Genetic Variation in Growth Characteristics and Wood Properties of *Ficus variegata* Blume First Generation Progeny Trials in Indonesia

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ABSTRACT

Two first-generation progeny trials of *Ficus variegata* Blume were planted in Yogyakarta, Indonesia, consisting of 17 families from the provenances of West Nusa Tenggara (WNT) and 19 families from the provenances of Cilacap-Pangandaran (C-P), respectively. The trials were evaluated after 10 years for growth characteristics [diameter (D), tree height (H) and stem volume (V)] and wood properties [stress-wave velocity (SWV) and Pilodyn penetration (P)]. Genetic variation, the coefficient of additive genetic variation (CV_A), and heritability estimation were analyzed. Subsequently, genetic correlation between traits was estimated. The analysis of variance showed that there were significant differences in growth characteristics and wood properties in the WNT families, with significance observed across most factors except for height and P in the C-P families. The CV_A in growth characteristics (D, H, V) was higher than for wood quality (SWV and P) in WNT and C-P families. Estimated family heritability (h^2_f) for growth characteristics, SWV, and P were high in the WNT families but moderate in the C-P families showing that genetic variation in the observed traits was more additive in the WNT families. The positive estimated genetic correlations between growth characteristics in two progeny trials, and the moderate to strong negative genetic correlation between D and P and also between P and SWV showed that growth characteristics and wood quality can be genetically improved simultaneously by using D as a selection criterion is an appropriate breeding strategy for *F. variegata*.

Keywords: *Ficus variegata* Blume, growth characteristics, heritability, genetic correlation, Pilodyn penetration

1. INTRODUCTION

The decline in the potential of Indonesia's natural forests to fulfill timber needs has led to the development of a plantation resource to help meet this demand. Promoting the use of native species is essential to meet the timber demand, as these species are expected to be well-suited and adapted to local biotic and abiotic conditions (Thomas *et al.*, 2014). It is also necessary to reduce the dependence of the wood industry, especially on members of the *Dipterocarpaceae* (Augustina *et al.*, 2020). Subsequently, nyawai (*Ficus variegata* Blume belongs to the Moraceae family) is a native species that has prospects for supplying plywood, face veneer

(Hendromono and Komsatun, 2008), packaging boxes, and materials for light construction (Sumarni *et al.*, 2009). It is a fast-growing tree species that has attracted the interest of private companies since 2003 (Effendi and Mindawati, 2015) and is being developed as an 'alternative' plant for plantations (Susanti and Halwany, 2017). In Indonesia, the natural distribution of this species includes Kalimantan (Haryjanto and Hadiyan, 2014; Wahyuningtyas *et al.*, 2022), Java (Nurtjahjaningsih *et al.*, 2019), Sumatra (Nur'aini *et al.*, 2013; Rofifah *et al.*, 2021), Sulawesi (Pitopang, 2012), West Lombok, Papua (van Heist *et al.*, 2010).

Implementing a selective breeding program is an effective way to increase plantation productivity and improve the genetic quality of trees (Nelson, 2023). Achieving effective selective breeding requires a thorough understanding of the heritability of growth and wood quality traits. Heritability is a statistical measure of the proportion of phenotypic variance explained by genetic variance (Waszak and Cieślik, 2016). Traits with high heritability can be targeted for improvement through selective breeding because they are more likely to be passed on to future generations. The correlations between traits is also important for plant breeding programs in order to create an understanding how one trait influences another through shared genetic factors (de Oliveira *et al.*, 2015). However, in-depth knowledge in these areas is currently lacking for *F. variegata*.

