



Effect of genotype on selected properties of young plantation-grown *Eucalyptus pellita* F. Muell. and its hybrids for structural applications

Oluwatosin Esther Falade¹ · Antanas Spokevicius¹ · Barbara Ozarska¹ · Gerd Bossinger¹ · Listya Mustika Dewi¹ · Umar Ibrahim¹ · Johannes Fehrmann² · Bala Thumma³ · Benoit Belleville¹

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Abstract

Short-rotation plantation hardwoods are increasingly used to meet timber demand but are often harvested before optimal structural properties are achieved. This limits their suitability for high-value timber applications. Improving the mechanical properties of young trees through selective breeding is a viable strategy, particularly when supported by molecular tools. However, limited information exists on how genetic and phenotypic variation influence structural traits across the stem profile. This study assessed variation in the mechanical properties of *Eucalyptus pellita* and its hybrids to support breeding for structural timber. Modulus of elasticity (MOE), modulus of rupture (MOR), and compressive strength (CS) were measured in inner and outer wood across multiple stem heights. These traits were correlated with physical properties, growth, and chemical traits. A single nucleotide polymorphism (SNP)-based genetic association analysis was also conducted. Outer wood and middle stem positions showed the highest values, with MOE up to 17,700 MPa, MOR up to 147 MPa, and CS up to 70 MPa, particularly in the *E. pellita* × *E. brassiana* hybrid. Mechanical traits correlated positively with height and diameter at breast height, while microfibril angle was negatively associated with CS ($r = -0.30$ inner; -0.24 outer). Lignin content showed positive associations with MOR and CS. SNP-based genetic analysis identified loci linked to MOE and MOR, including SNP4096 near *Eucgr.A00211*, a candidate gene potentially involved in cell wall regulation and wood strength. These findings highlight the potential of combining phenotypic and genomic tools to improve the selection of fast-grown hardwoods for high-value structural applications.

Introduction

Timber is a sustainable material valued for its strength-to-weight ratio, renewability, and aesthetic appeal. It is essential in both structural and industrial uses (Balasso et al. 2022; Kumar et al. 2022). Its versatility makes it crucial in construction, from residential housing to large-scale infrastructure. Timber can be sourced sustainably through well-managed plantations, aiding climate change mitigation efforts (González-Retamal et al. 2022; Tupenaite et al. 2023). *Eucalyptus pellita* is gaining prominence in Australian plantation forestry, especially in tropical and subtropical regions. It is a fast-growing species that thrives in challenging environments such as low-nutrient soils and high temperatures, making it suitable for plantations in tropical regions (Hutapea et al. 2023, 2024; Sukeno 2023). Its moderate density, good stability, and suitability for structural and pulpwood applications add to its value as a commercial species (Japarudin et al. 2021; Kien and Bien 2024). Hybrids of *E. pellita* with other *Eucalyptus* species show hybrid vigour, resulting in improved growth rates and mechanical properties compared to their parental inbred lines, enhancing their appeal for commercial forestry (Ibarra et al. 2023; Sharma et al. 2023).

Natural variability in timber properties, driven by genetic diversity and growth factors, presents a challenge for structural applications. Variations in growth traits, microstructural features, and wood chemical composition significantly impact timber's mechanical properties (Li et al. 2021a; Cabral et al. 2022; Peng et al. 2022). This variability often requires large safety margins in engineering designs, reducing material efficiency (Ratnam et al. 2014; Barrette et al. 2023). Identifying favourable genetic and environmental interactions can reduce properties' variability, enhancing wood reliability and efficiency (Gao et al. 2024). This supports the development of optimised *E. pellita* and hybrids for structural and industrial use, promoting sustainable forestry practices (Nickolas et al. 2020; Muneera Parveen et al. 2021; Ibarra et al. 2023).

Genetic and phenotypic relationships between growth traits and wood properties have been studied using non-destructive evaluation, where research has focused on traits affecting pulp yield, including basic density, cellulose, hemicelluloses, lignin, and extractives (Muneera Parveen et al. 2021). Understanding correlations between mechanical properties and wood traits, such as dimensional stability, growth traits, chemical composition, and pulp yield, is crucial for targeted breeding. However, direct measurements of mechanical properties, especially in plantation-grown *E. pellita*, are limited (Li et al. 2017; Prasetyo et al. 2018). Indirect methods, such as resistograph, acoustic tools, and near-infrared spectroscopy (NIRS) (Hung et al. 2015), are commonly used to predict wood density and mechanical properties in standing trees. More comprehensive studies using direct methods, such as static bending, compression, and shear tests, are needed to accurately assess mechanical properties. Such studies are essential to validate indirect approaches and ensure their reliability for industrial applications.

Advances in tree breeding and genetic selection have significantly improved wood quality and productivity in forest plantations. Techniques like genome-wide association studies (GWAS), marker-assisted selection (MAS), and genomic selection (GS) help identify genetic markers for desirable traits (Alves et al. 2020; Cortés et

al. 2020; Feng et al. 2024). GWAS has been used to identify genetic loci associated with wood properties in species like *Eucalyptus* and *Populus*. In *Eucalyptus*, several genetic markers associated with wood density and fibre length have been identified, which are crucial for pulp and paper production (Du et al. 2018). Similarly, research on *Populus* has revealed genetic loci related to wood formation and quality, providing insights into the genetic basis of these traits (Wang et al. 2023b). These advancements enable fast tracking of the breeding of genotypes with high yield and superior mechanical properties, such as modulus of elasticity (MOE) and modulus of rupture (MOR), critical for structural use (Japarudin et al. 2021, 2022a; Wongwachimaphet et al. 2024).

Building on these advancements, research on genetic variation in both hardwoods and softwoods has provided valuable insights into improving wood quality and productivity. In hardwoods, studies have examined species such as *E. globulus* (Hamilton et al. 2010; Nickolas et al. 2020; Tu 2021), *E. grandis* (Jurcic et al. 2023), *E. urogandis* (Marco de Lima et al. 2019) and *E. pellita* x *E. tereticornis* (Muneera Parveen et al. 2021). Quantitative genetic analyses of *E. pellita* x *E. tereticornis* showed significant genetic gains in diameter, density, acoustic velocity, MOE, cellulose, and lignin, with the highest gain in diameter (10.47% at 5% selection intensity) (Muneera Parveen et al. 2021). Studies on wood properties such as density, MOE, stiffness, and acoustic velocity have been conducted for hybrid poplars (Yanez et al. 2021), *E. globoides* (Iyiola et al. 2022), *E. globulus* (Nickolas et al. 2020) and *E. cloeziana* (Zhou et al. 2020). Studies have been conducted on softwood, which include species such as *Pinus koraiensis* (Kombi Kaviriri et al. 2021), *Larix kaempferi* (Pan et al. 2020), and *Pinus elliottii* (Lai et al. 2023; Wen et al. 2023). In white spruce, moderate to high genetic correlations exist between flexural properties and wood traits like density and ring width. However, flexural properties show negative correlations with tree growth (Rashidi-Jouybari et al. 2022). Most studies rely on indirect methods, such as density and acoustic velocity, to predict wood quality (Japarudin et al. 2022b; Rashidi-Jouybari et al. 2022). However, more direct measurements, especially for plantation-grown hardwoods like *E. pellita*, are needed to validate these approaches.

In this study, *E. pellita* and its hybrids were assessed for mechanical properties in both longitudinal and radial directions. The objectives were to: (i) evaluate the variability of MOE, MOR, and compression strength in both directions, (ii) investigate correlations between mechanical properties and wood traits. These traits included physical properties (density and shrinkage), growth traits (diameter at breast height (DBH) and height), and phenotypic traits such as lignin, cellulose, kraft pulp yield (KPY), microfibril angle (MFA), and extractives, and (iii) identify molecular markers associated with mechanical properties. Understanding genotype-trait relationships will help breeders improve mechanical properties for structural applications and optimise chemical traits for pulp production for sustainable wood production (Nickolas et al. 2020; Rashidi-Jouybari et al. 2022; Wen et al. 2023; Shang et al. 2024).

Materials and methods

Study area

This research was conducted at two *Eucalyptus pellita* trial sites on the Tiwi Islands in the Northern Territory of Australia: Kilu Impini 64, a high-productivity site, and Yapilika 28, a moderate-productivity site (Table 1). Both trials were planted in 2012 using a randomized complete block design, comprising four full replicates with 25 trees in each, totalling 1,000 trees per site. The trials included pure *Eucalyptus pellita* and its F1 and backcross (BC) hybrids. Individual genotypes representing each genetic group were randomly distributed within each block of the randomized complete block design. Trees were spaced at 3 m by 3 m to maintain a balanced stand density. Uniform silvicultural treatments, including weed management, pruning, and thinning, were implemented across the two sites.

