Variations of growth and wood traits in standing trees of the third-generation *Acacia mangium* families in Indonesia

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Abstract

The breeding of a fast-growing tree species, *Acacia mangium* Willd. has entered the third-generation cycle in Indonesia. To fulfill timber industry needs, wood traits, as well as growth traits, should be improved by conducting appropriate tree breeding programs for this species. In the present study, growth and wood traits were measured for the 10-year-old third-generation *A. mangium* from 40 half-sib families originating from four sub-lines from two provenances. The mean values of ten families in each sub-line ranged from 17.7 to 21.8 cm for stem diameter, 14.3 to 16.2 m for tree height, 3.60 to 3.77 km/s for stress-wave velocity, and 19.9 to 20.9 mm for Pilodyn penetration, respectively. The broad-sense heritability values in each sub-line ranged from 0.014 to 0.444 for stem diameter, 0.000 to 0.208 for tree height, 0.261 to 0.715 for stress-wave velocity, and 0.171 to 0.484 for Pilodyn penetration, respectively. These results suggested that families with higher density and Young's modulus of wood, suitable for solid wood production, can be selected from the third-generation *A. mangium*. Stem diameter significantly correlated with the other three measured traits, while phenotypic correlation coefficients between stem diameter and stress-wave velocity or Pilodyn penetration were very low. In addition, no significant phenotypic correlations were found between other measured traits. Furthermore, positive- or non-significant genetic correlations were found between growth and wood traits in all sub-lines. Thus, it is concluded that the selection of families with good growth characteristics will not always reduce the wood properties of this species.

Keywords: *stem diameter, tree height, stress-wave velocity, Pilodyn penetration, heritability*

Introduction

Growth traits, including stem volume and form, are the primary selection traits in tree breeding programs (Hai et al., 2008; Rojas et al., 2017). In addition to growth traits, wood traits, such as wood density and strength properties, have been considered essential for sustainable wood utilization. In tree breeding for wood quality, non-destructive and semi-destructive testing methods are applied to evaluate wood traits to decrease the cost and increase efficiency (Chen et al., 2010; Wu et al., 2011; Hidayati et al., 2013, 2019; Hai et al., 2015). For example, non-destructive testing, stress-wave velocity (Wu et al., 2011; Hidayati et al., 2013, 2019; Hai et al., 2015), and semi-destructive

DOI:10.2478/sg-2023-0016
edited by the Thünen Institute of Forest Genetics

testing, Pilodyn penetration (Chen et al., 2010; Wu et al., 2011; Hidayati et al., 2013, 2019; Hai et al., 2015) can evaluate Young's modulus and wood density of stems in standing trees, respectively.

Acacia mangium Willd. belongs to Fabaceae and is naturally distributed in Sula Islands, Seram, Aru Islands, Irian Jaya, Western Province of Papua New Guinea, and north-eastern Queensland (Lemmens et al., 1995). It is a fast-growing tree species (Lemmens et al., 1995). Thus, the species is extensively planted in Kalimantan and Sumatra, Indonesia (Lemmens et al., 1995). The wood from this species has been usually used for producing raw materials of pulp and paper materials (Rosli et al., 2009; Fiskari and Kilpeläinen, 2021). In addition to pulp and paper, wood is used as solid wood and raw materials for wood-based products (Wong et al., 1988; Ngadianto et al., 2020; Hadi et al., 2021).

A comprehensive tree breeding program for *A. mangium* in Indonesia was initiated by the Center for Forest Biotechnology and Tree Improvement, Yogyakarta, Indonesia (Nirsatmanto and Kurinobu, 2002; Nirsatmanto et al., 2003, 2004, 2013, 2015; Nirsatmanto, 2012; Hidayati et al., 2019; Rindarto et al., 2021; Sunarti et al., 2022). The first-generation seedling seed orchards were established in 1994 with about 200 families in four sub-lines (A, B, C, and D) from two different origins, Papua New Guinea (PNG; sub-lines A and B) and Far North Queensland (FNQ; sub-lines C and D), Australia (Nirsatmanto and Kurinobu, 2002; Nirsatmanto et al., 2003, Table 1 and Figure 1). Seeds obtained from the superior families in the first generation were used for establishing the second-generation seedling seed orchards in 2001 (Nirsatmanto et al., 2004, 2013; Nirsatmanto, 2012). The tree breeding program started for the third-generation cycle in 2012 (Nirsatmanto et al., 2015). Nirsatmanto et al. (2003) reported that the height growth of the first-generation trees was better than that of the local selections by 10–15 % in three-year-old trees. Compared to unimproved trees from the same provenances, tree height and stem diameter at breast height in the second-generation trees increased 3.1 % and 5.2 %, respectively (Nirsatmanto et al., 2004). Recently, the wood quality of *A. mangium* has also been required to be improved by tree breeding programs to fulfill the wood industry requirements. Hidayati et al. (2019) evaluated the heritability of growth and wood traits (stress-wave velocity and Pilodyn penetration) in 6-year-old third-generation *A. mangium*. They reported that the heritability of growth traits was higher than that of wood traits. However, information on genetic factors for wood traits is still limited in *A. mangium*.

To evaluate the possibility of selecting the candidate of the fourth-generation *A. mangium* in Indonesia, we estimated growth traits (stem diameter at 1.3 m above the ground and tree height) and wood traits (stress-wave velocity and Pilodyn penetration) in the third-generation trees planted in Central Java, Indonesia. Based on the obtained results, the broad-sense heritability of these traits and relationships between measured traits were discussed.

Table 1
Summary of the first- and second-generation families of *A. mangium* for producing the third-generation families used in the present study (Nirsatmanto et al., 2003, 2004, 2013).

Sub-line	Original provenance for first-generation	First-generation (planted in 1994)		Second-generation (planted in 2001)	
		Location	*n*	Location	*n*
A	PNG	SK	65	SK	52
B	PNG	SS	58	SK	55
C	FNQ	SK	55	SK	68
D	FNQ	SS	62	SK	55

Note: PNG, Papua New Guinea; FNQ, Far North Queensland (Australia); SK, South Kalimantan; SS, South Sumatra; *n*, number of families.