Measures of the heritability of height and diameter (D) of *F. variegata* in progeny tests established in 2012 showed that the genetic control of these traits was weak in the early growth phase (Haryjanto *et al.*, 2014). Accurate measurements of tree growth and wood quality at the time of harvesting are crucial from breeding and selection perspective. These measurements hold a high value for predicting the breeding values of tested genotypes. Wood density is regarded as the best single predictor of wood quality (Fundova *et al.*, 2018). Many breeding programs prioritize it as an initial trait for improvement due to its correlations with stiffness, strength, and shrinkage (Hong *et al.*, 2014). The specific gravity of *F. variegata* is 0.27, ranging from 0.20 to 0.43 (Sumarni *et al.*, 2009), indicating that the wood lacks strength and improving wood quality is necessary to make the species more attractive as a timber species. Wood quality is the main concern when using fast-growing plantations, especially when producing solid wood (Ghani and Lee, 2021). Therefore, improving these properties will expand the utilisation of wood more widely (Laksono *et al.*, 2023).

In breeding programs, the preferred approach for rapidly assessing wood properties in standing trees involves the use of non-destructive methods (Schimleck *et al.*, 2019). The Pilodyn, originally developed to test for wood decay, is often used to assess wood density (Fukatsu *et al.*, 2011). Meanwhile, stress-wave velocity (SWV) which measures the speed of sound waves in standing trees, has been used to measure the speed of sound waves in standing trees and has received considerable attention (Wang *et al.*, 2001). Many studies have used SWV on a standing tree as a stiffness selection criterion (Fukatsu *et al.*, 2015; Matheson *et al.*, 2008) and the potential for prediction of modulus of elasticity (Ishiguri *et al.*, 2008; Van Duong *et al.*, 2022; Wang *et al.*, 2001).

This study has two objectives: First, to investigate the inheritance of traits related to growth characteristics and wood quality. Second, to understand how these traits relate to each other, both genotypic and phenotypic correlations. The acquired information will be examined in the context of formulating suitable selection strategies for *F. variegata* breeding programs.

2. MATERIALS and METHODS

2.1. Study site

The study site was in Bantul, Yogyakarta Province,

Indonesia (latitude 07°57′30″−07°57′54″S, longitude 110°26′07″−110°26′29″ E, altitude of 75−145 m above sea level). The slope of the site varied between 5°−30°, and the soil was identified as an Oxisol. The climate according to the Köppen classification is Af (tropical rainforest climate) to Am (tropical monsoon climate), or type C (medium wet) of the climate classification by Schmidt and Ferguson (1951), with a mean annual rainfall of 1,502 mm (Bappeda Kabupaten Bantul, 2011).

2.2. Materials

In this study, two progeny trials involving the first generation from 17 and 19 open-pollinated *F. variegata* trees were conducted in a half-sib trial established in December 2012. The mother trees were selected from two regions, and the trial was divided into two sublines situated 300 m apart. The experimental design of the progeny test was a randomized complete block design. Subsequently, the provenances of West Nusa Tenggara (WNT) represented 17 families, 5 non-contiguous tree plots in six replicates and Cilacap-Pangandaran (C-P) represented 19 families, 4 non-contiguous tree plots in six replicates. The planting space was 5 × 5 m.

2.3. Measurement

D was measured at 1.3 m above ground, tree height (H) was measured from the ground to the tip of the tree, and stem volume (V) was measured using the equation of Qirom and Supriyadi (2013) for 10-year-old trees:

$$\ln V = a + b \ln (D) + c \ln (H) \qquad (1)$$

Where:

V: stem volume (m³), D: diameter at 1.3 m above ground (cm), H: tree height (m), a: −9.22846, b: 1.7456, c: 0.9759.

Stem SWV was measured using a commercially available handheld stress-wave timer (FAKOPP Microsecond Timer, FAKOPP Enterprise) according to previously described methods (Hidayati *et al*., 2013b; Ishiguri *et al*., 2007). The start and stop sensors were positioned at 150 and 50 cm from ground level, respectively. Using a small hammer, the start sensor was struck to generate a stress wave. When the stress-wave was received at the stop sensor, the travel time between the two sensors was recorded. Ten measurements of stress-wave propagation time were taken for each tree, and the mean value was calculated. The formula for the calculation of the stress-wave propagation time per unit length was described by Wang *et al*. (2000, 2004).