Growth trait assessment and genotyping

This study formed part of a broader project comprising three integrated studies focused on genomic selection, wood anatomy and chemistry, and mechanical performance of *Eucalyptus pellita* and its hybrids. The aim was to support breeding strategies for improved wood quality in tropical plantations. Approximately 1,500 trees across two trial sites were assessed for growth traits, including total height and diameter at breast height (DBH, ~130 cm). Cambial tissue was sampled at breast height using a chisel to target the meristematic zone, which is rich in nuclear DNA and suitable for high-throughput genotyping. Genomic DNA was isolated using a modified cetyltrimethylammonium bromide (CTAB) procedure adapted from Tibbits et al. (2006), which is well-suited for processing woody tissues and yields high-quality DNA from mature trees. Genotyping was carried out by Gondwana Genomics employing a Targeted Genotyping-by-Sequencing (TGS) approach with a custom *E. pellita* SNP array (Thavamanikumar et al. 2020; Thumma et al. 2022). In this method, specific genomic regions were captured using designed oligonucleotide probes, followed by

Table 1 Location and description of research trial sites (Falade et al. 2025)

	Kilu Impini 64	Yapilika 28
Geographical coordinates	11°25'6.00"S 30°30'0.00"E	11°33'45.00"S 130°34'39.00"E
Soil	Red sandy soils and grey to yellow sandy soil >2 m	Moonkinu Member sandstone >3 m
Rainfall	1200–1400 mm	1200–1400 mm
Year of establishment	2012	2012
Number of seedlots	10	10
Tree per plot	25	25
Replications	4	4
Number of trees planted	1,000	1,000
Spacing	3 × 3 m	3 × 3 m
Surviving trees (as of 2022)	763	666

amplification with universal primers, and sequencing of the amplified fragments on an Illumina platform (Illumina Inc., San Diego, USA). The sequencing achieved an average depth of approximately 30× per locus. SNP alignment was performed against the *Eucalyptus grandis* reference genome (version 2.0, Phytozome) to enable genetic structure and association analyses.

Five genetic groups were identified, consisting of pure *E. pellita*, first-generation (F1) hybrids, and backcross (BC) hybrids. *E. pellita* was represented by 456 trees at the KI64 site and 402 trees at YP28. The *E. pellita* × *E. brassiana* BC hybrid group included 59 trees at KI64 and 38 at YP28, while the corresponding F1 group included 17 trees at KI64 and 8 at YP28. For the *E. pellita* × *E. urophylla* hybrids, 160 BC individuals were sampled at KI64 and 153 at YP28, while the F1 hybrid group comprised 71 trees at KI64 and 65 at YP28 (Table 2). These hybrid materials were derived from ten seedlots representing different genetic origins. The genotyped subset was subsequently used for marker-trait association analysis to examine relationships between genetic variation and measured mechanical properties.

Tree selection, harvest, and collection of samples

Trees for wood property assessment were selected following standard practice for sampling forest trees for the determination of clear wood properties (ASTM 2017a). Due to the small diameter of plantation trees, random and cruciform sampling methods were used. Trees with a DBH of 15 cm and above were purposively chosen from the 1,500-tree pool and grouped by hybrid/genotype groups and plantation sites. To ensure proper representation, trees were classified into three density ranges using a three-bar histogram: high (≥ 620 kg/m³), medium (550–620 kg/m³), and low (≤ 550 kg/m³). Two trees were selected from each density range within each hybrid/genotype group and site. In total, 60 trees were selected and harvested at 10 years of age. Four mature trees (30 years old) from another site (Bremer) on Tiwi Island plantation were

Table 2 Distribution of genetic groups and trees selected for wood property assessment and genetic analysis

Hybrid/genotype group	Kilu Impini 64	Yapilika 28	Total genotyped	Selected Trees: Kilu Impini 64	Selected trees: Yapilika 28
Pure <i>E. pellita</i>	456	402	858	6	6
<i>E. pellita</i> × <i>E. brassiana</i> (BC)	59	38	97	6	6
<i>E. pellita</i> × <i>E. brassiana</i> (F1)	17	8	25	6	5
<i>E. pellita</i> × <i>E. urophylla</i> (BC)	160	153	313	6	6
<i>E. pellita</i> × <i>E. urophylla</i> (F1)	71	65	136	6	5
Total	763	666	1429	30	28
Pure <i>E. pellita</i> (Mature trees: Bremer site)	4 (30-year-old)				

F1 = first-generation hybrid; BC = backcross hybrid. Plantation-grown trees were sampled across three density classes (high, medium, low), with two trees selected per density class within each genetic group and site. Mature trees were sampled from a separate plantation (Bremer) for comparative purposes only. Experimental materials were derived from the same plantation trials described in Falade et al. (2025) and Falade et al. (2026), with sampling and analyses specific to the present study

also harvested to evaluate their strength properties compared to the younger trees (Table 2). After harvesting, 1.5 m billets were taken from the top, middle, and base of each log for mechanical property assessment (Fig. 1). The billets were sawn using a portable sawmill (LUCAS mill, model 6–18) in a plain sawing pattern to produce uniform boards. The boards were air-dried for 32 weeks in a well-ventilated shelter before undergoing kiln drying. The drying process followed a progressive schedule, starting at 40 °C and gradually increasing to 60 °C over three weeks, achieving a final wood moisture content of 12%. Test samples were prepared from each billet for bending strength (35 mm × 25 mm × 410 mm) and compression strength (25 mm × 25 mm × 100 mm). The density of each test sample was determined according to ASTM D2395 (ASTM 2017b).

Mechanical properties

The mechanical properties of *E. pellita* and hybrids were tested using a universal testing machine (Instron UTM). The test was done according to ASTM standard test methods for small clear specimens of timber ASTM D143:2021 (ASTM 2021) and the Australian/New Zealand standards for characterisation of structural timber AS/NZS 4063:2010 (AS/NZS 2010). The AS/NZS 4063:2010 procedures are harmo-

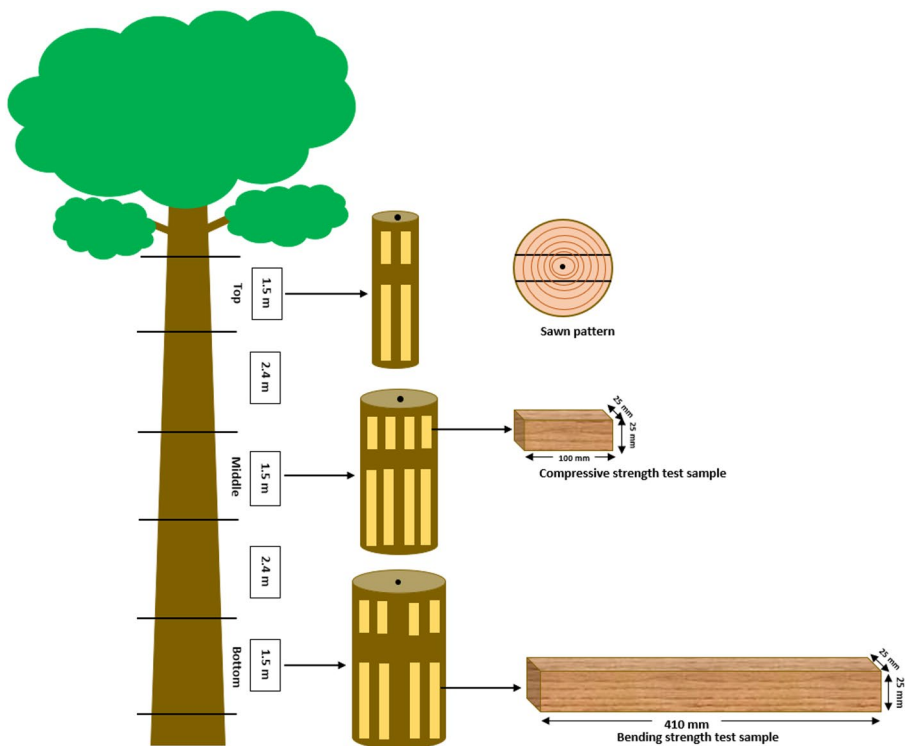


Fig. 1 Schematic diagram of sample collection for mechanical properties testing

nized with ASTM D143:2021, ensuring international comparability and repeatability of results.

Three-point bending tests were performed, and the modulus of elasticity (MOE, in MPa) and modulus of rupture (MOR, in MPa) were calculated using Eqs. 1 and 2. MOE was determined from the linear elastic portion of the load-displacement curve using crosshead displacement measurements. The Instron testing system was calibrated according to the manufacturer's specifications prior to testing. MOE values are reported rounded to the nearest 100 MPa to reflect the accuracy of the displacement measurement.

$$MOE \text{ (MPa)} = \frac{\ell_s^3 m}{4bd^3} \quad (1)$$

where ℓ_s is the test span (mm), m is the slope of the linear elastic region of load-deflection curve (N/mm), b is the width (mm), and d is the thickness (mm).

$$MOR \text{ (MPa)} = \frac{3P_{max} \ell_s}{2bd^2} \quad (2)$$

where P_{max} is maximum load failure at (N), ℓ_s is the test span (mm), b is the width (mm), and.

The compression value was calculated using Eq. 3.

$$R_{c,0} = \frac{P_{max}}{bd} \quad (3)$$

where $R_{c,0}$ is the compressive strength parallel to grain P_{max} is the value of P at failure (kN), while b , d are the cross-sectional dimensions of the test specimen (mm).

Physical, chemical and anatomical traits evaluation

Unit shrinkage in the tangential and radial directions was determined from discs collected at the base of the trees as part of a previous study (Falade et al. 2025). The unit shrinkage was carried out following Kingston and Risdon (1961).

Chemical traits were evaluated using near-infrared spectroscopy (NIRS). Wood chips were obtained from the outer stem behind the cambium at breast height (about 130 cm), oven-dried, and ground to produce 16-mesh woodmeal. Approximately 1 g of each sample was scanned on a Bruker MPA FT-NIR spectrometer over the range 4000–10,000 cm^{-1} . Calibration models for Klason lignin, total lignin, cellulose, extractives, and kraft pulp yield (KPY) were developed using partial least squares regression (PLSR) in the Bruker QUANT module of OPUS 5.5 (Bruker Optik, Ettlingen, Germany), following the procedures outlined by Poke and Raymond (2006) and Downes et al. (2011). Microfibril angle (MFA) was measured using X-ray diffractometry via the Silvican system on radial discs collected from the base, middle, and upper sections of felled logs. All data collected for chemical composition, anatomical

traits, and unit shrinkage were used to examine their correlations with the mechanical properties assessed in the present study.

