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GENETIC IMPROVEMENT FOR WOOD PRODUCTION IN *MELALEUCA CAJUPUTI*

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Genetic parameters was estimated for growth (tree height, diameter at breast height (DBH) and volume), stem form, MOE (wood stiffness), bark thickness and bark ratio in a half-sib family progeny trial of *Melaleuca cajuputi* comprising 80 families in South Vietnam. MOE of standing trees was measured indirectly by acoustic velocity using microsecond timer. Narrow-sense heritability ranged from 0.13 to 0.27 at age 7 years. MOE and stem form had positive genetic correlations with growth while negative correlation between bark ratio and growth was also favourable. Breeding for simultaneous improvement of multiple traits, faster growth with higher MOE and reduction of bark ratio should be possible in *M. cajuputi*. Index selection based on volume and MOE showed genetic gains of 31% in volume, 6% in MOE and 13% in stem form. In addition, heritability and age–age genetic correlations for growth traits increased with time and optimal early selection age for growth of *M. cajuputi* based on DBH alone was 4 years. Selected thinning resulted in an increase in heritability due to considerable reduction of phenotypic variation but had little effect on genetic variation.

Keywords: Heritability, age–age correlation, stiffness, acoustic velocity, bark thickness, optimum selection age, thinning effect

INTRODUCTION

Melaleuca cajuputi is a moderately fast-growing tree species considered to be a multipurpose species supplying fuelwood, piles and frame poles of construction, leaf essential oil and honey (Doran & Turnbull 1997). The species includes three recognised subspecies: *cajuputi, cumingiana* and *platyphylla*, which occur in Australia, Papua New Guinea and South-East-Asia (Craven & Barlow 1997, Brophy et al. 2013). *Melaleuca cajuputi* plantation can be harvested on 6–7-year rotations (Trung 2008, Nuyim 2001). Its timber can be used for pulp and paper, fibre and particle board, producing quality charcoal and potentially sawn timber (Trung 2008). The species is adapted to tropical environments and particularly to soils with higher salinities and/or aluminum levels as well as being tolerant to fire, drought, flooding and low soil pH (Yamanoshita et al. 1999, Nuyim 2001, Tran et al. 2013). It is well suited to sites in the Mekong Delta in Vietnam that are otherwise difficult for tree plantation establishment due to seasonal inundation and acid sulfate soils (Chuong et al. 1996, Doran & Turnbull 1997).

Species/provenance trials of melaleucas for wood and/or essential oil production were established in 1993 in the Mekong Delta (Kha et al. 1999). One of the species included in these trials, *M. cajuputi* subsp. *cumingiana* which is indigenous to Vietnam (Craven & Barlow 1997), was selected as a top priority for reforestation efforts in Mekong Delta, even though it was outperformed in growth by some exotic *Melaleuca* species introduced from Australia and Papua New Guinea (Kha et al. 1999, Pinypusarerk & Doran 1999). Three natural provenances of *M. cajuputi* subsp. *cumingiana* (Moc Hoa, Vinh Hung and Tinh Bien) were recognised by the Vietnamese Ministry of Agriculture and Rural Development as advanced varieties for commercial plantation establishment.

A breeding programme for *M. cajuputi* that aims primarily at improving yields of essential leaf oils has been conducted for many years in Indonesia (Doran et al. 1998). Genetic gains of 10 and 21% for the content of 1.8 cineole and oil yield respectively have been reported (Susanto et al. 2003). Genetic variation, mating system, fertility variation and genetic diversity of *M. cajuputi* were also studied (Kartikawati et al. 2013, Kartikawati 2016). Most *M. cajuputi* breeding programmes have been focused on oil production. After recognition of the potential of this species for wood production in acid sulfate soils of the Mekong Delta, a breeding programme aimed at improving tree growth for wood production was established in Vietnam in 2006. Preliminary works had been done to examine mechanical properties and anatomical characteristics of *M. cajuputi* timber (Junji 1999, Ban 2002). However, basic information about genetic variation in wood properties of *M. cajuputi* has not been reported.

This study was conducted to evaluate genetic variation in growth, stem form, MOE, bark thickness and bark ratio in an open-pollinated progeny trial of 7-year-old *M. cajuputi* in southern Vietnam. Estimates of heritability, genetic and phenotypic correlations between the traits are presented. The expected response from combined index selection, based on genetic parameters for growth and wood stiffness, i.e. modulus of elasticity (MOE) is discussed in relation to the breeding strategy to improve wood production.