Wood density measured indirectly by Pilodyn penetration (P) was carried out using Pilodyn tester (strength of spring, 6 J; D of pin, 2.5 mm, Proceq) at 1.3 m above ground level at three positions for each tree (Hidayati *et al*., 2013b, 2019; Ishiguri *et al*., 2008; Wu *et al*., 2010) and the mean value was calculated. The bark at the measurement points was removed prior to measurement.

2.4. Statistical analyses

Analyses of variance (ANOVA) were carried out to evaluate the differences in D, H, V, P, and SWV among the tested families based on an individual-tree following the linear model:

$$Y_{ijk} = \mu + B_i + F_j + \varepsilon_{ijk} \qquad (2)$$

Where Y_{ijk} is the individual tree observation, μ: the overall mean, B_i: fixed effect of the i-th block, F_j: random effect of the j-th family associated with the average genetic effects of the open-pollinated families, ε_{ijk}: the within-plot error.

Family heritability (h^2_f) was calculated using the

following formula of Zobel and Talbert (1984):

$$h_f^2 = \frac{\sigma^2 f}{\sigma_w^2 \; / \; TR \; + \; \sigma_f^2} \tag{3}$$

Where σ_f^2: the family component of variance, σ_w^2: the within-plot error component of variance, TR: the harmonic mean number of trees per plot by replication.

The coefficient of additive genetic variation (CV_A) is a mean-standardized index of the evolvability of a trait (Hill, 2010; Houle, 1992). It was described by Haapanen (2001):

$$CV_A = (\sqrt{\sigma_A^2} \; / \; \chi) \times 100 \tag{4}$$

Where CV_A: coefficient of additive genetic variation, σ_A^2: additive genetic variance. The additive genetic variance on a single-site basis was estimated by multiplying the among-family component of variance by four ($\sigma_A^2 = 4\sigma_f^2$; White *et al.*, 2007; Zobel and Talbert, 1984); χ: population mean for the trait.

Genetic correlation between pairs of traits (r_{Gxy}) was calculated following Zobel and Talbert (1984):

$$r_{Gxy} = \frac{\sigma_{f(xy)}}{\sqrt{\sigma_{f(x)}^2 \cdot \sigma_{f(y)}^2}} \tag{5}$$

Where $\sigma_{f(xy)}$ is the additive genetic covariance component between traits, and $\sigma_{f(x)}^2$ and $\sigma_{f(y)}^2$ are the additive variance components for traits x and y respectively.

The phenotypic correlation between pairs of traits (r_P) was calculated as given by Falconer (1989):

$$rP = \frac{covP}{\sigma Px \sigma Py} \tag{6}$$

Where cov_P is the covariance of the two traits, and σ_{Px} and σ_{Py} are the SD for traits x and y respectively.

3. RESULTS and DISCUSSION

3.1. Results

3.1.1. Mean values and variation among characteristics

The mean, range of values, SEM for D, H, V, SWV, and P of the 17 WNT families and the 19 C-P families are shown in Table 1. The mean growth traits (D, H, V) of WNT families were higher than those of C-P families. Subsequently, P was smaller in WNT than C-P,

Table 1. Mean value of growth characteristics and wood properties in WNT and C-P families

Trait	WNT families			C-P families		
	Mean	Range (min-max)	SEM	Mean	Range (min-max)	SEM
D (cm)	17.41	6.05−30.89	0.23	16.30	7.17−27.07	0.21
H (m)	9.74	5.34−14.13	0.09	9.07	5.04−16.10	0.10
V (m³)	0.141	0.006−0.340	0.004	0.121	0.009−0.407	0.004
SWV (km/s)	2.03	1.65−2.48	0.01	2.08	1.73−2.63	0.01
P (mm)	29.62	19.67−38.33	0.17	33.57	26.50−40.00	0.14

WNT: West Nusa Tenggara, C-P: Cilacap-Pangandaran, D: diameter, H: tree height, V: stem volume, SWV: stress-wave velocity, P: Pilodyn penetration.