Statistical analysis

Mechanical properties (MOE, MOR, and compression strength) were analysed using a mixed linear model (MLM) in R (version 4.3.3). The model assessed the significance of random effects (individual trees), fixed effects (hybrid group and plantation site), and their interactions. Pearson's correlation was used to examine the relationships between mechanical properties (MOE, MOR, compression strength), physical properties (density and dimensional stability), growth traits (height and DBH), and phenotypes (KPY, lignin, cellulose, extractives).

Genetic analysis was performed on data from 60 individuals, selected from 1,500 trees. Each tree had approximately 5,500 SNPs. SNPs were filtered using Trait Analysis by Association, Evolution, and Linkage (TASSEL, version 5.2.93). SNPs with multiple mutations or minor allele frequencies below 10% were removed, resulting in a final dataset of approximately 3000 high-quality SNPs. Association analysis was done using the BLINK method in GAPIT (version 3) with the SNPs from the *Eucalyptus pellita* marker panel. The BLINK analysis was conducted within a mixed linear model framework, in which SNP markers and covariates were fitted as fixed effects, while a kinship matrix was included as a random effect to account for relatedness among individual. Covariates included the first three principal components and the origin group. The BLINK method minimised false positives by iteratively including associated markers and optimising for linkage disequilibrium and Bayesian information content (Huang et al. 2018).

Results and discussion

Variation in density within trees, among genotype groups, and between plantation sites

Wood density varied across hybrids, radial positions, and plantation sites (Table 3). At KI64, density ranged from 707 to 816 kg/m³, with no significant hybrid differences ($p=0.60$). The highest density was recorded in *E. pellita* × *E. brassiana* (BC) (up to 816 kg/m³), followed by *E. pellita* × *E. brassiana* (F1) (725–784 kg/m³). *E. pellita* × *E. urophylla* (BC) had the lowest density (707–766 kg/m³). At YP28, density ranged from 665 to 853 kg/m³, with significant hybrid differences ($p=0.05$). *E. pellita* × *E. brassiana* (BC) again had the highest density (up to 853 kg/m³), followed by *E. pellita* × *E. urophylla* (BC), while *E. pellita* × *E. urophylla* (F1) had the lowest (665–770 kg/m³). At this site, *E. pellita* × *E. brassiana* (BC) differed significantly from *E. pellita*. Across the combined plantation sites, significant effects were observed for hybrid, site, and their interaction ($p<0.001$, $p=0.01$, and $p<0.001$, respectively).

The density values observed in this study are consistent with previous reports for *Eucalyptus* species (Elissetche et al. 2024; Neimsuwan et al. 2024). However, the densities observed in this study are higher than the mean density recorded for

Table 3 Mean table for density in Kilu Impini 64, Yapilika 28 and plantation combined

	Density (kg/m³)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
Kilu impini 64						
<i>E. pellita</i>	766.0 ^a (24.2)	716.0 ^a (24.6)	775.0 ^a (24.4)	724.0 ^a (24.6)	774.0 ^a (24.3)	724.0 ^a (24.3)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	808.0 ^a (24.5)	758.0 ^a (24.8)	816.0 ^a (24.8)	766.0 ^a (24.9)	816.0 ^a (24.4)	765.0 ^a (24.3)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	775.0 ^a (25.6)	725.0 ^a (26.3)	784.0 ^a (25.6)	733.0 ^a (26.1)	783.0 ^a (25.2)	733.0 ^a (25.6)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	757.0 ^a (24.4)	707.0 ^a (24.7)	766.0 ^a (24.5)	715.0 ^a (24.6)	765.0 ^a (24.4)	715.0 ^a (24.3)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	765.0 ^a (24.7)	715.0 ^a (25.1)	773.0 ^a (24.8)	723.0 ^a (25.0)	773.0 ^a (24.5)	722.0 ^a (24.6)
LSD (Tukey)	101.3					
<i>p</i> -value (Hybrid)	0.60					
<i>p</i> -value (Long_Pos)	0.60 (Top=a, Middle=a, Bottom=a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Yapilika 28						
<i>E. pellita</i>	746.0 ^a (23.2)	677.0 ^a (24.1)	751.0 ^a (23.5)	682.0 ^a (24.1)	744.0 ^a (23.4)	675.0 ^a (23.6)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	848.0 ^b (25.4)	779.0 ^b (26.3)	853.0 ^b (25.2)	784.0 ^b (25.9)	846.0 ^b (25.1)	777.0 ^b (25.4)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	736.0 ^{ab} (35.2)	667.0 ^{ab} (36.3)	742.0 ^{ab} (35.0)	673.0 ^{ab} (35.9)	734.0 ^{ab} (34.9)	665.0 ^{ab} (35.5)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	778.0 ^{ab} (20.6)	710.0 ^{ab} (21.7)	784.0 ^{ab} (20.7)	715.0 ^{ab} (21.4)	777.0 ^{ab} (20.4)	708.0 ^{ab} (20.6)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	770.0 ^{ab} (25.6)	701.0 ^{ab} (26.7)	776.0 ^{ab} (25.3)	707.0 ^{ab} (26.1)	769.0 ^{ab} (25.3)	700.0 ^{ab} (25.7)
LSD	125.6					
<i>p</i> -value (Hybrid)	0.05					
<i>p</i> -value (Long_Pos)	0.61 (Top=a, Middle=a, Bottom=a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Plantation combined						
<i>E. pellita</i>	759.0 ^{ab} (6.8)	684.0 ^{ab} (8.4)	757.0 ^{ab} (6.9)	717.0 ^{ab} (7.3)	745.0 ^{ab} (6.8)	707.0 ^{ab} (7.1)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	834.0 ^c (6.9)	760.0 ^c (8.4)	833.0 ^c (7.0)	793.0 ^c (7.66)	820.0 ^c (6.9)	783.0 ^c (7.2)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	775.0 ^{ab} (8.7)	701.0 ^{ab} (10.6)	773.0 ^{ab} (9.7)	733.0 ^{ab} (10.0)	761.0 ^{ab} (9.6)	723.0 ^{ab} (10.1)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	756.0 ^a (6.9)	681.0 ^a (8.6)	754.0 ^a (7.0)	714.0 ^a (7.3)	742.0 ^a (6.9)	704.0 ^a (7.6)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	776.0 ^b (7.4)	702.0 ^b (9.5)	775.0 ^b (7.9)	735.0 ^b (8.7)	762.0 ^b (7.4)	725.0 ^b (7.6)
LSD (Tukey)	25.0					
<i>p</i> -value (Hybrid)	0.00					

Table 3 (continued)

	Density (kg/m ³)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
<i>p</i> -value (Site)	0.01					
<i>p</i> -value (Hybrid x Site)	0.00					

*F1: first-generation hybrid; BC: backcross hybrid. Significance at $p < 0.05$, 95% confidence. Means with the same letter within each factor (hybrid, longitudinal position, radial position) are not significantly different (Tukey-adjusted, Mixed Linear Model). Different letters indicate significant differences. The same LSD value applies across all hybrid comparisons within each longitudinal and radial position. Standard error in parentheses

Eucalyptus hybrids using ultrasonic techniques (500 kg/m³) (Van Duong et al. 2024) and destructive testing method (462 kg/m³) (Mesquita Pimenta et al. 2024). The significant radial variation characterised by higher density in outer wood is typical of fast-grown plantation species and reflects the transition from juvenile to mature wood (Lachenbruch et al. 2011; Vega et al. 2020; Bento dos Santos et al. 2024). Additionally, increased density in the middle and upper stem positions was observed, consistent with findings in *E. nitens* (Gendvilas et al. 2022). In this study, backcross (BC) hybrids of *E. pellita* × *E. brassiana* and *E. pellita* × *E. urophylla* demonstrated higher wood density than their F1 counterparts. This improvement is likely due to the reinforcement of favourable traits from *E. pellita*, a parent known for high-density wood, and reduced linkage drag in backcross populations (Kullan et al. 2012a; Tourrette et al. 2021). Density is a moderately to highly heritable trait (Hung et al. 2015; Fadwati et al. 2023; Kien and Bien 2024), and similar patterns have been reported in *Eucalyptus* and *Populus*, where backcrossing to a superior parent enhanced wood quality (Myburg et al. 2003; Kullan et al. 2012a, b). Additionally, the larger population size of BC hybrids in this study may have supported greater genetic diversity and more effective selection for desirable traits.

Mechanical properties in relation to stem position, genotype, and site

Mechanical properties, including modulus of elasticity (MOE), modulus of rupture (MOR), and compressive strength (CS), were evaluated to determine the structural potential of *E. pellita* and its hybrids. Results highlight variation across hybrids, stem positions, and plantation sites. At KI64, MOE ranged from 10,700 to 16,600 MPa (Table 4). Although hybrid differences were not significant ($p = 0.27$), both radial and longitudinal variations were significant ($p < 0.001$), with outer wood and the middle section exhibiting higher stiffness. MOR ranged from 103 to 135 MPa. Hybrid differences were also not significant ($p = 0.91$), but radial variation was significant ($p < 0.001$). Longitudinal variation was marginal ($p = 0.07$). Despite the lack of a hybrid effect, *E. pellita* × *E. brassiana* (BC) had the highest MOE and MOR, followed by the F1 hybrid. The lowest values were observed in *E. pellita* × *E. urophylla* (F1), indicating better performance in hybrids with *E. brassiana*.

