GENETIC VARIATION OF GROWTH AND WOOD DENSITY IN A PROGENY TEST OF *RUBROSHOREA LEPROSULA* IN CENTRAL KALIMANTAN

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ABSTRACT. *One approach to reducing the rate of degradation and selecting superior genotypes for genetically improved plantations is the establishment of progeny test plantations. Rubroshorea leprosula is a potential species for progeny testing based on its growth performance and wood quality. The research objective was to evaluate the genetic variation and genetic parameters in progeny test of R. leprosula at PT. Sari Bumi Kusuma in Central Kalimantan, providing a basis for selection and breeding strategies. The experiment was arranged in a RCBD with five replicate blocks. Each block had 80 families (seedlot), with 4 trees per family. Growth characteristics (diameter, height, and bole height) and wood density were analyzed. Wood density was estimated using the Pilodyn penetration method. The results indicated significant genetic diversity between families for all measured traits. The estimated family heritability ranged from 0.025 – 0.320, was categorized as low to moderate across traits, suggesting a considerable environmental influence on trait expression. A robust and favorable genetic correlation recorded between diameter and height, as well as height and bole height. However, a negative correlation was observed within diameter and wood density, indicating a trade-off between the two. Multi-trait selection revealed that genetic gain based on a three-trait index (excluding wood density) was higher than that based on a four-trait index. A moderate selection intensity (30%) is recommended to establish a balance between genetic gain and genetic variety preservation.*

Keywords: *progeny test, genetic variation, wood density, Rubroshorea leprosula, Pilodyn*

ABSTRAK. Pembangunan pertanaman uji keturunan merupakan salah satu pendekatan untuk mengurangi laju degradasi hutan alam sekaligus menyeleksi genotipe unggul guna mendukung pembangunan hutan tanaman yang lebih produktif dan memiliki kualitas genetik yang lebih tinggi. *Rubroshorea leprosula* adalah salah satu jenis potensial untuk dikembangkan melalui uji keturunan karena memiliki pertumbuhan dan kualitas kayu yang baik. Tujuan penelitian ini adalah mengevaluasi variasi genetik dan parameter genetik pada pertanaman uji progeny *R. leprosula* di PT. Sari Bumi Kusuma, Kalimantan Tengah. Rancangan penelitian adalah Rancangan Acak Lengkap Berblok (RCBD) dengan 5 blok sebagai ulangan. Setiap blok terdiri dari 80 famili (*seedlot)*, dengan 4 pohon per famili. Karakter pertumbuhan (diameter, tinggi, tinggi batang bebas cabang) dan berat jenis kayu dianalisis. Berat jenis kayu di estimasi dengan metode non-destruktif menggunakan pilodyn. Hasil penelitian menunjukkan adanya variasi genetik nyata antar famili pada seluruh karakter yang diamati. Heritabilitas famili yang didapatkan berkisar antara 0.025 – 0.320, tergolong rendah hingga sedang pada semua sifat, yang menunjukkan adanya pengaruh lingkungan yang cukup besar terhadap ekspresi fenotipe. Korelasi genetik antara diameter dengan tinggi, serta antara tinggi dengan tinggi bebas cabang menunjukkan hubungan positif yang kuat, sedangkan korelasi negatif ditemukan antara diameter dan berat jenis kayu. Taksiran perolehan genetik menunjukkan bahwa perolehan genetik berdasarkan indeks tiga sifat (tanpa memasukkan berat jenis kayu) lebih tinggi dibandingkan indeks empat sifat. Intensitas seleksi sedang (30%) direkomendasikan untuk mencapai keseimbangan antara peningkatan perolehan genetik dan pelestarian keragaman genetik.

Kata kunci: uji keturunan, variasi genetik, berat jenis kayu, *Rubroshorea leprosula,* Pilodyn

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INTRODUCTION

Rubroshorea leprosula Miq., usually known as red meranti, is one of the important dipterocarp species in Southeast Asia, particularly in Indonesia. This species is highly valued economically because of its excellent wood characteristics as well as performs a crucial ecological function in tropical rainforests (Dwiyanti et al., 2024). Wood from this species is usually used for construction, joinery, veneer, plywood, etc. However, its natural population has declined significantly due to deforestation, habitat degradation, and overexploitation. This has resulted in a reduction in genetic variation and productivity. According to the IUCN Red List (2025), *Rubroshorea leprosula* is classified as Near Threatened due to continuing population decline across its natural range.

