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DEVELOPING *EUCALYPTUS PELLITA* BREEDING POPULATIONS FOR THE SOLID WOOD INDUSTRY OF EASTERN MALAYSIA

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Eucalyptus pellita progeny within provenance trials were used to predict responses that will result from several selection scenarios designed to improve productivity and solid wood properties. Comparisons of genetic gain estimates derived from genetic parameters and predicted breeding values for growth and wood properties were used to evaluate what may be achieved from developing seed orchards that will supply logs for conversion into high-value wood products. Significant genetic variation in *E. pellita*, for volume, straightness and dynamic modulus of elasticity (MOE) was evident, and heritability estimates were low to moderate (h^2 ranged from 0.13 to 0.39, 0.19 to 0.26, and 0.12 to 0.23 respectively). High genetic correlations were observed between volume and straightness, while the genetic correlation with dynamic MOE was low but highly significant in two of the three trials. Genetic parameters for wood stiffness in *E. pellita* indicated selection of parents for growth and straightness which may positively impact wood properties. Predictions of genetic gain for several selection strategies provided an indication of improvement that may be realised when trials are converted into seedling seed orchards, and seed is collected for reforestation.

Keywords: *Eucalyptus pellita*, solid wood, wood properties, genetic gain, seed orchads

INTRODUCTION

Tree domestication trials established in both wet and dry environments in the tropics have shown that *Eucalyptus pellita* is a reliable species for plantation forestry (Dickinson & Sun 1995, Harwood et al. 1997a, Nikles et al. 2000, Lee et al. 2012, Luo et al. 2006, Japarudin et al. 2020). Evaluation of provenance performance outside the species' natural range provided early indications of its adaptability (Pinyopusarerk et al. 1996, Harwood et al. 1997b, Bernardo et al. 1998, Hardiyanto 2003). These experimental populations are often converted into seed production areas and seedling seed orchards, and data are used by breeding programs to guide plantation development. *Eucalyptus pellita* is particularly resistant to foliar pathogens when compared to other *Eucalyptus* species evaluated in the wet tropics (Harwood 1998, Japarudin et al. 2020). Over the past 10 years, *E. pellita* has been planted extensively to replace *Acacia mangium* plantations that have been severely impacted by *Ceratocystis* wilt disease (Tarigan et al. 2010, Tarigan & Wingfield 2011, Brawner et al. 2015). The significant decline in *A. mangium* industrial tree plantations across eastern Malaysia led to a rapid replacement with *E. pellita* and other species.

Eucalyptus pellita planted forests provide an alternative wood supply to meet the large demand for logs, created by reduced harvesting of mixed tropical hardwood species from native forests. If *E. pellita* plantations are to sustain a viable timber industry in Sabah, it is necessary to ensure that the mechanical wood properties are suitable for commercial use and meet industry standards. *Eucalyptus pellita* grown in Queensland, Australia shows considerable promise for solid wood production (Baillères et al. 2008). Several studies in South East Asia have also indicated the potential of this species for veneer production

(Japarudin et al. 2021a). Although considerable effort has been placed on improving kraft pulp yield, little has been done in breeding programs to improve the solid wood properties of *E. pellita* so as to support plantations managed for the production of solid wood (Hung et al. 2015, Lukmandaru et al. 2016).

A study on plantation-grown *E. globulus* and *E. nitens* showed that variation in wood properties exists between genotypes, individuals, families and provenances (Raymond 2002). Given this variability, it is essential to quantify the extent to which important traits are under genetic control, if they are to be improved within breeding populations. Brawner et al. 2010 examined the genetic parameters of *E. pellita* in a breeding population in Indonesia and found large genetic differences between and within provenances which provided opportunities for genetic improvement. Well-established tree improvement programs in Sabah have also delivered higher-yielding planting stock through phenotypic selection based on growth and form. The increasing demand for solid-wood products in Sabah provides a clear objective for improving solid wood quality. Wood mechanical performance have been evaluated to guide the end use of the species as woodchip log. Based on the study by Japarudin (2021b), the good mechanical performance of *E. pellita* offers opportunity for use in higher value products. Among the mechanical properties of interest to the wood products industries, basic density and wood stiffness are the two most important. This study provided genetic parameter estimates for the determination of whether these traits may be used by breeders to enhance the utility of logs sourced from *E. pellita* plantations.

