al. (2011):

$$\mathbf{y}_i = \mathbf{X}\mathbf{b}_i + \mathbf{Z}\mathbf{u}_i + \mathbf{e}_i \quad (1)$$

where $\mathbf{y}_i$ refers to phenotypic observations that are indexed by trait i in bivariate models, $\mathbf{b}_i$ is the vector of fixed effects, $\mathbf{u}_i$ is the vector of random effects, $\mathbf{X}$ is the incidence matrix relating the $\mathbf{y}_i$ observations to the $\mathbf{b}_i$ fixed effects, $\mathbf{Z}$ is the incidence matrix relating the $\mathbf{y}_i$ observations to the $\mathbf{u}_i$ random effects, and $\mathbf{e}_i$ is the vector of random error terms.

2.2.1 Single-trial analyses

Single-trial analyses were first conducted separately to obtain estimates of variance components for each trait in each trial. The models included terms for random seed source and family (within seed source) effects in $\mathbf{u}_i$; where $\widehat{\sigma}^2 s$ and $\widehat{\sigma}^2_F$ are the estimated variance components associated with these random effects, respectively. The family by replicate interaction effect was used to account for plots within trial, and the seed source by replicate interaction was pooled with the residual to eliminate singularities caused by trials containing different sets of families within the same seed source. The overall trial mean and replicates within trial were included as fixed effects in $\mathbf{b}_i$. This model was used to generate estimates of the biased narrow-sense heritability and the proportion variance among seed source proportion (Table 3).

2.2.2 Bivariate analyses between traits

Bivariate analyses were then undertaken between the traits across the two trials. Variance components obtained from these analyses were used to estimate unbiased narrow-sense heritabilities and correlations referred to as type A genetic correlation (Table 5, White et al. 2007). For these bivariate analyses, variance and covariance estimates for all traits were taken from a linear mixed effects model as follows:

$$\mathbf{y}_i = \mathbf{X}_i\mathbf{b}_i + \mathbf{Z}_{qi}\mathbf{q}_i + \mathbf{Z}_{ui}\mathbf{u}_i + \mathbf{Z}_{pi}\mathbf{p}_i + \mathbf{e}_i \quad (2)$$

where $\mathbf{y}_i$ is the vector of observations that is indexed $\boldsymbol{i}$ by each trait, $\mathbf{y}_i = \begin{bmatrix} \boldsymbol{y}_{trait1} \\ \boldsymbol{y}_{trait2} \end{bmatrix}$; $\mathbf{b}_i$ is the vector of fixed effects representing the trial mean for each trait and replication; $\mathbf{X}_i$ is the incidence matrix relating the $\mathbf{y}_i$ to the $\mathbf{b}_i$ fixed effects, $\mathbf{X}_i\mathbf{b}_i = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix}$, $\mathbf{0}$ is the null matrix; $\mathbf{q}_i$ is the vector of random seed source effects ~MVN($\mathbf{0}$, $\mathbf{L}\otimes\mathbf{I}_i$), where $\mathbf{L} = \begin{bmatrix} \widehat{\sigma}^2_{S_1} & \widehat{\sigma}_{S_{1,2}} \\ \widehat{\sigma}_{S_{1,2}} & \widehat{\sigma}^2_{S_2} \end{bmatrix}$, $\otimes$ is the Kronecker product and $\mathbf{I}_i$ is an identity matrix of size equal to the number seed sources, $\widehat{\sigma}^2_{S_i}$ is the estimated seed source variance for trait i and $\widehat{\sigma}_{S_{1,2}}$ is the covariance between seed sources for traits 1 and 2; $\mathbf{u}_i$ is the vector of random open-pollinated family within seed source effects ~MVN($\mathbf{0}$, $\mathbf{G}\otimes\mathbf{I}_i$), where $\mathbf{G} = \begin{bmatrix} \widehat{\sigma}^2_{F_1} & \widehat{\sigma}_{F_{1,2}} \\ \widehat{\sigma}_{F_{1,2}} & \widehat{\sigma}^2_{F_2} \end{bmatrix}$ with estimated variance between families ($\widehat{\sigma}^2_{F_1}$) for the first and second traits, and between-trait family covariances ($\widehat{\sigma}_{F_{1,2}}$); $\mathbf{p}_i$ is the vector of random replicate by family within seed source interactions ~MVN($\mathbf{0}$, $\mathbf{M}\otimes\mathbf{I}_i$), where $\mathbf{M} = \begin{bmatrix} \widehat{\sigma}^2_{\mathrm{Repx}F_1} & \widehat{\sigma}_{\mathrm{Repx}F_{1,2}} \\ \widehat{\sigma}_{\mathrm{Repx}F_{1,2}} & \widehat{\sigma}^2_{\mathrm{Repx}F_2} \end{bmatrix}$, $\widehat{\sigma}^2_{\mathrm{Repx}Fi}$ is the estimated replicate variance for trait i, and $\widehat{\sigma}^2_{\mathrm{Repx}F_{1,2}}$ is the replicate covariance between traits 1 and 2; and $\mathbf{e}_i$ is the vector of

