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Genetic Improvement of *Araucaria cunninghamii* for Enhanced Industrial Pulp Production

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ABSTRACT

Araucaria cunninghamii has significant potential as a long-fiber pulpwood source in Indonesia; however, its utilization remains limited due to its dependence on imported raw materials. This study presents the results of a first-generation progeny trial designed to evaluate genetic variation and identify superior genotypes for future breeding programs. This study was conducted in Bondowoso, East Java; the experimental was included 80 families from six provenances (Fakfak, Jayapura, Serui, Wamena, Manokwari, and Queensland) and designed by a Randomized Complete Block Design (RCBD); comprised of 6 provenances, 80 families, 4 blocks, 4 trees per plot with a spacing of 4 m × 2 m. After six years, the survival rates ranged from 98.30% to 99.61%, indicating a strong potential for adaptability. Significant differences were observed among families for height, diameter, and volume growth traits. Heritability estimates for height, diameter, and volume at the individual level were 0.30, 0.25, and 0.27, respectively, and 0.48, 0.45, and 0.47 at the family level. Strong genetic correlations were found between height and diameter (r = 0.99), suggesting the potential for indirect selection through breeding. These findings highlight the genetic potential of *A. cunninghamii* for sustainable pulp production and inform future breeding strategies that focus on growth, adaptability, and wood quality.

1. Introduction

Forests are essential for supplying raw materials to the wood and non-wood industries, yet many countries, including Indonesia, face increasing difficulties in meeting this demand sustainably. The limited availability of commercially valuable timber from natural forests has created a raw material bottleneck for the wood-processing sector, particularly in plywood and pulp production (Belleville et al. 2020; Gusamo 2024). Indonesia, for example, has over 230 active plywood processing units with capacities exceeding 6,000 m³ per year; yet, much of the raw material supply is still imported due to declining domestic resources (Ministry of Environment and Forestry 2019). Over-reliance on natural forests contributes to deforestation and degradation, worsening environmental concerns (Austin et al. 2019; Ghazoul et al. 2015). Thus, to overcome forest degradation, the development and utilization of fast-growing species are important, especially species with high pulpwood potential (Kumar et al. 2015; Li et al. 2017, 2023; Martins et al. 2020; Wirabuana et al. 2024).

Araucaria cunninghamii, known as hoop pine, is commonly used for saw timber and plywood. This species has high potential for the pulp and paper industry, as it contains high cellulose (Orchads 2014; Setiadi et al. 2021a, 2021b), similar to *Pinus merkusii* and *Agathis loranthifolia* (Purusatama et al. 2021). It is native to Papua, Indonesia, and northern Australia. According to Rizqiani et al. (2019), the total raw material requirements for Indonesia's national pulp and paper industry amounted to 45 million m³ per year. Indonesia exported 4.7 million tons of pulp and 4.3 million tons of paper in 2017, with the majority of the raw materials sourced from Acacia and Eucalyptus. Due to the limited supply and cultivation scale, Araucaria has not been widely utilized at the industrial level. A study reveals that Araucaria timber can be an alternative raw material for high-quality pulp and paper as its cellulose content is very high (49.28%), and the lignin content reaches 29.15%, which is suitable for pulp (Setiadi et al 2021). Furthermore, this species has a straight pole, long fibers, and is adaptable to climate change, making it a priority for breeding (Bernardinis et al. 2023; Du et al. 2024; Li et al. 2017; Moreno et al. 2020; Osterkamp et al. 2017; Prasetyo et al. 2022).

Therefore, it can be stated that *A. cunninghamii* presents considerable potential as a sustainable raw material for the pulp industry. Nonetheless, its incorporation into large-scale plantations has been constrained by the absence of high-quality planting material. According to Li et al. (2017) and Du et al. (2024), the natural population of *A. cunninghamii* exhibits limited genetic variation, which complicates achieving uniform growth performance and resilience to pests, diseases, and climate stress. To overcome this limitation, tree improvement through selective breeding and the establishment of progeny tests should be undertaken to achieve desirable traits, such as rapid growth, high biomass, and resilience to climate stress (Kumar et al. 2015; Matos et al. 2024).

