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Estimation of Genetic Parameters for Growth and Wood Traits in Endemic *Neolamarckia macrophylla* in Parungpanjang, Indonesia

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ABSTRACT

Neolamarckia macrophylla is an endemic, fast-growing tree naturally distributed across Sulawesi and the Maluku Islands, Indonesia. *N. macrophylla* is a species used for plantations and community forests; however, its propagation is constrained by limited high-quality seed sources. This study estimated genetic variation, heritability, genetic correlations, and predicted genetic gains for growth and wood-quality traits in a 6-y-old progeny test at Parungpanjang Research Station, Bogor, consisting of 72 families from 10 populations. The traits measured were tree height, diameter at breast height (DBH), tree volume, pilodyn penetration, wood moisture content, wood density, and specific gravity. Family effects were statistically significant for height, DBH, volume, moisture content, and density; block × family interactions were statistically significant for several traits. Stem diameter showed strong genetic correlations with tree height (0.502), volume (0.582), and pilodyn penetration (0.464). Pilodyn penetration was also genetically correlated with wood density (–0.507) and moisture content (0.595). The key selection traits identified were stem diameter and pilodyn penetration, which were strongly correlated with growth and wood traits. Pilodyn penetration is a practical, fast, and non-destructive method that does not require laboratory testing, making selection based on wood quality more efficient. By applying within-family selection at 25% (one best tree per four) combined with a ~40% family retention (43 retained of 72 families), results show meaningful increases in diameter and volume while producing only moderate, correlated changes in wood-quality traits.

Keywords: diversity, family, heritability, genetic parameter, genetic gain

1. INTRODUCTION

The forestry sector is integral to Indonesia's economy as a supplier of primary raw materials to the downstream sector, mainly in the form of logs, and as an engine for economic growth through increased investment, improved export performance, and internal revenue generated by governments through tax and non-tax activities. The forestry sector also contributes substantially to employment and business opportunities (Mutaqin *et*

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al., 2022). Indonesia's forestry industry is in a state of stagnation and declining productivity and is often referred to as a "sunset industry". One considerable challenge is the limited supply of raw materials, which has led to a steady decline in wood-processing production (Benyamin *et al.*, 2019; Maharani *et al.*, 2025). According to the 2019–2045 Production Forest Development Road Map, Indonesia aims to produce 269.05 million m^3 of wood annually from plantation forests and 14.31 million m^3 from natural forests by 2045. The number of logs produced in Indonesia in 2022 was only 64.65 million m^3 (BPS, 2022). To meet the need for industrial raw materials, some wood raw materials are imported from other countries (KLHK, 2022). The existing gap between the demand for and production of wood materials highlights the urgent need to improve demand fulfillment to meet future targets. Wood demand can be met through measures such as growing fast-growing species in plantations (Hadi *et al.*, 2022). One alternative, a potentially fast-growing species native to Indonesia, is *Neolamarckia macrophylla* (Roxb.). Bosser (Cahyono *et al.,* 2015; Halawane *et al.,* 2011; Sandalayuk *et al.,* 2023).

N. macrophylla is a fast-growing tree species endemic to Indonesia, with an area of natural distribution ranging from Sulawesi to Maluku (Augustina *et al.*, 2023). This species can grow in lowland areas up to 1,000 m above sea level (asl) and is commonly found in several forest landscapes, including secondary forests, riverbanks, valleys, and hill ridges (Cahyono *et al.,* 2015; Halawane *et al.,* 2011; Shi *et al.,* 2020). This species is also known for its adaptability to various soil types and rapid growth, and is widely planted in industrial and community forests (Irawan and Purwanto, 2014; Mpapa *et al.*, 2025; Sandalayuk *et al.,* 2023; Yuniarti *et al.,* 2023). *N. macrophylla* growth can be optimized by growing in more favorable areas, such as damp areas, and is less tolerant of drought stress (Yulianti and Sudrajat, 2016). The species can reach 45 m in height with a branch-free height of 30 m; a diameter of 40–50 cm; and straight, self-pruning trunks, making it suitable for timber production without intensive silvicultural intervention. The wood characteristics of *N. macrophylla* are classified as durability class IV and strength class II–III, with long, straight fibers, and a smooth texture (Augustina *et al.*, 2023; Priadi *et al.*, 2021). These wood characteristics make it ideal for use in pulp, paper, plywood, particleboard, and construction materials (Cahyono *et al.,* 2015; Halawane *et al.,* 2011; Lempang, 2014).

The development of *N. macrophylla* in forest plantations is limited by the availability of genetically-superior seed sources and requires support for high-quality seeds. The procurement of high-quality seeds for native species is often an obstacle to reforestation activities, both nationally in Indonesia and globally (Bosshard *et al.*, 2021; Di Sacco *et al.*, 2021). Sources of high-quality genetic seeds have been unavailable (DPTH, 2022) and the initiation of tree breeding activities involving diversity from a relatively wide growing distribution is required. Several initial progeny tests have been conducted for the development of *N. macrophylla* seed sources (A'ida *et al.,* 2019) with 108 families from Sulawesi, and 55 families from Konawe, Southeast Sulawesi (Surip *et al.,* 2017).

The results presented by A'ida *et al.* (2019) and Surip *et al.* (2017) showed low-to-moderate heritability estimates for individual and family tree heights and diameters, indicating that genetic material from a broader distribution is necessary to optimize *N. macrophylla* breeding programs. Additional wood quality parameters are needed, considering that for specific purposes, the wood quality *of N. macrophylla* is still low (Augustina *et al.,* 2023; Priadi *et al.*, 2020), especially for solid wood, so that breeding activities to produce plantations with shorter cycles and a higher quantity of timber can be realized (Nugroho *et al.,* 2024). To enhance the effectiveness of breeding programs, genetic material from a wide geographical range must be incorporated.