Estimating wood mechanical properties using acoustic-based methods allows breeders to sample large numbers of standing trees in breeding populations. Standing tree acoustic velocity has been shown to correlate well with modulus of elasticity measurements, taken through destructive sampling (Wang et al. 2005, Legg and Bradley 2016). Standing tree acoustic velocity (AV), log AV and basic density are all positively related with AV in predicting the mechanical properties, although the strength of the correlation depends on the tree section being measured (Baier 2008). Numerous studies have been conducted using non-destructive testing methods to obtain information on the within-tree variation in wood mechanical properties. As part of the *E. pellita* evaluation of mechanical wood properties in Sabah, the acoustic velocity to board modulus of elasticity (MOE) calibration indicates that the correlation with standing trees is strongly positive (Japarudin et al. 2021a). While this relationship is favourable, indirect assessments of mechanical properties are complex and the level of genetic control for mechanical properties in *E. pellita* remains unclear.

A breeding objective to improve the mechanical properties of wood must also take volume and form into consideration. Genetic gain may be achieved in individual traits, however multi-trait selection is usually required, and index selection is typically used to differentiate the importance of traits. The level of genetic improvement that may be realised from this depends on the level of additive genetic variability in each trait, the selection intensity and the genetic correlations between traits (Falconer & Mackay 1996).

This study used three *E. pellita* progeny trials established in Sabah by members of the Borneo Forestry Cooperative (BFC). Trials were established with open-pollinated families derived from both native range provenance collections, local land race populations and third-party seed orchards. The objective of the trials were to estimate genetic parameters and provide breeding value predictions for growth, form and wood stiffness. Genetic analyses were used to compare diameter at breast height (DBH), form and wood stiffness (dynamic MOE) among the seed sources, partition variation for all traits into genetic and environmental components and estimate the heritability of traits and estimate the genetic correlations between traits. The solutions of the mixed models provide predictions of parental breeding values that may be used to estimate the response to selection. Predictions of response to selection may also be derived from genetic parameter estimates. Combining breeding values for different traits into a selection index, setting different selection intensities, and culling for low wood stiffness were strategies used to evaluate trade-offs that must be made in an operational tree breeding program. Understanding the potential genetic gain that may be realised for different traits helps to develop tree improvement strategies to advance breeding populations of *E. pellita* in Borneo, aimed at developing plantation forests to produce high value solid wood and engineered wood products.

MATERIALS AND METHODS

Pedigreed *Eucalytus pellita* progeny trials

The *Eucalyptus pellita* breeding populations evaluated in this study are part of the BFC tree improvement program, and a larger network of trials that have been established in the Malaysian states of Sarawak and Sabah. The experimental design used randomised incomplete blocks within ten replications of three-tree row-plots representing each family with 30 trees. Seed was collected from the native range of the species in both Australia and Papua New Guinea, as well as from various seedling seed orchards derived from the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO), and the Queensland Forestry Research Institute (QFRI), and other collaborators (Harwood 1998). The populations were subsequently defined into four distinct populations i.e. Papua New Guinea (PNG)-wild, Queensland-wild and seedling seed orchards developed in situ or ex situ. The germplasm included in these three progeny trials provided a broad genetic base from which an advanced generation breeding program can be developed using forward selection of progeny from a diverse set of families. Table 1 summarises the progeny trials that were used in this study, established by Sabah Softwoods.

Growth characteristics and acoustic-wave velocity of the stem

Data collected 3 years after trial establishment were used to estimate genetic parameters and predict breeding values for a range of traits that were assessed in these progeny trials. Data for this study was based on phenotypic assessments of stem volume [a function of tree height (m) and DBH (cm)], stem straightness (1–6 subjective score) and acoustic velocity for individual trees within each trial. Acoustic velocity was used to predict wood stiffness (dynamic MOE) (Japarudin et al. 2021a). Acoustic wave velocity data is strongly correlated with timber stiffness and was directly measured using a microsecond timer (Legg & Bradley 2016). To obtain acoustic wave velocity data, probes were inserted into each standing tree stem with an inter-probe distance (d) of 1 m, centred approximately at breast height (ca. 1.2 m above ground). The measured time of flight (t) was converted to velocity (velocity, $V = dt^{-1}$) and a correction factor of 14 ms^{-1} was added to each stem to account for model bias (Japarudin et al. 2021b). The dynamic modulus of elasticity (dMOE) was determined according to the following formula:

$$MOE_{dynamic} = V^2 \times \rho$$

where ρ is the green density, which is assumed to be the value of 1 in green wood.