A. cunninghamii is a rare tropical tree species undergoing continuous genetic enhancement for over fifty years (Lott and Read 2021). The commercialization and genetic improvement of this species exemplify the dual economic and conservation advantages achievable in tropical tree species. Therefore, this study evaluated the growth and adaptability of *A. cunninghamii* at a provenance trial that comes from several provenances, which is established at Bondowoso, East Java. The findings will facilitate the establishment of enhanced genetic criteria for commercial cultivation, ensuring a sustainable and efficient provision of superior raw materials for the Indonesian pulp sector.

2. Materials and Methods

2.1. Study Site

The first generation (F-1) *A. cunninghamii* progeny test plot in Bondowoso District, East Java Province, served as the study's location. Wringinanom Village, Sukosari Sub-District, Bondowoso District, is the administrative location of the research forest (**Fig. 1**). With an average annual rainfall of 2,400 mm, the progeny test site has a climatic type B. The soil type is Andosol.

The site, situated 800 meters above sea level (masl), features level terrain with an average slope of 0–10% (Setiadi et al. 2021a).

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Fig 1. Study site of first generation (F-1) *A. cunninghamii* progeny test.

2.2. Materials

The study involved a 6-year-old *A. cunninghamii* progeny test, and the genetic material used to build the test came from six provenances: one population from Queensland (CSIRO), which included 20 families, and five natural provenances of Papua (Fakfak, Sorong, Serui, Wamena, and Manokwari), which included 60 families. **Table 1** lists the geographic locations and elevations of the six provenances. Fertilization was carried out every 6 months, starting at 1 and 2 years of age, using 60 g of NPK fertilizer per plant. Maintenance in the form of weed control was also carried out annually in the progeny test.

Table 1. Seed sources information of progeny test of *A. cunninghamii* in Bondowoso, East Java (Setiadi and Susanto 2012)

No	Provenances	Number of families	Latitude (°S)	Longitude (°W)	Altitude (masl)
1	Serui	11	02° - 34'	135° - 11'	800
2	Wamena	28	04° - 21'	135° - 11'	1600
3	Manokwari	12	02° - 59'	139° - 09'	1200
4	Jayapura	6	04° - 25'	140° - 38'	1600
5	Fakfak	7	02° - 34'	132° - 31'	900
6	Queensland	16	26° - 52'	152° - 25'	1000

2.3. Design and Data Analysis

A Randomized Completely Block Design (RCBD) with 6 provenances, 80 families, 4 blocks, and 4 trees per plot, spaced 4 m × 2 m, was used to create the progeny test. Every single tree was measured for the following characteristics: height, diameter, volume, and survival rate. By dividing the number of surviving plants by the number of original plants and multiplying the result by 100%, the survival rate was determined. The stem diameter was measured at chest height (1.3 m), but the measured tree height was the entire height of the tree. Equation 1 was used to determine tree volume based on information on stem diameter and tree height (Setiadi et al. 2021a; 2021b).

$$V = \tfrac{1}{4}\,\pi \times (D)^2 \times T \times f \qquad (1)$$

where V is the tree volume (m^3), D is the stem diameter (cm), T is the tree height (m), and f is the shape factor (0.486).

Data on the average percentage of live plants per plot were used to analyze variance for plant adaptation using Equation 2 (Baskorowati et al. 2022; Setiadi et al. 2021a; 2021b).

$$Yijk = \mu + Bi + Pj + Fk(Pj) + Eijk \qquad (2)$$

where $Yijk$ is the plot means of the k^{th} family, j^{th} provenances, i^{th} replicate, μ is the overall mean, Bi is the effect of the i^{th} replicate, Pj is the effect of the j^{th} provenances, $Fk(Pj)$ is the effect of the k^{th} family nested in the j^{th} provenances and $Eijk$ is the residual error with a mean of zero.

Analysis of variance was 119 performed using individual data for plant growth parameters (height, stem diameter, and tree volume). The analysis was conducted using Equation 3 (Baskorowati et al. 2022; Setiadi et al. 2021a; 2021b).

$$Yijk = \mu + Bi + Pj + Fk(Pj) + B_i{*}F_k(P_j) + Eijk \qquad (3)$$

where $Yijk$ is the plot means of the k^{th}family, j^{th} provenances, i^{th}replicate, μ is the overall mean, Bi is the effect of the i^{th} replicate, Pj is the effect of the j^{th} provenances, $Fk(Pj)$ is the effect of the k^{th}family nested in the j^{th} provenances, $B_i{*}F_k(P_j$ is the interaction effect of i^{th} replicate and k^{th}family nested in the j^{th} provenances, and $Eijk$ is the residual error with a mean of zero.