Collecting genetic material from a wider geographical distribution is believed to increase genetic diversity and improve the effectiveness of breeding activities (Zobel and Talbert, 1984).

The current study evaluated the growth and wood quality of 72 families from 10 populations across Sulawesi and Maluku using a progeny test established at the Parungpanjang Forest Research Station in Bogor. The objective of this study was to estimate the genetic parameters for growth and wood quality traits of 6-y-old *N. macrophylla* to select progeny tests for solid wood seed sources in Parungpanjang, Bogor.

2. MATERIALS and METHODS

2.1. Materials

The progeny test of *N. macrophylla* was established using genetic material from plus trees (mother trees) that were growing naturally in 10 populations, i.e., eight populations from the Sulawesi region (Konawe, East Luwu, Muna, Buton, Banggai, Wajo, Manado, and Kotamobagu) and two populations from the Maluku region (Tidore and Seram islands; Fig. 1). Plus tree selection was conducted following the method described by Clark and Wilson (2005). The distance between

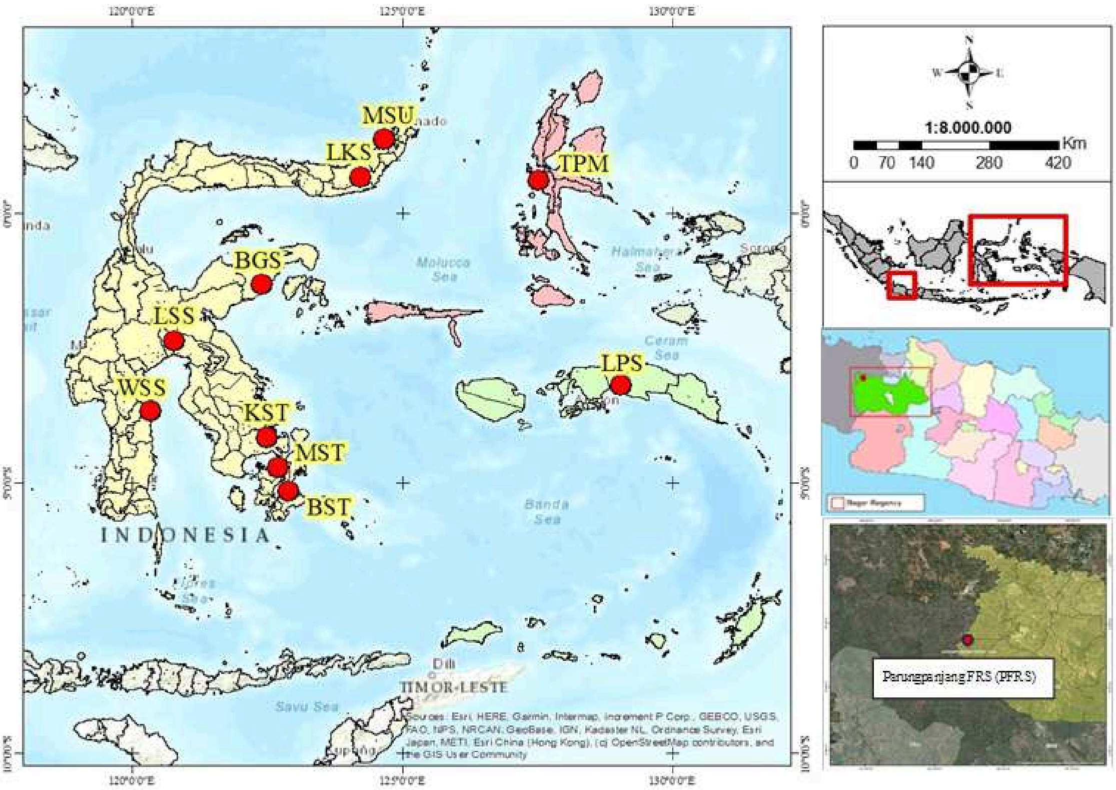

Fig. 1. Location of the 10 tree populations (Sulawesi and Maluku regions) and the progeny test at the Parungpanjang Forest Research Station (PFRS), Bogor, Indonesia. MSU: Manado, North Sulawesi, LKS: Lolayan, Kotamobagu, BGS: Banggai, Central Sulawesi, LSS: East Luwu, South Sulawesi, WSS: Wajo, South Sulawesi, KST: Konawe, Southeast Sulawesi, MST: Muna, Southeast Sulawesi, BST: Buton, Southeast Sulawesi, TPM: Tidore, Maluku, LPS: Layeni, Seram Island.

selected mother trees in each population was set at 100 m to prevent the collection of seeds from related mother trees. Geoclimatic information and the number of *N. macrophylla* mother trees used to establish the progeny tests are presented in Table 1.

2.2. Progeny test establishment

The *N. macrophylla* progeny tests were conducted at the Parungpanjang Forest Research Station in Bogor, West Java, Indonesia (06°23'09.226" S, 106°31'23.138" E), with an altitude of 52 m asl. The land cover of this location was previously classified as open, relatively flat, and overgrown with bushes dominated by *Imperata cylindrica, Melastoma malabatricum*, *Acacia* spp., and *Schima wallichi* coppices. The soil in this area is classified as marginal with relatively low nutrient content (C-organic 1.97%, N-total 0.22%, P 10.88 ppm, Ca 4.98 $cmol^{(+)}$ kg^{-1}, Mg 3.47 $cmol^{(+)}$ kg^{-1}, K 0.12 $cmol^{(+)}$ kg^{-1}, cation exchange capacity 34.08 $cmol^{(+)}$ kg^{-1}, base saturation 25.59%), soil pH 4.8, and soil texture dominated by clay (68.39%). The soil was a composite of sand (19.63%) and silt (11.98%).