Total height and basal area [$BA = pi * (DBH/2)^2$] were used to estimate total tree volume (m^3) under bark. Stem volume was calculated using a general volume equation that incorporates a form factor of 0.365.

$$\text{Volume under bark (ub)} = \text{Basal area} \times \text{height} \times \text{form factor}$$

Stem straightness is based on visual assessment following a subjective scoring system of

Table 1 Description of progeny trials and assessments used to evaluate *Eucalyptus pellita* populations

Trial	Location	Established	Material[a]	Design[b]	Latitude	Longitude	Assess[c]	Stocking[d]	Total stems	WQ stems[e]
Progeny 2012	83C	Sep-12	3 (51)	10, 10, 3	4.609° N	117.714° E	12, 24, 36	58	1045	959
Progeny 2013	116A	Dec-13	3 (137)	10, 23, 3	4.644° N	117.744° E	12, 24, 36	80	3330	2668
Progeny 2014	133KH	Dec-14	4 (120)	10, 20, 3	4.686° N	117.722° E	12, 24, 36	78	2819	2818

a = genetic material established in trials with number of population groups followed with number of open pollinated families in parenthesis, b = design lists number of replications, incomplete blocks per replication and trees per contiguous familyplot, respectively, c = age of diameter at breast height and total tree height assessments in months from planting, d = Percent of trees remaining at assessment age of 36 months, e= number of stems assessed for wood quality

straightness score (1 to 6) where 1 = poor stem straightness with tree deviating significantly from its vertical axis, 6 = excellent stem straightness, and intermediary scores indicate increasingly straight stems.

Statistical analyses

Statistical analysis was conducted using R Studio version 1.3. Data were analysed to provide descriptive statistics for each trial (Table 2) and the different populations evaluated within each trial (Table 3). A mixed linear model was fit using the R package LME4 for the estimation of variance components, derivation of genetic parameters and prediction of breeding values for parents (Bates et al. 2014). While the LME4 package provides an open-source method for variance component estimation and solving mixed models for fixed and random effects, the authors did not recommend significance tests for random effects and no methods were provided for estimating the standard errors of ratios of variance component of its heritability estimates. Clonal controls and non-pedigreed treatments were removed prior to genetic analysis. For each trial, variance component estimates were obtained from fitting a parental model to individual tree data for each trait.

$$Y_{ijk} = \mu + R_i + S_j + F_k(S_j) + RF_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the individual tree data for the i-th replication of the k-th family within the j-th source, μ is the overall mean, R_i is the fixed effect of i-th replication, S_j is the fixed effect of j-th source, $F_k(S_j)$ is the k-th family within the j-th source, RF_{ij} is the plot effect or the interaction between replication and family effects and ε_{ijk} is the residual error variance.

For the derivation of genetic parameter estimates, variance components for each trait were estimated to provide heritability estimates. Narrow-sense heritability (h_i^2) was calculated for each of the three experiment as the ratio of additive genetic variance to phenotypic variance.

$$h^2 = \frac{V_A}{V_p} = \frac{3\sigma_F^2}{\sigma_F^2 + \sigma_{Error}^2}$$

where V_A is the estimated additive genetic variance, V_p is the estimated phenotypic variance, σ_F^2 is the estimated among family variance (within seed source) and σ_{Error}^2 is the estimated error or residual variance. This heritability estimate assumes that the coefficient of relationship among families is one-third rather than one-fourth in order to account for the mixed mating that is expected in eucalypt species (Griffin & Cotterill 1988, Brawner et al. 2012). The between trait genetic correlations were estimated as the correlation between parental breeding values for a pair of traits. Genetic correlation estimates were approximated using the Pearson correlation between parental breeding value predictions with the base R 'cor' function and the significance of correlation estimates was provided with the base R 'cor.test' function.

Breeding value predictions used to identify parents that would be suitable for inclusion in future seed production facilities were produced using the mixed model described, however the source effect was removed and population effects were pooled with family effects. Both genetic parameters and breeding value predictions were used to evaluate the response to selection and predict genetic gain.