Table 3 Growth and wood traits from two progeny trials of *Eucalyptus pellita* established in Vietnam

Trait[a]	Trial	Mean	Range[b]		$\widehat{h}^2$	$\widehat{P}^2$
			Min	Max		
Diameter (cm)	Pleiku	16.8 (0.2)	10.8	25.5	0.14 (0.08)	0.01 (0.02)
	Bau Bang	21.0 (0.3)	9.3	34	0.33 (0.11)	0.04 (0.04)
Density (kg/m^3)	Pleiku	657 (3)	554	829	0.23 (0.13)	0.04 (0.04)
	Bau Bang	665 (3)	569	779	0.25 (0.10)	0.05 (0.04)
Kraft pulp yield (%)	Pleiku	46.8 (0.1)	42.6	51.7	0.29 (0.14)	0.03 (0.02)
	Bau Bang	45.5 (0.2)	39.3	50.3	0.47 (0.13)	0.11 (0.07)
Modulus of elasticity (GPa)	Pleiku	19.0 (0.2)	13.3	27	0.36 (0.14)	0.03 (0.03)
	Bau Bang	19.5 (0.2)	13.6	29.5	0.51 (0.14)	0.10 (0.07)
Microfibril angle (°)	Pleiku	15.1 (0.1)	11	18.7	0.14 (0.12)	0.02 (0.02)
	Bau Bang	14.5 (0.2)	9	19	0.48 (0.13)	0.10 (0.06)

Overall mean, range of variation, estimates of biased narrow-sense heritability and seed source proportion of phenotypic variance from single-trial analyses (standard errors of means in parentheses)

[a] Diameter=diameter at breast height over bark

[b] Minimum and maximum values of individual traits observed in each trial

random residuals ~MVN($\mathbf{R}\otimes\mathbf{I}$) where residuals were heterogeneous across traits, where $\mathbf{R} = \begin{bmatrix} \widehat{\sigma}^2_{Error_1} & \widehat{\sigma}_{Error_{1,2}} \\ \widehat{\sigma}_{Error_{1,2}} & \widehat{\sigma}^2_{Error_2} \end{bmatrix}$, $\widehat{\sigma}^2_{Error_1}$ is the estimated error variance for trait *i*, and $\widehat{\sigma}^2_{Error_{1,2}}$ is the estimated between-trait error covariance.

2.2.3 Across-trial analyses

Across-trial analyses for the same trait measured in two different trials were conducted to investigate environmental stability with type B correlations (Burdon 1977) and to estimate population-wide genetic parameters (Table 6). A similar linear mixed model (Eq. 2) as that described above for paired-trait analyses was used for the across-trial analyses of each trait, except the model was indexed by trial identification rather than assessment trait, where $\mathbf{y_i}$ is the vector of observations indexed (*i*) by trial: $\mathbf{y}_i = [\boldsymbol{y_{trial1}}\ \boldsymbol{y_{trial2}}]$; $\mathbf{b_i}$ and $\mathbf{X_i}$ are defined as above; $\mathbf{q_i}$ is the vector of random seed source effects ~MVN($\mathbf{0}$, $\mathbf{L}\otimes\mathbf{I_i}$), where $\mathbf{L} = \begin{bmatrix} \widehat{\sigma}^2_{S_1} & r_{S_{1,2}} \\ r_{S_{1,2}} & \widehat{\sigma}^2_{S_2} \end{bmatrix}$ is a uniform correlation matrix, r_{S_x} is a constant between-trial correlation, and $\widehat{\sigma}^2_{S_N}$ is estimated among-seed source variance in trials 1 to 2 for the trait; $\mathbf{u_i}$ is the vector of random family within seed source effects ~MVN($\mathbf{0}$, $\mathbf{G}\otimes\mathbf{I_i}$), where $\mathrm{G}_i = \begin{bmatrix} \widehat{\sigma}^2_{F_1} & \widehat{\sigma}_{F_{1,2}} \\ \widehat{\sigma}_{F_{1,2}} & \widehat{\sigma}^2_{F_2} \end{bmatrix}$ is an unstructured variance/covariance matrix with $\widehat{\sigma}^2_{F_N}$ estimated for trait in each of the two trials, and $\widehat{\sigma}_{F_{N,N}}$ is the estimated genetic covariance estimated between each pair of trials; $\mathbf{n_i}$ and $\mathbf{p_i}$ is defined as above; $\mathbf{M}$ is a diagonal matrix of heterogeneous trial-specific plot variances; $\mathbf{e_i}$ is defined as above; $\mathbf{R}$ is a diagonal matrix of the between-trial error variances.

Estimates of all model parameter were unconstrained, with the exception of the model used for the supplementary analysis of seed source interaction where all covariance components were constrained to keep parameters within the theoretical parameter space.