Seedling preparation was carried out at the nursery of Nagrak Research Station, Bogor (06°6'74" S, 106°51'27" E, altitude 254 m asl). Seeds resulting from exploration were sown in germination boxes containing a mixture of sand, compost, and husk charcoal (5:3:1, *v/v*; Sudrajat *et al.,* 2016). Normal seedlings that had grown a pair of leaves were transplanted into polybags measuring 10 cm × 15 cm and filled with a mixed medium of soil, compost, and rice husks (3:2:1 by volume). The seedlings were grown for 3 m under a shading net at 60% intensity and then moved to an open area for hardening for 1 m. Seedlings ready for planting were transported to the planting site while maintaining their family identities. The progeny test planting used a completely randomized block design with six blocks, each containing 72 families from 10 populations. Each family consists of four-row tree plots with a planting distance of 4 m × 4 m. At planting, 4 kg of basic fertilizer (manure compost) was added to each planting hole. Weed control was carried out every 6 m until the tree stand was 5 y old.

Table 1. Geo-climatic information and number of parent trees for the establishment of progeny test in Parungpanjang Forest Research Station in Bogor

Populations	Latitude	Longitude	Altitude (m asl)	Precipitation (mm $year^{-1}$)	Number of mother trees
Konawe, Southeast Sulawesi (KST)	4°416'N	121°459'E	65–242	1,740	7
East Luwu, South Sulawesi (LSS)	5°404'N	120°412'E	100–317	3,109	4
Muna, Southeast Sulawesi (MST)	5°404'N	122°442'E	39–85	1,949	4
Buton, Southeast Sulawesi (BST)	5°410'N	122°453'E	32–445	3,068	7
Banggai, Central Sulawesi (BGS)	1°19’N	122°20’E	19–107	3,463	9
Wajo, South Sulawesi (WSS)	3°440'N	120°420'E	40–48	4,038	7
Manado, North Sulawesi (MSU)	1°56’'S	124°416'E	36–41	4,526	3
Lolayan, Kotamobagu (LKS)	0°39’S	124°13’E	302–410	2,543	7
Tidore, Maluku (TPM)	0°19’S	127°32’E	21–369	4,250	7
Layeni, Seram Island (LPS)	3°05’S	129°404'E	168–676	2,016	17

2.3. Growth and wood quality measurement

Growth and wood quality measurements were conducted on 6-y-old stands. The percentage tree survival was calculated by dividing the number of living trees by the number of seedlings planted in each block, as per the research design. Tree height measurements (in meters) were carried out for all individual trees using a Haga altimeter, and stem diameter measurements were carried out 1.30 m above ground level (diameter at breast height, in centimeters) using a diameter measuring tape. The tree volume (m^3) was calculated using the following formula (Saputra *et al.,* 2019):

$$V = 0.25 \times 3.14 \times D^2 \times 10^{-4} \times T \times f \tag{1}$$

where V is tree volume (m^3), D is stem diameter at breast height (cm), T is tree height (m), and f is a form factor.

The wood qualities measured were pilodyn penetration, moisture content (MC), wood density, and specific gravity (SG). Pilodyn penetration was measured using Pilodyn (strength = 6 J, pin diameter = 2.5 mm) by measuring pin penetration at three points on the tree trunk horizontally at a distance of 120°, which was then averaged at a height of 1.30 above the ground surface (Anna *et al.,* 2020; Chaerani *et al.,* 2019).

Wood quality was assessed based on sample cores taken using an increment borer (Haglöf three -Thread Increment Borers; https://www.forestry-suppliers.com/p/63261/hagl%C3%B6f-8-replacement-bit-3-thread-0169-43 mm). Small wood core samples with a diameter of 4.3 mm were taken to a depth approaching the pith at a tree height of 1.3 m from the ground surface to determine the wood MC, density, and SG (Anna *et al.*, 2020; Sudrajat *et al.*, 2021). The samples were then wrapped in plastic and aluminum foil and analyzed at the Forest Products Technology Laboratory of the Faculty of Forestry and Environment, IPB University. Fresh wood samples 2 cm in length (outer growth layers obtained from the core sample) were weighed using a digital balance to obtain the initial weight of the wood (Cown, 1982). The volume of the wood sample was measured using Archimedes' principle, and the sample was then dried in an oven at 103 ± 2℃ for 24 h. The dried samples were weighed to determine the dry weight. The physical properties tested were MC, wood density (ρ), and SG (ASTM, 2005; Kien *et al.,* 2009). In general, the MC of wood is inversely proportional to wood density and SG (Hadi *et al.,* 2022). The higher the MC of the wood, the lower the wood density and SG.

$$\rho\left(\frac{g}{cm^3}\right) = \frac{FSW}{WV} \tag{2}$$

$$SG = \frac{ODW\ /\ WV}{\rho\ water} \tag{3}$$

$$WC\ (\%) = \frac{FSW - ODW}{ODW} \times 100\% \tag{4}$$

where *FSW* = fresh wood sample weight (g), *WV* = wood volume (cm^3), *ODW* = oven-dry weight (g), ρ *water* = 1 g/cm^3.