Predicted genetic gain and selection index weights

Theoretical predictions of genetic gain were estimated using the heritability (h^2) of the trait and the selection differential (S), and these parameters may be derived from assessments of field trials ($G = h^2S$) (Falconer & Mackay 1996). The narrow sense heritability is used to reflect gains that would be realised from selection based on additive breeding value predictions of the open pollinated parents evaluated in these trials. The selection differential may be calculated directly as the difference between the mean value (arithmetic average) of the entire population and the mean value of the selected individuals. Alternatively, the selection differential may be calculated using two factors: the intensity of selection (i) and phenotypic standard deviation (σ_p), where $S = i\sigma_p$ and the predicted genetic gain that may be derived from direct selection (ΔG = genetic gain) for any single trait is given by the following formula:

$$\Delta Gt = h^2 \times \sigma_p \times i$$

Selection intensity values were taken from standard tables (Falconer & Mackay 1996). As the linear model used to produce genetic parameters for theoretical gain estimates including a

'source' or 'population' effect, these genetic gain estimates are indicative of what may be achieved from selection within any population of *E. pellita*. Selection of the correct population for a particular environment would provide additional improvements, and this level of improvement may be estimated using the fixed estimates of source effects provided in Table 3. The linear model used to produce the breeding values that were in turn used to estimate genetic gain realised from index selection and culling, excluded the source effect so that the total genetic effect (family and population) is included in the gain estimates. Gain estimates are therefore indicative of what may be achieved from selection among the families of the populations that are specific to these trials.

Genetic gain prediction for each trial were produced assuming selection was based on an index that differentially weighs the traits assessed in these trials. In this study, a selection index was created with subjective weighting of three traits: stem volume, stem straightness and dMOE. Parental breeding values were used in predicting the change that would be realised from selection based on a weighted index of 60% for volume, 20% for stem straightness and 20% for dMOE. Breeding values were standardised to have a mean of zero and standard deviation of one:

$$sBVx = (BVx - \text{mean}(BVx)) / \text{standard deviation}(BVx)$$

Standardisation was used to centre and scale breeding values so that they could be readily combined into a single index value:

$$\text{Index} = 0.6 \times sBV_{VOL} + 0.2 \times sBV_{STR} + 0.20 \times sBV_{dMOE}$$

Breeding values for each parent were sorted by the summed indexed value, and a constant proportion of trees were selected from each trial. In the first selection scenario, predicted genetic gain was estimated as the ratio of the average breeding value of the top 10% of parents, relative to the population average, assuming selections were available and allowed to out-cross at random. For comparison, in the second scenario, the selection intensity was reduced to the top 50% of parents selected using the same index. No selection index was applied in the third and fourth scenario, and a different approach using culling from below was considered. A simple culling from below strategy, to improve wood stiffness, was used for the third selection scenario, where the poorest 20% of the parents for dMOE breeding values were removed. For comparison, the same culling approach of the poorest 20% of the population was applied before selection of 10% of the population for volume, as the fourth scenario.

RESULTS

The progeny trials were established following a period of silvicultural development, and a common intensive silvicultural prescription was used across all trials. The trials were maintained in a weed-free condition until canopy closure, to minimise confounding effects among the trial plots. Descriptive statistics for each progeny trial are presented in Table 2.

The summary of trial performance shows that trees produce an average DBH between 11.2 and 13.1 cm and average height between 11.7 and 14.5 m after three years. This is comparable to the results from progeny trials evaluated in Sumatra, Indonesia (Brawner et al. 2010). The 2012 progeny had the highest mean DBH and straightness, and the 2013 progeny trial had the highest mean stiffness as well as volume and height. By contrast, the 2014 progeny had the lowest average performance for all parameters. The populations established in the trial network comprised of seed collected from the wild in PNG and Queensland, as well as in situ (Borneo) and ex situ seedling seed orchards. Estimates of the relative performance of seed sources from these populations are presented in Table 3 as best linear unbiased estimates of fixed effects with standard errors, and number of trees provided for each trial.

Mean values of traits varied significantly among populations and among trials. The stem volume of sources from managed seed production areas and seedling seed orchards tended to be greater than the wild sources. In general, unimproved population originating from the native forests of PNG and Queensland had poorer performance relative to population from local or external seed orchards. With the exception of the 2012 trial, mean values for all traits were marginally higher for the domestically developed populations, followed by externally improved populations and wild populations respectively. For straightness, the best source in the 2012 trial was from overseas populations while the best source in the 2013 and 2014 trials

Table 2 Descriptive statistics for growth [diameter at breast height (DBH, cm), height (HT, m), volume (VOL, m^3), stem straightness (STR), dynamic stiffness (dMOE, GPa)] in three *Eucalptus pellita* progeny trials assessed three years after planting