2.2.4 Genetic parameter estimates

Narrow-sense heritability estimates for single-trial and across-trial (biased and unbiased heritability estimates, respectively (Falconer and Mackay 1996)) analyses were estimated for all traits using the following formulae, which is the proportion of additive genetic variance to the within-seed source phenotypic variance:

$$\widehat{h}^2 = \frac{\widehat{V}_A}{\widehat{V}_P} \approx \frac{3\widehat{\sigma}^2_F}{\widehat{\sigma}^2_F + \widehat{\sigma}^2_{Error}}, \quad (3)$$

where $\widehat{V}_A$ is the estimated additive genetic variance, $\widehat{V}_P$ is the estimated phenotypic variance, $\widehat{\sigma}^2{}_F$ is the estimated between-family variance (within seed source), and $\widehat{\sigma}^2{}_{Error}$ is the estimated unexplained error (residual) variance. This heritability estimate assumes that the coefficient of relationship among families was one third due to the mixed mating that is expected in eucalypt species (Griffin and Cotterill 1988; Brawner et al. 2012), rather than one quarter as is appropriate for true half-sibs (Falconer and Mackay 1996). Between

family variance components when estimated from a single site are biased upwards (Dieters et al. 1995), because the family and family × site variance components are confounded. Therefore, heritability estimated from a single site is referred to as 'biased narrow-sense heritability estimates'. The standard errors for heritability estimates were calculated using Dickerson's approximation following Dieters et al. (1995).

The proportion of seed source variance was used to estimate the relative importance of the among-provenance variance (Hodge and Dvorak 2001) and estimated as follows:

$$\widehat{P}^2 = \frac{\widehat{\sigma}^2 s}{\widehat{V}_p}, \quad (4)$$

where $\widehat{\sigma}^2 s$ is the estimated variance between seed sources, and $\widehat{V}_p$ is the estimated phenotypic variance as used to calculate heritability. Similarly estimates of $\widehat{P}^2$ from a single site are biased upwards due to confounding effects of any seed source by site variance.

Types A and B genetic correlations were calculated at the level of both family and seed source. Type A (family and seed source trait-trait) is a correlation between two different traits, whereas type B measures the genetic correlation between the same trait expressed on two different sites (Williams et al. 2002). These correlations can theoretically range between −1 and +1, and estimates approaching ±1 indicate a very high degree of similarity of family performance for different traits or/and environments (Burdon 1977).

Types A and B correlations for family level were estimated as follows:

$$r_F = \frac{\widehat{\sigma}_{F_{1,2}}}{\sqrt{\widehat{\sigma}^2_{F_1}\widehat{\sigma}^2_{F_2}}}, \quad (5)$$

with the estimated genetic covariance $\widehat{\sigma}_{F_{1,2}}$ specific to a pair of traits for type A correlations or a pair of trials for type B correlations.

Types A and B correlations at the seed source level were estimated as follows:

$$r_{Prov} = \frac{\widehat{\sigma}_{S_{1,2}}}{\widehat{\sigma}^2_{S_1}\widehat{\sigma}^2_{S_2}}, \quad (6)$$

where $\widehat{\sigma}_{S_{1,2}}$ is the estimated covariance among seed sources for either pairs of traits or trials. The standard errors for genetic correlation estimates were calculated following the equation described by Falconer (1981).

3 Results

3.1 Results from single-trial analyses

3.1.1 Variation among trials

Summary statistics, biased narrow-sense heritability and seed source proportion of phenotypic variance estimates are given in Table 3. Mean values of most traits differed significantly between the two progeny trials. For growth, the mean value of diameter was significantly ($p<0.001$) greater in the Bau Bang trial, 21.0 cm compared to 16.8 cm in the Pleiku trial. In terms of wood properties, density and modulus of elasticity had higher overall means in the Bau Bang trial; trial means for density were statistically different ($p<0.001$), but trial means for modulus of elasticity did not differ significantly ($p=0.098$). Nonetheless, significantly ($p<0.01$) greater Kraft pulp yield and microfibril angle were observed in the Pleiku trial, 46.8 % and 15.1° compared with 45.5 % and 14.5° in the Bau Bang trial. Estimates of both biased narrow-sense heritability and provenance proportion of phenotypic variance for most traits were much larger in the Bau Bang trial. The only exception was density, where estimates of single-trial genetic parameters were almost identical in the two trials. When comparing among traits, modulus of elasticity had the highest single-trial heritability estimates for the trait assessed at both trials, while diameter and microfibril angle were the lowest at the Pleiku trial, and density was lowest at the Bau Bang trial.

3.1.2 Variation among seed sources

The differences between seed sources were statistically significant ($p=0.013$ to <0.001) for all the traits evaluated.

Of the nine seed sources included in the two trials, two (19616 and 19718) grew consistently well in both trials. These originated from the SSOs in the highlands of Queensland and the monsoonal lowland environment of the Northern Territory, Australia, with 19616 ranked first and second, and 19718 ranked third in both the Pleiku and Bau Bang trials. DBH of these sources were significantly different from most other sources and from the trial means ($p=0.013$ and $p<0.001$ in the Pleiku and Bau Bang trials, respectively). There were two interactive seed sources, 18197 and 19673 (originating from south of Kiriwo, Papua New Guinea and Cardwell SSO in Queensland, Australia, respectively), which performed well in only one of the two trials. Source 18197 ranked second highest in the Pleiku trial but ranked lowest in the Bau Bang trial, while 19673 ranked first in the Bau Bang trial but ranked sixth in the Pleiku trial (Table 4). With the exception of 18197, populations from the wild did not grow as well as the improved sources in either trial, demonstrating the combined effect of selection and increased out-crossing in these first generation trials. Interestingly, some evidence of local