One approach to reducing the population decline is the establishment of progeny test plantations. Progeny tests also allow us to select superior genotypes for genetically improved plantations. Central Kalimantan represents a major distribution area for *R. leprosula* and offers diverse environmental conditions suitable for evaluating genetic adaptability. The progeny test evaluated is located within the forest concession area of PT Sari Bumi Kusuma (SBK), which has implemented a tree improvement program for *shorea* species. This breeding initiative was established through a collaborative project between PT SBK, the International Tropical Timber Organization (ITTO), and Universitas Gadjah Mada (UGM), aiming to enhance the genetic quality and productivity of dipterocarp species for sustainable forest management.

In progeny tests, genetic variation provides fundamental information for tree breeding programs. It reflects the potential genetic improvement achieved through selection as well as the adaptive capacity of populations to changing environmental conditions (Lai et al., 2017). Measuring growth traits and wood density is essential because growth performance indicates adaptability and productivity, while wood density is a key parameter that affects mechanical strength, durability, and suitability for end-use applications of wood products (Mo et al., 2024).

Previous literature has documented various aspects of this species. Genetic variation and the estimation of genetic parameters have been assessed using both conventional approaches (Muin, 2021) and molecular methods (Hasnah et al., 2014). Nevertheless, neither of those studies investigated the genetic components of wood characteristic qualities. In addition, studies examining growth traits and wood properties have also been carried out. However, the studies focused solely on phenotypic aspects, without taking genetic factors into account (Aiso et al., 2025; Dwiyanti et al., 2024). Several other studies have also examined genetic diversity and genetic parameters of growth characteristics and Pilodyn penetration in different species, such as *Tectona grandis*, *Neolamarckia macrophylla*, *Acacia mangium* and *Ficus variegata* (Hidayati et al., 2014; Anna et al., 2018; Hidayati et al., 2019; Haryjanto et al., 2024). However, studies that specifically investigate the genetic aspects of growth and wood characteristic, particularly wood density in *R. leprosula* remain limited.

This limitation constrains the development of efficient selection strategies, particularly in balancing the enhancement of growth characteristics and wood density of *R. leprosula*. To solve such a gap, the present research provides a comprehensive genetic evaluation by simultaneously analyzing growth traits and wood density, including their genetic relationships and expected selection responses, to support more balanced breeding strategies. This study is among the first to integrate genetic gain prediction in terms of growth and wood density using a multi-trait selection index in *R. leprosula* progeny tests in Indonesia.

Accordingly, this study was performed to identified the genetic variation, estimates the heritability, correlation of genetic, and expected genetic gain in growth as well as wood density of *R. leprosula* in a progeny test established in Central Kalimantan. The findings will provide valuable information to support the breeding program and contribute to conserving and sustainably managing dipterocarp genetic resources.

MATERIALS AND METHODS

Location and Research Materials

The study was conducted in a 10-year-old *Rubroshorea leprosula* progeny trial located in the forest concession of PT. Sari Bumi Kusuma. The site lies between 00°36′00″ and 01°10′00″ S latitude and 111°39′ and 112°25′ E

longitude, with an elevation from 100 to 400 m above sea level. The area has a tropical humid climate with a standard annual precipitation of roughly 2,739.4 mm, an average temperature ranging from 22–33 °C. The soil, derived from tonalite and granodiorite with minor diorite and gabbro, has moderate fertility typical of lowland dipterocarp forests. The progeny test was established as part of a breeding program aimed at improving the quality of *R. leprosula* for sustainable plantation development, conducted through a collaborative program between ITTO, Universitas Gadjah Mada (UGM), and PT. Sari Bumi Kusuma (SBK).