Trials	Traits	N	mean	sd	min	max	range	se
Progeny 2012	DBH	966	13.10	2.76	3.30	25.20	21.90	0.09
	HT	966	12.94	2.66	4.10	19.80	15.70	0.09
	VOL	966	0.06	0.03	0.00	0.30	0.30	0.00
	dMOE	959	6.47	0.77	4.10	9.89	5.79	0.02
	STR	966	4.19	0.98	1.00	6.00	5.00	0.03
Progeny 2013	DBH	3302	11.69	3.62	0.70	21.10	20.40	0.06
	HT	3302	14.45	4.49	1.30	23.10	21.80	0.08
	VOL	3301	0.07	0.05	0.00	0.25	0.25	0.00
	dMOE	2668	8.30	1.20	2.94	13.72	10.78	0.02
	STR	3302	3.59	0.95	1.00	6.00	5.00	0.02
Progeny 2014	DBH	2819	11.21	3.31	2.30	19.50	17.20	0.06
	HT	2819	11.68	3.04	2.30	19.60	17.30	0.06
	VOL	2819	0.05	0.03	0.00	0.19	0.19	0.00
	dMOE	2818	7.99	1.24	2.83	10.14	7.31	0.02
	STR	2819	3.37	0.89	1.00	6.00	5.00	0.02

DBH = diameter at breast height (cm), HT= height (m), VOL = volume (m^3), dMOE = dynamic wood stiffness (GPa), STR = straightness on a 1–6 scale, N = number, sd = standard deviation, se = standard error

Table 3 Estimates of growth, straightness and dynamic stiffness for the population evaluated in three *E. pellita* open-pollinated progeny trials

Population	3-year volume (m^3)			3-year straightness (STR)			3-year dynamic stiffness (GPa)		
	Progeny 2012	Progeny 2013	Progeny 2014	Progeny 2012	Progeny 2013	Progeny 2014	Progeny 2012	Progeny 2013	Progeny 2014
Domestic population	0.06 (0.03) n = 323	0.08 (0.05) n = 2188	0.05 (0.03) n = 655	4.13 (0.99) n = 323	3.69 (0.95) n = 2189	3.46 (0.87) n = 655	6.49 (0.64) n = 321	8.39 (1.17) n = 1757	8.15 (1.18) n = 655
Foreign population	0.06 (0.03) n = 634	0.07 (0.05) n = 518	0.05 (0.03) n = 1259	4.22 (0.97) n = 634	3.62 (0.97) n = 518	3.34 (0.87) n = 1259	6.47 (0.83) n = 630	8.38 (1.23) n = 423	7.94 (1.22) n = 1259
Wild, Papua New Guinea (PNG)			0.04 (0.03) n = 401			3.40 (0.78) n = 401			7.97 (1.22) n = 401
Wild, Queensland	0.05 (0.03) n = 9	0.05 (0.04) n = 595	0.04 (0.03) n = 504	3.67 (1.00) n = 9	3.23 (0.81) n = 595	3.32 (1.02) n = 504	6.27 (0.93) n = 8	7.89 (1.20) n = 488	7.90 (1.36) n = 503

Overall mean from single trial analysis (standard deviation of means in parenthesis) with n indicating the number of observations

were domestic populations. For dMOE, all trials showed that the domestic improved population was the best source, however the differences between both improved and wild population were small in the 2014 trial. The moderate standard error estimates indicated that significant variation exists within populations. Table 4 shows the differences among populations that were statistically significant.

Table 4 shows highly significant replication effects in all trials that were evident for growth traits, whereas less significant replication effects were evident for dMOE in the 2012 and 2014 trials. In the 2012 trial, there were no significant differences among sources for all traits, which contrasts with others trials where significant differences among populations were highly significant for volume but less significant for other traits. Both wild PNG &

Table 4 Analysis of variance (ANOVA) for significance of random effects

Progeny 2012						
Volume (m^3)						
Source of variation	Sum square	Mean square	DF	F value	Pr (> F)	Significance codes
Source population	0.002115	0.001057	2	1.2254	0.3001	
Rep	0.07893	0.00877	9	10.1635	$3.61E^{-10}$	***
Straightness (scale 1–6)						
Source population	3.225	1.6125	2	2.0172	0.141792	
Rep	31.236	3.4707	9	4.3417	$1.13E^{-04}$	***
Dynamic MOE (GPa)						
Source population	0.0423	0.02114	2	0.0447	0.9563	
Rep	14.1984	1.5776	9	3.3329	$1.60E^{-03}$	**
Progeny 2013						
Volume (m^3)						
Source population	0.089645	0.044823	2	23.3794	$1.74E^{-09}$	***
Rep	0.057575	0.006397	9	3.3368	$8.06E^{-04}$	***
Straightness (scale 1–6)						
Source population	34.521	17.2606	2	21.4998	$7.18E^{-09}$	***
Rep	22.829	2.5366	9	3.1595	$8.37E^{-04}$	***
Dynamic MOE (GPa)						
Source population	39.246	19.623	2	17.5051	$1.69E^{-07}$	***
Rep	44.22	4.9134	9	4.3831	$3.02E^{-05}$	***
Progeny 2014						
Volume (m^3)						
Source population	0.033668	0.011223	3	16.9771	$2.89E^{-09}$	***
Rep	0.043934	0.004882	9	7.3847	$4.35E^{-09}$	***
Straightness (scale 1–6)						
Source population	3.0049	1.0016	3	1.5405	$2.07E^{-01}$	
Rep	23.2285	2.581	9	3.9696	$1.28E^{-04}$	***
Dynamic MOE (GPa)						
Source population	10.17	3.3901	3	2.7416	$4.63E^{-02}$	*
Rep	21.811	2.4234	9	1.9598	$4.65E^{-02}$	*