Table 4 Best linear unbiased predictions (standard deviations as given by Genstat version 16.0 in parentheses) for growth and wood quality traits for the seed sources evaluated in two *Eucalyptus pellita* open-pollinated progeny trials in Vietnam

Source	*N*		Trait									
			Diameter (cm)		Density (kg/m^3)		Kraft pulp yield (%)		Modulus of elasticity (GPa)		Microfibril angle (°)	
	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang
17854	48	77	16.8 (2.4)	20.7 (2.9)	666 (35)	675 (32)	46.8 (1.5)	45.5 (1.8)	19.2 (1.8)	19.2 (1.6)	15.1 (1.2)	14.8 (1.3)
18197	17	24	17.5 (2.9)	20.0 (3.4)	664 (35)	660 (29)	47.0 (1.4)	46.3 (1.2)	19.8 (1.7)	19.7 (1.6)	14.7 (1.2)	14.2 (1.1)
18199	131	202	16.6 (2.2)	20.1 (3.5)	648 (38)	659 (33)	46.7 (1.6)	45.5 (1.7)	18.4 (2.2)	18.8 (1.9)	15.4 (1.2)	14.9 (1.3)
18955	31	40	16.1 (2.0)	20.1 (4.4)	640 (33)	655 (36)	46.8 (1.4)	45.6 (2.1)	18.3 (2.3)	18.4 (2.1)	15.4 (1.3)	15.2 (1.4)
19206	19	39	16.2 (2.0)	20.0 (4.0)	655 (33)	668 (32)	46.5 (1.2)	46.0 (1.3)	18.6 (1.7)	19.7 (1.4)	15.4 (1.3)	14.2 (0.8)
19207	33	40	16.4 (2.3)	20.9 (3.4)	651 (27)	670 (33)	46.2 (1.5)	45.7 (1.8)	18.7 (1.7)	19.5 (1.6)	15.0 (1.2)	14.3 (1.1)
19616	31	37	17.9 (2.1)	22.1 (3.2)	666 (43)	665 (23)	46.3 (1.6)	44.0 (1.5)	19.0 (1.9)	19.7 (1.8)	15.0 (1.2)	14.6 (1.4)
19673	40	67	16.5 (2.3)	22.2 (3.4)	658 (39)	651 (36)	47.5 (1.4)	45.1 (1.9)	19.3 (2.1)	20.9 (2.6)	15.1 (1.6)	13.6 (1.7)
19718	120	131	17.2 (2.4)	21.9 (3.1)	667 (43)	676 (36)	47.0 (1.5)	46.0 (1.7)	19.6 (2.3)	19.8 (2.0)	14.8 (1.2)	14.2 (1.3)
Mean	52	73	16.8 (2.3)	21.0 (3.5)	657 (39)	665 (34)	46.8 (1.5)	45.5 (1.8)	18.9 (2.1)	19.5 (2.1)	15.1 (1.2)	14.5 (1.4)

N number of observations assessed from each seed source

adaptation was noted, as the highland seed orchard (19616) performed best in the highland trial (Pleiku) but changed rank across trials, while the lowland seed orchard (91673) performing best in the lowland trial. While this may reflect the genetic composition of the families included in these trials from the first-generation orchards, the lowland trial demonstrates a reversal of the SSO rankings with no significant differences between the two first-generation trials evident.

In terms of wood quality traits, sources 19718, 19616, 17854 and 18197 had the highest density and were significantly different from the Pleiku trial mean ($p<0.001$), with 19718 and 17854 demonstrating superiority in the Bau Bang trial. The other sources had lower density and/or were not significantly different ($p>0.05$) from the trial mean. For Kraft pulp yield, rankings were inconsistent for most sources across the two trials; however, 18197 and 19718 ranked well in both the Pleiku and Bau Bang trials. The inconsistency in rankings is demonstrated by 19673, which ranked first in the Pleiku trial and ranked eighth in the Bau Bang trial for Kraft pulp yield. Differentiation among seed lots reflects the seed source proportion of phenotypic variance $\left(\widehat{P}^2\right)$ estimates of Table 3 with a much smaller level of variation accounted for by seed sources evident in Pleiku (0.03) relative to Bau Bang (0.11). While only one source (19673) was found to have significantly ($p=0.005$) greater Kraft pulp yield than the trial mean at the Pleiku trial, significant ($p<0.001$) differences in Kraft pulp yield from the trial mean were found for three sources (18197, 19206 and 19718) at the Bau Bang trial. In contrast to Kraft pulp yield, three sources (18197, 19718 and 19673) had significantly higher modulus of elasticity than the trial mean in the Pleiku trial; however, there was only one source (19673) in the Bau Bang trial with modulus of elasticity significantly higher than the trial mean. For microfibril angle, the best source in the Bau Bang trial was 19673 with the lowest microfibril angle (13.6°). Three other sources (18197, 19206 and 19718) also had significantly ($p<0.001$) lower microfibril angle than the trial mean in this trial. In the Pleiku trial, two sources (18197 and 19718) had the lowest microfibril angle (14.7 and 14.8, respectively) and were significantly less than the trial mean ($p=0.009$) (see Table 4).