Materials and Methods

Materials

Table 1 summarizes tree breeding programs using seedling seed orchards in *Acacia mangium* in Indonesia (Nirsatmanto et al., 2003, 2004, 2013). Seedling seed orchards with four sub-lines of provenances were established in South Kalimantan and South Sumatra, Indonesia, in 1994 as the first generation of *A. mangium*. Each sub-line contained about 50 families from a provenance. The provenances of seed origin were Papua New Guinea (PNG) for sub-lines A and B, and Far North Queensland (FNQ), Australia, for sub-lines C and D, respectively (Figure 1). Seeds of the second generation were collected from superior mother trees in the seedling seed orchards of the first generation. Then, the second-generation seedlings were planted for establishing seedling seed orchards in South Kalimantan in 2001. Among the second-generation families in the seedling seed orchards, seeds were again collected from 10 superior mother trees in each sub-line of provenances (a total of 40 families from four sub-lines) as the third generation (Table 2).

A seedling seed orchard was established using these third-generation seeds in Alas Kethu Special Purpose Forest Area, Wonogiri, Central Java, Indonesia (7°47'S, 110°56'E; Figure 2) in 2012 with 4 by 4 m spacings, single tree-plot and 30 replications (Table 2). The topographic conditions of the seedling seed orchard are as follows: 141 m above sea level in elevation, vertisol soil, and flat topography. Figure 2 also shows the climatic conditions of the seedling seed orchard used in the present study. No thinning was applied in the seedling seed orchard site before this experiment.

Growth and wood traits

Growth traits (stem diameter at 1.3 m above the ground and tree height) and wood traits (the stress-wave velocity of stems and Pilodyn penetration) were measured for a total of 789 trees from 40 families (ca. 20 trees per family) in July 2022 (10-year-old). The stem diameter and tree height were measured using a diameter tape (Yamayo Million Diameter Tape, Japan) and an altimeter (Haga, Germany). The stress-wave velocity of the stem was measured between 0.5 and 1.5 m above the ground

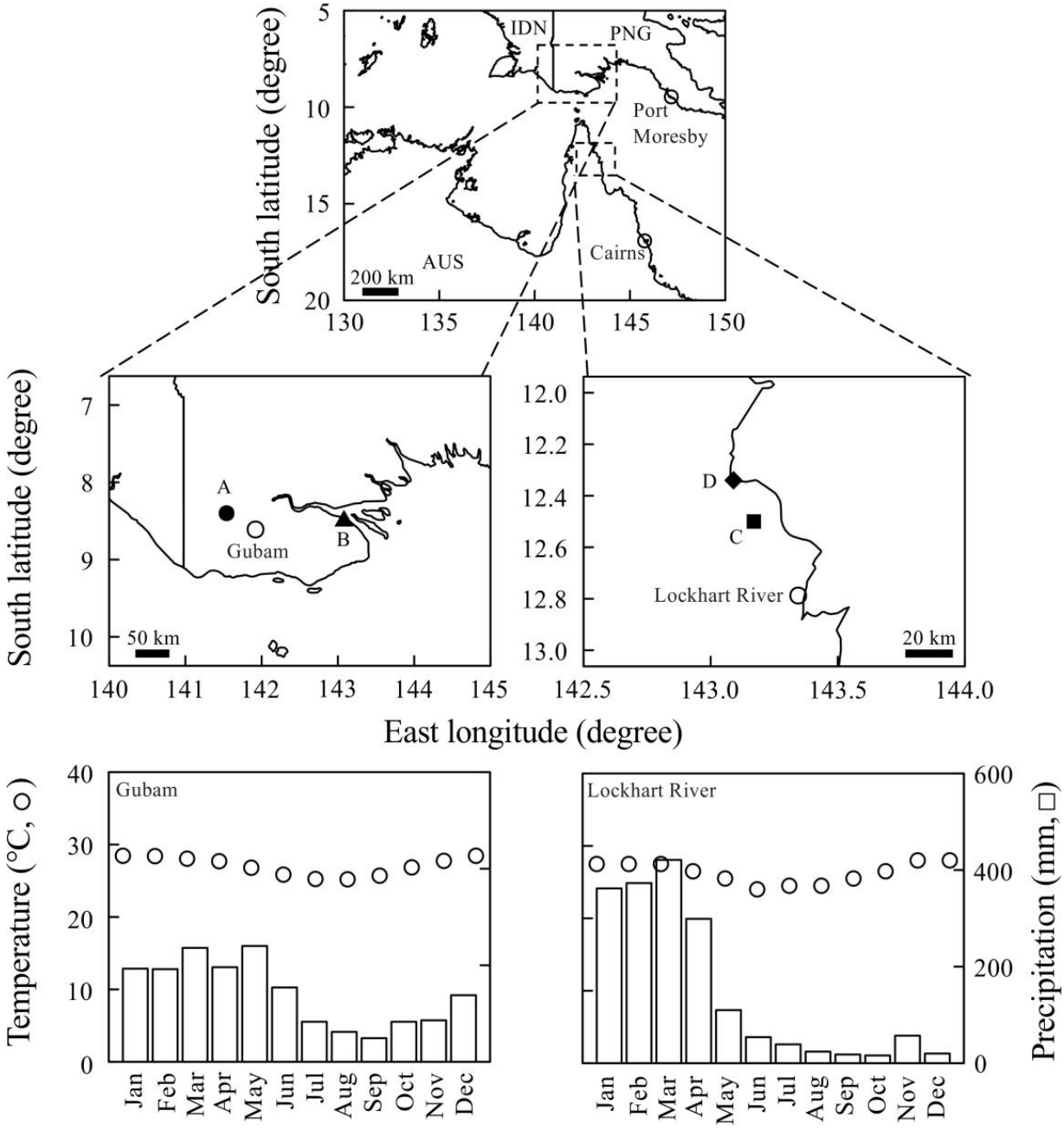

Figure 1
Seed origins for the first generation of *A. mangium*

Note: Closed symbols of circle, triangle, square, and diamond in maps indicate seed origins of sub-lines A, B, C, and D, respectively. IDN, Indonesia; PNG, Papua New Guinea; AUS, Australia. The climatic data of Gubam, Papua New Guinea and Lockhart River, Australia in 2021 was obtained from Papua New Guinea Government National Weather Service and Bureau of Meteorology, Australia, respectively. Mean monthly temperature and annual precipitation were 27.0 °C and 1,712 mm in Gubam, Papua New Guinea, and 26.3 °C and 1,793 mm in Lockhart River, Australia, respectively.