2.4. Data analysis

The data normality test was conducted using the Kolmogorov–Smirnov test (Hanusz and Tarasińska, 2015). The growth and wood quality data of *N. macrophylla* progeny test showed an abnormal distribution for tree height (D = 0.052473, p < 0.0100), diameter at breast height (D = 0.038166, p < 0.0100), tree volume (D = 0.111286, p < 0.0100), pilodyn penetration (D = 0.069043, p < 0.0100), MC (D = 0.102879, p < 0.0100), wood density (D = 0.067639, p < 0.0100), and SG (D = 0.118279, p < 0.0100). The normality of the data was improved through data transformation using the SQRT(x) function because the data distribution exhibited moderate positive skewness (Hatem *et al.,* 2022).

Trait distributions were tested using the Kolmogorov–Smirnov test and positively-skewed traits were square-root transformed prior to analysis. The variance components were estimated using a mixed model (Johnson *et al.,* 2001):

$$Y_{ijk} = \mu + B_i + F_j + BF_{ij} + E_{ijk} \tag{5}$$

where: Y_{ijk} = observation of the phenotype of the individual tree, μ = general average value; B_i = random effect of the i^{th} block; F_j = random effect of j^{th} family; BF_{ij} = interaction effect between the i^{th} block and the j^{th} family; E_{ijk} = error (random effect of the k^{th} individual of the j^{th} family in the i^{th} block); $i = 1, \cdots, r$ (r = number of blocks); $j = 1, \cdots, f$ (f = number of families), $k = 1, \cdots, f$ (f = number of trees per family).

Analysis of variance was conducted to determine the effects of family and block factors on the growth and wood quality of *N. macrophylla* using the GLM procedure in SAS for Windows, version 9.0 (SAS Institute, Cary, NC, USA). The value of the family variance (σ^2_f), the block variance (σ^2_r), as well as the error variance (σ^2_e) components were obtained from the results of the PROC VARCOMP analysis using SAS for Windows version 9.0. Family (h^2f) and individual heritability (h^2i) were calculated based on variance components (Falconer and Mackay, 1996), which were calculated using Equations (6) and (7):

$$h^2 i = \frac{4\sigma^2_f}{\sigma^2 f + \sigma^2 fr + \sigma^2 e} \tag{6}$$

$$h^2 f = \frac{\sigma^2 f}{\sigma^2 f + \frac{\sigma^{2\ fr}}{n} + \frac{\sigma^2 e}{jn}} \tag{7}$$

where σ^2_f, σ^2_{fr}, σ^2_e, n, r were the variance components of family, block-family interaction, error, number of trees per plot, and number of blocks, respectively. According to Robinson *et al.* (1951), heritability is categorized as low (0–0.3), moderate (0.3–0.6), and high (> 0.6).

The additive genetic variance coefficient (CV_G) was calculated based on family variance using Equation (8) (Cornelius, 1994):

$$CV_G\ (\%) = 100 \times \sqrt{\frac{4\sigma^2 f}{\overline{X}}} \tag{8}$$

where $\overline{X}$ = average of each parameter and σ^2_f = variance of family.

Phenotypic ($R_{p(xy)}$) and genetic ($R_{f(xy)}$) correlation were calculated from the variance components and their covariance (Falconer and Mackay, 1996), and were substituted into the standard formulae for the product-moment correlation coefficient:

$$R_{P(xy)} = \frac{COV_{p(xy)}}{\sqrt{\sigma^2_{P(x)}\sigma^2_{P(y)}}} \tag{9}$$

$$R_{f(xy)} = \frac{COV_{f(x,y)}}{\sqrt{\sigma^2_{f(x)}}\sqrt{\sigma^2_{f(y)}}} \tag{10}$$

where: x and y = compared parameters, $\sigma^2_{p(x)}$ and $\sigma^2_{f(x)}$ = phenotypic and genetic variance components for character x, $\sigma^2_{p(y)}$ and $\sigma^2_{f(y)}$= phenotypic and genetic variance components for character y, $COV_{P(xy)}$ dan $COV_{f(x,y)}$ = phenotypic and genetic covariance components between characters x and y. To obtain the magnitude of the covariance components of two characters, x and y, Equations (11) and (12) were used (O'Neill *et al.,* 2001):

$$COV_{p(x,y)} = 0.5\left(\sigma^2_{p(x+y)} - \sigma^2_{p(x)} - \sigma^2_{p(y)}\right) \tag{11}$$

$$COV_{f(x,y)} = 0.5\left(\sigma^2_{f(x+y)} - \sigma^2_{f(x)} - \sigma^2_{f(y)}\right) \tag{12}$$

where: $\sigma^2_{f(x+y)}$ = variance component for characters x and y, $\sigma^2_{f(x)}$ = variance component for character x, $\sigma^2_{f(y)}$ = variance component for character y.

The genetic gain (*GG, %*) was predicted using Equation (13) (Diao *et al.,* 2016; Falconer and Mackay, 1996):

$$GG\ (\%) = ih^2\sqrt{\frac{\sigma_p^2}{\overline{X}}} \times 100 \qquad (13)$$

where: i = intensity of individual selection within the family and family selection referring to Zobel and Talbert (1984) using 25% selected individuals (selection intensity of 75%) within family and intensity for family selection of 10%, 20%, 30%, 40%, 50%, and 60%; h^2 = heritability; σ_p = phenotypic variance; $\overline{x}$ = average of each parameter. The realized gain consisted of four categories: low if *GG* = 0%–3.30%, medium if *GG* = 3.31%–6.60%, high if *GG* = 6.61%–10.00%, and very high if *GG* > 10% (Singh and Chaudhary, 1987).