3.2 Results from across-trial analyses

3.2.1 Genetic parameter estimates from trait-trait correlations

The across-trial (unbiased) narrow-sense heritability, seed source proportion of phenotypic variance, family genetic correlation and seed source genetic correlation estimates estimated using Eq. 2 are presented in Table 5. For all traits, heritability estimates were far larger than the proportion of variance between seed sources; this indicates that additive variation was greater than the variance between seed sources. It should be noted that seed was sourced exclusively from New Guinea, and it is highly likely that the inclusion of populations from Queensland would have increase the proportion of variance between seed sources. Of these, the greatest heritability estimates were found for modulus of elasticity and microfibril angle (0.39±0.09 and 0.37±0.08, respectively) while the heritability of DBH was moderate (0.32±0.08) and low for density (0.20±0.07). In contrast to many other forest tree species, there was zero genetic correlation found for DBH

Table 5 Genetic parameter estimates from bivariate across-trial analyses of growth and wood traits assessed in two *Eucalyptus pellita* progeny trials

Trait	DBH	DEN	KPY	MOE	MfA
Family level parameter estimates					
DBH	**0.32 (0.08)**				
DEN	0.00 (0.00)	**0.20 (0.07)**			
KPY	−0.12 (0.17)	0.07 (0.20)	**0.34 (0.08)**		
MOE	0.26 (0.16)	0.78 (0.08)	0.52 (0.12)	**0.39 (0.09)**	
MfA	−0.19 (0.16)	−0.65 (0.11)	−0.36 (0.14)	CF	**0.37 (0.08)**
Seed source level parameter estimates					
DBH	**0.02 (0.02)**				
DEN	0.76 (0.21)	**0.04 (0.02)**			
KPY	−0.31 (0.55)	0.17 (0.42)	**0.04 (0.03)**		
MOE	0.93 (0.08)	0.29 (0.35)	0.05 (0.46)	**0.07 (0.04)**	
MfA	−0.82 (0.17)	−0.26 (0.33)	−0.22 (0.41)	CF	**0.06 (0.03)**

Family parameter estimates include narrow-sense heritability on the diagonal (bold) and type A additive genetic correlations below the diagonal. Seed source parameter estimates include proportion of phenotypic variance on the diagonal and type A seed source correlations below the diagonal (approximate standard errors of estimates are given in parentheses)

DBH diameter at breast height over bark, *DEN* wood basic density, *KPY* Kraft pulp yield, *MOE* modulus of elasticity, *MfA* microfibril angle, *CF* convergence failed

and density at the family level and a high correlation at the seed source level was associated with a high standard error (Table 5). Similarly, a very high correlation between DBH and modulus of elasticity was found for seed sources, but the correlation was low at the family level. DBH was negatively correlated with both Kraft pulp yield and microfibril angle at both the family and seed source levels. Among wood quality traits, microfibril angle was moderately (−0.36) and strongly (-0.65) correlated at the family level with Kraft pulp yield and density, respectively. Unfortunately, the genetic relationship between microfibril angle and modulus of elasticity was not estimable for this species as the convergence of these REML analyses failed. A very low additive genetic correlation with high standard error was found between density and Kraft pulp yield with these two traits highly correlated with modulus of elasticity (Table 5).

3.2.2 Genetic parameter estimates from trial-trial correlations

Unbiased narrow-sense heritability and the seed source proportion of phenotypic variance estimates from across-trial analyses (Table 6) were similar to those estimated from single-trial analyses (Table 5) with single-trial heritability estimates typically higher than estimates from across-trial analyses. All type B seed source correlations were moderate to strong with the exception of Kraft pulp yield (Table 6). The same pattern was evident for type B additive genetic correlations indicating genotype by environment interactions not significant.

4 Discussion

4.1 Trial means and variation among seed sources

The representation of seed sources and families within seed source were similar in the two trials; therefore, trial differences expressed in mean values are assumed to be caused largely by differences in the environmental conditions (Pliura et al. 2007) experienced by the progeny trials. The slower growth rate observed in the Pleiku trial was likely due to cooler and drier climatic conditions as this trial is located on the high central plateau in Vietnam. Significantly higher ($p<0.001$) growth found in the Bau Bang trial, most probably resulting from higher annual rainfall and warmer temperatures associated with lower elevation and latitude of this trial (Table 1). Significant site effects for growth traits (tree height and diameter) have been reported for *E. pellita* at four sites in Indonesia (Leksono et al. 2008). In comparison with a temperate eucalypt at a similar age (11 years of age), trial mean found for diameter at Bau Bang was similar with the overall mean of diameter of *E. globulus* reported by Apiolaza et al. (2005). Unexpectedly, higher wood density and modulus of elasticity, and lower microfibril angle were not observed in the less productive trial (Pleiku), as higher growth rates are expected to result in decreasing wood density and modulus of elasticity, and increasing microfibril angle (Zobel and van Buijtenen 1989). In contrast, significantly ($p<0.05$) greater Kraft pulp yield was evident at the Pleiku trial. Density, modulus of elasticity and microfibril angle means found in the present study are somewhat higher than those previously reported in