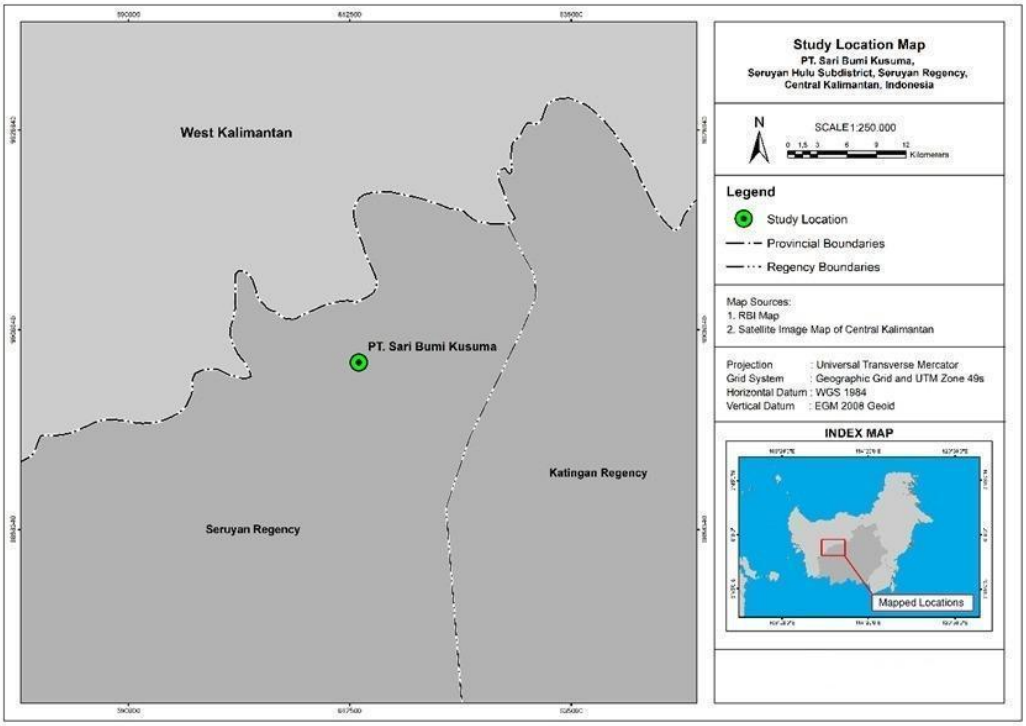

Figure 1. Study Location Map

Experimental Design

The progeny test was arranged in a Randomized Complete Block Design (RCBD) consisting of 80 families, each of which was replicated five times (i.e. five blocks). Within each block, four trees per family were planted in a single-row plot arrangement, resulting in a total of 1,600 trees (80 families × 5 blocks × 4 trees per plot). Randomization of families within each block was conducted to minimize environmental bias across the experimental site. The seeds were collected from phenotypically superior mother trees originating from natural populations in Central Kalimantan and the surrounding regions.

Data Collection

Data collection began with the measurements of tree growth traits as well as Pilodyn penetration for the entire population conducted across five blocks of the *Rubroshorea leprosula* progeny test. Diameter measurement was taken at the level of 1.3 m high. Entire tree height and bole height were measured using a Haga hypsometer. Wood density was estimated by pilodyn penetration using an instrument of Pilodyn 6J Forest (PROCEQ, Switzerland). Pilodyn penetration was measured at the same level of diameter measurement on two opposite sides of the trunk for every single tree, and the analysis was based on the mean values.

To calibrate Pilodyn readings, 15 trees from each block (n = 75) were sampled using an increment borer (diameter 5 mm) at breast height. The subsampling approach was designed to capture the range of Pilodyn penetration values and to provide sufficient calibration data for regression analysis. The extracted increment cores were oven-dried at 103 ± 2 °C until a constant weight was achieved. Basic wood density (g/cm³) was

subsequently calculated as the ratio of oven-dry mass to green volume. Then, a linear regression equation between Pilodyn penetration and actual wood density was developed to estimate the wood density of all trees in the progeny test (see results).