Significance codes: *** = 0, ** = 0.001, * = 0.01, DF = degree of freedom

Queensland populations were less productive across all trials, however the significance of differences between trials was not consistent. The ANOVA table showed no difference among sources for straightness and dMOE in the 2012 trial while the populations in the 2014 trials were similar in straightness, and differences in dMOE or populations were smaller.

Variance component estimates were used to approximate the level of genetic control in each trial. Heritability and genetic correlations are presented in Table 5.

Heritability estimates were low to moderate for all traits with moderate heritability found in the 2013 and 2014 trials, and a low heritability estimate was estimated for volume in 2012. In contrast, the heritability of dMOE in the 2012 trial was moderate, and the other two trials produced low heritability estimates.

The genetic correlations approximated by the correlation between parental breeding values were inconsistent for both; volume:dMOE and dMOE:straightness. In particular, the 2012 trial provided correlation estimates that differed from the 2013 and 2014 trials. With the exception of the insignificant correlations in the 2012 trial, all genetic correlation estimates were favourable. The genetic correlation estimates for volume:dMOE and dMOE:straightness were low in the 2013 and 2014 trials, however they were highly and moderately significant. Volume and straightness

Table 5 Heritability and between trait genetic correlation estimates from analysis of each progeny trial

Heritability estimates	Progeny 2012	Progeny 2013	Progeny 2014
Volume (VOL)	0.13	0.39	0.26
Straightness (STR)	0.19	0.21	0.26
Dynamic MOE (dMOE)	0.23	0.17	0.12
Correlations:			
$r_{VOL,dMOE}$	-0.13 -	0.37 ***	0.18 **
$r_{VOL,STR}$	0.91***	0.87 ***	0.70 ***
$r_{dMOE,STR}$	-0.20 -	0.29 ***	0.25 ***

Significance of correlation estimates $p < 0.001$ = ***, 0.01 = **, $p < 0.05$ = *, NS = -

were strongly correlated whereas the genetic correlations between volume and dMOE, and straightness and dMOE were low and inconsistent.

The heritability estimates of the selected traits were used to provide a theoretical genetic gain estimate expected from selecting for these traits alone. Theoretical genetic gain estimates were calculated using genetic parameters and selection differentials for a single trait. These were compared to predicted genetic gain estimates calculated using differentials in breeding value estimates (Table 6). Gains, expected from culling the poorest 20% of the population for dMOE were also included.

The theoretical gain estimates for each trait ranged from 10.4 to 48.3% for volume, 7.8 to 12.2% for straightness and 3.2 to 4.9% for dMOE. These estimates provided an upper boundary of improvement from selection of each trait. As expected, theoretical gain estimates were greater than genetic gain estimates derived from index selection for multiple traits. Selecting the best 10% of the families with a weighted index provided some gain across all traits, and as expected, the larger (60%) weighting on volume resulted in larger predicted improvements for volume. The exception was the volume in the 2012 trial, which may be attributed to the small sample size of the population selected with the index (5 parents of the 51 families evaluated), as well as the low heritability estimates in the 2012 trial. Furthermore, there were no significant differences in volume among sources of population (Table 4), as only improved in-situ and ex-situ populations were selected in this trial using an index. Compared to theoretical gain, the 60% weighting on volume led to a drop in volume improvement by 12 and 2.6% in 2013 and 2014 trials, and reduction in dMOE improvement by 6, 2.3 and 1.8% in 2012, 2013 and 2014 respectively. Substantial gain for volume in both 2013 and 2014 trials reflected higher heritability, associated increase in variation among family