The selection simulation was conducted with a 25% selection rate for individual trees within a family using a four-line tree plot planting design with the goal of retaining one best individual per family in each block. The family selection simulations used selection intensities of 10% (64 families selected), 20% (58 families selected), 30% (50 families selected), 40% (43 families selected), 50% (36 families selected), and 60% (29 families selected). The optimal strategy was chosen based on relatively high growth increases while maintaining wood quality.

3. RESULTS and DISCUSSION

The progeny test of *N. macrophylla* in this study showed that tree survival at 6 y of age was not influenced by family (p = 0.655). Family 65 from Layeni, Seram Island, had the lowest tree survival rate (30%). In contrast, the family with the highest tree survival rate was family 72, which was also from Layeni on Seram Island (75%). The growth and wood quality of the progeny were quite diverse. The coefficient of variation was dominated by growth traits obtained from tree volume (39.67%), followed by stem diameter (16.16%), and tree height (12.32%). The lowest coefficients of variation were observed for pilodyn penetration (3.91%) and wood density (6.44%; Table 2).

Analysis of variance based on a linear model indicated that the family had an effect on several key traits, including tree height (p = 0.0003), stem diameter (p = 0.0339), tree volume (p = 0.0241), wood MC (p = 0.0055), and wood density (p = 0.0477). Family effects were not significant for pilodyn penetration (p = 0.2649)

Table 2. Statistical description of growth and wood quality characteristics in *Neolamarckia macrophylla* progeny tests at the Parungpanjang Forest Research Station in Bogor

Characters	Individual mean	Minimum–maximum	SD	Coefficient of variation (%)
Tree height (m)	13.52	11.10–16.17	3.61	12.32
Stem diameter (cm)	17.21	13.04–22.34	5.79	16.16
Tree volume (m^3)	0.276	0.145–0.485	0.22	39.67
Pilodyn penetration (mm)	29.42	27.95–31.99	2.42	3.91
Moisture content (%)	83.97	71.49–102.58	21.02	10.54
Wood density (g cm^{-3})	0.567	0.520–0.633	0.065	6.44
Specific gravity	0.387	0.279–0.755	0.062	8.36

or wood SG (p = 0.0765).

The interaction between block and family influenced the growth and wood quality parameters, except for wood density (p = 0.0560) and wood SG (p = 0.1199), which were unaffected by the interaction between block and family (Table 3). In this study, although the trial blocks were uniformly set up by selecting flat, uniform test locations, in practice, the soil and environmental characteristics (tree density) differed slightly between the planting blocks (Anna *et al.*, 2020; Chaerani *et al.*, 2019). This condition caused blocks and their interactions with families to affect growth parameters and wood quality. Differences in blocks affect nutrient availability and plant physiological processes, which, in turn, influence wood growth and quality (wood density and SG).

Family differences affected tree height, stem diameter, tree volume, wood MC, and wood density, but did not affect pilodyn penetration or wood-SG (Table 3). Family effects on growth and wood quality traits have been reported in *Picea jezoensis* (Tanabe *et al.,* 2014), *Neolamarckia cadamba* (Anna *et al.,* 2020; Chaerani *et al.,* 2019; Que *et al.,* 2021), *Swietenia macrophylla* (Sudrajat *et al.,* 2021), *Ficus variegata* (Haryjanto *et al.,* 2024), and *Cupressus sempervirens* (Özbey *et al.,* 2024). These influences demonstrate the contributions of genetic and environmental factors and their interactions to wood growth and quality (Fadwati *et al.,* 2023; Özbey *et al.,* 2024). Wood has different cell compositions; therefore, its characteristics vary among tree species, and even within the same species (Park *et al.,* 2024).

The variance component analysis of growth and wood quality traits in the *N. macrophylla* progeny test at 6 y of age indicated that the contribution of family to total variation was relatively low, from 0.50% for tree height to 2.97% for wood-SG. The interaction between the block and family accounted for a substantially higher proportion of variation in several traits, with the highest variance; tree height (17.70%), wood MC (15.10%), and stem diameter (14.13%). The lowest interaction effects were observed for wood SG (2.97%) and wood density (6.67%; Table 4).

The contribution of family to total variation was lower than that of the block variation, interaction of block and family, and the error component. This has been observed in previous studies on *N. cadamba* (Sudrajat *et al.,* 2016) and *F. variegata* (Haryjanto *et al.,* 2024). Environmental heterogeneity and genotype × environment (G × E) interactions contribute substantially to phenotypic variation, as demonstrated in *Pinus sylvestris*, where environmental factors account for up to 31% of the variation in stem diameter and 20% of the variation in tree height (Chmura *et al.,* 2021).

As an endemic tree with a relatively narrow natural distribution, *N. macrophylla* is estimated to have lower

Table 3. Mean square for growth and wood quality traits in the linear model of the *Neolamarckia macrophylla* progeny test at Parungpanjang Forest Research Station in Bogor

Source of variation	DF	Tree height (m)	Stem diameter (cm)	Tree volume (m^3)	Pilodyn penetration (mm)	Wood moisture content (%)	Wood density (g cm $^{-3}$)	Wood specific gravity
B	5	2.3603**	2.7091**	0.2796**	0.1162*	16.3107**	0.0277**	0.0387**
F	71	0.3562*	0.5796*	0.0509*	0.0498^{ns}	1.4199*	0.0083*	0.0028^{ns}
B × F	315	0.3116**	0.6216**	0.0506**	0.0557*	1.2538*	0.0068^{ns}	0.0025^{ns}
E	516	0.2014	0.4357	0.0365	0.0448	0.9206	0.0053	0.0022

Analyzed from the transformed data: B = block, F = family, * = significant effect at p < 0.05, ** = significant effect at p < 0.01, ^{ns} = no significant effect.