Data Analysis

1. Statistical Analysis

   The statistical analyses were performed using the following model, adapted from Steel and Torrie (1991) :

   $$Y_{ij} = \mu + B_i + F_j + BF_{ij} + E_{ij}$$

   Where : Y_{ij} represents the observed value for the *j*-th family within the *i*-th block; μ denotes the grand mean; B_i is the fixed effect associated with the *i*-th block; F_j is the random effect associated with the *j*-th family; BF_{ij} is the interaction effect between the *i*-th block and *j*-th family; E_{ij} is the random residual error, assumed to be normally distributed (mean 0, variance σ^e_2)

   The significance of block, family, and block × family interaction effects was assessed using F-tests obtained from the mixed-model analysis. The variance components were then calculated using the Restricted Maximum Likelihood (REML) and subsequently used to calculate the genetic parameters including heritability, genetic correlations, and expected genetic gain. REML was used because the progeny test data were unbalanced due to missing observations resulting from tree mortality and damage, leading to unequal numbers of observations among families. This method provides unbiased estimates of variance components in unbalanced datasets and is appropriate for mixed models with random family effects. SAS 9.4. was used to perform all analyses.

2. Heritability

Heritability estimates represent the portion of phenotype variation attributable to genetic variance. It used to determine the proportion of genetic factors in parents that are passed on to their offspring. The estimates of individual and family heritability were calculated with the subsequent formula developed by Falconer & Mackay (1996):

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{fr}^2 + \sigma_e^2}$$

$$h_f^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \frac{\sigma_{fr}^2}{r} + \frac{\sigma_e^2}{nr}}$$

Where : h_i^2 is individual heritability; h_f^2 is family heritability; σ_f^2 is variance of family; σ_{fr}^2 is variance of replication and family; σ_e^2 is variance of error; *n* represents the harmonic mean of the number of trees per plot; *r* signifies the harmonic mean of the number of blocks.

3. Genetic correlations

   A genetic correlation analysis was conducted to assess the genetic correlation among the height and diameter characteristics; height and bole height; as well as between diameter and wood density using the formula according to Zobel and Talbert (1984). :

   $$r_G = \frac{Cov_G(x,y)}{\sqrt{\sigma_{G(x)}^2 . \sigma_{G(y)}^2}}$$

   $$Cov_G(x,y) = 0.5(\sigma_{f(x+y)}^2 - \sigma_{f(x)}^2 - \sigma_{f(y)}^2)$$

   Where : r_G is genetic correlation; $Cov_G(x,y)$ is covariance component between traits x and y; $\sigma_{f(x+y)}^2$ is variance component of traits x and y; $\sigma_{f(x)}^2$ is family variance component for trait x; and $\sigma_{f(y)}^2$ is the family variance component for trait y.

4. Genetic gain

Genetic gain was estimated for each individual trait (diameter, height, bole height, and wood density) as well as for multiple traits using a selection index. This study used selection intensities 25%, 30% and 40%. Two multi-trait scenarios were applied: (1) a four-trait index incorporating all traits, and (2) a three-trait index incorporating only growth traits (diameter, height, and bole height). The genetic gain was determined using the formula established by Zobel and Talbert (1984) :

$$G_f = i \cdot h_f^2 \cdot \sigma_{pf}$$

Where : G_f is genetic gain from family selection; i is selection intensity, h_f^2 is family heritability; σ_{pf} is phenotypic standard deviation of families.

RESULTS AND DISCUSSION

Pilodyn Penetration and Wood Density Correlation

The correlation coefficient of Pilodyn penetration value with wood density in this study was -0.867 (Figure 1). Previous studies have also consistently reported strong negative correlations between Pilodyn penetration and wood density across various tree species, typically ranging from −0.80 to −0.90 (Chen et al., 2015; Gao et al., 2017). This confirms the reliability of the Pilodyn as a proxy for wood density, especially in tree breeding programmes and in young trees with easily removed bark. The observed negative correlation means an opposite relationship, the greater the Pilodyn penetration value, the smaller the wood density value, and vice versa. This relationship is explained by the physical structure of wood, where higher density is associated with thicker cell walls and smaller lumen spaces, which leads to a higher resistance to penetration (Nopens et al., 2020; Fundova et al., 2018).