Using mixed model analysis, variance components were calculated. Additional tests using the Duncan Multiple Range Test (DMRT) at the 1% or 5% significance level were conducted to determine if there were differences among treatments, given that the results of the analysis of variance indicated significant differences. Individual ($h^2{}_i$) and family ($h^2{}_f$) heritability values were estimated using the variance component of the family in the provenances using Equations 4 and 5 (Baskorowati et al. 2022).

$$h^2{}_i = \frac{3\sigma^2{}_f}{\sigma^2{}_f + \sigma^2{}_{fb} + \sigma^2{}_e} \qquad (4)$$

$$h^2{}_f = \frac{3\sigma^2{}_f}{\sigma^2{}_f + \sigma^2{}_{fb}/B + \sigma^2{}_e/NB} \qquad (5)$$

where $h^2{}_i$ is the individual tree heritability, $h^2{}_f$ is the family tree heritability, $\sigma^2 f$ is the variance between families-within-provenances groups, $\sigma^2{}_{fb}$ is the variance between families and replications, $\sigma^2{}_e$ is the variance error, B is the mean of the number of replications, and N is the harmonic mean number of individuals per plot.

Given that seeds were taken from open-pollinated parent trees in natural forests, where some seeds might be the product of family mating, the family variance component ($\sigma^2{}_f$) was taken to represent one-third of the additive genetic variation ($\sigma^2 A$). Using Equations 6 and 7, estimated genetic (r_g) and phenotypic (r_p) correlations were determined (Baskorowati et al. 2022).

$$r_g = \frac{\sigma_{f(xy)}}{(\sigma^2{}_{f(x)} + \sigma^2{}_{fy})^{1/2}} \qquad (6)$$

$$r_p = \frac{\sigma_{p(xy)}}{(\sigma^2{}_{p(x)} + \sigma^2{}_{py})^{1/2}} \tag{7}$$

where r_g is the genetic correlations, $\sigma_{f(xy)}$ is the covariance of the two traits at the family level, $\sigma^2{}_{f(x)}$ is the family-level variance components of trait (x), $\sigma^2{}_{f(y)}$ is the family-level variance components of trait (y), r_p is the phenotypic correlations, $\sigma_{f(xy)}$ is the phenotypic covariance of the two traits at the family level, $\sigma^2{}_{p(x)}$ is the phenotypic variance components of trait (x), and $\sigma^2{}_{p(y)}$ is the phenotypic variance components of trait (y).

Equation 8 was used to forecast the genetic gain (ΔG) from selection-tested progeny (Baskorowati et al. 2022; Setiadi et al. 2021a; 2021b).

$$\Delta G = h^2{}_i \times i \times \sigma_p \tag{8}$$

where $h^2{}_i$ is the individual heritability of a trait, i is the selection intensity, and σ_p is the phenotypic variance components of trait (x).

3. Results and Discussion

3.1. Survival and Adaptability

Survival rate is a crucial indicator of adaptability in progeny tests, particularly for exotic species introduced to new environments. At six years of age, the survival rate of *A. cunninghamii* ranged from 98.30% to 99.61%, with a mean value of 98.93%. This suggests that the species exhibits excellent adaptability to the environmental conditions of Bondowoso, East Java (Resende et al. 2021; Stuepp et al. 2020). This performance exceeds survival rates reported for long-term trials in Brazil, where survival decreased to 78% by age 29 (Santos et al. 2021). These values are also significantly higher compared to *Pinus sylvestris* (97.748) at age five, which was planted at Bayanbulag, Mongolia (Sukhbaatar et al. 2020). The high survival observed here may be attributed to ecological similarities between the test site and the species' native range. Nikels and Arnold (2018) stated that *A. cunninghamii* is primarily found in montane forests from West Papua (around 1°S) through the Owen Stanley Range in PNG (to about 10°30′S), occurring at elevations between 500 and 3,355 masl. In Queensland, this species is found from Shelburne Bay (11°40′S) to northern New South Wales (approximately 31°S), with an altitudinal range from sea level to 1,000 masl. Therefore, this finding is consistent with Resende et al. (2021), who noted that exotic conifers often retain high survival when planted in ecoclimatic analogues. Santos et al. (2021) emphasize that the survival rate is a key early indicator of successful genetic transfer in provenance trials, particularly under uniform silvicultural practices.