MATERIALS AND METHODS

Trial site, genetic material and experimental design

An open-pollinated progeny trial of *M. cajuputi* subsp. *cumingiana* was established in July 2009 at Thanh Hoa, Long An province (10° 35' N, 106° 11' E, 12 m above sea level) on seasonally inundated acid sulphate soil (pH 2.9–3.7). Average temperature is 27.3 °C and annual rainfall ranges from 1325 to 1670 mm. Rainy season starts from May and ends in November. About 93% of total annual rainfall occurs in the rainy seasons. Inundation of the local area usually begins in the middle of August and lasts till November. Maximum water level can reach above 1.5 m.

The trial comprised 80 families collected from individual plus trees with fast growth, good stem form (straightness and narrow crown), fruiting and no visible insect or disease damage. All plus trees were selected in three natural provenance locations, namely, Moc Hoa, Vinh Hung and Tinh Bien in the Mekong Delta. The trial was planted as randomised complete block design and represented by 51 replicates. Each replicate consisted of a 4-tree row plot of each family, with a spacing of 1 m between trees within rows and 1.5 m between rows. The entire trial was thinned at age 4 years to retain the best two trees in each family plot. Felled trees were either dead or had other deficiencies (slow growth, broken stems or attacked by stem borer).

Data collection and analysis

Eighteen replicates in the trial were assessed for diameter at breast height (DBH) and total height from 2010 to 2016. Volume, stem form, bark thickness, bark ratio and acoustic velocity were evaluated in 2016, and MOE was computed using acoustic velocity. DBH and tree height (H) were measured using tapeline and measurement pole. Stem volume (V) was calculated by the formula:

$$V\ (\mathrm{dm}^3) = \frac{\pi \mathrm{DBH}^2}{4} \times \mathrm{H} \times \mathrm{f} \qquad (1)$$

where, f is a form index and was estimated to be 0.5 (Kha et al. 1999).

Bark thickness was measured at three points around 1.3 m height of the stem using nail and callipers. Bark ratio was calculated by volume basis (bark volume/under-bark stem volume). Tree form was scored as one of four categories based on construction pole requirements, i.e. 1 = bad, 2 = average, 3 = good and 4 = very good. A non-destructive testing method was used for computing MOE using acoustic velocity on standing tree (Jayawickrama 2001). Two probes were inserted into a tree stem, 1 m apart, between 0.7 and 1.7 m and three horizontal points on the same stem (e.g. 120° between each point) were measured. The acoustic velocity (AV) were calculated using the equation:

$$\mathrm{AV}\ (\mathrm{ms}^{-1}) = \frac{s}{t} \qquad (2)$$

where, s is the distance between probes and t is the transit time. MOE was estimated from the acoustic velocity through the one-dimensional wave equation (Johnson & Gartner 2006):

$$\text{MOE (GPa)} = AV^2\rho \qquad (3)$$

where, ρ is green density of the material (kg m^{-3}). Seven-year-old *M. cajuputi* green density (968 kg m^{-3}) was assumed to be constant.

Variance and covariance components for all phenotypic traits were estimated by mixed-model equation (Isik et al. 2017):

$$Y_{ijk} = \mu + B_i + P_j + F_{k(j)} + BF_k + e_{ijk} \qquad (4)$$

where, Y_{ijk} is the plot mean of kth family within provenance jth within replicate ith; μ is the overall mean; B_i, P_j and $F_{k(j)}$ are the effects of ith block (or replicate), jth provenance and kth family effect; BF_{ik} is the random family by block interaction effect; and e_{ijk} is the residual error with a mean of zero. For these analyses, provenances were regarded as fixed effects while families, block and family by block interaction were regarded as random.