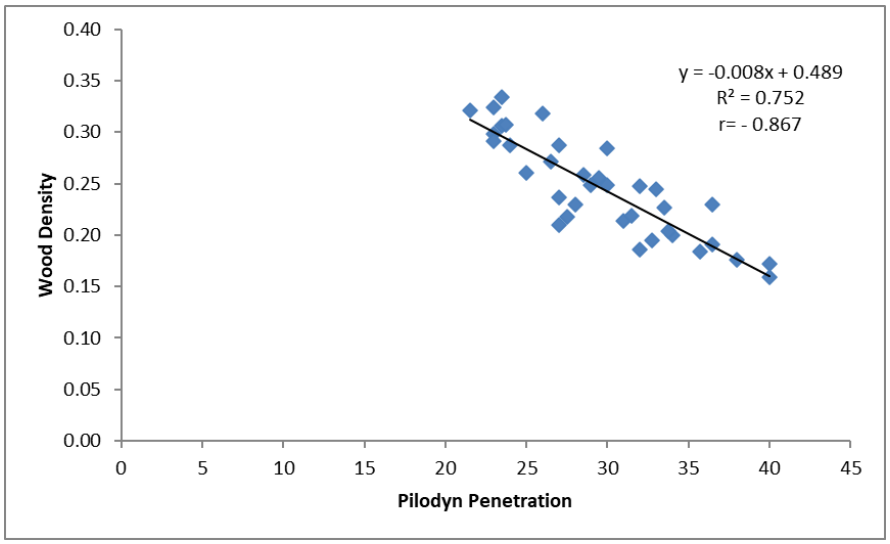

Figure 2. Correlation between Wood Density and Pilodyn Penetration

Genetic Variation

The findings of the statistical analysis of diameter, height, bole height, and wood density are presented in Table 1.

Table 1. Analysis of Variance on Growth Traits and Wood Density in *R. leprosula* Progeny Test

Variation Source	F-Value			
	Diameter	Height	Bole Height	Wood Density
Block	2.076*	10.312**	34.785**	0.819^{ns}
Family	1.364**	1.498**	1.067**	1.270**
Block*Fam	1.600**	2.140**	2.772**	1.831**

Note : ** significant at p < 0.01; * significant at p < 0.05; ns = not significant

Significant variance in diameter, height, bole height, and wood density corresponded to both family effect and the interaction of block × family effects, suggesting that selection can be effectively applied to improve these traits. The presence of significant variation in block × family interaction suggests that the performance of progenies (families) varies across environmental conditions. This has important implications for breeding and deployment strategies, as it emphasizes the need to consider adaptability and stability

when selecting superior genotypes. This finding is in line with previous results in *R. leprosula*, where differences among families resulted in significant variation in growth traits (Muin, 2021). The observed variation reflects the combined influence of genetic factors, environmental conditions, and their interaction (Callister et al., 2024).

Among the observed traits, height and bole height were more strongly affected by block effects, as indicated by higher F-values, suggesting greater sensitivity to environmental variation across the study site. In contrast, wood density was not significantly affected by block, implying greater stability of this trait across environmental conditions. These results suggest that selection for height and bole height may be more influenced by local site conditions, whereas selection for wood density may be more robust across environments. Consequently, families with consistently superior performance across blocks are more suitable for deployment in operational breeding and planting programs.

Although genetic variation was observed, this does not necessarily reflect the extent to which the traits are genetically controlled. Therefore, heritability estimates are required to quantify the genetic contribution to phenotypic variation and to evaluate potential responses to selection.

Heritability

Heritability estimates varied across traits, reflecting differences in genetic control. Heritability of family values observed for diameter (h_f^2 = 0.253) and height (h_f^2 = 0.320) classified as moderate based on Cotterill and Dean (1990), suggest that these growth traits are partially genetically controlled and may respond to selection, although environmental influence remains substantial. In contrast, bole height showed very low heritability (h_f^2 = 0.025), indicating that it is considerably more affected by environmental factors involving stand competition and availability of light, rather than genetic effects. Wood density showed moderate heritability (h_f^2 = 0.194), which agrees with earlier findings demonstrating that wood properties exhibit higher genetic stability compared to growth traits (Fundova et al., 2018; Pelawi et al., 2020) although age and environment conditions may still influence its expression.

Table 2. Estimated Heritability Values for All Traits Observed in *R. leprosula* Progeny Test

Variable	Individual Heritability (h_i^2)	Family Heritability (h_f^2)
Diameter	0.127	0.253
Height	0.199	0.320
Bole Height	0.012	0.025
Wood Density	0.160	0.194

The relatively low to moderate heritability estimates observed in this study are supported by the significant values of block × family interaction (Table 1), highlighting the importance of genotype × environment interactions. This suggests that the performance of genotypes is not consistent across environmental conditions, which has important implications for breeding strategies, particularly in the selection of broadly adapted versus site-specific genotypes.