At YP28, MOE ranged from 10,500 to 17,700 MPa. Hybrid effects were significant ($p = 0.01$). *E. pellita* × *E. brassiana* (BC) had the highest MOE, followed by *E. pellita* × *E. urophylla* (BC). The F1 hybrid had the lowest. The two BC hybrids

Table 4 Mean table for modulus of elasticity (MOE) in Kilu Impini 64, Yapilika 28 and plantation combined

	MOE (MPa)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
Kilu impini 64						
<i>E. pellita</i>	15,700 ^a (707)	13,800 ^a (722)	16,100 ^a (715)	14,200 ^a (722)	14,200 ^a (709)	12,300 ^a (709)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	16,100 ^a (718)	14,200 ^a (731)	16,600 ^a (731)	14,700 ^a (736)	14,700 ^a (713)	12,800 ^a (712)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	15,700 ^a (763)	13,800 ^a (791)	16,200 ^a (762)	14,300 ^a (781)	14,300 ^a (746)	12,400 ^a (761)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	15,600 ^a (713)	13,700 ^a (727)	16,000 ^a (717)	14,100 ^a (722)	14,200 ^a (713)	12,300 ^a (712)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	14,000 ^a (725)	12,100 ^a (745)	14,400 ^a (725)	12,500 ^a (741)	12,600 ^a (717)	10,700 ^a (723)
LSD (Tukey)	2,957					
<i>p</i> -value (Hybrid)	0.27					
<i>p</i> -value (Long_Pos)	0.00 (Top=a, Middle=ab, Bottom b)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Yapilika 28						
<i>E. pellita</i>	16,000 ^{ab} (665)	13,600 ^{ab} (715)	16,300 ^{ab} (679)	13,900 ^{ab} (721)	15,200 ^{ab} (676)	12,800 ^{ab} (684)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	17,400 ^a (726)	15,000 ^a (781)	17,700 ^a (715)	15,300 ^a (756)	16,600 ^a (710)	14,200 ^a (728)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	14,200 ^{ab} (1,067)	11,800 ^{ab} (1,125)	14,500 ^{ab} (1,056)	12,100 ^{ab} (1,103)	13,400 ^{ab} (1,055)	11,000 ^{ab} (1,087)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	16,400 ^a (627)	14,100 ^a (683)	16,700 ^a (627)	14,400 ^a (667)	15,600 ^a (618)	13,300 ^a (630)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	13,700 ^b (741)	11,300 ^b (801)	14,000 ^b (722)	11,600 ^b (770)	12,900 ^b (722)	10,500 ^b (746)
LSD (Tukey)	3,666					
<i>p</i> -value (Hybrid)	0.01					
<i>p</i> -value (Long_Pos)	0.00 (Top=ab, Middle=b, Bottom a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Plantation combined						
<i>E. pellita</i>	16,300 ^{bc} (262)	14,700 ^{bc} (270)	16,400 ^{bc} (262)	14,300 ^{bc} (264)	15,000 ^{bc} (262)	13,000 ^{bc} (264)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	17,200 ^d (263)	15,600 ^d (279)	17,300 ^d (263)	15,300 ^d (265)	15,900 ^d (263)	13,900 ^d (265)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	15,600 ^b (276)	14,000 ^b (295)	15,700 ^b (276)	13,700 ^b (288)	14,300 ^b (276)	12,300 ^b (288)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	16,300 ^c (260)	14,700 ^c (268)	16,400 ^c (260)	14,300 ^c (261)	15,000 ^c (260)	13,000 ^c (261)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	14,300 ^a (268)	12,700 ^a (284)	14,400 ^a (268)	12,400 ^a (270)	13,000 ^a (268)	11,000 ^a (270)
LSD (Tukey)	709					
<i>p</i> -value (Hybrid)	0.00					

Table 4 (continued)

	MOE (MPa)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
<i>p</i> -value (Site)	0.92					
<i>p</i> -value (Hybrid x Site)	0.00					

*F1: first-generation hybrid; BC: backcross hybrid. Significance at $p < 0.05$, 95% confidence. Means with the same letter within each factor are not significantly different (Tukey-adjusted, Mixed Linear Model). Different letters indicate significant differences. The same LSD value applies across all hybrid comparisons within each longitudinal and radial position for each trait. Standard error in parentheses

were not significantly different but were higher than the F1 hybrid. Radial and longitudinal effects were also significant ($p < 0.001$). Outer and middle sections showed higher stiffness. MOR ranged from 68 to 147 MPa. Hybrid differences were significant ($p = 0.01$). *E. pellita* × *E. brassiana* (BC) had the highest MOR. The F1 hybrid had the lowest and was significantly different from the others. *E. pellita* and *E. pellita* × *E. urophylla* (F1) were not significantly different. Radial variation was significant ($p < 0.001$), while longitudinal variation was not ($p = 0.07$) (Table 5).

At the combined plantation level, no significant site effect was observed for MOE ($p = 0.92$); however, the interaction between hybrid and site was significant ($p < 0.001$) (Table 4). For MOR, a significant plantation effect was detected ($p = 0.01$), along with a significant hybrid × site interaction ($p < 0.001$) (Table 5).

The CS values across hybrids and plantation sites are summarised in Table 6. At KI64, outer wood CS ranged from 56.8 to 69.9 MPa, and inner wood from 48.7 to 61.7 MPa. At YP28, outer values ranged from 56.6 to 68.9 MPa, and inner from 47.4 to 59.6 MPa. The middle section had the highest CS, followed by the top, and bottom. Radial and longitudinal effects were significant ($p < 0.01$), but hybrid effects were not (KI64: $p = 0.29$; YP28: $p = 0.23$). However, *E. pellita* × *E. brassiana* (BC) had the highest CS at both sites, followed by *E. pellita*. The lowest values were observed in *E. pellita* × *E. urophylla* (BC) at KI64 and *E. pellita* × *E. urophylla* (F1) at YP28. At the plantation combined, there were no significant hybrid and site effects.

The mechanical properties, MOE, MOR and CS, measured in this study are generally within or above the expected range for *Eucalyptus* species such as *E. globulus*, *E. nitens*, and *E. grandis*. For these species, MOE ranges from 13,000 to 22,000 MPa, MOR from 80 to 140 MPa, and CS from 40 to 70 MPa (Vega et al. 2020; Balasso et al. 2022; Ettelaie et al. 2022; Neimsuwan et al. 2024). These results align closely with previous findings on *E. pellita* (Hii et al. 2017; Japarudin et al. 2022a; Kien and Bien 2024), although it is slightly lower than the values reported by Kien and Bien (Kien and Bien 2024). Furthermore, Júnior & Garcia (Júnior and Garcia 2023) reported lower MOE and MOR values for *E. urophylla* compared to those observed in this study for *E. pellita* × *E. urophylla* (Júnior and Garcia 2023). The CS values obtained (up to 70 MPa) are comparable with those reported for *Eucalyptus* used in structural applications (Lahr et al. 2018; Zhou et al. 2020; Japarudin et al. 2021; Van Duong et al. 2024). The results are comparable with other hardwood species (Van Duong and Ridley-Ellis 2021). Although hybrid effects were not always statistically significant, observable trends suggest a genetic influence, with *E. pellita* × *E. brassiana* hybrids performing favourably across all three traits on both plantation sites (Hii et al. 2017;

Table 5 Mean table for modulus of rupture (MOR) in Kilu Impini 64, Yapilika 28 and plantation combined