Table 4. Components of variance (relative contribution in parentheses) of growth and wood quality characteristics in the *Neolamarckia macrophylla* progeny test at the Parungpanjang Forest Research Station in Bogor

Component of variance	Tree height	Stem diameter	Tree volume	Pilodyn penetration	Wood moisture content	Wood density	Wood specific gravity
$\sigma^2 B$	0.7187 (5.46%)	1.3081 (3.76%)	0.0028 (5.57%)	0.0419 (0.69%)	38.5882 (8.60%)	0.00029 (6.71%)	0.00041 (10.15%)
$\sigma^2 F$	0.0663 (0.50%)	0.4674 (1.34%)	0.0003 (0.59%)	0.0527 (0.87%)	2.389 (0.53%)	0.00005 (1.16%)	0.00012 (2.97%)
$\sigma^2 BF$	2.3267 (17.70%)	4.9132 (14.13%)	0.0059 (11.75%)	0.5591 (9.33%)	67.3297 (15.10%)	0.00029 (6.71%)	0.00012 (2.97%)
$\sigma^2 e$	10.0310 (76.32%)	28.0927 (80.76%)	0.0412 (82.07%)	5.3392 (82.07%)	340.242 (75.85%)	0.00369 (85.42%)	0.00339 (83.91%)
$h^2 i$	0.02	0.06	0.03	0.04	0.02	0.05	0.13
$h^2 f$	0.06	0.16	0.09	0.13	0.07	0.18	0.41
CV_G (%)	14.01	32.96	6.59	8.46	33.74	1.87	3.52

$\sigma^2 B$: component of variance of block, $\sigma^2 BF$: component of variance of interaction between block and family, $\sigma^2 e$: component of variance of error, $h^2 i$: individual heritability, $h^2 f$: family heritability, CV_G: coefficient of genetic variance.

genetic diversity than its widely-distributed congener, *N. cadamba*. Naturally, *N. macrophylla* is found only in Sulawesi and Maluku (Cahyono *et al.,* 2015; Shi *et al.,* 2020). Several studies on the genetic variation in *N. macrophylla* using molecular markers have shown that this species exhibits low to moderate population-level genetic diversity. According to Larekeng *et al.* (2018), *N. macrophylla* shows moderate genetic variation, whereas Arif *et al.* (2019) reported relatively low genetic variation. Long-standing cultivation in certain regions, particularly Sulawesi, may have facilitated gene flow between provenances (Halawane *et al.,* 2011), potentially increasing intrafamilial variation.

Low genetic diversity appears to have affected the differences in growth, height, and diameter of *N. macrophylla*, which were greater between families than between populations. Soltis and Soltis (1991) also reported lower diversity among populations of endemic species than among populations of widely-distributed species. Lowe *et al.* (2018) supported this claim by stating that species with a wide natural distribution generally have a higher diversity than species with a limited distribution. Widely-distributed species can maintain a larger effective population size, thereby reducing the influence of genetic drift on genetic diversity (Sudrajat, 2016; White *et al.,* 2007). Despite its limited distribution, *N. macrophylla* presented a relatively high family level variation in growth traits. The CV_G were classified as high to moderate for wood MC (33.74%), stem diameter (32.96%), tree height (14.01%), pilodyn penetration (8.46%), and tree volume (6.59%; Milligan *et al.,* 2003).

Family heritability was greater than individual heritability (Table 4). Family heritability was 0.06 (tree height) to 0.41 (wood SG), whereas individual heritability was 0.02 (tree height and wood MC) to 0.13 (wood SG). The highest coefficient of genetic variation was observed for wood MC (33.74%), followed by stem diameter (32.96%), and tree height (14.01%).

Family heritability estimates ($h^2 f$) were 0.06 (height) to 0.41 (SG), whereas individual heritabilities ($h^2 i$) were low (0.02–0.13). Because several variance components were small relative to the residual variance, this study reported 95% confidence intervals for each heritability [for example, h^2f (height) = 0.06], indicating limited precision for the early age selection of some traits. The CV_G were high for MC and DBH, but the combination of low h^2i and substantial block × family interactions suggests caution when implementing individual selection at 6 y of age (Cornelius, 1994; Robinson *et al.,* 1951). The lowest CV_G were observed for wood density (1.87%) and SG (3.52%; Table 4).

Heritability estimates indicated that family heritability was consistently higher than individual heritability across all measured traits. Family heritability was 0.06 for tree height to 0.41 for wood SG; individual heritability values were lower, from 0.02 for tree height and wood MC to 0.13 for wood SG. Heritability is categorized as low (0–0.3), moderate (0.3–0.6), or high (> 0.6; Fernandes *et al.*, 2022; Robinson *et al.*, 1951), so in the current study, the heritability value was categorized as low to moderate. The highest CV_G was observed for wood MC (33.74%), followed by stem diameter (32.96%) and tree height (14.01%), whereas wood density (1.87%) and SG (3.52%) had the lowest CV_G (Table 4).