Table 6 Genetic parameter estimates from analyses for growth and wood traits in two *Eucalyptus pellita* progeny trials

Trial/trait	Diameter		Density		Kraft pulp yield		Modulus of elasticity		Microfibril angle	
	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang	Pleiku	Bau Bang
Family level parameter estimates										
Pleiku	**0.30 (0.13)**		**0.25 (0.13)**		**0.28 (0.13)**		**0.35 (0.14)**		**0.14 (0.12)**	
Bau Bang	1.0 (0.0)	**0.41 (0.12)**	0.71 (0.16)	**0.25 (0.1)**	0.85 (0.07)	**0.46 (0.13)**	0.60 (0.15)	**0.51 (0.14)**	1.0 (0.0)	**0.49 (0.13)**
Seed source level parameter estimates										
Pleiku	CF		**0.04 (0.03)**		**0.03 (0.04)**		**0.04 (0.03)**		**0.02 (0.02)**	
Bau Bang			0.97 (0.04)	**0.05 (0.03)**	0.10 (0.61)	**0.11 (0.08)**	0.78 (0.21)	**0.11 (0.07)**	0.60 (0.23)	**0.16 (0.04)**

Narrow-sense heritability estimates or the proportion of variance between seed sources are given on the diagonals (bold). Type B (among trials) additive genetic and seed sources correlations are given below the diagonal. Approximate standard errors of each estimate are given in the parentheses

Notes: CF = convergence failed

ITTO (2006) for *E. pellita* at 13 years of age (630 kg/m^3, 17.3 GPa and 10.2°, respectively). Likewise, *E. pellita* had greater wood density means (657 and 665 kg/m^3 in the Pleiku and Bau Bang trials, respectively) when compared with trial means of *E. globulus*, with ranges from 520 to 547 kg/m^3 (Miranda and Pereira 2002), 492 kg/m^3 (Apiolaza et al. 2005), and 482 to 488 kg/m^3 (Downes et al. 2006). Tran et al. (2010) also found lower wood density (521 kg/m^3) for *E. urophylla* in a progeny trial established in northern Vietnam. However, wood density observed in the present study was similar to that reported for *E. pellita* by Lee et al. (2011) and much lower than estimates (750 kg/m^3) reported by Brawner et al. (2012) for another eucalypt species, *Corymbia citriodora*. In contrast with wood density, mean values of Kraft pulp yield found here (45.5 and 46.8 %) were lower than those found for *E. globulus*: 56.9 to 60.9 % (Miranda and Pereira 2002), 51.57 % (Apiolaza et al. 2005) and 52.2 % (Costa e Silva et al. 2009).

In this study, comparisons among the Kairi and Cardwell orchards are of interest as Kairi and Pleiku are at higher elevation and experienced lower mean annual temperatures and precipitation than Cardwell and Bau Bang. The Northern Territory SSO was established in a monsoonal environment at Yapilika on Mellville Island to the north of Darwin—a site with very distinct wet and dry seasons. The data allowed for an estimate of local adaptation brought about by selection for growth in contrasting first-generation trials, with families selected from a first-generation trial on the Tablelands of Queensland shown to be more productive (i.e. larger average diameter, $p<0.001$ for the contrast between 19616 and 19673 at Pleiku) than families selected from the first-generation trial in the Queensland lowlands when tested in the Vietnamese highlands. While the reverse was true in the lowland Vietnamese trial where the ranking of these seed lots reversed, differences were not significant.

Of the three seed sources that were collected from progeny trials that had been thinned into SSOs in Australia, two (19616 from the highland tropics of Atherton Tablelands and 19718 from the monsoonal tropics of Melville Island) grew well across both trials. The third seed source, which originated from a progeny trial established in a high rainfall, lowland Australian environment, did not perform well in the drier, highland Vietnamese trial. The better seed sources were represented by open-pollinated families from trees selected in thinned SSOs in Australia, with 19616 represented as open-pollinated families from six trees selected from within the Kairi progeny trial and 19718 represented by 13 or 14 families selected on Melville Island. The entire Kairi orchard was derived from Bupul-Muting (PNG) families, and the Melville trial was derived from seven provenances representing the range of the species in Australia and New Guinea. Both first- and second-generation families from New Guinea were used to establish the trials in Vietnam, and this allowed comparisons between New Guinea populations sourced from either the wild or planted forests managed as SSOs established in Australia. These comparisons demonstrate improvement that has been achieved through selection and/or increased out-crossing in managed orchards. The average diameters of families sourced from the three Australian orchards were 4 to 9 % larger than the diameters of the families sourced from natural populations in New Guinea. This difference is still evident even after thinning of inferior trees. This may be interpreted as a genetic gain but may be inflated by competition effects (i.e. between row plots).