	MOR (MPa)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
Kilu impini 64						
<i>E. pellita</i>	131.0 ^a (6.3)	114.0 ^a (6.4)	134.0 ^a (6.3)	117.0 ^a (6.4)	124.0 ^a (6.3)	108.0 ^a (6.3)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	135.0 ^a (6.4)	118.0 ^a (6.5)	138.0 ^a (6.5)	121.0 ^a (6.6)	128.0 ^a (6.3)	112.0 ^a (6.3)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	131.0 ^a (6.8)	115.0 ^a (7.1)	135.0 ^a (6.8)	118.0 ^a (7.0)	125.0 ^a (6.6)	108.0 ^a (6.8)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	130.0 ^a (6.3)	114.0 ^a (6.5)	133.0 ^a (6.4)	117.0 ^a (6.4)	124.0 ^a (6.3)	107.0 ^a (6.3)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	126.0 ^a (6.4)	110.0 ^a (6.6)	130.0 ^a (6.5)	113.0 ^a (6.6)	120.0 ^a (6.4)	103.0 ^a (6.4)
LSD (Tukey)	26.2					
<i>p</i> -value (Hybrid)	0.91					
<i>p</i> -value (Long_Pos)	0.00 (Top=ab, Middle=b, Bottom=a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Yapilika 28						
<i>E. pellita</i>	128.6 ^{ab} (6.7)	104.9 ^{ab} (7.4)	138.2 ^{ab} (6.9)	114.5 ^{ab} (7.4)	134.5 ^{ab} (6.9)	110.8 ^{ab} (7.0)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	137.2 ^a (7.4)	113.5 ^a (8.1)	146.7 ^a (7.2)	123.0 ^a (7.8)	143.0 ^a (7.2)	119.3 ^a (7.4)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	92.0 ^b (11.2)	68.3 ^b (11.9)	101.6 ^b (11.0)	77.9 ^b (11.7)	97.9 ^b (11.0)	74.2 ^b (11.5)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	129.3 (6.6) ^a	105.6 ^a (7.3)	138.8 ^a (6.6)	115.1 ^a (7.1)	135.2 ^a (6.5)	111.5 ^a (6.6)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	109.8 ^{ab} (6.6)	86.1 ^{ab} (8.4)	119.0 ^{ab} (7.3)	95.6 ^{ab} (8.0)	115.7 ^{ab} (7.3)	92.0 ^{ab} (7.6)
LSD (Tukey)	37.6					
<i>p</i> -value (Hybrid)	0.01					
<i>p</i> -value (Long_Pos)	0.07 (Top=a, Middle=a, Bottom=a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Plantation combined						
<i>E. pellita</i>	131.2 ^b (3.3)	114.7 ^b (3.5)	132.7 ^b (3.3)	119.2 ^b (3.3)	123.6 ^b (3.3)	102.7 ^b (3.3)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	143.5 ^c (3.3)	127.0 ^c (3.6)	145.0 ^c (3.3)	131.6 ^c (3.4)	136.0 ^c (3.3)	115.0 ^c (3.4)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	118.5 ^a (3.5)	102.0 ^a (3.9)	120.0 ^a (3.5)	106.6 ^a (3.7)	111.0 ^a (3.5)	90.0 ^a (3.7)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	133.0 ^b (3.3)	116.5 ^b (3.6)	134.5 ^b (3.3)	121.1 ^b (3.3)	125.5 ^b (3.3)	104.5 ^b (3.3)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	122.8 ^{ab} (3.4)	106.3 ^{ab} (3.7)	124.3 ^{ab} (3.4)	110.8 ^{ab} (3.5)	115.2 ^{ab} (3.4)	94.3 ^{ab} (3.5)
LSD (Tukey)	11.2					
<i>p</i> -value (Hybrid)	0.00					
<i>p</i> -value (Site)	0.01					
<i>p</i> -value (Hybrid x Site)	0.00					

F1: first-generation hybrid; BC: backcross hybrid. Significance at $p < 0.05$, 95% confidence. Means with the same letter within each factor are not significantly different (Tukey-adjusted, Mixed Linear Model). Different letters indicate significant differences. The same LSD value applies across all hybrid comparisons within each longitudinal and radial position for each trait. Standard error in parentheses

Table 6 Mean table for compressive strength in Kilu Impini 64, Yapilika 28 and plantation combined

	Compressive strength (MPa)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
Kilu impini 64						
<i>E. pellita</i>	64.2 ^a (2.6)	56.0 ^a (2.7)	66.0 ^a (2.7)	57.8 ^a (2.7)	60.4 ^a (2.7)	52.2 ^a (2.7)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	68.1 ^a (2.7)	59.9 ^a (2.7)	69.9 ^a (2.7)	61.7 ^a (2.7)	64.3 ^a (2.7)	56.1 ^a (2.7)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	61.6 ^a (2.7)	53.4 ^a (2.7)	63.4 ^a (2.7)	55.2 ^a (2.7)	57.8 ^a (2.7)	49.7 ^a (2.7)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	60.6 ^a (2.6)	52.4 ^a (2.6)	62.4 ^a (2.7)	54.2 ^a (2.7)	56.8 ^a (2.7)	48.7 ^a (2.7)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	62.0 ^a (2.7)	53.9 ^a (2.7)	63.8 ^a (2.7)	55.7 ^a (2.7)	58.0 ^a (2.7)	50.1 ^a (2.7)
LSD (Tukey)	10.9					
<i>p</i> -value (Hybrid)	0.29					
<i>p</i> -value (Long_Pos)	0.00 (Top=b, Middle=ab, Bottom=a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Yapilika 28						
<i>E. pellita</i>	63.3 ^a (2.3)	54.1 ^a (2.4)	64.7 ^a (2.4)	55.4 ^a (2.4)	60.2 ^a (2.4)	51.0 ^a (2.4)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	67.5 ^a (2.4)	58.2 ^a (2.5)	68.9 ^a (2.4)	59.6 ^a (2.4)	64.4 ^a (2.4)	55.1 ^a (2.4)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	61.8 ^a (2.8)	52.6 ^a (3.1)	63.2 ^a (2.9)	54.0 ^a (3.0)	58.8 ^a (2.8)	49.5 ^a (3.0)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	62.2 ^a (2.2)	52.9 ^a (2.4)	63.6 ^a (2.2)	54.3 ^a (2.3)	59.1 ^a (2.2)	49.9 ^a (2.2)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	59.7 ^a (2.6)	50.5 ^a (2.8)	61.1 ^a (2.6)	51.8 ^a (2.7)	56.6 ^a (2.5)	47.4 ^a (2.6)
LSD	10.8					
<i>p</i> -value (Hybrid)	0.23					
<i>p</i> -value (Long_Pos)	0.00 (Top=b, Middle=ab, Bottom=a)					
<i>p</i> -value (Rad_Pos)	0.00 (Inner=a, Outer=b)					
Plantation combined						
<i>E. pellita</i>	63.4 ^a (1.8)	55.7 ^a (1.9)	65.6 ^a (1.8)	56.3 ^a (1.9)	60.3 ^a (1.8)	51.6 ^a (1.8)
<i>E. pellita</i> x <i>E. brassiana</i> (BC)	67.5 ^a (1.8)	59.8 ^a (1.9)	69.7 ^a (1.9)	60.3 ^a (1.9)	64.3 ^a (1.8)	55.7 ^a (1.8)
<i>E. pellita</i> x <i>E. brassiana</i> (F1)	61.5 ^a (2.0)	53.8 ^a (2.1)	63.7 ^a (2.0)	54.3 ^a (2.1)	58.3 ^a (2.0)	49.7 ^a (2.1)
<i>E. pellita</i> x <i>E. urophylla</i> (BC)	61.1 ^a (1.7)	53.4 ^a (1.84)	63.3 ^a (1.8)	54.0 ^a (1.8)	58.0 ^a (1.7)	49.3 ^a (1.8)
<i>E. pellita</i> x <i>E. urophylla</i> (F1)	60.7 ^a (1.9)	53.0 ^a (2.1)	62.9 ^a (1.9)	53.5 ^a (2.0)	57.5 ^a (1.9)	48.9 ^a (1.9)
LSD (Tukey)	7.4					
<i>p</i> -value (Hybrid)	0.05					

Table 6 (continued)

	Compressive strength (MPa)					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
<i>p</i> -value (Site)	0.69					
<i>p</i> -value (Hybrid x Site)	0.94					

FI: first-generation hybrid; BC: backcross hybrid. Significance at $p < 0.05$, 95% confidence. Means with the same letter within each factor (hybrid, longitudinal position, radial position) are not significantly different (Tukey-adjusted, Mixed Linear Model). Different letters indicate significant differences. The same LSD value applies across all hybrid comparisons within each longitudinal and radial position. Standard error in parentheses

Seng Hua et al. 2022). Across all mechanical properties, consistent longitudinal and radial trends were observed. Values were highest in the middle stem sections, moderate at the top, and lowest at the base, while outer wood outperformed inner wood.

These patterns reflect wood maturation and are well-documented in *Eucalyptus* studies (Lima et al. Jr 2018; Amer et al. 2021). These trends are characteristic of fast-growing *Eucalyptus* species. The higher mechanical performance in the outer wood is associated with mature xylem, which has thicker cell walls and greater density (Ślupianek et al. 2021). The inner wood, formed earlier, tends to have lower density and thinner walls, contributing to reduced strength. It also contains tissue with shorter fibres and lower lignification, making it structurally weaker. Middle stem sections also showed higher values, likely due to improved anatomical structure, while lower performance at the base may relate to early-formed wood and growth stress (van Leeuwen et al. 2011; Ślupianek et al. 2021). The differing strength performance of hybrids across sites highlights the role of environmental factors in trait expression and the importance of matching hybrids to suitable site conditions for optimal performance (Raymond 2002; Nguyen et al. 2014). In this study, hybrid differences were minimal at the more productive site (Kilu Impini 64), which features favourable soil conditions, resulting in consistent mechanical properties across hybrids (Nguyen et al. 2014). Conversely, greater variability among hybrid classes was observed at the less productive site (Yapilika 28), suggesting that less favourable soils amplify genetic differences and influence trait variability (Raymond 2002). This reinforces the need to consider site productivity and soil conditions when deploying specific hybrids for structural applications. These findings underscore the importance of position-specific grading in wood processing and support targeted selection in breeding programs aimed at improving structural wood quality (Lima et al. Jr 2018; Rodriguez-Perez et al. 2022).

Comparative analysis of wood strength and density in mature and young *Eucalyptus pellita* and hybrids

Measured mechanical and physical properties obtained from the middle stem sections differed between age classes and sites. Comparisons were made between 30-year-old *E. pellita* trees from the Bremer site and 10-year-old *E. pellita* and hybrid material from the KI64 and YP28 plantation sites. Across the measured traits, mature trees exhibited higher values than younger material. Outer wood from mature trees showed

the highest modulus of elasticity (MOE), modulus of rupture (MOR), compressive strength (CS), and density, while inner wood values, although lower than outer wood, remained higher than those observed in most 10-year-old trees (Table 7).