For each trait, the narrow-sense heritability (h_i^2), family mean heritability (h_{fm}^2) and within family heritability (h_w^2) were estimated from univariate analyses as follows:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_p^2} = \frac{4\sigma_f^2}{\sigma_p^2} \quad (\sigma_p^2 = \sigma_f^2 + \sigma_{bf}^2 + \sigma_e^2) \qquad (5)$$

$$h_{fm}^2 = \frac{\sigma_f^2}{\sigma_{fm}^2} \quad (\sigma_{fm}^2 = \sigma_f^2 + \tfrac{1}{b}\sigma_{bf}^2 + \tfrac{1}{bn}\,\sigma_e^2) \qquad (6)$$

$$h_w^2 = \frac{3\sigma_f^2}{\sigma_w^2} \quad (\sigma_w^2 = \tfrac{(b-1)}{b}\sigma_{bf}^2 + \tfrac{(bn-1)}{bn}\,\sigma_e^2) \qquad (7)$$

where, σ_A^2 and σ_p^2 are the additive and phenotypic variances; σ_f^2 and σ_e^2 are the family and residual variances; σ_{bf}^2 is the variance of family by block interaction; σ_{fm}^2 and σ_w^2 are the family mean and within family variances; and b and n are number of blocks and plants per block respectively. Coefficients of variation (CV) was calculated as:

$$CV_1 = \frac{100\sqrt{\sigma_1^2}}{\bar{X}} \qquad (8)$$

where, σ_1^2 is the considered variance and $\bar{X}$ is the phenotypic mean of the trait.

Genetic (r_g) and phenotypic (r_p) correlations between traits were calculated as:

$$r_g = \frac{Cov_{f(x,\,y)}}{[\sigma_f^2(x).\,\sigma_f^2(y)]^{1/2}} \qquad (9)$$

$$r_p = \frac{Cov_{p(x,\,y)}}{[\sigma_p^2(x).\,\sigma_p^2(y)]^{1/2}} \qquad (10)$$

where, $Cov_f(x, y)$ and $Cov_p(x, y)$ are family covariance component and phenotypic covariance (based on family means) between traits x and y respectively; and $\sigma_f^2(x)$ $\sigma_f^2(y)$ and are family level variance components of trait x and y. Expected genetic gain (ΔG) is the amount of increase in performance from mass selection in the trial and estimated by the formula:

$$\Delta G = h_i^2 \text{ x } i \text{ x } \sigma_p \qquad (11)$$

where, i is selection intensity, σ_p is the phenotypic standard deviation for the trait of interest and h_i^2 is individual tree heritability for the trait of interest. The correlated responses were calculated as:

$$CR_Y = ih_Xh_Yr_g\sigma_{PY} \qquad (12)$$

where, character X is selected directly and then Y is a correlated character selected indirectly. Breeding selection was based on selection indices (I) constructed for improvement of single and multiple traits and with or without restriction among traits (Falconer & Mackay 1996).

$$I = b_1P_1 + b_2P_2 + \ldots + b_mP_m \qquad (13)$$

where P_1 to P_m are phenotypic measurements of m characters on which selection is to be based, and b_1 to b_m are the corresponding weighting factors to be determined. A total of six different selection scenarios were considered:

A—selection for each independent trait,

B—selection based on DBH, but calculating indirect effect on other correlated traits,

C—selection based on volume, but calculating indirect effect on other correlated traits,

D—index selection based on volume and stem form,

E—index selection based on volume and MOE, and

F—index selection based on volume and MOE with the restriction of no change on bark thickness.

The index coefficients were obtained from

$$b = P^{-1} \times G \times a \qquad (14)$$

where P and G are the phenotypic and additive genetic variance–covariance matrices for selected traits, and a is vector of weighting coefficients assigned as reciprocals of the phenotypic standard deviations for each of objective traits (equal economic values are assigned to one standard deviation for change in each character). For restricted selection index, equation 14 could be modified as (Mrode & Thompson 2005):

$$b^* = \begin{bmatrix} P^* & G^* \\ G^* & 0 \end{bmatrix}^{-1} \times \begin{bmatrix} G^{**} \\ 0 \end{bmatrix} \times a \qquad (15)$$

where P* is the phenotypic variance–covariance matrix for selection traits; G* is the additive genetic variance–covariance matrix between selected traits and traits excluding restricted traits; G** is the additive genetic variance–covariance matrix between selected traits excluding restricted traits; and 0 is the zero vector. Statistical analyses were conducted using ASReml 4.0 (2014).

RESULTS

Mean, variation and heritability

Mean values, ranges, standard deviations and coefficients of variation of DBH, height, volume, stem form, acoustic velocity, MOE, bark ratio and thickness traits at 7 years are presented in Table 1. Acoustic velocity showed the smallest phenotypic variation (6.30%), followed by tree height, MOE and DBH (between 12.17–20.19%), while bark ratio, bark thickness and stem form showed large phenotypic variation (24.29–32.26%) and the largest phenotypic variation was volume (50.14%).