Analysis of variance (**Table 2**) indicated no significant difference in survival among provenances ($p > 0.05$), which is consistent with findings in exotic conifer trials under homogeneous site conditions (Stuepp et al. 2020). Among the provenances, Fakfak, Queensland, and Manokwari demonstrated slightly higher survival, while Jayapura, Wamena, and Serui exhibited relatively lower survival, potentially due to site-specific pest or disease pressures (**Fig. 2a**). The uniformly high survival across provenances suggests ecological compatibility, yet minor differences, with Fakfak and Queensland performing best, may indicate genetic influences on site adaptation.

Table 2. Variance analysis of survival rate and growth of *A. cunninghamii* progeny trial at 6 years in Bondowoso, East Java

Source of variation	Degrees of freedom	Survival rate	Height	Diameter	Volume
Replications	3	70.42155	55.37785**	30.85839**	0.00106**
Provenances	5	11.29144 ns	1.71488**	1.67252**	0.00004**
Family (Provenances)	74	32.07948ns	3.00613**	2.83807**	0.00007**
Rep*Fam (Prov)	236		1.50901**	1.52663**	0.00004**
Error	946		0.55192	0.00001	0.00001
Error	237	29.435592			

Notes: ns = not significantly different, ** = significantly different at the 0.01 level.

3.2. Growth Performance Across Provenances

Significant variation in growth traits (height, diameter, and volume) among provenances, families, and block interactions indicates a strong genetic basis and micro-site influence on phenotype (**Table 2**). Provenances from Jayapura and Serui exhibited higher growth (Costa et al. 2016; Xie et al. 2024), i.e., diameter, height, and volume (**Fig. 2b-d**), likely due to environmental similarity between their origin and the trial site, particularly in elevation. Altitude has previously been shown to affect tree performance in tropical species (Costa et al. 2016; Xie et al. 2024).

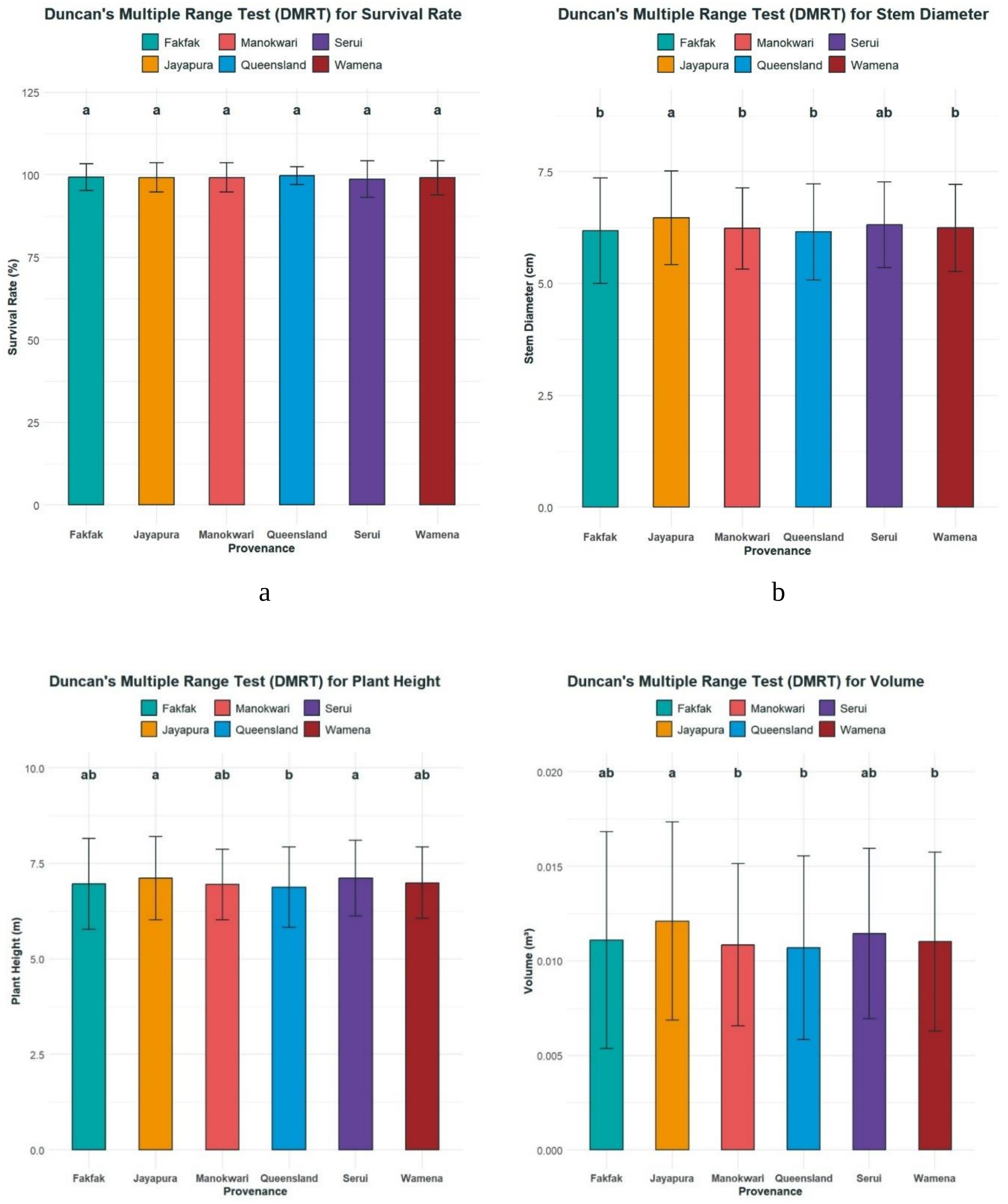
According to Raymond and Johnson (2022) and Santos et al. (2021), growth differences among provenances of *A. cunninghamii* are heavily influenced by altitude, precipitation regimes, and photoperiod (Huang et al. 2020). Raymond and Johnson (2022) found that altitude and photoperiod at the origin sites significantly affected early growth and form traits. Provenances from higher altitudes showed slower growth but better form, likely due to photoperiodic cues. This aligns with the superior performance of Jayapura (1,600 masl) in Bondowoso (800 masl), where similarities in temperature and rainfall may enhance growth vigor.