Age had a significant effect on all measured traits (Table 8). Mean MOE increased from 15,600 MPa in 10-year-old material to 18,700 MPa in 30-year-old trees ($p < 0.001$), while MOR increased from 129.8 MPa to 143.1 MPa ($p = 0.05$). Similarly, CS increased from 63.6 MPa to 69.5 MPa ($p = 0.02$), and density increased from

Table 7 Mean values of modulus of elasticity (MOE), modulus of rupture (MOR) and compressive strength (CS) for older trees from Bremer plantation site and younger trees from KI64 and YP28

Site	Hybrid	Age (years)	MOE (MPa)		MOR (MPa)		CS (MPa)		Density (kg/m ³)	
			Outer	Inner	Outer	Inner	Outer	Inner	Outer	Inner
Bremer	<i>E. pellita</i>	30	19,900 (1,612.3)	17,400 (1,884.3)	161.4 (8.9)	122.3 (32.8)	73.9 (3.8)	64.5 (4.7)	904.5 (58.4)	822.4 (78.6)
Kilu Impini 64	<i>E. pellita</i>	30	17,000 (2,678.1)	13,300 (1,153.6)	140.9 (27.2)	107.9 (15.9)	68.6 (11.4)	58.3 (10.3)	779.3 (93.7)	701.9 (65.2)
	<i>E. pel- lita</i> x <i>E. brassiana</i> (BC)	10	16,800 (765.6)	16,200 (1,365.9)	142.8 (14.8)	139.6 (11.4)	73.7 (2.8)	73.2 (2.2)	841.5 (22.6)	804.1 (73.2)
	<i>E. pel- lita</i> x <i>E. brassiana</i> (F1)	10	16,800 (1,041.34)	14,200 (1,384.0)	138.9 (11.4)	118.8 (14.4)	63.4 (7.7)	54.1 (3.2)	803.1 (71.6)	737.8 (41.2)
	<i>E. pel- lita</i> x <i>E. urophylla</i> (BC)	10	15,600 (2,296.5)	13,700 (1,835.7)	132.1 (21.3)	109.2 (19.1)	64.6 (6.1)	51.0 (7.5)	768.1 (65.4)	712.2 (56.3)
	<i>E. pel- lita</i> x <i>E. urophylla</i> (F1)	10	15,000 (2,242.3)	13,900 (1,099.6)	133.9 (20.0)	128.4 (16.7)	66.9 (7.4)	59.5 (11.4)	819.0 (55.6)	749.6 (55.7)
	<i>E. pellita</i>	10	16,800 (1,865.6)	15,900 (2,710.1)	144.4 (3.7)	131.5 (26.2)	64.6 (1.3)	63.3 (6.0)	748.5 (45.9)	746.0 (11.7)
Yapi- lika 28	<i>E. pel- lita</i> x <i>E. brassiana</i> (BC)	10	17,900 (1,310.2)	16,100 (186.2)	153.8 (12.2)	114.6 (17.4)	67.6 (8.7)	66.2 (7.5)	862.2 (63.5)	776.2 (15.2)
	<i>E. pel- lita</i> x <i>E. brassiana</i> (F1)	10	15,000 (3,168.3)	NA	112.4 (47.0)	NA	68.1 (6.6)	NA	740.5 (54.2)	NA
	<i>E. pel- lita</i> x <i>E. urophylla</i> (BC)	10	16,500 (1,927.7)	14,900 (2,723.3)	130.9 (18.3)	123.5 (21.8)	65.5 (8.1)	62.3 (11.8)	779.7 (60.8)	699.7 (60.3)
	<i>E. pel- lita</i> x <i>E. urophylla</i> (F1)	10	14,000 (2,715.9)	13,000 (792.9)	120.1 (29.0)	99.9 (19.0)	60.5 (8.8)	48.1 (4.7)	766.7 (68.6)	710.3 (16.1)

F1: first-generation hybrid; BC: backcross hybrid; Standard deviation in parentheses

Table 8 Summary of modulus of elasticity (MOE) and modulus of rupture (MOR) for young trees (10 years) and older trees (30 years)

Wood property	(Young, age 10)	(Older, age 30)	<i>p</i> -value
MOE (MPa)	15,600±2367.7	18,700±2105.1	0.00*
MOR (MPa)	129.8±23.9	143.1±30.1	0.05
Compressive strength (MPa)	63.6±9.4	69.5±6.3	0.02*
Density (kg/m ³)	772.3±73.6	866.2±78.4	0.00*

772.3 kg/m³ to 866.2 kg/m³ ($p < 0.001$). These results highlight the strong influence of cambial age on wood mechanical and physical properties.

The observed age-related differences are consistent with established understanding of wood development, whereby increasing cambial age is associated with enhanced fibre maturity, greater cell wall thickness, and increased latewood proportion, resulting in higher stiffness, strength, and density (Vega et al. 2021; Piispanen et al. 2025). While the present comparison provides insight into how wood properties differ between young and mature material, the limited number of mature trees and the use of small clear specimens mean that no prediction of future structural performance can be made. Long-term trials incorporating larger sample sizes, multiple environments, and structural-sized members are required to evaluate how these properties evolve with age and management interventions such as thinning.

Correlation among mechanical properties, density, and sapwood proportion

Correlation analysis revealed several statistically significant relationships ($p < 0.01$) across the combined plantation dataset. These involved mechanical properties (MOE, MOR, CS), wood density from bending and compression samples (Density_b, Density_c), and sapwood proportion (SW_b, SW_c) (Fig. 2; Table 9). MOE exhibited a strong positive correlation with MOR ($r = 0.86$), Density_b ($r = 0.68$), and a moderate correlation with CS ($r = 0.57$). MOR was also positively correlated with CS ($r = 0.52$) and Density_b ($r = 0.66$). CS showed the strongest association with Density_c ($r = 0.75$). In addition, Density_b and Density_c were highly correlated ($r = 0.74$), indicating good consistency in wood density measurements across mechanical testing types. Sapwood proportion showed weak but statistically significant positive correlations with mechanical properties. Specifically, SW_b was positively correlated with MOE ($r = 0.26$), and SW_c with CS ($r = 0.35$). These findings suggest that a higher proportion of sapwood is mildly associated with improved mechanical performance (MOE, MOR, and CS), although the relationship is weak.

The observed correlations offer valuable insight into the mechanical performance of *E. pellita* and its hybrids, particularly in relation to wood density and sapwood allocation. The strong positive relationship between MOE and MOR ($r = 0.86$) and their respective associations with density reinforces established biomechanical principles where stiffer wood tends to resist bending forces better (Nenning et al. 2024). CS also demonstrated notable relationships, particularly its strong correlation with density (Density_c, $r = 0.75$) and moderate correlation with MOE ($r = 0.57$). This highlights the role of density in influencing both bending and compressive strength, confirming density's utility in structural performance assessments. The high correlation between Density_b and Density_c ($r = 0.74$) further indicates consistency across

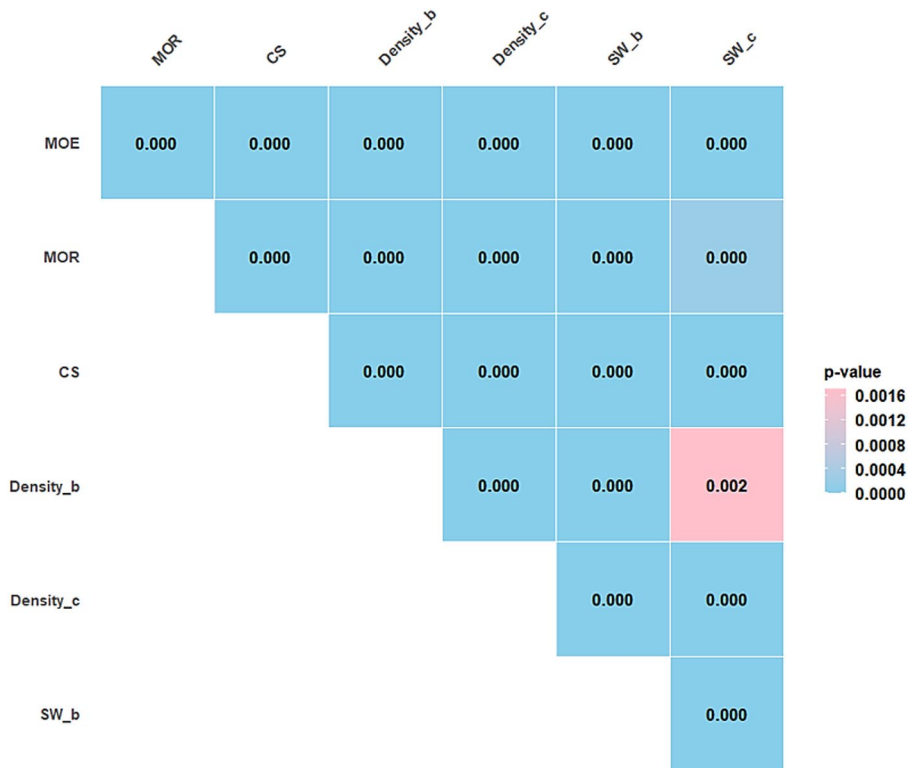


Fig. 2 Matrix of Pearson correlation p -values among MOE, MOR, CS, density, and sapwood proportion measured from bending (Density_b, SW_b) and compression (Density_c, SW_c) samples. Color intensity indicates the level of statistical significance, with p -values shown inside each cell for the upper triangle

Table 9 P -values for Pearson correlation tests among mechanical properties (MOE, MOR, CS), wood density (bending and compression samples: Density_b and Density_c), and sapwood proportion (SW_b and SW_c) across the combined plantation dataset

	MOE	MOR	CS	Density_b	Density_c	SW_b	SW_c
MOE	1	0.86*	0.57*	0.68*	0.50*	0.26*	0.25*
MOR		1	0.52*	0.66*	0.49*	0.23*	0.20*
CS			1	0.55*	0.75*	0.23*	0.35*
Density_b				1	0.74*	0.22*	0.16*
Density_c					1	0.22*	0.29*
SW_b						1	0.38*
SW_c							1

*Significance at $p=0.05$. All values are $p<0.01$

testing methods, supporting the use of density measurements from either bending or compression tests in wood property evaluations. This pattern is consistent with findings in *Eucalyptus* and other fast-growing hardwoods (Kovryga et al. 2020; Júnior and Garcia 2023). The strong correlations between density and mechanical traits

confirm density as a practical and reliable predictor of wood strength and stiffness (Morin-Bernard et al. 2020; Pramreiter et al. 2023).