Table 6 Genetic gain for each population in trial using the theorical gain estimate for each trait independently ($Gt = h^2 \times \sigma p \times i$) and a selection index using weightings of 60, 20 and 20% for volume, straightness and dynamic MOE (dMOE), respectively, were used to select proportions of the parents and provide predictions of genetic gain

Selection response	Dynamic MOE (GPa)			Volume (m^3)			Straightness (score 1–6)		
Progeny trial	2012	2013	2014	2012	2013	2014	2012	2013	2014
Theoretical	4.9%	4.4%	3.2%	10.4%	48.3%	29.9%	7.8%	9.9%	12.2%
Top 10% index weighting	-1.2%	2.1%	1.5%	11.7%	36.2%	27.4%	5.1%	8.8%	10.4%
Top 50% index weighting	0.3%	1.4%	0.7%	4.7%	15.8%	10.7%	2.1%	3.6%	3.5%
Removed 20% family with low dMOE and no selection for VOL	0.8%	1.2%	0.8%	-0.1%	2.6%	1.0%	0.3%	0.5%	0.6%
Removed 20% family with low dMOE and select top 10% family for VOL	0.8%	1.2%	0.8%	11.5%	36.3%	27.0%	2.8%	8.3%	9.5%

VOL = volume (m^3), STR = straightness on a 1–6 scale, dMOE = dynamic wood stiffness (GPa)

breeding values and significant differences among sources (Tables 3 and 4). On the other hand, increasing the index weighting for volume to 80% was similar to the 60% index weighting for volume and dMOE across trials. An index weighting of 80% on dMOE resulted in relatively greater predicted improvements for dMOE compared to selecting the top 10%. Compared to theoretical gain, dMOE for 2013 and 2014 were just 0.5 and 0.4% lower respectively.

To understand what may be realised by eliminating families with low dMOE, a third strategy was adopted whereby the poorest 20% of the population for dMOE were culled. As expected, predicted gains in volume and straightness from leaving 80% of the population after this culling were small. As shown in Table 6, this strategy resulted in little change in volume (-0.1 to 2.6%), straightness (0.3 % to 0.6%), or dMOE (0.8 % to 1.2 %) across these progeny trials. While consistent improvements in dMOE were predicted to result from culling families with poor MOE, improvements were similar to that predicted from selecting the top 50% of the families using the 20% weighted index for dMOE. Much higher gain would be realised for volume and straightness.

Finally, gains from both culling and selecting the top 10% of the families for volume were predicted. Some improvement in dMOE and majority gain in volume by selecting an index would be realised. Culling and selection for volume led to predicted volume gains of 11.5, 36.3 and 27.0% for the 2012, 2013 and 2014 trials respectively. Given the high genetic correlation between straightness and volume and the removal of low MOE parents in the combined culling and index selection scenario, predictions of gain were similar to using an index that included all three traits. The final scenario of selecting the top 10% of the population for volume production after removing the poorest 20% for dMOE provided a scenario that could be applied in the breeding program.

DISCUSSION

The productivity of *E. pellita* observed in these trials was comparable to previous estimates of productivity for this species in the tropics (Brawner et al. 2010, Hung et al. 2015). Major differences in volume among populations in the 2013 and 2014 trials were associated with larger differences between improved and unimproved sources. Genetic parameters were estimated to elucidate the level to which selection traits were under genetic control. Low to moderate heritability estimates were found for all traits and corresponded with the heritability estimates in Luo et al. (2006) at younger ages (0.19 to 0.25 for diameter growth), and were slightly lower than those presented for other *E. pellita* trials. For example, the heritability for growth and wood traits estimated by Hung et al. (2015) at 10 years old ranged from 0.14 to 0.33 and 0.36 to 0.51 for DBH and near infrared (NIR) predicted MOE, respectively. The heritability estimates for dynamic MOE were also lower than those found by Blackburn et al. (2014) in *E. nitens*.

Wood stiffness (MOE) is a key trait that impacts wood quality in developing a breeding population of *E. pellita* for solid wood products requiring superior mechanical properties (Japarudin et al. 2021b). The price that may be obtained for veneer and boards produced for the solid wood market may be influenced by these quality traits. Prasetyo et al. (2017) found superior growth characteristics that tended to produce higher quality solid wood properties. For dMOE, the results from these trials indicated that there is potential to improve *E. pellita* through the exploitation of genetic variation among families, while differences among populations were inconsistent. The low heritability estimated for growth and inconsistent correlations of growth MOE in 2012 could be attributed to family differences in survival. The 2012 trial was affected by high mortality resulting in only 58% trees remaining at the time of assessment. The influence and impact of silviculture and genotype were evident as stressed by Punches (2004), where tree growth and wood formation are produced by a complex interaction of site, climate, genetics and competition. The correlation estimates between growth and straightness are typical for the species and similar to estimates found in other *Eucalyptus* breeding programs (Hamilton & Potts 2008). The high and significant correlation between volume and straightness were strongly positive and indicated that selection for one trait would achieve improvement in the other. While standard error estimates were not available using the LME4 package, the heritability estimates provided an indication that differences in family composition and trial management led to inconsistencies in the level of genetic control.