At six years, mean height ranged from 6.87 to 7.12 m, and diameter from 6.15 to 6.47 cm, reflecting a vigorous growth pattern compared to other conifer trials. For example, *A. angustifolia* in Brazil attained only 5.48 m in height at age seven (Resende et al. 2021), while *P. sylvestris* in Northern Mongolia showed 5.46 m at age five (Sukhbataaral 2020). This underscores the suitability of *A. cunninghamii* for plantation forestry in tropical highlands.

The observed family and provenance variation provide substantial scope for selection and genetic improvement. As previously noted in studies of *P. radiata*, *A. angustifolia*, and *P. caribaea*, early height and diameter traits exhibit significant inter-provenance differences that can be harnessed in breeding programs (Mingliang et al. 2023; Nantongo et al. 2020). Kanowski and Vanclay (2021) found a significant genotype-by-environment interaction. Growth was optimized when provenances were matched to rainfall regimes and altitude conditions similar to those of their native habitats (Mingliang et al. 2023; Nantongo et al. 2020).

3.3. Heritability and Genetic Control

Heritability is a key parameter in quantifying the genetic control over phenotypic traits. The moderate to high heritability estimates observed: 0.30 (height), 0.25 (diameter), and 0.27 (volume) at the individual level, suggest substantial genetic control over these traits (Lock and Whittle 2021; White et al. 2020) (**Table 3**). According to Sanchez et al. (2024), in the study of *P. pinaster*, these values indicate moderate to strong genetic control, validating the potential for effective selection, particularly at the family level. Family-level heritabilities were even higher, suggesting that selection at the family level could accelerate genetic gain in breeding programs.



a b

c d

Fig. 2. The average survival rate and growth parameters of *A. cunninghamii* progeny trial at 6 years old (the numbers followed by the same letters were not significantly different at the 0.01 level).

Comparable findings were reported by Espinoza et al. (2014), who showed similar individual heritability values for the first-generation *P. radiata* in South African trials (0.12-0.20). These results were also supported by Balkrishna et al. (2025) and Baskorowati et al. (2022) in other tropical tree species. These values are well within the range (0.20-0.45) typically considered adequate for tree improvement (Nambiar 2019). Resende et al. (2021) argued that heritability in early ages is a reliable predictor for rotation age traits, especially under uniform site conditions. As expected, heritability tends to decrease over time due to increased environmental influence; thus, early-age selection (5-10 years) is optimal for species with rotation ages of 25-50 years (Lai et al. 2017; Ornella et al. 2024).