Sapwood proportion showed statistically significant but weak correlations with mechanical traits. Although SW_b was positively correlated with MOE ($r=0.26$) and SW_c with CS ($r=0.35$), the strength of these associations was limited. This suggests that while sapwood may contribute to mechanical variability, it is not a reliable predictor of strength or stiffness in isolation. Overall, the results reinforce the value of wood density as a key selection criterion in breeding programs aimed at improving mechanical properties (Kien and Bien 2024). In contrast, sapwood proportion may have limited utility as a selection criterion due to its weak and inconsistent associations with mechanical properties.

Regression analyses among mechanical properties, density, and sapwood proportion

To build on the correlation results, simple linear regressions were performed to quantify the predictive strength of density, MOE, MOR, compressive strength (CS), and sapwood proportion. These analyses clarify the relative influence of each trait on mechanical performance, with key outcomes summarised in Table 10; Figs. 3, 4 and 5. Across all models, density consistently explained a large proportion of variation in mechanical traits, especially compressive strength ($R^2 = 0.56$). It showed a substantial influence on MOE ($R^2 = 0.46$) and MOR ($R^2 = 0.44$). A strong regression relationship was also observed between MOE and MOR ($R^2 = 0.74$), reflecting their mechanical interdependence. In contrast, CS contributed to the prediction of MOE and MOR but with lower explanatory power. Sapwood proportion consistently showed weak predictive strength across models, with R^2 values below 0.13, indicating a limited role in explaining mechanical performance variation in these hybrids.

The regression analyses reinforce the central role of wood density as a key determinant of mechanical performance in *E. pellita* hybrids. The high R^2 values

Table 10 Simple linear regression models predicting compressive strength (CS), modulus of elasticity (MOE), and modulus of rupture (MOR) from individual predictors

Predictor	Response variable	R^2 value	Coefficient	Std. error	p -value
MOE	CS	0.33	0.00	0.00	0.00
MOR	CS	0.27	0.22	0.02	0.00
Density	CS	0.56	0.08	0.00	0.00
Sapwood proportion	CS	0.12	0.21	0.03	0.00
MOR	MOE	0.74	97.16	3.00	0.00
CS	MOE	0.33	155.75	11.68	0.00
Density	MOE	0.46	23.76	1.36	0.00
Sapwood proportion	MOE	0.07	39.11	7.49	0.00
MOE	MOR	0.74	0.01	0.00	0.00
CS	MOR	0.27	1.25	0.11	0.00
Density	MOR	0.44	0.21	0.01	0.00
Sapwood proportion	MOR	0.05	0.30	0.07	0.00

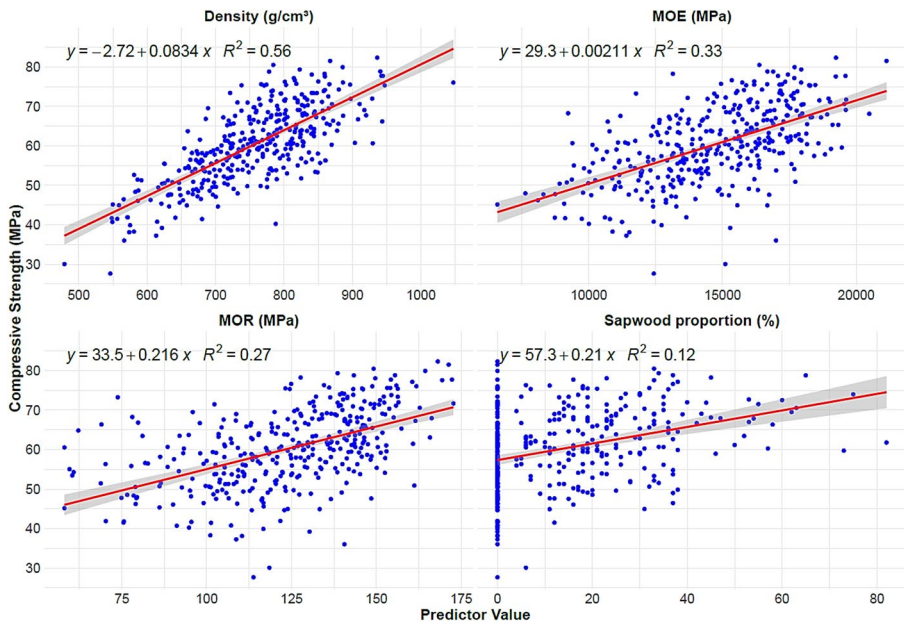


Fig. 3 Regression plots showing the relationship between compressive strength (CS) and key predictors: density, modulus of elasticity (MOE), modulus of rupture (MOR), and sapwood proportion

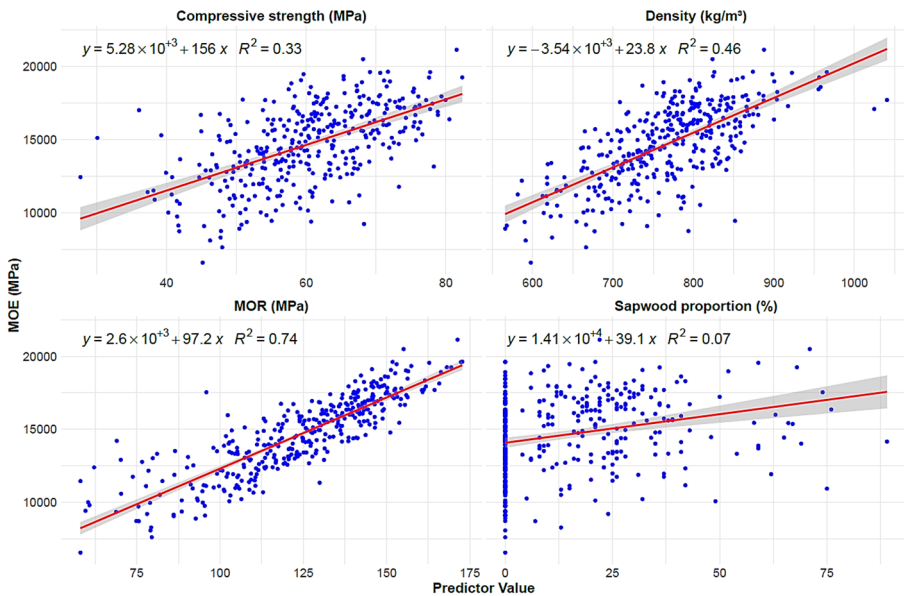


Fig. 4 Regression plots showing the relationship between modulus of elasticity (MOE) and its predictors: compressive strength (CS), density, modulus of rupture (MOR) and sapwood proportion

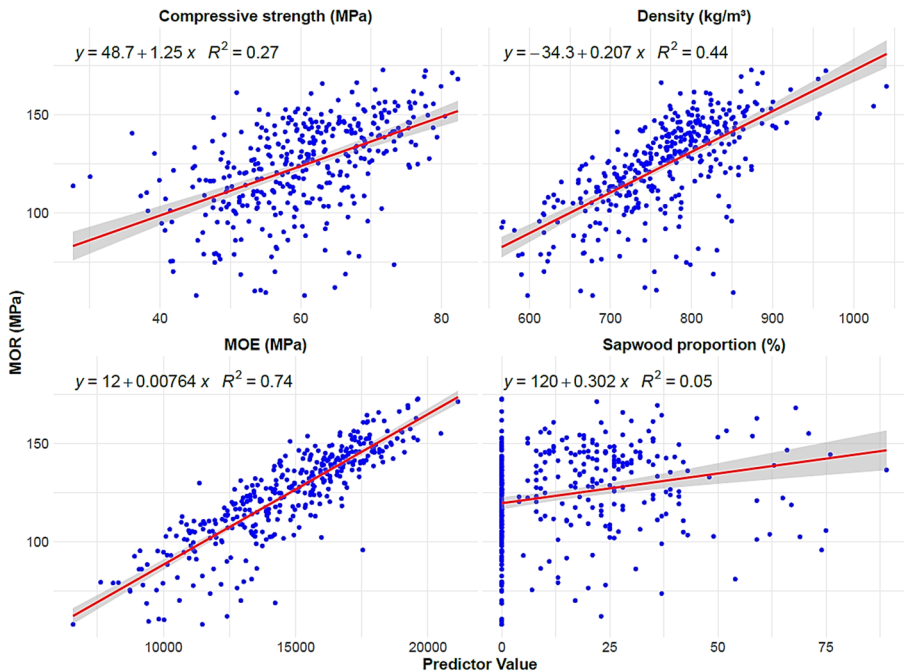


Fig. 5 Regression plots showing the relationship between modulus of rupture (MOR) and its predictors: compressive strength (CS), density, modulus of elasticity (MOE) and sapwood proportion

for models predicting MOE, MOR, and especially CS highlight density as an effective proxy trait. These findings align with prior studies that have established strong links between wood density and mechanical strength in hardwoods (Miyoshi et al. 2018; Marini et al. 2022; Arriaga et al. 2023). The strong regression between MOE and MOR ($R^2 = 0.74$) further supports the well-known mechanical interdependence between stiffness and bending strength (Nenning et al. 2024; Górska et al. 2025). Although CS also contributed to predicting MOE and MOR, its influence was moderate compared to that of density. This suggests that while compressive strength is associated with structural performance, it may not serve as a primary predictor in early screening programs.