Table 2
Detailed information about the third-generation seedling seed orchard located in Wonogiri, Central Java, Indonesia.

Sub-line (Origin)	*n*	Seed origin of the first generation
A (PNG)	3	Gubam NE Morehead
	1	Derideri E Morehead
	2	Bimadebun
	1	Boite NE Morehead
	1	Dimisisi
	2	Arufi Village
B (PNG)	3	Oriomo
	7	Kini
C (FNQ)	8	Claudie River
	2	135k NNE Coen
D (FNQ)	8	Pascoe River
	2	Cassowary

Note: *n*, number of families; PNG, Papua New Guinea; FNQ, Far North Queensland, Australia. Detailed information about the provenances and location of the third-generation seedling seed orchard refer to Figures 1 and 2.

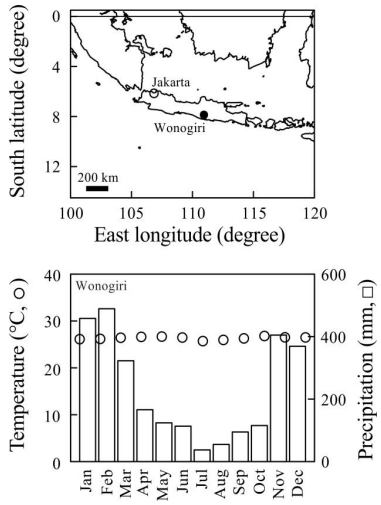

Figure 2
Location of the seedling seed orchard of the third-generation *A. mangium* in Wonogiri, Central Java, Indonesia.

Note: Climate data was provided in 2021 by Central Management of Regional River Flow, Gajah Mungkur Basin, Indonesia. Mean monthly temperature and annual precipitation were 26.4 °C and 2,750 mm, respectively.

of the tree by a stress wave timer (Fakkop Microsecond Timer, Fakkop Enterprise, Hungary) according to the methods of previous research (Ishiguri et al., 2008). Ten measurements were made in each tree, and the mean value was calculated. The Pilodyn penetration was measured by a Pilodyn tester (6J Forest, Proceq, Switzerland) according to the method described by previous researchers (Ishiguri et al., 2008; Nezu et al., 2021a). The bark at four positions randomly selected on the circumference of the stem at 1.3 m above the ground was removed. Then, Pilodyn penetration was measured at the four debarked positions. The mean value of four measurements was used as a penetration value for a tree.

Statistical analysis

The statistical analysis was performed using R software version 4.2.1 (R Core Team, 2022). To eliminate the outlier values, Smirnov–Grubbs test at a 95 % confidence level was applied for measured data. As the results, the outlier values were found in stem diameter (five trees), tree height (three trees), stress-wave velocity (seven trees), and Pilodyn penetration (nine trees): A total of 23 trees (one tree showed outlier values in both stem diameter and Pilodyn penetration). Thus, of 789 trees, a total of 766 trees were finally used for further statistical analysis.

The variance components of the family in each measured trait were estimated separately for each sub-line using the "breedR" package (Muñoz and Sanchez, 2020). The estimation of the variance components in each trait is expressed in the following linear mixed-effects model:

$$Y_{ij} = \mu + A_j + e_{ij} \quad \text{(Eq. 1)}$$

where Y_{ij} is the trait at the *i*th individual tree of the *j*th family, μ is the general mean value, A_j is the additive genetic effect of the *j*th mother trees, and e_{ij} is residual. Each variance component ratio in each trait was also calculated. The variance component ratio of family and residual in each trait was calculated as a percentage of the total variance components in the model (Nakagawa and Schielzeth, 2010). In addition, the broad-sense heritability of each trait was calculated using the following formula (Falconer and Mackay, 1996):

$$H^2 = \sigma^2_f / [\sigma^2_f + \sigma^2_e] \quad \text{(Eq. 2)}$$

where H^2 is broad-sense heritability, and σ^2_f and σ^2_e are variance components of family and residual, respectively. Furthermore, principal component analysis (PCA) and cluster analysis were applied to categorize the families in each sub-line. Breeding values of the mother tree in each measured trait were used for PCA. The breeding values were estimated by an "individual-tree model" of the best linear unbiased prediction (BLUP). The cluster analysis using the Ward hierarchical clustering algorithm used the 1st and 2nd principal component scores from PCA as variables.

The phenotypic relationships between the traits were evaluated using Pearson's correlation coefficient. In addition, to clarify the effect of the sub-line on the relationships between the traits which showed a significant correlation coefficient, the following linear mixed-effects models were developed using the "lmer" function in "lme4" package (Bates et al., 2015). The developed models are as follows:

$$Y_{ij} = (\alpha_0 + Sub\text{-}line_{0j}) X_{ij} + \alpha_1 + Sub\text{-}line_{1j} + e_{ij} \quad \text{(Eq. 3)}$$
$$Y_{ij} = (\alpha_0 + Sub\text{-}line_{0j}) X_{ij} + \alpha_1 + e_{ij} \quad \text{(Eq. 4)}$$
$$Y_{ij} = \alpha_0 X_{ij} + \alpha_1 + Sub\text{-}line_{1j} + e_{ij} \quad \text{(Eq. 5)}$$

where Y_{ij} and X_{ij} are the objective variable and explanation variable of the *i*th individual tree within the *j*th sub-line, respectively, α_0 is the fixed slope, α_1 is the fixed intercept, $Sub\text{-}line_{0j}$ is the random slope of the *j*th sub-line, $Sub\text{-}line_{1j}$ is the random intercept of the *j*th sub-line, and e_{ij} is residual. Model selection was conducted using the Akaike Information Criterion (AIC) (Akaike, 1998). The model with the lowest AIC was selected among the three models. The significance of the fixed-effect parameters of the best model was determined using the lmerTest package (Bates et al., 2015). In addition, the variance component ratio of the sub-line to the total variance was calculated. Furthermore, genetic correlation coefficients between measured traits were also calculated in the form of Pearson's correlation coefficients using breeding values.