Table 3. Estimated values of individual and family heritability of height, diameter, and volume in test plots of 6-year-old *A. cunninghamii* progeny test

Traits	**Individual heritability (h^2_i)**	**Family heritability (h^2_f)**
Height	0.30	0.48
Diameter	0.25	0.45
Volume	0.27	0.47

3.4. Genetic and Phenotypic Correlations

High genetic correlations between height and diameter (0.99), height and volume (0.99), and diameter and volume (0.98), along with high phenotypic correlations, suggest that indirect selection for height can effectively improve overall yield (Chen et al. 2018; Dias et al. 2022) (**Table 4**). This finding is consistent with those in *P. radiata* and *Eucalyptus* spp., where high correlations facilitate simplified selection arrangements (Chen et al. 2018). Strong positive phenotypic correlations among the traits were also recorded in the progeny test of indigenous *P. merkusii* from East Java (Purwanto et al. 2022).

Furthermore, Dias et al. (2022) highlighted that genetic correlations above 0.80 often suggest pleiotropic effects, enabling breeders to prioritize traits with easier or less expensive phenotyping methods. In this case, stem diameter measurements could substitute for total height in mature trees, where height measurements can be challenging in older stands.

Table 4. Estimated genetic (r_g) and phenotypic correlation (r_p) among traits of the 6-year-old progeny test of *A. cunninghamii* in Bondowoso, East Java

r_g **r_p**	**Height**	**Diameter**	**Volume**
Height	-	0.99	0.99
Diameter	0.86	-	0.98
Volume	0.91	0.96	-

Notes: genetic correlation (r_g) between traits (above diagonal), phenotypic correlation (r_p) between traits (below diagonal).

3.5. Genetic Structure and Provenance Clustering

Cluster analysis based on Nei (1972) standard genetic distance revealed the existence of two distinct genetic groups among the six *A. cunninghamii* provenances tested in Bondowoso: Group 1: Serui and Wamena, and Group 2: Fakfak, Jayapura, Manokwari, and Queensland (**Table 5** and **Fig. 3**). Interestingly, this clustering does not reflect the geographical proximity of the provenances. For instance, Serui and Manokwari, despite being relatively close geographically, were assigned to separate clusters. This suggests that genetic divergence is not solely shaped by geographic distance, but is likely influenced by factors such as oceanic barriers and limited gene flow, a pattern similarly reported in mangrove forests (Da Silva et al. 2021; Wee et al. 2020).

Table 5. Genetic distance (bottom diagonal) and genetic identity (top diagonal) in the 6-year-old *A. cunninghamii* progeny test in Bondowoso, East Java, based on Nei's standard genetic distance (1972)

Provenance	Fakfak	Jayapura	Manokwari	Queensland	Serui	Wamena
Fakfak	-----	3.881	0.625	3.636	1.490	4.680
Jayapura	3.881	-----	1.833	2.777	3.207	2.462
Manokwari	0.625	1.833	-----	4.218	0.957	3.406
Queensland	3.636	2.777	4.218	-----	2.363	4.218
Serui	1.490	3.207	0.957	2.363	-----	0.595
Wamena	4.680	2.462	3.406	4.218	0.595	-----

Such disjunctions indicate reproductive isolation and fragmented gene pools, which are common in archipelagic systems where allopatric differentiation occurs due to physical barriers such as seas and mountains (Moeinizade et al. 2019). The clustering pattern emphasizes the need for strategic crossing between different clusters to maximize heterosis (hybrid vigor). This method is promoted by Principe et al. (2024) to combine complementary genetic traits while preserving allelic richness. Furthermore, understanding the structure of genetic diversity is vital for conservation and breeding. It helps identify potential inbreeding risks, ensures broad genetic representation in seed orchards, and enhances the long-term adaptability of plantations to biotic and abiotic stressors, which is particularly significant in the context of climate variability (Daetwyler et al. 2015; Rangan et al. 2023).