29.62 mm, and 33.57 mm, respectively. SWV of WNTs was smaller than that of C-P, 2.03 km/s and 2.08 km/s, respectively. Significant variations (1% level) were observed for all measured characteristics among WNT families. Additionally, differences in D, V, and SWV within the C-P families were found to be significant at the 5% level, as shown in Table 2.

3.1.2. Genetic variation and heritability

The estimated CV_A, variance components, and family heritability estimates are shown in Table 3. The estimated CV_A depending on the analyzed traits, and growth traits was higher than wood quality. In the WNT, CV_A ranged from 16.47% to 46.61% for the growth traits (D, H, and V) and it was 4.68% (SWV) and 6.20% (P); in C-P, CV_A ranged from 5.16% to 24.02% for the growth traits (D, H, and V) and it was 2.58% (SWV) and 2.54% (P).

In the WNT, the estimated contribution of the family component of variance (σ^2_f) to the total phenotypic variance ranged from 15.80% to 21.47% for the growth traits (D, H, and V). For wood quality, it was 8.95% (P)

and 10.43% (SWV). In C-P, the estimated contribution of the family component of variance (σ^2_f) to the total phenotypic variance ranged from 0.46% to 3.95% for the growth traits (D, H, and V). For wood quality, it was 2.18% (P) and 3.04% (SWV).

In the WNT, family heritability (h^2_f) for the growth traits (D, H, and V) ranged from 0.81 to 0.86, and for wood quality, it was 0.69 (P) and 0.73 (SWV); in C-P, family heritability for growth traits ranged from 0.26 (H) to 0.49 (V) and for wood quality, it was 0.32 (P) and 0.39 (SWV).

3.1.3. Phenotypic and genetic correlations between characteristics

In both WNT and C-P families, highly positive and significant phenotypic correlations were observed for the growth traits (D, H, and V). The correlations ranged between 0.811−0.969 for WNT families and 0.631−0.922 for C-P families, as shown in Table 4. Subsequently, no phenotypic correlations were observed between growth traits (D, H) and wood quality (SWV and P). Significant negative phenotypic correlations were observed between

Table 2. Differences in growth characteristics, stress-wave velocity (SWV), Pilodyn penetration (P) of the WNT and C-P families

Parameter	Trait				
	Diameter	Height	Volume	SWV	Pilodyn
WNT					
Mean square					
Family	85.034**	17.171**	0.029**	0.071**	27.844**
Error	15.900	2.351	0.004	0.019	8.569
C-P					
Mean square					
Family	27.538*	4.441ns	0.009*	0.038*	12.065ns
Error	14.844	3.303	0.004	0.023	8.187

[*] Significant at $p < 0.05$; [**] Significant at $p < 0.01$; [ns] Non-significant at $p > 0.05$.
WNT: West Nusa Tenggara, C-P: Cilacap-Pangandaran.

Table 3. Estimated coefficient of additive genetic variation (CV_A), estimated the family component of variance (σ^2_f), estimated the within-plot error component of variance (σ^2_w) and family heritability (h^2_f) for diameter, height, volume, SWV and Pilodyn penetration (P) of the WNT and C-P families

Trait	CV_A (%)	σ^2_f	σ^2_w	h^2_f
WNT				
Diameter	19.84	2.984 (15.80%)[a]	15.900 (84.20%)[b]	0.81
Height	16.47	0.643 (21.47%)	2.351 (78.53%)	0.86
Volume	46.61	0.001 (19.61%)	0.004 (80.39%)	0.85
SWV	4.68	0.002 (10.43%)	0.019 (89.57%)	0.73
Pilodyn	6.20	0.843 (8.95%)	8.569 (91.04%)	0.69
C-P				
Diameter	9.58	0.610 (3.95%)	14.843 (96.05%)	0.46
Height	5.16	0.055 (1.63%)	3.302 (98.37%)	0.26
Volume	24.02	0.0002 (0.46%)	0.044 (95.58%)	0.49
SWV	2.58	0.0007 (3.04%)	0.023 (96.96%)	0.39
Pilodyn	2.54	0.182 (2.18%)	8.186 (97.82%)	0.32