Individual heritability ranged from 0.13 to 0.27 while family mean heritability for these traits was higher (0.49–0.64) than both the individual heritability and the within family heritability (0.11–0.22) (Table 2). Individual heritability estimates for growth (DBH, height and volume) were in a narrow range of 0.25–0.27. Stem form had the lowest heritability (0.13), while MOE and acoustic velocity had moderate heritability of 0.21 and bark thickness and ratio had 0.23 and 0.21 respectively.

Phenotypic and genetic correlations between traits

The phenotypic and genetic correlations between DBH, height, volume, stem form, acoustic velocity, MOE, bark thickness and bark ratio for *M. cajuputi* at 7 years are shown in Table 3. There were very strong genetic (r_g = 0.88 to 0.99) and phenotypic (r_p = 0.73 to 0.97) correlations between growth traits. MOE had positive genetic and phenotypic correlations with growth, stem form and bark thickness. The genetic correlations between MOE and growth were moderate, i.e. 0.33–0.50. Negative correlations were found between bark ratio and growth traits

Table 1 Mean, range (minimum and maximum), standard deviation (SD) and coefficient of variation (CV) for growth, stem form, acoustic velocity, MOE, bark ratio and thickness of 7-year-old *Melaleuca cajuputi* in the progeny trial at Thanh Hoa, Long An, Vietnam

Trait	Mean	Minimum	Maximum	SD	CV (%)
DBH (cm)	7.77	3.20	14.60	1.57	20.19
Tree height (m)	8.64	4.10	12.90	1.05	12.17
Volume (dm^3)	22.08	1.65	108.00	11.07	50.14
Stem form	2.64	1.00	4.00	0.85	32.26
Acoustic velocity (km s^{-1})	3.65	2.63	4.35	0.23	6.30
MOE (GPa)	12.94	6.69	18.33	1.61	12.44
Bark ratio (%)	50.72	16.80	100.20	12.32	24.29
Bark thickness (cm)	0.68	0.21	1.65	0.17	25.25

DBH = diameter at breast height, MOE = modulus of elasticity

Table 2 Estimated individual (h^2_i), family mean (h^2_{fm}) and within family (h^2_w) heritability values of 7-year-old *M. cajuputi*

Trait	h^2_i	h^2_{fm}	h^2_w
DBH	0.25 (0.06)	0.64 (0.06)	0.21 (0.05)
Height	0.27 (0.07)	0.62 (0.06)	0.22 (0.06)
Volume	0.26 (0.06)	0.64 (0.06)	0.21 (0.05)
Stem form	0.13 (0.04)	0.49 (0.09)	0.11 (0.04)
Acoustic velocity	0.21 (0.06)	0.59 (0.07)	0.18 (0.05)
MOE	0.21 (0.06)	0.60 (0.07)	0.18 (0.05)
Bark ratio	0.23 (0.06)	0.59 (0.07)	0.19 (0.05)
Bark thickness	0.21 (0.06)	0.58 (0.07)	0.18 (0.05)

DBH = diameter at breast height, MOE = modulus of elasticity; standard errors are given in parentheses

Table 3 Genetic (above the diagonal) and phenotypic (below the diagonal) correlation between traits of 7-year-old *M. cajuputi* progeny trial

Trait	DBH	Height	Volume	Stem form	Acoustic velocity	MOE	Bark ratio	Bark thickness
DBH		0.88 (0.04)	0.99 (0.01)	0.76 (0.09)	0.33 (0.16)	0.33 (0.16)	-0.22 (0.16)	0.76 (0.07)
Height	0.73 (0.01)		0.92 (0.03)	0.88 (0.07)	0.50 (0.13)	0.50 (0.13)	-0.34 (0.15)	0.57 (0.11)
Volume	0.97 (0.00)	0.79 (0.01)		0.76 (0.09)	0.36 (0.15)	0.36 (0.15)	-0.23 (0.16)	0.73 (0.08)
Stem form	0.60 (0.01)	0.63 (0.01)	0.56 (0.01)		0.49 (0.16)	0.49 (0.16)	-0.23 (0.18)	0.56 (0.14)
Acoustic velocity	0.14 (0.02)	0.39 (0.02)	0.16 (0.02)	0.28 (0.02)		1.00 (0.00)	0.03 (0.17)	0.34 (0.16)
MOE	0.14 (0.02)	0.39 (0.02)	0.16 (0.02)	0.27 (0.02)	1.00 (0.00)		0.02 (0.17)	0.34 (0.16)
Bark ratio	-0.13 (0.02)	-0.19 (0.02)	-0.12 (0.02)	-0.15 (0.02)	-0.09 (0.02)	-0.09 (0.02)		0.47 (0.13)
Bark thickness	0.73 (0.01)	0.49 (0.02)	0.70 (0.01)	0.40 (0.02)	0.07 (0.02)	0.07 (0.02)	0.54 (0.02)	