Results

The statistical values of the growth and wood traits are listed in Table 3. The mean values of ten families in each sub-line ranged from 17.7 to 21.8 cm for stem diameter, 14.3 to 16.2 m for tree height, 3.60 to 3.77 km/s for stress-wave velocity, and 19.9 to 20.9 mm for Pilodyn penetration, respectively (Table 3). The minimum and maximum broad-sense heritability values in each sub-line were 0.014 (sub-line C) and 0.444 (sub-line D) for stem diameter, 0.000 (sub-lines B and C) and 0.208 (sub-line D) for tree height, 0.261 (sub-line C) and 0.715 (sub-line D) for stress-wave velocity, and 0.171 (sub-line A) and 0.484 (sub-line C) for Pilodyn penetration, respectively (Table 3).

The variance component ratio of measured traits in each sub-line is shown in Figure 3. Values of variance components of family in stress-wave velocity and Pilodyn penetration (ranging from 17.6 to 75.2 %) showed relatively higher than those in growth traits (ranging from 0.0 to 46.3 %).

Figure 4 shows PCA scores of breeding value in the mother tree and dendrogram based on the principal component score. In addition, loading values from PCA are listed in Table 4. The cumulative proportion of variance in principle component (PC) 1 and PC2 ranged from 71.3 % (sub-line C) to 81.5 % (sub-line D) (Figure 4). Based on the cluster analysis results, families were divided into four groups in each sub-line.

Relationships between measured traits are shown in Figure 5. Stem diameter significantly correlated with the other three measured traits. However, no significant correlations were found between other measured traits. A mixed-effects model with a random effect of the sub-line was applied for significantly correlated traits (Table 5). For stem diameter and tree height, all equations did not converge. On the other hand, the model with a random intercept of sub-line (Eq. 5) showed the minimum AIC value for stem diameter and stress-wave velocity or Pilodyn penetration. However, the fixed-effect parameters of the model with minimum AIC value were not significant, and the variance component ratios in the sub-line were also very low (around 5.0 %, Table 6).

Table 7 shows genetic correlations between measured traits in each sub-line. Stem diameter genetically correlated with tree height in sub-lines A ($r_g = 0.722$, $p = 0.018$) and D ($r_g = 0.898$, $p < 0.001$). A positive genetic correlation coefficient ($r_g = 0.675$, $p = 0.032$) was also found between tree height and Pilodyn penetration in sub-line B.

Discussion

Growth and wood traits

Annual growth rate (growth trait value / tree age) was calculated to compare growth trait data obtained from trees with different ages. Annual growth rate was 2.06 cm/yr (18.5 cm / 9 yrs) in stem diameter for 9-year-old *A. mangium* plantation trees in Indonesia (Arisman et al., 2005). In addition, Makino et al. (2012) reported that the annual growth rate of stem diameter was 3.13 cm/yr (21.9 cm / 7 yrs) for 18 trees of 7-year-old *A. mangium* planted in Indonesia. In the present study, annual growth rates ranged from 1.77 (sub-line C) to 2.18 cm/yr (sub-line A) for stem diameter and 1.43 (sub-line C) to 1.62 m/yr (sub-line A) for tree height for 10-year-old trees. Thus, the annual growth rate of stem diameter in the present study is the same or slower than those in previous studies (Arisman et al., 2005; Makino et al., 2012).

In the stress-wave velocity of stems, the mean value (3.60 to 3.77 km/s, Table 3) of this study was almost the same as that measured in 6-year-old trees of 65 families in the third-generation *A. mangium* in Indonesia (3.42 km/s, Hidayati et al., 2019), and 5- and 7-year-old *A. mangium* trees (seed source was unknown) planted in Indonesia (3.92 and 3.75 km/s, respectively, Makino et al., 2012). The results of the stress-wave velocity of the stem suggested that Young's modulus of wood in the present study is the same as that reported in the previous study. On the other hand, Pilodyn penetration showed a higher mean value (20.4 mm, Table 3) compared to that obtained in 3- to 4-year-old *A. mangium* trees with 164 open-pollinated families from six different genetic groups of trees planted in Vietnam (13.68 to 17.52 mm, Hai et al., 2015) and 6-year-old *A. mangium* trees planted in Southern China (13.6 mm, Chen et al., 2010), suggesting that wood density of outer part of the stem is relatively low compared to that in *A. mangium* planted outside Indonesia.