[a,b] The proportion of the family component variance (σ^2_f) and the within-plot error component of variance (σ^2_w) to the total phenotypic variance in parenthesis, respectively.
SWV: stress-wave velocity, WNT: West Nusa Tenggara, C-P: Cilacap-Pangandaran.

SWV and P in both families, −0.281 (WNT) and −0.125 (C-P), respectively.

Strong estimated positive genetic correlations were observed between D and H (r_G = 0.918), and (r_G = 0.765) in WNT and C-P families, respectively. Between other growth traits (D and V) and (H and V) they were low (0.047) and moderate (0.502), respectively. Estimated negative genetic correlations among growth characteristics (D, H, V) and P in the WNT families and C-P families were −0.179 to −0.731 and −0.375 to −0.664, respectively.

Estimated negative genetic correlations observed between D and P were strong (r_G = −0.731) and moderate (r_G = −0.375), and between P and SWV were moderate (r_G = −0.460) and strong (r_G = −0.786) in WNT families and C-P families, respectively.

3.2. Discussion

3.2.1. Mean values populations and variation among characteristics

In this study, the growth of *F. variegata* was comparatively lower than that observed in other sites. For instance, in Riam Kiwa (South Kalimantan), *F. variegata* planted there exhibited a mean annual increment (MAI) in D of 2.10–2.36 cm/yr (Fitriani, 2011), whereas in this study the MAI was 1.74 cm/yr and 1.63 cm/yr for the WNT and C-P populations, respectively. This difference may be attributed to the tropical climate in Riam Kiwa (South Kalimantan) characterized by high humidity and consistent rainfall throughout the year (Yasin *et al.*, 2020). *F. variegata,* being a tropical tree, thrives in seasonal wet tropical rainforests, often found along watercourses (Spencer *et al.*, 1996).

Table 4. Genetic (upper diagonal) and phenotype (lower diagonal) correlation coefficients between traits in WNT and C-P families

Characteristics	Diameter	Height	Volume	SWV	Pilodyn
WNT					
Diameter	-	0.918	0.180	−0.194	−0.731
Height	0.811[**]	-	0.302	0.091	−0.640
Volume	0.969[**]	0.863[**]	-	−0.367	−0.179
SWV	−0.011[ns]	0.063[ns]	0.040[ns]	-	−0.460
Pilodyn	−0.086[ns]	−0.099[ns]	−0.107[*]	−0.281[**]	-
C-P					
Diameter	-	0.765	0.047	−0.051	−0.375
Height	0.631[**]	-	0.502	0.144	−0.664
Volume	0.922[**]	0.819[**]	-	0.706	−0.502
SWV	−0.176[ns]	−0.080[ns]	−0.150[**]	-	−0.786
Pilodyn	0.016[ns]	0.076[ns]	0.050[ns]	−0.125[*]	-

[*] Significant at $p < 0.05$; [**] Significant at $p < 0.01$; [ns] Non-significant at $p > 0.05$.
WNT: West Nusa Tenggara, C-P: Cilacap-Pangandaran, SWV: stress-wave velocity.

The SWV values of *F. variegata* (2.03 km/s and 2.08 km/s for WNT and C-P families, respectively) may be relatively lower than other tropical tree species. Subsequently, the SWV values were at 2.83 km/s for *Gmelina arborea* 5-year-old (Hidayati *et al*., 2017) and 3.08 km/s for 13-year-old *Falcataria moluccana* (Ishiguri *et al*., 2007). This indicates that *G. arborea* and *F. moluccana* are stiffer than *F. variegata.* This difference may be due to differences in the anatomical characteristics and basic density of these species.