Genetic parameters and breeding value predictions for these traits were used to compare

selection strategies. The similarity of genetic parameter estimates with other studies provided confidence that genetic gain estimates used to compare selection scenarios will be close to expectations. To provide a measure of certainty in gain estimates, each trial was used to provide independent estimates. Variation in genetic parameter estimates was reflected in the range of the gain estimates that were used to compare the impact of selection strategies.

The intent of gain estimates from single site progeny trials is to provide a metric for comparing selection strategies, rather than an attempt to quantify expectations of improvements from selection (Stanger et al 2011). Gain estimates are likely biased upwards through the exclusion of genotype by environment interaction and the differential competition in small row plots. Accurate empirical estimates of gains that may be achieved in a breeding program require extremely long periods of time in forest tree improvement. Large-plot genetic gain trials comparing baseline of selected populations were established across the targeted planting estate, which was required to correct the competition differentials and genotype by environment interactions. Data were also collected three years after planting, and gain estimates related to change at three years of age, rather than at harvest age. However, in order to provide guidance to forest and mill managers as to what may be achieved from selection, theoretical and predicted genetic gain estimates were approximated using genetic parameters and breeding value predictions, respectively. While selection of the parents for seed orchards was infeasible as parents were not captured as grafted ramets at seed collection, the backwards selection strategy using more reliable parental predictions was used, rather than relying on individual tree predictions for estimates. These parental predictions will provide more conservative approximations of genetic gain. Theoretical gain estimates predicted the level of improvement that selection may achieve when a single trait is in focus. This is rarely the case in tree improvement programs and a selection index that includes multiple traits, which is typically used to identify parents to include in production seed orchards or individuals to clone for deployment.

Selection of individuals using an index that combines growth and wood quality traits requires index weightings for each trait which may be set using a variety of methods (Brawner et al. 2012). Therefore, a better approach in realising gain using selection of multiple traits is required. Selecting the top 10% of families using an index will have a large impact on the genetic diversity of the population that is advanced to the next generation. This loss in diversity may be reduced by selecting a larger proportion of the population but reducing the selection intensity which will result in lower levels of genetic improvement. As most breeding programs are built on a long-term population improvement, strategies should be in place to balance immediate genetic gain with the maintenance of population diversity, to ensure long-term progress (Jannink 2010). With reference to the genetic correlation of growth and wood traits, particularly the low correlation of volume with dMOE found this study, there will be a negative effect on volume gain resulting from the removal of low dMOE families. Selecting a small proportion of the population for volume has a large impact on the gain estimates for other traits, and this study provided predictions of gain that reflected trade-offs in selection pressure applied among different traits.

CONCLUSIONS

Superior breeding value predictions led to the selection of a greater number of families from improved populations with few selections made from wild populations. The predicted response to selecting the top 10% of families using a 60% weighting on volume indicated that significant gain could be achieved in volume and straightness. These comparisons provided estimates of the trade-offs that would be realised by using different strategies to improve several traits, taken into consideration the size of selected population and the trait importance. Application of a higher selection intensity led to the development of a clonal seed orchard for maximising gain, while lower selection intensity resulted some gain whilst preserving genetic diversity. Selection of a broader cohort of families to advance the next generation will reduce the improvements that may be realised from more intensive selection. This difference is offset by an increase in genetic diversity that may be utilised in the future, allowing a continuation of the genetic improvement program through open pollinated breeding which provides options for responding to diseases or changes in climatic variables that impact productivity.

Selecting the top 10% of the population for volume production after removing the poorest

20% for dMOE provided a practical approach to reducing low stiffness stems and increasing volume in the resulting breeding population. This led to improvements in dMOE and volume over what was expected in using index selection. Further improvements in the quantity and quality of wood in planted forests, delivering to the wood processing industries in eastern Malaysia, will require continued investment in silvicultural and genetics research. Development of the forest industry through applied research and collaboration will accelerate the delivery of sustainable planation forests in the tropics.

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