Several seed sources achieved high growth rates at only one site. For instance, 19673 (from the Cardwell SSO in the humid lowlands of Queensland) performed best (ranked first) in the Bau Bang trial but grew relatively poorly in the upland Pleiku trial. Unimproved material originating from the native forests of Papua New Guinea and Indonesia typically did not

have high growth rates relative to families selected from the Australian SSOs. Nonetheless, at earlier ages in a trial established in Malaysia, the growth of two New Guinean provenances clearly outperformed the SSO seed sources, and Papua New Guinean provenances were superior to all Queensland provenances tested at a trial in the Northern Territory, Australia (Harwood et al. 1997). The growth of *E. pellita* found in the literature varies markedly. Kha et al. (2003) reported that at 8 years of age at central Vietnam diameter of six provenances ranged from 8.4 to 10.2 cm. At the same time, Hardiyanto (2003) showed that *E. pellita* grew much faster in Indonesia, with diameter of 20.6 to 21.5 cm at 7.5 years of age. While studies on the growth rates for *E. pellita* are available in the published literature, little can be found for the wood properties of *E. pellita*. In this study, the source from Melville Island SSO (19718) was superior for wood quality traits across the two trials. This seed source not only grew well but also had relatively high density, Kraft pulp yield and modulus of elasticity, and low microfibril angle. Another seed source from the Kairi SSO in Queensland (19616) also grew well across the two trials; however, this seed source had lower Kraft pulp yield, but its density and modulus of elasticity were quite high.

4.2 Genetic parameter estimates

Estimates of biased narrow-sense heritability at younger ages (Luo et al. 2006) ranged from 0.19±0.03 to 0.25±0.05 for diameter seem to fit reasonably with those found in the present study. However, the current across-trial (or unbiased) heritability estimates found for diameter are somewhat greater than those previously reported, with a range of 0.30±0.13 to 0.41±0.12 compared with 0.22 to 0.25 at six years of age (Leksono et al. 2006), and 0.15 to 0.25 (Leksono et al. 2008) and 0.15 to 0.33 (Brawner et al. 2010) at younger ages (1 to 3 years of age). A reason for this may be the use of one third rather than one quarter for the coefficient of relationship (Hodge et al. 2002). Another factor may be due to the fact that these trials were thinned twice and thinning can inflate heritability estimates (Matheson and Raymond 1984). Across-trial heritability estimates for wood quality traits indicated that these traits are under moderate levels of genetic control. As the present study is the first to provide pair-site genetic parameter estimates for wood properties of *E. pellita*, comparisons are made with other *Eucalyptus* species.

The heritability estimate for wood density (0.20±0.07) found here was low when compared to the range of values reported previously for other eucalypts. Sanhueza et al. (2002) reported heritability estimates for pilodyn penetration (an indirect measurement of wood density) of *E. globulus* at 4 and 5 years of age of 0.33 and 0.35, respectively. Moderate heritability (0.37) was also found for pilodyn penetration of *E. globulus* grown in a range of sites in Portugal, with ages ranging from 4 to 11 years (Costa e Silva et al. 2009). These differences may be caused by a number of reasons, such as different tree species assessed, the methods of estimation of wood density (pilodyn penetration versus NIR spectroscopy) and the ages of trees. However, heritability estimates for Kraft pulp yield, modulus of elasticity and microfibril angle in the present study are within the range of those previously published elsewhere for eucalypts (Raymond 2002; Schimleck et al. 2004; Apiolaza et al. 2005; Costa e Silva et al. 2009). Estimates of the proportion of variance among seed source were consistently lower than heritability estimates, suggesting that additive variance is more important than variation among PNG sources; however, as noted earlier, this may result from the deliberate exclusion of north Queensland sources.

Genetic correlations are useful to understand the importance of acclimation for the species in a range of sites and to make inferences about indirect responses on one trait from selection on others. Of these traits, growth, wood density and Kraft pulp yield are of particular importance as they can strongly impact pulp productivity (Borralho et al. 1993; Greaves et al. 1997). However, the present study found that there was no additive genetic correlation among diameter and wood density, which agrees with Miranda et al. (2001) who also found no correlation between growth and wood density in *E. globulus*. The additive genetic correlation between diameter and Kraft pulp yield found here was unfavourable (negative, see Table 5). Nevertheless, reports from previous studies upon the correlations among growth and wood density, and growth and Kraft pulp yield are often conflicting. For *E. globulus*, MacDonald et al. (1997) and Sanhueza et al (2002) reported slightly positive correlations among pilodyn and diameter, and for mean annual volume increment and pilodyn (0.25 and a range of 0.09 to 0.22, respectively); however, other authors report weak (Hamilton et al. 2010) to moderate (Wei and Borralho 1997; Apiolaza et al. 2005) negative correlations between wood density and diameter. Further, on two sites investigated for *Eucalyptus nitens*, Hamilton et al. (2009) report the additive genetic correlations among wood density and diameter were moderate and negative for one site and positive for the other. Similarly, for *E. globulus*, although the genetic correlation between Kraft pulp yield and diameter was positive in Costa e Silva et al. (2009), it was negative in Apiolaza et al. (2005). These differences in the genetic correlations among growth and wood density, and growth and Kraft pulp yield may be due to the different ages of assessment at the same site (MacDonald et al. 1997;