P serves as an indicator of wood density; higher values correspond to lower wood density, and vice versa (Kha *et al*., 2012). The P value was higher than other tropical tree species. Specifically, the P value was at 25.9 mm for 4.5-year-old in white jabon (*Neolamarckia cadamba*; Chaerani *et al*., 2019), 18.7−27.6 mm for 12-year-old *Tectona grandis* (Hidayati *et al*., 2013b), 15.7−18.9 mm for 6-year-old *Acacia mangium* (Hidayati *et al*., 2019). This indicates that *F. variegata* has a lower

wood density compared to these species.

In this study, a comparison of the growth and wood quality traits between the two populations (WNT and C-P) reveals the following: the WNT families exhibit superior growth and wood density compared to the C-P families. Wood density, as indicated by P, is lower for WNT families than for C-P families. Lower penetration shows denser and stronger wood and is negatively correlated with P (Wei and Borralho, 1997; Wu *et al*., 2010). Conversely, for wood stiffness, SWV in the WNT families is slightly smaller than the C-P families (2.03 and 2.08, respectively). Although higher values of SWV show greater stiffness (Ishiguri *et al*., 2007; Wang *et al*., 2001), it does not always correlate with smaller P as observed in *T. grandis* (Hidayati *et al*., 2013a; Seta *et al*., 2021), *A. mangium* (Hidayati *et al*., 2019). In summary, it can be concluded that growth characteristics and wood density are superior in WNT compared to the C-P family. However the wood stiffness are similar for

WNT to CP.

With the exception of height (H) and P in the C-P families, all measured traits between the two populations (WNT and C-P) were statistically significantly different. These significant differences in characteristics indicate that these traits are influenced by genetic factors rather than the environment. Similar results were reported in other studies, where significant differences were observed in growth characteristics (D, H) and wood quality (SWV and P) among 65 families of *A. mangium* (Hidayati *et al.,* 2019), as well as in D, H, and P among 105 families of white jabon (Chaerani *et al*., 2019). The significant differences observed among the families in these traits suggest the possibility of selecting superior families to support breeding programs.

3.2.2. Genetic variation and heritability

The CV_A is recommended for reporting the results of studies on adaptive variation, as it provides a better guide than heritability to the long-term evolvability of a trait (Houle, 1992). This CV_A serves as a valuable indicator for assessing the long-term evolution of a trait and its potential for adaptation under changing environmental conditions (Houle, 1992). This reflects the potential for a given trait to respond to selection pressures in a given population, the larger the coefficient, the greater the evolvability of the trait (Cheung, 2020). In this study, CV_A in growth traits (D, H, V) was higher than for wood quality (SWV and P) in WNT and C-P families (Table 3). This suggests that growth traits could be hypothesized as being more related to species adaptation. Additionally, the CV_A of V was higher than that of H or D in both populations. This result may reflect the fact that volume is a function of both H and D. Specifically, the CV_A of D was higher than that of height in both populations, at 19.84% and 16.47% for WNT, and 9.58% and 5.16% for C-P, respectively. This finding contrasts with a previous study on *Pinus elliottii*, where the CV_A for height (H) was higher at 5.06% compared to the CV_A for D at 2.99% (Lai *et al*., 2017). Therefore, this study suggests that there is a greater scope for selection of D among families compared to height.

Family heritability (h^2_f) was higher in WNT families compared to C-P families for all traits (Table 3). Additionally, the proportion of the family component variance (σ^2_f) to the total phenotypic variance was consistently greater in WNT families for specific traits. For instance, in the D trait, the contribution of WNT families to the family component variance was 15.80%, whereas for C-P families, it was 3.95% (Table 3). The genetic variation in WNT families resulted in higher heritability values, indicating that the variation in these traits was primarily due to genetic differences among families (Lai *et al*., 2017; Ranjan and Gautam, 2020). This suggests a greater additive genetic effect passed on to offspring from WNT families compared to C-P families, emphasizing the significance of genetic variation in breeding programs (Mihai *et al*., 2014). The observed high heritability implies that selective breeding is more feasible for the considered traits.