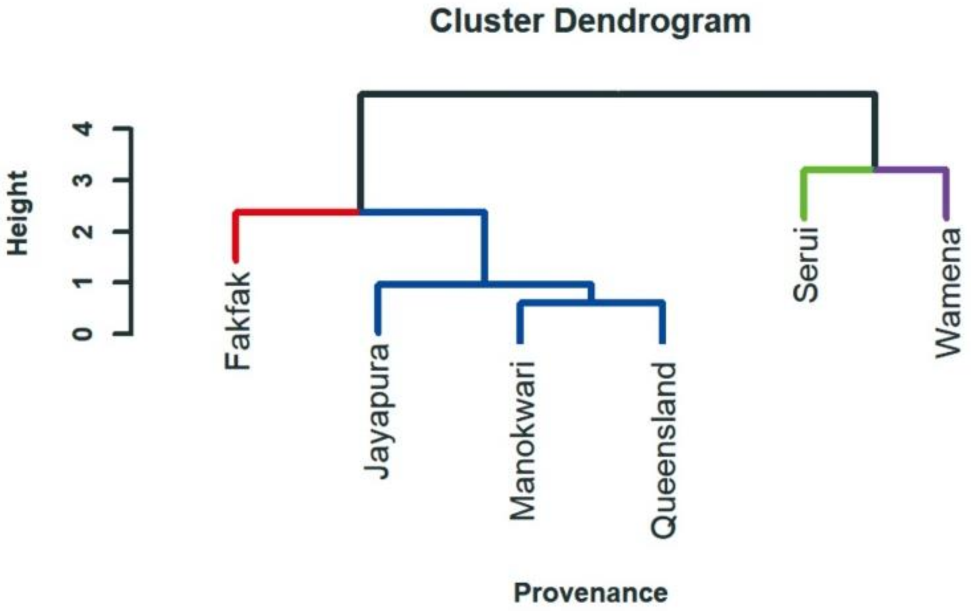


Fig. 3. Kinship relationship of 6 provenances of *A. cunninghamii* based on standardised genetic distance according to Nei (1972) by the UPGMA method.

4. Conclusions

The six-year evaluation of *A. cunninghamii* in Bondowoso revealed strong genetic variation in survival and growth traits, high heritability estimates, and positive genetic correlations, demonstrating the species' substantial potential for selective breeding in tropical pulpwood plantations. A growth performance of *A. cunninghamii* at six years showed a survival rate between

98.30% and 99.61%. The estimated heritability values for height, diameter, and volume were 0.30, 0.25, and 0.27, respectively. The family level heritability ranges from 0.45 to 0.48 for the growth parameter. Meanwhile, genetic, and phenotypic correlation between height and diameter were positive and substantial, with values of 0.99 and 0.86, respectively. The elevated survival rates and growth performance from several genetic origins validate the species' tolerance to the climatic circumstances of Bondowoso, East Java. Heritability estimates for height, diameter, and volume attributes, ranging from moderate to high, provide significant evidence of genetic influence, affirming the viability of early selection in breeding programs. The robust genetic relationships among growth parameters support indirect selection strategies, facilitating selection regardless of geographic proximity, and highlighting the importance of preserving extensive genetic diversity in population breeding. This diversity is crucial for enhancing long-term adaptability and resilience, especially in a changing climate. The findings advocate for prompt progress in identifying superior families and establishing seed orchards. Future research should assess long-term performance to confirm the initial benefits of selection and incorporate genomic tools to further enhance progress.

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Author Contributions

B.P.: Conceptualization, Software, Formal Analysis, Data Curation, Writing – Review and Editing; D.S.: Conceptualization, Methodology, Software, Formal Analysis, Data Curation, Writing – Original Draft Preparation, Writing – Review and Editing; L.B.: Conceptualization, Formal Analysis, Data Curation, Writing – Original Draft Preparation, Writing – Review and Editing; M.S.: Methodology, Resources, Writing – Original Draft Preparation, Funding Acquisition; R.L.H.: Methodology, Resources; Writing – Original Draft Preparation, Funding Acquisition; P.Y.A.P.W: Software, Formal Analysis, Data Curation, Writing – Original Draft Preparation, Visualization; M.: Validation, Investigation, Project Administration; S.P.: Validation, Investigation; S.: Investigation, Project Administration; Y.S.A.F.: Validation, Investigation, Project Administration; I.L.G.N.: Resources, Writing – Original Draft Preparation, Funding Acquisition.

Conflict of Interest

The authors declare no conflict of interest.

Declaration of Generative AI And AI-Assisted Technologies in the Manuscript Preparation

Not applicable.

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