Hamilton et al. 2010) and different sites of assessment (Apiolaza et al. 2005; Costa e Silva et al. 2009). In the present study, the genetic correlation obtained for wood density and Kraft pulp yield were positive but not significantly different from zero. This correlation for wood density and Kraft pulp yield is consistent with Costa e Silva et al. (2009) who showed a genetic correlation between pilodyn and pulp yield was 0.05. The strongly positive genetic correlation between modulus of elasticity and wood density observed here corresponds with other studies on *E. nitens* (Blackburn et al. 2010) and softwood species (Dungey et al. 2006). While we were unable to calculate a correlation between microfibril angle and modulus of elasticity due to convergence failure in REML analyses, genetic correlations between microfibril angle and all other traits were favourable in the current study, suggesting the genetic correlation between microfibril angle and modulus of elasticity is also likely to be favourable. This was consistent with previous estimates of correlations among microfibril angle and diameter, microfibril angle and wood density, and microfibril angle and Kraft pulp yield for other species (Apiolaza et al. 2005; Baltunis et al. 2007).

Different traits had different magnitudes of genotype by environment interaction found in this study for *E. pellita*. On one hand, type B genetic correlations among sites for diameter and microfibril angle were both 1.0, indicating that there was no genotype by environment interaction for these traits. This suggests that estimated breeding values for these two traits will rank similarly across sites. This corresponds with the findings of Brawner et al. (2010b) for diameter, where the correlation between sites in Indonesia was reported to be moderate to strong (0.49 to 0.79). Type B genetic correlations for wood density and Kraft pulp yield among trials were above 0.70, indicating low genotype by environment interaction. However, genetic correlation estimates for modulus of elasticity between the two trials were lower at 0.60, suggesting genotype by environment interaction may be more important for this trait. On the other hand, at the seed source level (with the exception for diameter as the convergence failed in REML analysis), type B correlation for microfibril angle among trials was only moderately high (0.60). In addition, type B seed source correlation for Kraft pulp yield was very small and not significantly different from zero. This implies that for Kraft pulp yield, the performance of provenances was inconsistent across the two trials. Nonetheless, type B seed source correlations for wood density and modulus of elasticity were very high and positive (0.97 and 0.78, respectively), indicating a low level of seed source by environment interaction observed in these trials. The results presented herein suggest that all assessed traits, at the family level, are likely to be moderately-high to highly stable across environments.

5 Conclusion

The results of this study indicate that the growth rates of *E. pellita* were good on contrasting sites in Vietnam and that its wood properties are suitable for both pulping and solid timber production. Genetic parameters were estimated for five industrially important traits in red mahogany from two open-pollinated progeny trials. Heritability estimates were lower for diameter and wood density than for Kraft pulp yield, modulus of elasticity and microfibril angle. However, these traits are under moderate genetic control and therefore the species can offer good opportunities for substantial genetic improvement of these traits. The negative correlations between microfibril angle and other traits were favourable. However, the negative correlation between diameter and Kraft pulp yield, as well as the zero or low correlations between diameter and wood density, and between Kraft pulp yield and wood density were neutral. The largest correlation between wood traits was between wood density and modulus of elasticity at the family level. Variation was much higher at the family level than the seed source level, and genotype by environment interactions were low between these two trials.

These results indicate that selection of the best individuals (i.e. those with highest breeding values) across all seed sources of *E. pellita* is likely to lead to significant gains in key growth and wood property traits, as heritability of these traits were moderate to high and variation between the PNG seed sources evaluated was relatively small compared to variation between families for all traits except density. Given the observed trait-trait correlations, multi-trait selection in *E. pellita* can be expected to lead gains in both growth and wood property traits, improving the suitability of the species for production of both timber and pulpwood. The results are important to improve the understanding the genetic control of economically important traits and for directing ongoing *E. pellita* breeding and improvement programs in Vietnam and elsewhere.

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Appendix 1

Table 7 The calibration statistics for the near infrared (NIR) calibration models used in the prediction of pulp yield, density, modulus of elasticity and microfibril angle

Trait	R_C^2	RMSEC	RMSEV	No. of factors	Outliers excluded	No. of samples	R_P^2	RMSEP	SEP	Reference
Kraft pulp yield (%)	0.94	2.1	2.1	5	24	729	0.80	2.1	2.1	(Meder et al. 2011)
Density (kg/m^3)	0.64	47	49	7	27	1,028	0.61	49	49	Unpublished data
Modulus of elasticity (GPa)	0.78	2.2	2.3	5	75	1,923	0.77	2.2	2.3	Unpublished data
Microfibril angle (°)	0.65	2.2	2.3	5	10	1,923	0.63	2.2	2.2	Unpublished data

All models used second derivative in treatment procedure

R_C^2 coefficient of determination for the calibration model, *RMSEC* root mean square error of calibration, *RMSEV* root mean square error of cross validation, *No. of factors* number of factors used in NIR model development, *No. of samples* number of samples used in model calibration, R_P^2 coefficient of determination for the prediction, *RMSEP* root mean square error of prediction, *SEP* standard error of predicted residuals

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