Broad-sense heritability of measured traits

The narrow-sense heritability and broad-sense heritability (repeatability) on *Acacia* species have been reported by many researchers (Nirsatmanto and Kurinobu, 2002; Ginwal and Mandal, 2004; Hai et al., 2008, 2009; Nirsatmanto, 2012; Hidayati et al., 2019; Chan and Isik, 2021). The narrow-sense heritability at the age of 2.7 in two seedling seed orchards of *A. mangium* was 0.240 and 0.283 for stem diameter and 0.158 and 0.236 for tree height (Nirsatmanto and Kurinobu, 2002). Hai et al. (2015) reported that the narrow-sense heritability of stem diameter, tree height, and Pilodyn penetration was 0.26, 0.22, and 0.25 for 4-year-old *A. mangium* planted in Vietnam. The broad-sense heritability of these growth and wood traits obtained in

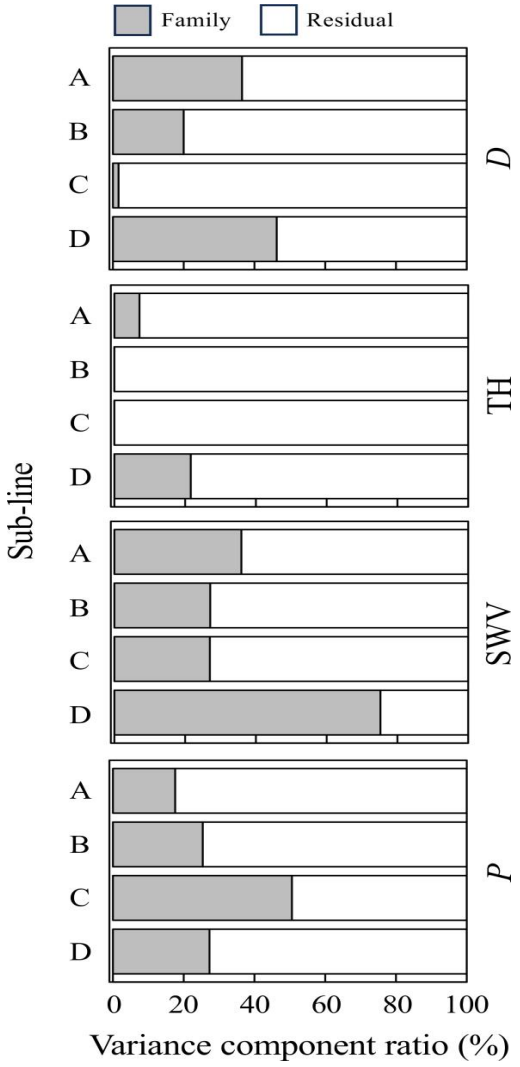

Figure 3.
Variance component ratio of measured traits in each sub-line.

Note: *D*, stem diameter; TH, tree height; SWV, stress-wave velocity; *P*, pilodyn penetration.

Table 3
Growth and wood traits of 766 trees from 40 families of the third-generation *A. mangium*

Sub-line (Origin)	Family ID	*n*	*D* (cm)	TH (m)	SWV (km/s)	*P* (mm)
A (PNG)	1	21	19.9	15.5	3.71	20.4
	2	24	21.1	16.7	3.77	19.6
	3	21	19.8	13.7	3.82	19.6
	4	19	20.5	14.4	3.83	20.4
	5	19	25.4	18.0	3.95	18.8
	6	22	23.7	16.4	3.56	20.7
	7	22	20.8	17.0	3.58	19.5
	8	20	21.3	16.3	3.69	19.7
	9	21	22.8	16.5	3.69	20.3
	10	21	23.0	17.7	3.76	20.4
	Mean ± SD	10	21.8 ± 1.8	16.2 ± 1.4	3.74 ± 0.12	19.9 ± 0.6
	H^2 ± SE		0.352 ± 0.243	0.069 ±0.126	0.347 ±0.241	0.171 ±0.170
B (PNG)	11	19	21.5	15.2	3.47	20.0
	12	21	21.2	15.7	3.76	20.3
	13	23	21.4	16.9	3.85	20.5
	14	23	22.3	15.3	3.87	20.6
	15	19	21.0	15.4	3.88	20.3
	16	17	18.5	14.4	3.74	18.7
	17	23	20.5	15.7	3.89	19.9
	18	17	17.0	17.0	3.74	21.0
	19	20	19.8	15.1	3.73	19.5
	20	24	20.9	14.3	3.72	19.9
	Mean ± SD	10	20.4 ± 1.6	15.5 ± 0.9	3.77 ± 0.12	20.1 ± 0.6
	H^2 ± SE		0.194 ± 0.185	0.000 ± 0.000	0.263 ± 0.209	0.246 ± 0.207
C (FNQ)	21	13	19.2	14.2	3.75	20.2
	22	22	18.7	14.7	3.64	20.4
	23	17	17.9	13.2	3.61	21.7
	24	11	17.0	12.7	3.55	20.0
	25	21	16.2	14.3	3.68	20.6
	26	16	17.4	16.3	3.62	20.0
	27	15	15.9	12.3	3.66	20.8
	28	17	19.2	14.9	3.39	19.7
	29	16	17.7	15.6	3.68	22.4
	30	19	17.9	15.2	3.67	20.5
	Mean ± SD	10	17.7 ± 1.1	14.3 ± 1.3	3.63 ± 0.10	20.6 ± 0.8
	H^2 ± SE		0.014 ± 0.122	0.000 ± 0.000	0.261 ± 0.232	0.484 ± 0.318
D (FNQ)	31	19	19.9	17.1	3.82	21.0
	32	22	20.3	15.0	3.62	20.2
	33	22	18.5	14.8	3.44	20.4
	34	21	16.0	13.4	3.72	22.0
	35	19	19.9	15.9	3.72	21.1
	36	17	17.0	14.5	3.73	20.7
	37	21	18.2	14.9	3.58	20.8
	38	15	16.9	13.3	3.34	21.0
	39	15	20.9	17.1	3.55	22.0
	40	12	14.9	11.2	3.48	20.1
	Mean ± SD	10	18.3 ± 2.0	14.7 ± 1.8	3.60 ± 0.15	20.9 ± 0.7
	H^2 ± SE		0.444 ± 0.297	0.208 ± 0.208	0.715 ± 0.390	0.264 ± 0.222

Note: PNG, Papua New Guinea; FNQ, Far North Queensland (Australia); *n*, number of trees or families; *D*, stem diameter; TH, tree height; SWV, stress-wave velocity; *P*, Pilodyn penetration; SD, standard deviation; SE, standard error; H^2, broad-sense heritability.