Heritability and genetic correlations are important factors influencing the effectiveness of breeding programs, particularly in forest trees. A notable and crucial adverse genetic correlation is observed between tree productivity and wood density, commonly characterized by a strong negative relationship (Klápště *et al*., 2022). Meanwhile, heritability and genetic correlation are important genetic parameters for the effectiveness of indirect selection. When the genetic correlation between traits is high but heritability is low, indirect selection tends to be less effective in producing offspring with the desired parent traits. Low heritability means that the genetic influence on the traits is not strongly transmitted to the next generation, diminishing the impact of indirect selection. High family heritability was found in the WNT population for the D and P at 0.81 and 0.69, respectively (Table 3), and the strong genetic correlation

of D and P r_G = −0.731 (Table 4). This indicates that indirect selection of the D trait in the WNT population will improve wood quality.

In this study, family heritability (h^2_f) for the growth characteristics was higher than for wood quality in the WNT families, and except for H, also for the C-P families. In the WNT families, the family heritability of growth traits (D, H, V) ranged from 0.81 to 0.86, while the family heritability of wood quality traits (SWV, P) ranged from 0.69 to 0.73. Meanwhile, the family heritability in the C-P families ranged from 0.46 to 0.49 and ranged from 0.32 to 0.39 for growth (D, V) and wood quality (SWV, P) respectively, and other studies confirm this findings. The family heritability for height and P were 0.69 and 0.46, respectively in white jabon (Chaerani *et al*., 2019); in *A. mangium,* family heritability for height and P were 0.37 and 0.25 respectively (Hidayati *et al*., 2019). This indicates that growth traits are passed on to offspring more than wood quality traits.

The study showed that high heritability can also be obtained by using a limited number of families, for example, 17 families for WNT and 19 for C-P. The result was similar to in *Quercus serrata* with a family heritability of 0.80 with 17 families (Kang *et al*., 2007). However, it is important to note that high heritability does not necessarily mean that the trait is entirely determined by genetic or that it cannot be influenced by environmental factors. Subsequently, heritability estimates are specific to the population being studied and the range of environments and genetic variations present in that population. Traits with high heritability in one population may exhibit lower heritability in another population with different genetic and environmental factors.

3.2.3. Phenotype and genetic correlations between traits

Phenotypic and genetic correlations play important roles in tree improvement programs. Subsequently, phenotypic correlations help identify relationships between observable traits, while genetic correlations inform breeders about how they can prioritize the selection of certain traits, knowing that improvement in one trait may have a positive or negative effect on others. By considering both phenotypic and genetic correlations, breeders can formulate comprehensive strategies aimed at simultaneously enhancing multiple traits. This method allows for the development of forest plantations with desired outcomes, taking into account the interplay and relationships between different traits in the breeding process.

This study showed highly significant phenotypic correlations among growth traits (D, H, V) in both WNT families (0.811 to 0.969) and C-P families (0.631 to 0.922; Table 4), consistent with prior results observed in *T. grandis* (Hidayati *et al*., 2013a). Positive correlations between D and H were similarly reported in *A. mangium* (Hidayati *et al*., 2019), and *Eucalyptus urophylla* (Wei and Borralho, 1997), suggesting a strong interdependence between growth characteristics, with their values exhibiting predictable simultaneous changes.