Previous studies on *Rubroshorea leprosula* reported relatively low heritability values in early-stage progeny trials (Naiem et al., 2014). The relatively higher heritability estimates observed in this study likely result from the implementation of a structured progeny test that incorporates broader genetic representation and improved experimental control. However, the values remain within the low to moderate range, which suggests that environmental factors continue to have a prominent role in forming phenotypic performance at this stage of growth.

Individual heritability is typically lower than family heritability, primarily because environmental influences are more pronounced at the individual level than at the family level (Zhou et al., 2020). From a breeding perspective, these results imply that family-based selection may be more effective than individual selection. Furthermore, the low genetic control of bole height suggests that this trait may be better managed through silvicultural practices rather than genetic improvement. The moderate heritability

observed at the age of 10 years also suggests that selection at this stage could provide a reasonable balance between early selection efficiency and genetic gain.

Genetic Correlation

While heritability estimates quantify the genetic control of individual characteristics, tree breeding programs often need a combined selection of multiple characteristics. Consequently, understanding genetic associations among characteristics is important for determining how selection on one trait may influence responses to selection on another..

Table 3. Genetic Correlation Among Traits Observed in *R. leprosula* Progeny Test

Trait Variables	Genetic Correlation
Diameter-Height	0.618
Height-Bole Height	0.552
Diameter-Wood Density	-0.600

High favorable genetic correlations have been observed between diameter and height (0.618), as well as between height and bole height (0.552). These findings indicate that growth characteristics are likely to be influenced by partially common genetic factors, so that selection for one trait will result in favorable correlated responses in the others. This pattern is helpful for breeding programs, as it increases the efficiency of selection for the overall growth performance. Conversely, a robust negative genetic correlation (−0.600) was detected between diameter-wood density, indicating that these traits are governed by largely distinct genetic mechanisms that may respond antagonistically to selection. Another possible explanation is the differential allocation of assimilates, where increased growth may be related to decreased wood density (Tang et al., 2022).

This finding contrasts with Aiso et al. (2025), who reported no significant phenotypic association between growth traits and mechanical properties of wood. However, the lack of phenotypic correlation does not exclude the presence of genetic correlation. Genetic correlations indicate shared genetic control (van Rheenen et al., 2019), where phenotypic relationships are subject to environmental influences and measurement error that can mask the true genetic associations.

Overall, the genetic correlation structure showed a favorable association among growth traits, but a negative association between growth and wood characteristics. This emphasizes the importance of careful application of multi-trait selection strategies to balance productivity and wood quality in *R. leprosula* breeding programs. To further evaluate the practical implications of these genetic parameters, the expected response to selection was quantified through genetic gain estimates.

Expected Genetic Gain

Expected genetic gain for individual traits is presented in Table 4. Genetic gain increased with higher selection intensity (lower proportion of selected families), with the highest gains obtained at 25% selection intensity (selection of the top 20 families). This pattern reflects the selection differential, where more stringent selection captures superior genotypes with higher genetic gains (Falconer and Mackay, 1996; He et al., 2023).

Table 4. Expected Genetic Gain based on Individual Traits in *R. leprosula* Progeny Test

Variable	25% (20 Family)		30% (28 Family)		40% (32 family)	
	value	%	value	%	value	%
Diameter	0.728 cm	3.571	0.608 cm	2.980	0.556 cm	2.727
Height	0.285 m	1.852	0.237 m	1.540	0.217 m	1.410
Bole Height	0.040 m	0.418	0.033 m	0.345	0.030 m	0.314
Wood Density	0.010	3.690	0.008	2.952	0.007	2.583

Among the traits, diameter and wood density showed the highest genetic gains (2.727–3.571% and 2.583–3.690%, respectively), indicating good potential for genetic improvement. This may be related to their relatively higher genetic control and greater phenotypic variability compared to other traits, as indicated by heritability estimates. In contrast, height showed moderate gains (1.410–1.852%), while bole height exhibited very low gains (0.314–0.418%), consistent with its low heritability. These results confirm that the magnitude of genetic gain is strongly influenced by heritability and phenotypic variation, as traits with higher genetic control respond more effectively to selection (Sinha et al., 2021).