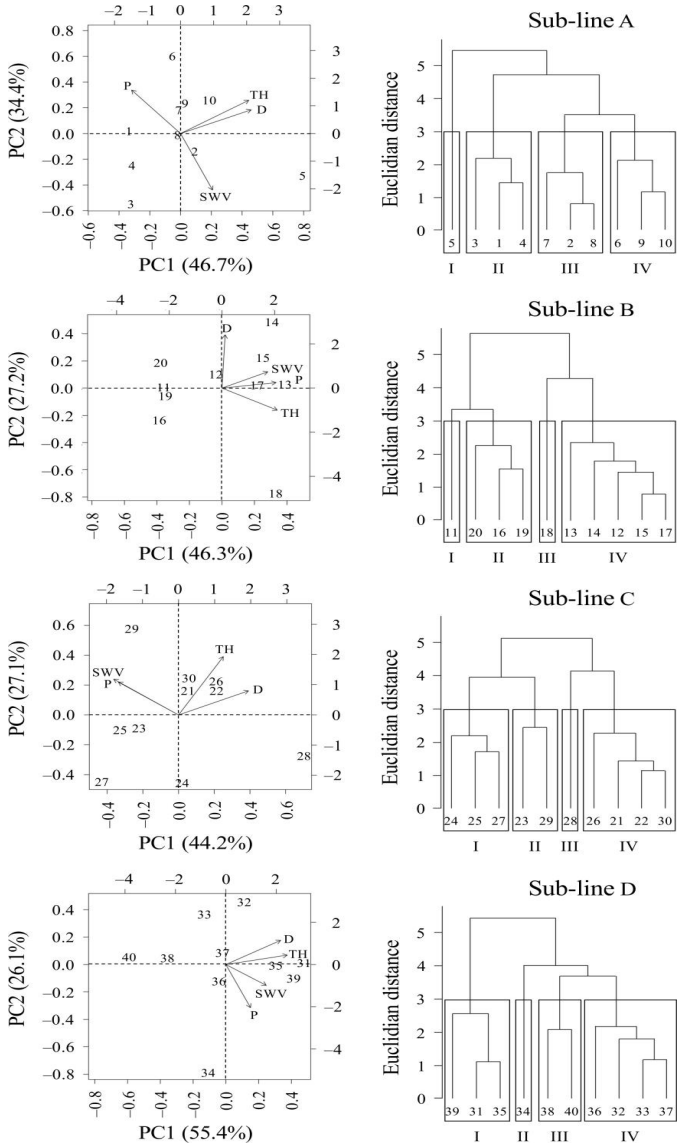

Figure 4
Principle component (PC) analysis scores of the breeding value measured traits in mother trees in each sub-line and dendrogram based on the principal component score.

Note: *D*, stem diameter; TH, tree height; SWV, stress-wave velocity; *P*, pilodyn penetration; Number in PCA scores, family ID.

Table 4
Loading values from the principal component analysis for the families in each sub-line.

Sub-line (origin)	Trait	Loading value	
		PC1	PC2
A	*D*	0.618	0.288
	TH	0.597	0.404
	SWV	0.280	–0.688
	P	–0.429	0.529
B	*D*	–	0.916
	TH	0.639	–0.311
	SWV	0.417	0.246
	P	0.643	–
C	*D*	0.576	0.303
	TH	0.369	0.732
	SWV	–0.534	0.449
	P	–0.496	0.413
D	*D*	0.577	0.444
	TH	0.647	0.173
	SWV	0.425	–0.383
	P	0.260	–0.791

Note: PC, principal component; *D*, stem diameter; TH, tree height; SWV, stress-wave velocity; *P*, Pilodyn penetration; -, approximately 0.

Table 5
AIC values of mixed-effect models for explaining relationships between measured traits.

Trait 1 (X_{ij})	Trait 2 (Y_{ij})	Eq. 3	Eq. 4	Eq. 5
D	TH	–	–	–
	SWV	–	464.715	<u>460.575</u>
	P	3186.41	3184.60	<u>3184.47</u>

Note: AIC, Akaike Information Criterion; *D,* stem diameter; TH, tree height; SWV, stress-wave velocity; *P,* Pilodyn penetration, –, failed to converge. Values with underline indicate the selected model with minimum AIC values. Relationships were only evaluated for phenotypic correlation coefficient with less than a *p*-value of 0.05 in Figure 5.

Table 6
Fixed-effect parameters and variance components in mixed-effects models for explaining relationships between measured traits.

Trait 1 (X_{ij})	Trait 2 (Y_{ij})	Parameter	Fixed-effect parameter				Variance component	
			Estimate	SE	*t*-value	*p*-value	Sub-line	Residual
D	SWV	α_0	0.0014	0.0024	0.561	0.575	0.0053 (4.9)	0.1027 (95.1)
		α_1	3.6580	0.0608	60.160	<0.001		
	P	α_0	–0.0123	0.0143	–0.863	0.389	0.1705 (4.5)	3.6302 (95.5)
		α_1	20.6509	0.3554	58.107	<0.001		

Note: SE, Standard error; *D*, stem diameter; SWV, stress-wave velocity; *P*, Pilodyn penetration. The formula is Eq. 5 ($Y_{ij} = \alpha_0 X_{ij} + \alpha_1 + Sub\text{-}line_{ij} + e_{ij}$). Values in parenthesis of variance components indicate variance component ratios (%) of the sub-line to the total variance.

Table 7
Genetic correlation coefficients between measured traits.

Trait 1	Trait 2	Sub-line A		Sub-line B		Sub-line C		Sub-line D	
		r_g	*p*-value	r_g	*p*-value	r_g	*p*-value	r_g	*p*-value
D	TH	<u>0.722</u>	0.018	–0.147	0.685	0.380	0.279	<u>0.898</u>	< 0.001
	SWV	0.151	0.677	0.107	0.769	–0.352	0.318	0.256	0.476
	P	–0.150	0.680	0.166	0.648	–0.228	0.526	0.049	0.894
TH	SWV	–0.104	0.776	0.289	0.418	–0.026	0.944	0.465	0.175
	P	–0.239	0.506	<u>0.675</u>	0.032	–0.101	0.782	0.270	0.451
SWV	*P*	–0.494	0.147	0.255	0.476	0.396	0.257	0.265	0.459

Note: *D*, stem diameter; TH, tree height; SWV, stress-wave velocity; *P*, Pilodyn penetration; r_g, genetic correlation coefficient. Values with underline in genetic correlation coefficients indicate *p*-values less than 0.05.