Family heritability was higher than individual heritability. Several studies in other species reported similar findings, where family values were higher than individual heritability values, such as in *Araucaria angustifolia* (Sebbenn *et al.*, 2003), *Pinus brutia* (Gülcü and Çelik, 2009), *N. cadamba* (Anna *et al.,* 2020; Chaerani *et al.,* 2019), *Bursaphelenchus xylophilus* (Menéndez-Gutiérrez *et al.,* 2021), and *F. variegata* (Haryjanto *et al.,* 2024). In the current study, family heritability was 0.06–0.41, whereas individual heritability was 0.02–0.13. High heritability values indicate that the additive genetic influence is relatively high for a trait or character and vice versa (Santos *et al.,* 2021; Zhang *et al.,* 2024). High heritability values indicate that selective breeding is promising for obtaining greater genetic gains (Haryjanto *et al.,* 2024).

Phenotypic correlation analysis indicated strong positive associations between growth traits. The tree height was highly correlated with stem diameter (0.830) and tree volume (0.871). Stem diameter was also strongly correlated with tree volume (0.940), indicating a close relationship between these parameters. Genetic correlation analysis indicated similar patterns: tree height was positively correlated with stem diameter (0.502) and tree volume (0.563), whereas stem diameter was strongly correlated with tree volume (0.582). Generally, the growth traits were negatively correlated with wood density and SG (Table 5).

Tree height showed a relatively strong negative genetic correlation with wood density (−0.461) and a moderate negative genetic correlation with SG (−0.233). All growth trait correlations with wood density and SG were negative, suggesting an inverse association between growth rate and wood compactness. The effects of growth rate on various wood properties have been intensively studied across several tree species (Fujimoto *et al.*, 2024). However, these results have not been consistent across species, individuals, or wood properties (Fujimoto and Koga, 2010; Kimura and Fujimoto, 2014). In these studies, growth was generally negatively correlated with wood properties (e.g., density and SG). The same finding was also reported by Anna *et al.* (2020) and Chaerani *et al.* (2019) for *N. cadamba* and Sudrajat *et al.* (2021) in *S. macrophylla*. Fast-growing trees usually have more earlywood and less latewood than do slow-growing trees (Anna *et al.*, 2020; Mäkinen *et al.*, 2002; Wang *et al.*, 2002). This composition results in low moduli of rupture and elasticity and density (Anna *et al.*, 2020; Clark *et al.*, 2006). Pilodyn penetration demonstrated strong genetic correlations with several traits, including stem diameter (0.464), tree volume (0.647), and wood MC (0.595), as well as a negative correlation with wood density (−0.507). The resulting pilodyn value

Table 5. Phenotypic correlation (lower diagonal) and genetic correlation (upper diagonal) between growth and wood quality traits in the progeny test of *Neolamarckia macrophylla* at the Parungpanjang Forest Research Station in Bogor

Characters	Tree height	Stem diameter	Tree volume	Pilodyn penetration	Wood moisture content	Wood density	Wood specific gravity
Tree height		0.502	0.563	0.031	0.231	−0.461	−0.233
Stem diameter	0.830		0.582	0.464	0.392	−0.007	−0.086
Tree volume	0.871	0.940		0.647	0.431	−0.087	−0.023
Pilodyn penetration	0.043	0.146	0.108		0.595	−0.507	−0.165
Wood moisture content	−0.017	−0.199	0.129	0.385**		−0.114	−0.092
Wood density	0.061	−0.151	−0.135	−0.255*	−0.160		0.228
Wood specific gravity	0.028	−0.172	−0.121	−0.309**	−0.586**	0.753**	

* = significant at $p < 0.05$, ** = significant at $p < 0.01$.

is based on the depth to which the pilodyn needle penetrates the wood layer, with a greater depth indicating a lower wood density (Anna *et al.*, 2020; Chen *et al.*, 2015; Cown, 1982). In the present study, pilodyn penetration values were negatively correlated with wood quality (wood density and SG) and positively correlated with tree diameter (faster-growing trees were likely to have deeper pilodyn penetration and lower wood quality) and MC. Fast-growing individuals (large diameter) generally contain more earlywood with a higher MC (Mäkinen *et al.,* 2002; Wang *et al.*, 2002), making them more easily penetrated by pilodyn needles. These results highlight the genetic relationships between growth and wood quality traits in *N. macrophylla* progeny at 6 y of age (Table 5).

Correlations between characters or traits can indicate which characters are the most important or most strongly correlated with others. They can therefore be used as the main characters in the selection. In the present study, phenotypic and genetic correlations among the growth traits (tree height, stem diameter, and volume) of *N. macrophylla* trees showed a positive (strong) correlation. Strong correlations between growth parameters (height and stem diameter) have also been reported for the same species by Dharmawati *et al.* (2024). This indicates that growth traits are controlled by the same genes (pleiotropic genes) or inherited simultaneously (genetic linkage), as reported by Longui *et al.* (2024), who found positive genetic correlations between height and wood density in *Balfourodendron riedelianum*.

The positive correlation between growth traits and the negative correlation between growth and wood quality traits have been widely reported in tree species, such as *Enterolobium contortisiliquum* (Sant'ana *et al.,* 2013), *Acacia mangium* (Nurhasybi and Sudrajat, 2019), *Dipteryx alata* (Santos *et al.,* 2021), and *F. variegata* (Haryjanto *et al.,* 2024). The wood quality trait that was most genetically-related to growth traits was pilodyn penetration. Pilodyn penetration shows a strong genetic correlation with wood MC and density, making it a useful indicator for selecting wood quality traits.

Different correlation patterns were observed among the tree growth traits, with growth traits being genetically negatively correlated with wood density and SG. This leads to selection based on wood density, resulting in a negative increase in tree volume (Hong *et al.,* 2014).