However, selection based on single traits may not be optimal in practical breeding programs, where multiple traits are targeted simultaneously. Estimating genetic gain for more than two traits simultaneously is more complex, particularly when the correlations among traits are negative (Xu et al., 2017). To address this issue, selection was also based on a combined selection index. Therefore, in addition to estimating genetic gain for individual traits, this study also calculated genetic gain based on selection indices combining four traits and three traits, representing simultaneous selection. The use of a selection index provides more comprehensive and realistic estimation of genetic gain (Moeinizade et al., 2020), as it accounts for genetic parameters and trait interrelationships observed in this study.

Table 5. Expected Genetic Gain Based on Multitraits (Selection Index) in *R. leprosula* Progeny Test

Variable	4 traits			3 traits		
	25 % (%)	30 % (%)	40 % (%)	25 % (%)	30 % (%)	40 % (%)
Diameter	1.381	1.262	1.055	3.950	3.608	3.017
Height	1.016	0.928	0.776	3.478	3.176	2.656
Bole Height	1.134	1.036	0.866	1.535	1.402	1.172
Wood Density	0.762	0.696	0.582			

The expected genetic gain based on the three-trait index was higher than that of the four-trait index, mainly because of the adverse genetic association between diameter and wood density. This correlation indicates a trade-off between growth and wood characteristics, improving one trait may be at the expense of the other. Consequently, inclusion of wood density in the selection index reduced overall genetic gain due to antagonistic relationships among traits. These results highlight the importance of genetic correlations in determining selection efficiency and emphasize the need for appropriate trait weighting in more than one trait selection approaches (Moeinizade et al., 2020; Besson et al., 2020).

From a breeding perspective, the option of selection strategy relies on the objective. If the primary goal is to maximize growth, a three-trait selection approach may be more efficient. However, if both productivity and wood quality are targeted, a multi-trait index including wood density remains necessary despite lower genetic gain.

In terms of selection intensity, higher selection intensity (25%) resulted in greater genetic gain due to a larger selection differential, where only the best-performing families are retained. However, more stringent selection also leads to a reduction in the genetic base of the population, which may limit long-term adaptive potential and increase vulnerability to environmental changes (Stange et al., 2021; Rajora & Zinck, 2021). Conversely, lower selection intensity (40%) helps maintain greater genetic diversity but results in reduced expected gain. Therefore, a moderate selection intensity (approximately 30%) represents a balanced strategy, allowing substantial genetic gain while keeping sufficient genetic variety for long-term breeding sustainability and resilience.

This study provides valuable information for the breeding of *Rubroshorea leprosula*, however it still has several limitations. The genetic evaluation was conducted in a single progeny test site at one assessment age (10 years), which may not fully capture genotype × environment interactions or age related changes in genetic parameters. Furthermore, this study focused on quantitative genetic

parameters without incorporating molecular or genomic information that could improve the accuracy of selection. Therefore, future studies should include multi-site and multi-age evaluations, larger calibration datasets for wood density estimation, and integration of genomic approaches to improve understanding of the genetic basis and to enhance breeding efficiency.

CONCLUSIONS

This study records significant genetic diversity in diameter, height, bole height as well as wood density in the progeny test of *Rubroshorea leprosula*, indicating substantial potential for genetic improvement. However, heritability estimates were generally low to moderate, suggesting strong environmental influence and genotype × environment interaction. Genetic correlation analysis revealed positive relationships among growth traits, suggesting that selection in one growth trait may result in simultaneous improvement in others. In contrast, a significant negative correlation within diameter and wood density indicates a trade-off between those two characteristics, which needs to be carefully considered in breeding strategies. Expected genetic gain showed that higher selection intensity resulted in greater improvement, particularly for diameter and wood density. However, multi-trait selection including negatively correlated traits may reduce overall gain, emphasizing the importance of selection index design in line with the objective.

Overall, a moderate selection intensity (30%) is recommended to balance genetic gain and the maintenance of genetic diversity. These results offer valuable perspectives for optimizing breeding programs and support the continuous improvement and conservation of *Rubroshorea leprosula* genetic resources.

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