DBH = diameter at breast height, MOE = modulus of elasticity; standard errors are given in parentheses

as well as between bark ratio and stem form. Bark ratio had moderate positive correlation with bark thickness. The correlation between bark ratio and MOE was nearly zero.

Trends of growth and heritability, and the effect of thinning

The age trends for growth and heritability for DBH and height are shown in Figure 1. The heritability for height increased from age 1 to 7. Heritability for DBH and height increased considerably after thinning at age 4. The highest values of heritability for growth were reached at 7 years. Selective thinning of 50% of trees resulted in reduction of phenotypic coefficient of variation of DBH and height (Figure 2).

The correlations between DBH and height from age 1 to 7 were moderate to strong and ranged from 0.45 to 0.99 (Figure 3). The phenotypic correlations were weaker than genetic correlations between DBH and height

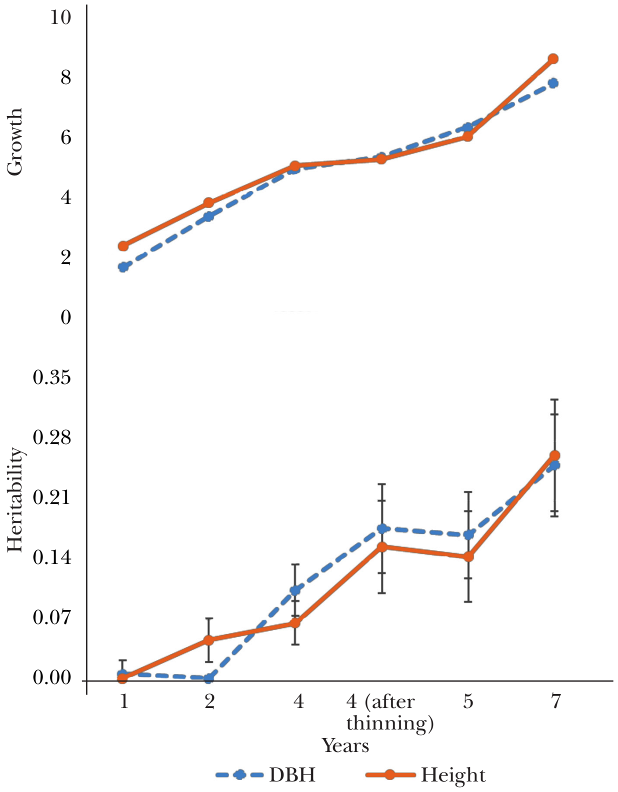

Figure 1 Diameter at breast height (DBH) (cm) and height (m) growth and heritability for *Melaleuca cajuputi* from ages 1 to 7 years old

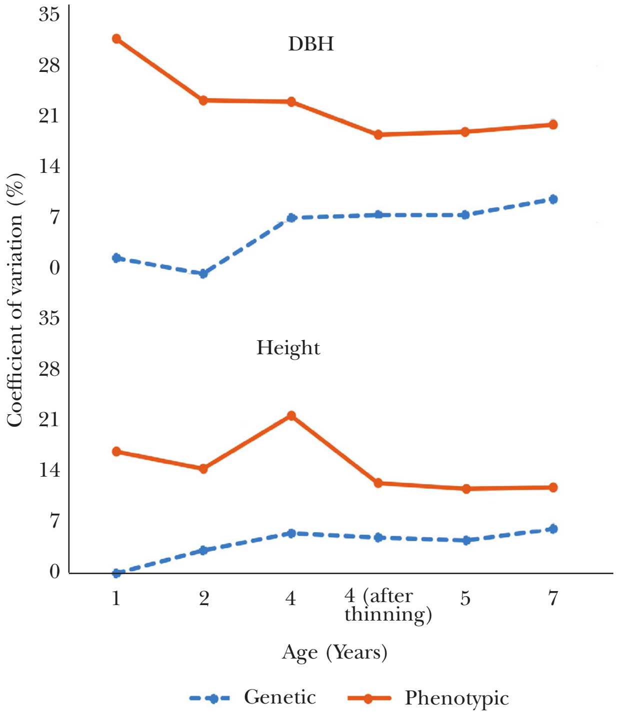

Figure 2 Genetic and phenotypic coefficient of variation trend for DBH and height for *Melaleuca cajuputi* from ages 1 to 7 years old