There was no phenotype correlation between wood traits (SWV and P) and growth traits (D and height; Table 4). Similarly, no significant phenotype correlation was observed between growth characteristics (D and H) and SWV in teak (Hidayati *et al*., 2013b). This finding aligns with previous results on *A. mangium* (Hidayati *et al*., 2019), but in contrast to *G. arborea*, which exhibits a positive significant phenotype correlation between D and SWV (Hidayati *et al*., 2017). In this study, wood traits appear to be independent of growth traits, suggesting that families with superior characteristics for both growth and wood traits can be selected.

Positive genetic correlation between growth traits (D, H, V) ranged from 0.180 to 0.918 in the WNT families and ranged from 0.047 to 0.765 in the C-P families (Table 4). This indicates that these traits tend to be influenced by similar genetic factors. In other words, individuals with favorable genes for one of these traits

are likely to also have favorable genes for the others. These results are consistent with other studies, such as those conducted on *Populus ussuriensis* Kom (Jin *et al.*, 2019), *P. elliottii* (Lai *et al.*, 2017) and *Eucalyptus pellita* (Fadwati *et al.*, 2023). These traits are interconnected at the genetic level, and improving one trait can lead to improvements in the others.

P is closely related to the wood density at the outer part of the stem (Wessels *et al.*, 2011; Wu *et al.*, 2010). The estimated negative genetic correlations between P and D were strong ($r_G = -0.731$) in the WNT families and moderate ($r_G = -0.375$) in the C-P families (Table 4). Meanwhile, the genetic correlation of SWV with growth traits (D and H) of both ENT and C-P was both positive and negative, but the correlation was weak ($r_G = -0.194-0.144$; Table 4). The strong and negative correlation observed between P and D implies that as D increases, there is a corresponding decrease in P. This association indicates that increasing D is linked to low P, which, in turn, is indicative of high wood density. This finding is consistent with previous study on white jabon (Chaerani *et al.*, 2019), and *E. urophylla* (Kien *et al.*, 2008). Some studies have shown an unfavourable relationship between the two traits found in Norway spruce (Nguyen *et al.*, 2022), *Catalpa bungei* (Xiao *et al.*, 2021), *T. grandis* (Hidayati *et al.*, 2013b), and *E. urophylla* (Wei and Borralho, 1997), making it difficult to improve growth and wood quality at the same time. This study shows that the correlations is favourable for breeding both traits (growth and wood quality) simultaneously.

The genetic correlation between P and SWV was moderate ($r_G = -0.460$) to strong ($r_G = -0.786$) negative in the WNT and C-P families, respectively. In other words, selecting trees for increased P (which may be associated with wood density) could lead to a decrease in SWV and vice versa. Subsequently, higher SWV corresponded to lower P values, indicative of denser and stronger wood. This finding is consistent with previous studies on *E. urophylla* (Wei and Borralho, 1997), and *Larix kaempferi* (Fukatsu *et al.*, 2015). The result indicates that P was a reliable indirect measure of wood density in *F. variegata*.

4. CONCLUSIONS

The genetic study on the growth and wood characteristics of *F. variegata* in Yogyakarta Province, Indonesia aimed to investigate the inheritance of traits related to growth characteristics and wood quality; and to understand how these traits relate to each other, both genotypic and phenotypic correlations. The results obtained are summarized as follows:

a. Significant differences were observed between all measured characteristics in WNT families, except for height, and in the C-P families, except for height and P, indicating that these characteristics were influenced by genetic factors.

b. The family heritability of all traits was much higher in the WNT than in C-P families, demonstrating (1) much higher variability of all traits in the WNT was due to genetic differences among families; (2) greater additive effect passed on to offspring from WNT families than C-P families.

c. Positive genetic correlations between growth traits (D, H, V) were found in the WNT and C-P families. The observed moderate to strong negative genetic correlation between D and P, as well as between P and SWV, suggested that using D as a selection criterion could be a suitable breeding strategy for *F. variegata*. This method allows for the simultaneous genetic improvement of both growth and wood quality traits in the species.

CONFLICT of INTEREST

No potential conflict of interest relevant to this article was reported.

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