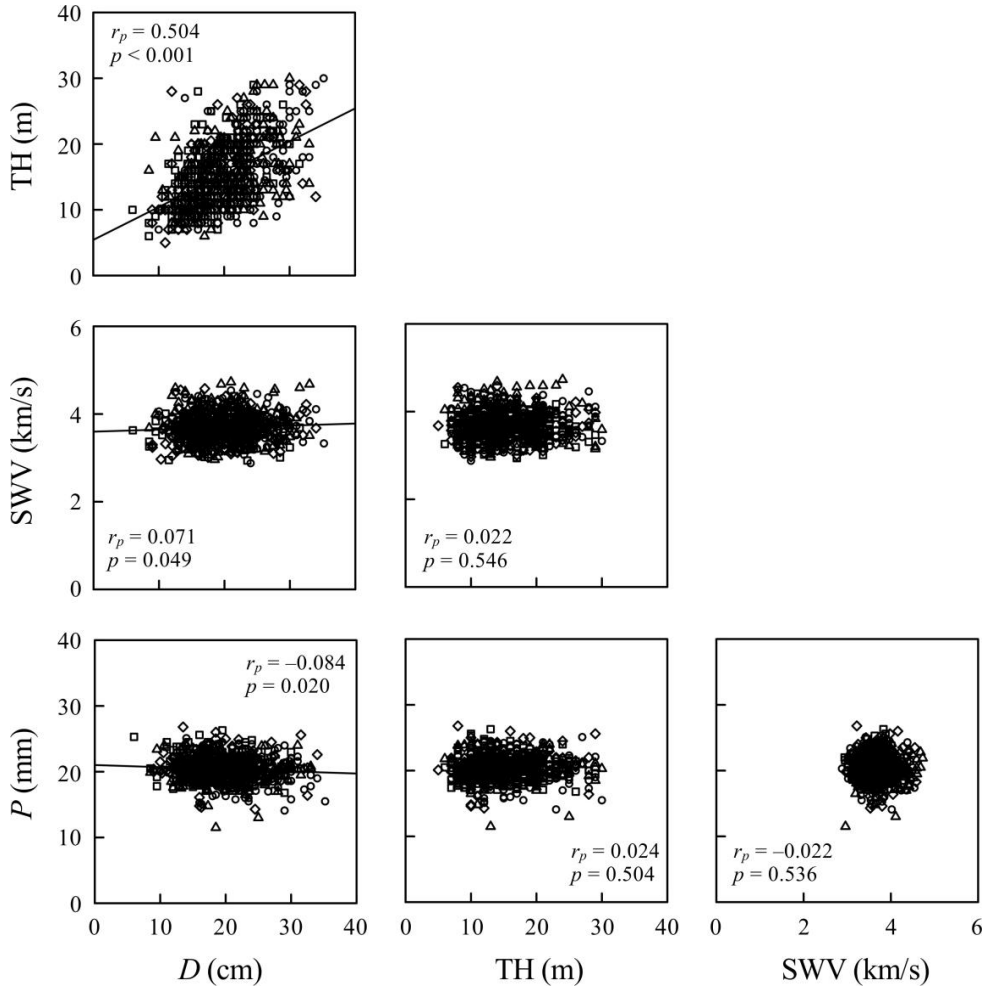

Figure 5
Phenotypic relationships between measured traits in the third-generation *A. mangium*

Note: Number of trees = 766; *D*, stem diameter; TH, tree height; SWV, stress-wave velocity; *P*, Pilodyn penetration; r_p, phenotypic correlation coefficient; *p*, *p*-value.

this study (Table 3) was almost the same or higher than the heritability reported in the previous research, with a few exceptions (Nirsatmanto and Kurinobu, 2002; Hai et al., 2015). In addition, although the broad-sense heritability of growth traits was almost zero in several sub-lines, the broad-sense heritability of wood traits showed moderate to high in all sub-lines (Table 3). In the tree breeding program of *A. mangium* in Indonesia, the selection criteria of superior families from the first and second generations were mainly growth traits, such as stem diameter, tree height, and stem form. Thus, relatively lower broad-sense heritability might be found in growth traits than wood traits. The higher broad-sense heritability of wood traits in each sub-line in this study indicated that families with higher density and Young's modulus of wood, which are suitable for solid wood products, can be selected from the third-generation *A. mangium* in all sub-lines.

As shown in Figure 3, relatively lower values of variance component ratio of family were found for stem diameter in sub-line C and tree height in sub-lines A, B, and C. The result suggested that the genetic diversity of growth traits might be reduced in some sub-lines. The height growth of the first-generation *A. mangium* was better than that of locally selected *A. mangium* trees in Indonesia by 10 to 15 % at three years old (Nirsatmanto et al., 2003). In addition, stem diameter and tree height of the second-generation trees showed about 5 and 3% higher values compared to those of the unimproved population at one year old (Nirsatmanto et al., 2004). Thus, lower values of variance component ratio in tree height might be related to the selection results in the first and second generations. Therefore, if new families with superior growth traits were added to the seed orchard of this generation from the same original seed provenance, the growth traits of the next generation would be improved. On the other hand, the variance component ratio of the family for wood traits showed relatively higher values in all sub-lines (Figure 3). These results indicated that the production of the next generations with superior wood

traits is possible in all sub-lines of the third generation of this species.