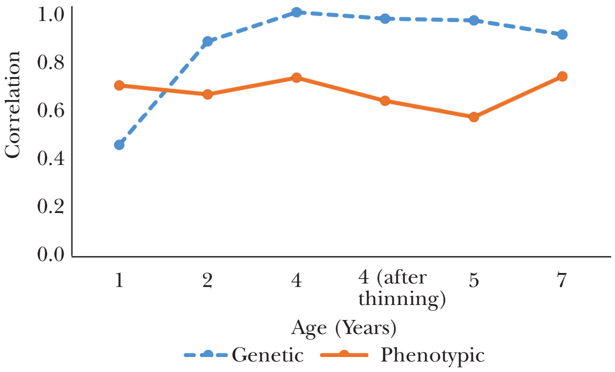

Figure 3 Genetic and phenotypic correlations between DBH and height for *Melaleuca cajuputi* from age 1 to 7 years old

at all ages except for age 1. Genetic correlations increased sharply from age 1 to 2, moderate from age 2 to 4 and decreased slightly after age 4. However, strong genetic correlations between DBH and height started from age 2.

Age–age correlation

Age–age correlations from age 1 to 7 years are shown in Figure 4. The age–age genetic correlation values were weak to moderate between ages 7 and 1 and ages 7 and 2 but stronger between ages 7 and 4 (both before and after thinning), and ages 7 and 5. For DBH and height, the trend of age–age correlation increased sharply from ages 2 to 4 and was nearly constant thereafter. DBH had higher age–age correlations than height after age 2.

Response for different selection scenarios

The results of six different selection scenarios are presented in Table 4 with the same selection intensity of 2.67 (i.e. 1%). In scenario A, genetic gains reached 7 to 34% as selection was based on each independent trait. Selections based on DBH alone (scenario B), volume (scenario C), volume and form (scenario D) showed negligible differences of genetic gains for growth traits. Genetic gains reached about 33% for volume, 9–13% for stem form and 1–4% for MOE. However, selection based on volume and MOE (scenario E) had less genetic gain of volume (31%, relative to 33%) but considerable increase in MOE (6%) compared with scenarios B, C and D. There were considerable differences in expected responses between selection based

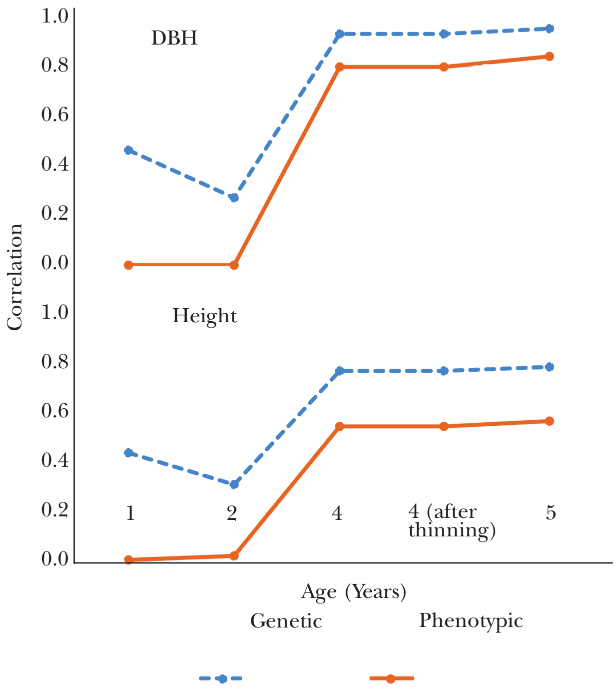

Figure 4 Genetic and phenotypic correlations for DBH and height of *Melaleuca cajuputi* between age 7 and earlier ages

on volume and MOE with the restriction of no change on bark thickness (scenario F) and all other scenarios. Restriction of no change on bark thickness in breeding selection resulted in decreasing expected responses of 16% in volume, 7% in stem form and 5% in MOE.