Therefore, Missanjo and Matsumura (2017) recommended selecting a multi-trait index that included growth characteristics and wood quality. Anatomical studies have shown that *N. cadamba* trees with larger stem diameters tend to have lower proportions of fiber parenchyma and thinner cell walls (Pertiwi *et al.,* 2018), although this does not always translate into inferior wood properties (Pertiwi *et al.,* 2018). Hence, it is possible to obtain better wood properties from trees with larger diameters. Pang *et al.* (2015) reported that wood formation (xylogenesis and lignin biosynthesis) in *N. cadamba* was controlled by several key genes, enabling genetic improvement of wood quality through targeted breeding (focusing on plant-trait prioritization).

Based on the genetic correlation estimates presented in Table 5, stem diameter and pilodyn penetration were selected to simulate genetic gain. Stem diameter is strongly genetically correlated with other growth parameters, such as tree height and volume. Stem diameter is also correlated with wood properties, such as pilodyn penetration and MC. The relatively easy and highly accurate measurement makes stem diameter readily applicable as a selection parameter in the field. Similarly, pilodyn penetration was strongly genetically correlated with wood density and MC. Pilodyn penetration is a practical, fast, and nondestructive method because it does not require laboratory testing (Chen *et al.*, 2015; Cown, 1982), making selection based on wood quality more efficient.

Two selection stages were simulated, i.e., individual within-family and family selection. Using the individual within-family selection approach (selection intensity of 75%), the predicted genetic gains were 6.23% for stem diameter and 1.26% for pilodyn penetration. A family selection intensity of 40% (retaining the top 43 families) yielded optimal genetic gains for growth and wood traits, with the genetic gain for stem diameter categorized as very high (14.51%) and low for pilodyn penetration (3.59%). This low pilodyn penetration indicated that wood density and SG did not decrease substantially due to the selection for stem diameter (a growth trait). At a 40% selection intensity, the genetic increase in pilodyn penetration was low; therefore, the decrease in wood density and SG due to this selection would be less substantial. In other words, growth increased without substantially reducing wood quality (Table 6). These results suggest that family based selection offers greater potential for improving the growth and wood-quality

Table 6. Estimation of genetic gains (GG, %) of tree height, stem diameter, and pilodyn penetration based on the heritability and selection intensity level

Selection	Selection intensity level	Genetic gain (%)	
		Stem diameter	Pilodyn penetration
Individual within family	75%	6.23 (high)	1.26 (low)
Family	10% (65 families)	4.37 (moderate)	1.08 (low)
	20% (58 families)	7.82 (high)	1.94 (low)
	30% (50 families)	11.28 (very high)	2.79 (low)
	40% (43 families)	14.51 (very high)	3.59 (low)
	50% (36 families)	18.19 (very high)	4.51 (medium)
	60% (29 families)	21.87 (very high)	5.42 (medium)

Realized gain consists of four categories: low if GG = 0%–3.30%, medium if GG = 3.31%–6.60%, high if GG = 6.61%–10.00%, and very high if GG > 10% (Singh and Chaudhary, 1987).

traits of *N. macrophylla* at this stage of evaluation.

The selection criteria were more effective when several parameters (stem diameter, tree height, and pilodyn penetration) were used for multi-trait selection (combining more than one key trait, such as stem diameter and pilodyn penetration). Based on the heritability values, family selection is expected to provide greater genetic gains than individual selection within a family. Selection simulations were based on heritability values and selection intensity in individuals within a family using an intensity of 75% with one best individual per family per block. Family selection with an intensity of 40% (43 selected families) provided optimal results, particularly for stem diameter (growth trait) and pilodyn penetration (wood quality trait).

Selection strategies must balance improvement (genetic advantage) with genetic conservation (effective population size; de Araujo *et al.*, 2021). A number of unrelated individuals (families) from 30–50 families will be sufficient to carry out a breeding program in several generations for one trait, as long as the breeding objectives do not change (Johnson *et al.,* 2001). The requirements for certified seed sources in Indonesia stipulate that a minimum of 25 families should be maintained after thinning (BSN, 2019), with the effective population size calculated to ensure that genetic drift and inbreeding rates are less than 2% (ITTO, 2020).

4. CONCLUSIONS

The results of this 6-y progeny test of *N. macrophylla* indicated that the contribution of family variation to total phenotypic variance was relatively low compared to the effects of block, block × family interaction, and residual error. The family heritability estimates were consistently higher than the individual heritability estimates, suggesting that selection at the family level offered greater potential for genetic improvement than selection within families. This supports the use of family-based selection strategies in early breeding cycles. Selection based solely on wood quality traits, such as density and SG, was associated with negative genetic gains in growth traits, highlighting the trade-off between productivity and wood properties. Therefore, a multi-trait selection approach is recommended to balance growth performance and wood quality. Based on genetic correlation analysis, stem diameter and pilodyn penetration were identified as key traits for selection given their strong associations with both growth and wood density. A family selection intensity of 40% (retaining the top 43 families) yielded optimal genetic gains for growth and wood traits, with the genetic gain for stem diameter categorized as very high (14.51%) or low for pilodyn penetration (3.59%). This low pilodyn penetration indicated that wood density and SG did not decrease substantially due to selection for stem diameter (a growth trait). At a 40% selection intensity, the genetic increase in pilodyn penetration was low; therefore, the decrease in wood density and SG due to this selection would be less substantial; i.e., growth would increase without reducing wood quality considerably. The proposed selection strategy, which retained one superior individual per four-tree plot and selected the top 43 families, demonstrated promising genetic gains while maintaining sufficient genetic diversity. This approach effectively balances genetic superiority with the conservation of an effective population size, aligning with both breeding objectives and long-term sustainability goals.

CONFLICT of INTEREST

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

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