Characterization of families in each sub-line

In the present study, growth and wood traits in the third-generation trees of *A. mangium* were examined. The main selection criteria in the first and second generations were growth traits such as stem diameter and tree height (Nirsatmanto and Kurinobu, 2002; Nirsatmanto et al., 2003, 2004, 2013, 2015; Nirsatmanto, 2012). Wood traits should be considered in addition to growth traits for producing the next generation of this species. The wood with higher Young's modulus is produced from trees of families showing higher values of stress-wave velocity (Ishiguri et al., 2008). In addition, pulp yield is increased using wood with higher density (Nezu et al., 2021a,b) obtained from trees of families showing lower values of Pilodyn penetration. In the present study, as the results of cluster analysis based on PCA for mother trees, families with superior characteristics in both growth and wood traits were found (Figure 4). For example, group I in sub-line A might be suitable for both solid wood and pulpwood production. Group IV in sub-line B, group II in sub-line C, and group I in sub-line D are suitable for solid wood production. In addition, group IV in sub-line D might have higher wood density, although growth traits and stress-wave velocity showed average values. Wood properties might be improved in the next generation by using these families.

Relationships among measured traits

Positive phenotypic and genetic correlations have been reported between growth traits in tropical tree species (Hai et al., 2008; Rojas et al., 2017; Hidayati et al., 2019). For example, a positive phenotypic and genetic correlation between stem diameter and tree height was found in four-year-old *Acacia auriculiformis* clone trees planted in Vietnam (Hai et al., 2008), five- to six-year-old *Eucalyptus globulus* planted in Chile (Rojas et al., 2017), and six-year-old *A. mangium* families in the third-generation progeny trial (Hidayati et al., 2019). The phenotypic correlation in this study (r_p = 0.504, Figure 5) was similar to those obtained in many tropical tree species (Hai et al., 2008; Rojas et al., 2017; Hidayati et al., 2019). In addition, positive genetic correlations were found between stem diameter and tree height in sub-lines A and D, indicating that selecting superior trees or families by stem diameter may increase wood yield in this species in these sub-lines.

Positive phenotypic correlations between stem diameter and stress-wave velocity of trees were found in nine-year-old *Eucalyptus grandis* (r_p = 0.81, $p < 0.01$) and *Eucalyptus urophylla* (r_p = 0.44, $p < 0.05$) planted in Indonesia (Prasetyo et al., 2017), and five-year-old *Gmelina arborea* (r_p = 0.336, $p < 0.01$) planted in Indonesia (Hidayati et al., 2017). In contrast, phenotypic negative correlation (r_p = –0.465, r_p^2 = 0.216) was found in 13-year-old *Falcataria falcata* (syn. *Paraserianthes falcataria*) planted in Indonesia (Ishiguri et al., 2007). In addition, no significant phenotypic correlations were found in *Tectona grandis* (Hidayati et al., 2013), *A. mangium* (Hidayati et al., 2019), and *Eucalyptus camaldulensis* (Nezu et al., 2021a). These results indicated that the phenotypic relationships between growth and wood traits might differ among tree species. Similar results were obtained in the relationship between stem diameter and Pilodyn penetration: significant phenotypic correlations in clones of 12-year-old *T. grandis* planted in Indonesia (r_p = 0.86, $p <$ 0.01, Hidayati et al., 2013) but not in *E. globulus* and *Eucalyptus nitens* at age six growing in commercial plantation in Chile (Carillo et al., 2017) and *A. mangium* families at age six in Indonesia (Hidayati et al., 2019). In this study, phenotypic correlation coefficients between growth and wood traits were very low (Figure 5). The results indicate that, in *A. mangium*, wood traits are independent of growth characteristics at the individual tree level. In addition, significant positive or no significant genetic correlations were found between growth and wood traits in all sub-lines (Table 7). Similar results were found in several tropical tree species in the previous studies (Wu et al., 2011; Blackburn et al., 2014; Hai et al., 2015). Thus, it is concluded that selecting the families with higher wood yield does not always reduce density and Young's modulus of wood.

To evaluate the effect of sub-line differences on relationships between measured traits, the linear mixed-effects model with random effect of sub-line was developed for the relations with a *p*-value less than 0.05 (Figure 5). The model was not obtained between stem diameter and tree height (Table 5). In the relation between stem diameter and stress-wave velocity or Pilodyn penetration, the model with a random effect of sub-line in intercept was selected based on the AIC value (Table 5). However, the *p*-value of the fixed-effect parameter estimates exceeded 0.05, and the variance component ratio in the sub-line also showed lower values (Table 6). Thus, sub-line differences might not largely affect the relationships between measured traits in this species: relationships between measured traits in this study might be common relationships in this species. It is suggested that superior trees in both growth and wood traits in this species can be efficiently selected from other provenances by using these common relationships.

Conclusion

The growth and wood trait variations and their relationships were evaluated for the third-generation *A. mangium* in Indonesia. Broad-sense heritability values for wood traits were higher than those for growth traits in all sub-lines, with several exceptions. Superior families in both growth and wood traits were found based on the PCA and cluster analysis results in each sub-line using the breeding value of mother trees in the measured traits. These results suggest that wood traits in relation to Young's modulus and density of wood can be improved through family selection within the sub-lines in the third-generation *A. mangium* in Indonesia. Except for the relationship between stem diameter and tree height, no significant or lower values of phenotypic correlation coefficients were obtained between measured traits. In addition, almost no sub-line effects were found in the relationships between stem diameter and other traits. Furthermore, positive- or non-significant

genetic correlations were found between growth and wood traits in each sub-line. Thus, it is considered that, despite the origin of seeds, the selection of superior families in growth characteristics will not lead to deterioration of wood properties for solid wood production in the third-generation *A. mangium* in Indonesia. In conclusion, the fourth-generation *A. mangium* in Indonesia can be selected from the superior families in terms of growth characteristics and wood properties in the third generation.

Acknowledgements

We thank the students of the Department of Bioresources Technology and Veterinary, Vocational College, Universitas Gadjah Mada, Indonesia, and the staff of the Center for Forestry Instrument Standard Assessment, Yogyakarta, Indonesia, for their help in field sampling.

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