DISCUSSION

Mean, variation and heritability

The growth of 7-year-old *M. cajuputi* in this study reached 7.77 cm in DBH, 8.64 m in height and 22.08 dm^3 in volume. This result was similar to the previous studies in Vietnam (Hong et al. 2010). The phenotypic variations of growth traits were also close to the results of *Melaleuca* species/provenance trial (25.8% in DBH, 12.0% in height and 58.8% in volume) at the same age in Mekong Delta (Hong et al. 2010).

One of the main wood properties of interest to the wood industry is MOE. Acoustic tools have been used to measure MOE of standing trees, stems and logs (Jayawickrama 2001, Grabianowski et al. 2006). Previous studies of mechanical properties of *Melaleuca* wood used destructive methods (Junji 1999, Ban 2002, Wahyudi et al. 2014). In this study, non-destructive evaluation of mechanical properties of wood was conducted. The average MOE of *M. cajuputi* was 12.94 GPa at age 7 years, higher than the results reported by Ban (2002) on some wood characteristics of *M. cajuputi* at 6 years old (10.69 GPa) and *M. viridiflora* (11.38 GPa) but lower than *M. leucadendra* (13.83 GPa) at the same age. From these results, it seems that the larger the diameter, the higher the MOE of *M. cajuputi*. *Melaleuca cajuputi* showed lower acoustic velocity than *Eucalyptus globulus* at 10 years (Hamilton et al. 2017), but close to *E. nitens* at 14–19 years (Blackburn et al. 2014) and *Acacia melanoxoxylon* at 18 years old (Bradbury et al. 2011). Generally, *Melaleuca* wood has strong properties and high possibility to be used as a structural component (Junji 1999).

The heritability for MOE of *M. cajuputi* was moderate ($h_i^2 = 0.21$) and lower compared with the estimates of 10-year-old *E. globulus* (0.26) (Hamilton et al. 2017) and 8-year-old *E. urophylla* (0.47) (Wu et al. 2013) but higher than 24-year-old Norway spruce ($h_i^2 = 0.15$) (Chen et al. 2015). *Eucalyptus nitens* had a large range of heritability (0.16–0.74) at different sites (Blackburn et al. 2014). The bark of *M. cajuputi* species is very thick and the bark to under-bark stem volume ratio can reach 100%. Bark thickness and its percentage of volume of the tree or log are important in forest inventory and has a major effect on the amount of usable wood (Kleinn 2007). According to Van et al. (2000), variations in *Melaleuca* bark thickness were large at different sites in southern Florida. The percentage of bark fluctuates depending on species and size of tree which varies from 8% in volume for some large hardwood species to 40% for small tropical pines (Zobel & Jett 1995). In this study, *M. cajuputi* had high bark ratio of 50.72%. It was considerately higher than those of *Eucalyptus grandis* (7.43%) and *E. urophylla* (17.31%) (Retief & Stanger 2009). Thus, actual wood volume will be overestimated when tree diameter over bark is measured.

Phenotypic and genetic correlations between traits

The phenotypic and genetic correlations between all traits except for bark ratio of *M. cajuputi* were positive. This suggests that selection for one of these traits should result in a simultaneous positive response in other traits. The results of this study are comparable with different studies

Table 4 Expected response for DBH, height, volume, stem form, MOE, bark ratio and bark thickness of *Melaleuca cajuputi* when different selection criteria were used under selection intensity of 1% (i = 2.67)

Scenario	DBH (cm)	Tree height (m)	Volume (dm^3)	Stem form	MOE (GPa)	Bark ratio (%)	Bark thickness (cm)
A	1.05 (13.51%)	0.72 (8.33%)	7.50 (33.97%)	0.30 (11.50%)	0.09 (6.92%)	6.71 (13.24%)	0.10 (14.05%)
B	1.05 (13.51%)	0.62 (7.19%)	7.35 (33.27%)	0.32 (11.96%)	0.47 (3.66%)	-1.54 (-3.03%)	0.08 (11.51%)
C	1.05 (13.47%)	0.66 (7.59%)	7.50 (33.97%)	0.24 (8.94%)	0.15 (1.16%)	-0.86 (-1.69%)	0.07 (10.81%)
D	1.03 (13.30%)	0.66 (7.71%)	7.39 (33.48%)	0.34 (12.84%)	0.37 (2.86%)	-1.64 (-3.24%)	0.08 (11.16%)
E	0.93 (11.96%)	0.66 (7.66%)	6.80 (30.81%)	0.34 (12.87%)	0.79 (6.09%)	-1.01 (-1.99%)	0.07 (10.88%)
F	0.42 (5.43%)	0.42 (4.88%)	3.48 (15.77%)	0.20 (7.40%)	0.61 (4.69%)	-3.99 (-7.86%)	0.00 (0.00%)

DBH = diameter at breast height, MOE = modulus of elasticity; scenarios A: selection for each independent trait; B: selection based on DBH, but calculating indirect effect on other correlated traits, C: selection based on volume, but calculating indirect effect on other correlated traits, D: selection based on volume and form, E: selection based on volume and MOE, F: selection based on volume and MOE with the restriction of no change on bark thickness

of trees, in that diameter, height and volume are strongly inter-correlated (Butcher et al. 1996, Whittock et al. 2003, Gonçalves et al. 2005, White et al. 2007, Retief & Stanger 2009). These mean that bigger trees tend to have thicker bark. However, selection for bigger tree would reduce the bark to volume ratio due to negative genetic correlation between bark ratio and tree volume.

MOE had positive moderate genetic and phenotypic correlations with growth (0.33–0.50) which were similar to *Eucalyptus nitens* and *E. globulus* (Blackburn et al. 2014, Hamilton et al. 2017), but with the exception in *Eucalyptus urophylla* (Wu et al. 2013). This positive correlation is in contrast to most studies in conifer species where high or moderate negative genetic correlations were observed, such as *Pinus radiata* (Wu et al. 2008), *Pseudotsuga menziesii* (Johnson & Gartner 2006) and *Picea abies* (Chen et al. 2015). The positive correlation between growth and MOE in hardwood, particularly in *Melaleuca* species indicated that it was possible to select trees for larger stem and higher MOE.

Trends of growth and heritability and effect of thinning

The increased heritability for growth after the thinning at age 4 showed significant effects of selective thinning which caused considerable reduction of phenotypic variation but slight change in additive genetic variation. Increasing heritability for growth may be caused by normal development of the genetic parameter with time and/or selective thinning (Franklin 1979). Effect of selective thinning on heritability were reported in *E. urophylla* (Kien et al. 2009), *P. radiata* (Wu et al. 2007) and *P. sylvestris* (Hannrup et al. 1998). Selective thinning produced higher heritability than unthinned progeny trial. Commercial thinning inflates heritability estimates of growth (DBH), but had less impact on heritability of wood quality traits (Wu et al. 2007).

Age–age correlation

Age–age genetic correlations for DBH and height were strong between age 7 and earlier ages except for ages 1 and 2. DBH had strong correlation relative to height at all ages except for age 1. Therefore, early selection for growth of *M. cajuputi* based on DBH alone may be sufficient and could reduce costs of multiple early measurements.

Selection response

The positive genetic correlation between growth, stem form, MOE and adverse correlation between these traits and bark ratio are a considerable advantage for simultaneous improvement of multiple traits in advanced breeding programmes of *M. cajuputi*. However, deciding a breeding selection scenario is dependent on the use purpose of *Melaleuca* wood. As observed, selection based on volume and MOE would result in an increase in MOE (6%) which was higher than selection based on volume (1%) or DBH alone (4%).

CONCLUSIONS

This study observed increased heritability for growth traits with tree age and also as a consequence of selective thinning. Such thinning reduced phenotypic variation but had little effect on genetic variation. The age–age genetic correlations for growth traits increased with time and was higher than 0.77 from age 4. Optimal selection age for a 7-year rotation of *M. cajuputi* based on DBH was 4 years. Positive genetic correlations between growth traits and MOE indicated that simultaneous improvement of growth and stiffness were possible in *M. cajuputi*. Negative genetic correlation between tree volume and bark ratio meant that selection for bigger tree would reduce bark to volume ratio, which was favourable for sawn timber production. However, no change in bark thickness can reduce genetic gain for volume. Therefore, selection for volume and MOE simultaneously would be the best strategy for *M. cajuputi* breeding selection for production of sawn timber.

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