The consistently weak predictive relationships observed for sapwood proportion ($R^2 < 0.13$) confirm its limited predictive value for mechanical performance in the studied hybrids. While such associations have been occasionally reported, their significance remains minor, and this study adds confirmatory evidence for its limited utility in structural assessment (Balboni et al. 2020). Importantly, the results underscore the practical benefits of using density in breeding and selection programs. With the availability of field-based tools such as resistance drills, density can be measured non-destructively and cost-effectively, making it a suitable trait for early-stage genetic selection aimed at improving structural wood quality (Arriaga et al. 2023).



Fig. 6 Heatmap showing p-values from Pearson correlations between mechanical properties and wood traits in *Eucalyptus hybrids*. Color intensity reflects the level of statistical significance, with blue indicating more significant correlations (lower p-values) and red indicating less significant correlations (higher p-values). Modulus of elasticity (MOE); modulus of rupture (MOR); compressive strength (CS); diameter at breast height (DBH); unit shrinkage at tangential and radial direction (UnitShr_T and UnitShr_R); kraft pulp yield (KPY); micro fibril angle (MFA)

Table 11 Pearson correlation coefficients between mechanical properties and phenotypic traits in *Eucalyptus hybrids*

	MOE Inner	MOE Outer	MOR Inner	MOR Outer	CS Inner	CS Outer
Height	0.38*	0.46*	0.26	0.48*	0.22	0.37*
DBH	0.32*	0.38*	0.11	0.51*	0.12	0.25
UnitShr_T	0.57*	0.61*	0.38*	0.63*	0.22	0.27
UnitShr_R	0.32	0.43*	0.15	0.44*	0.05	0.03
Total lignin	0.12	0.30*	0.10	0.37*	0.10	0.28*
Klason Lignin	-0.01	0.19	0.02	0.36*	0.15	0.30*
Extractives	-0.13	0.07	-0.08	0.27*	-0.13	0.29*
KPY	0.22	0.10	0.12	-0.10	0.09	-0.15
Cellulose	0.18	0.12	0.12	-0.01	0.17	-0.09
MFA	-0.09	-0.11	0.04	-0.07	-0.30*	-0.24*

*Significant at $p \leq 0.05$; modulus of elasticity (MOE); modulus of rupture (MOR); compressive strength (CS); diameter at breast height (DBH); unit shrinkage at tangential and radial direction (UnitShr_T and UnitShr_R); kraft pulp yield (KPY); micro fibril angle (MFA)

Correlation between mechanical properties and growth, physical and chemical traits

Pearson correlation was performed between mechanical properties and growth traits and other wood traits, including DBH, height, unit shrinkage, lignin, extractives, KPY, cellulose, and MFA. The wood property was derived from chips col-

lected near the cambium, which represents the most recent season of growth. As such, correlations were primarily interpreted in relation to the outer wood properties, where the data origin aligns. The correlation heatmap (Fig. 6) and associated p -values (Table 11) revealed several significant relationships between mechanical properties (MOE, MOR, and CS) and phenotypic traits. Strong positive correlations were observed between unit shrinkage in the tangential direction (UnitShr_T) and both MOE of outer wood ($r=0.61$) and MOR of outer wood ($r=0.63$). Similar patterns were seen for unit shrinkage in the radial direction (UnitShr_R) with MOE of outer wood ($r=0.43$) and MOR of outer wood ($r=0.44$), all of which were statistically significant ($p<0.001$).

Tree height and DBH also showed significant correlation with MOE of outer wood and MOR of outer wood (e.g., height vs. MOR of outer wood: $r=0.48$, $p<0.001$). Among chemical traits, Klason lignin (KLignin) and total lignin (Tlignin) had moderate positive correlations with MOR of outer wood ($r=0.36$ and $r=0.37$, respectively), both significant at $p\leq 0.05$. Extractives correlated modestly with several mechanical traits, including MOE of outer wood ($r=0.27$) and CS of outer wood ($r=0.29$). In contrast, microfibril angle (MFA) was negatively correlated with most mechanical properties, most notably with MOR of outer wood ($r=-0.30$, $p=0.04$) and CS of outer wood ($r=-0.24$, $p=0.03$). Cellulose and KPY showed weak or non-significant correlations overall. For example, KPY and CS of inner wood correlated $r=0.09$ ($p=0.59$), which was not statistically significant.

The strong correlations between unit shrinkage (especially in the tangential direction) and both MOE and MOR highlight a close link between shrinkage behaviour and bending performance. This relationship is probably driven by shared anatomical features and density-related factors (Yang et al. 2021; Arriaga et al. 2023). The observed positive correlations between tree height, DBH, and outer wood mechanical properties are consistent with previous studies that found faster-growing trees tend to produce stronger, stiffer wood (Górska et al. 2025; Huang et al. 2025). Moderate positive correlations between lignin content and mechanical properties, particularly MOR, support lignin's known role in reinforcing cell wall stiffness (Salmén et al. 2016; Mariana et al. 2021). Negative correlations between MFA and CS are in line with findings that lower MFA enhances stiffness and strength (Li et al. 2021b; Jakob et al. 2022; Górska et al. 2025).

The correlations between chemical traits and mechanical properties varied in strength and direction. Extractives content showed modest positive correlations with MOE and CS of outer wood, which may reflect their contribution to cell wall densification in some hybrids (Zhao et al. 2020). Cellulose content showed weak or no correlation with MOE, MOR, and CS, indicating a limited association with mechanical performance in *E. pellita* and its hybrid. Wood strength is influenced not only by cellulose but also by factors such as microfibril angle (MFA), lignin content, density, and anatomical structure (Carrillo et al. 2018; Lourenço et al. 2020; Jakob et al. 2022). Furthermore, these results suggest that kraft pulp yield is not a strong predictor of mechanical strength. This may indicate that chemical traits influencing pulp yield, such as lower lignin content, do not align with those that contribute to structural strength, like higher lignin and denser wood. Previous studies have reported similar findings, where weak or inconsistent relationships were reported between

pulp and mechanical properties (Hamilton et al. 2010; Nickolas et al. 2020; Varghese et al. 2024). Overall, growth and chemical properties, particularly in outer wood, offer practical selection targets for improving wood quality in structural and engineered applications.

Genetic analysis of mechanical properties

A SNP-based genetic association analysis identified SNP markers linked to mechanical traits in *Eucalyptus* hybrids, including modulus of elasticity (MOE), modulus of rupture (MOR), and compressive strength (CS), assessed from both outer and inner wood. Although the sample size was limited, distinct associations were observed, particularly for outer wood traits, highlighting potential genomic regions influencing wood mechanical performance. The Manhattan and Q-Q plots (Fig. 7) illustrate the negative log-transformed p -values of SNP associations across the genome. Significant markers were observed for MOE and MOR in the outer position, suggesting possible candidate loci influencing these traits, which were further confirmed with the Q-Q plots. Despite the small sample size, these findings highlight the potential for identifying trait-associated markers for these traits in *Eucalyptus*.

Only a few SNPs associated with mechanical properties exceeded the significance threshold ($p < 0.001$), however, the top-ranked SNPs for each trait based on the lowest p -values are listed in Table 12. While these markers did not surpass the significant threshold line, they may hold biological relevance given the small sample size and complex genetic architecture of mechanical traits. These associations provide a preliminary basis for further investigation and potential candidate gene discovery. Table 12 includes the associated SNPs for MOE, MOR, and CS for MOE, MOR, and CS along with their alleles, chromosomal locations, physical positions, p -values, minor allele frequencies (MAF), and estimated allelic effects.

Among the notable associations, SNP4096 surpassed the significance threshold. It was significantly linked to MOE_outer, MOR_outer, and MOR_inner ($p < 0.001$). It showed consistent negative effects, suggesting that the minor allele may reduce stiffness and bending strength. Its moderate minor allele frequency (MAF = 0.245) indicates it is not rare in the population. SNP3683 also exceeded the significance threshold. It is a rare variant (MAF = 0.091) and showed a positive effect on MOR_outer. SNP1573, while not surpassing the threshold, was associated with MOE_outer and MOR_outer. It showed a positive effect, indicating that the minor allele may enhance mechanical performance.

Other notable SNPs include SNP4462, which was associated with CS in both outer and inner wood. A group of SNPs, including SNP4423, SNP4424, and SNP4426, was linked to MOE_inner. These SNPs shared identical MAF and effect sizes, suggesting they belong to the same genomic region. SNP134 and SNP3664 were associated with CS_outer and showed moderate effect sizes. The ability to identify SNP markers associated with key mechanical properties can enhance the efficiency of breeding programs by enabling early selection of superior genotypes. This approach can accelerate the development of genotypes with improved structural qualities, reducing the time and cost associated with traditional breeding methods (Estopa et al. 2023). All SNPs significantly associated with mechanical traits (MOE, MOR, and

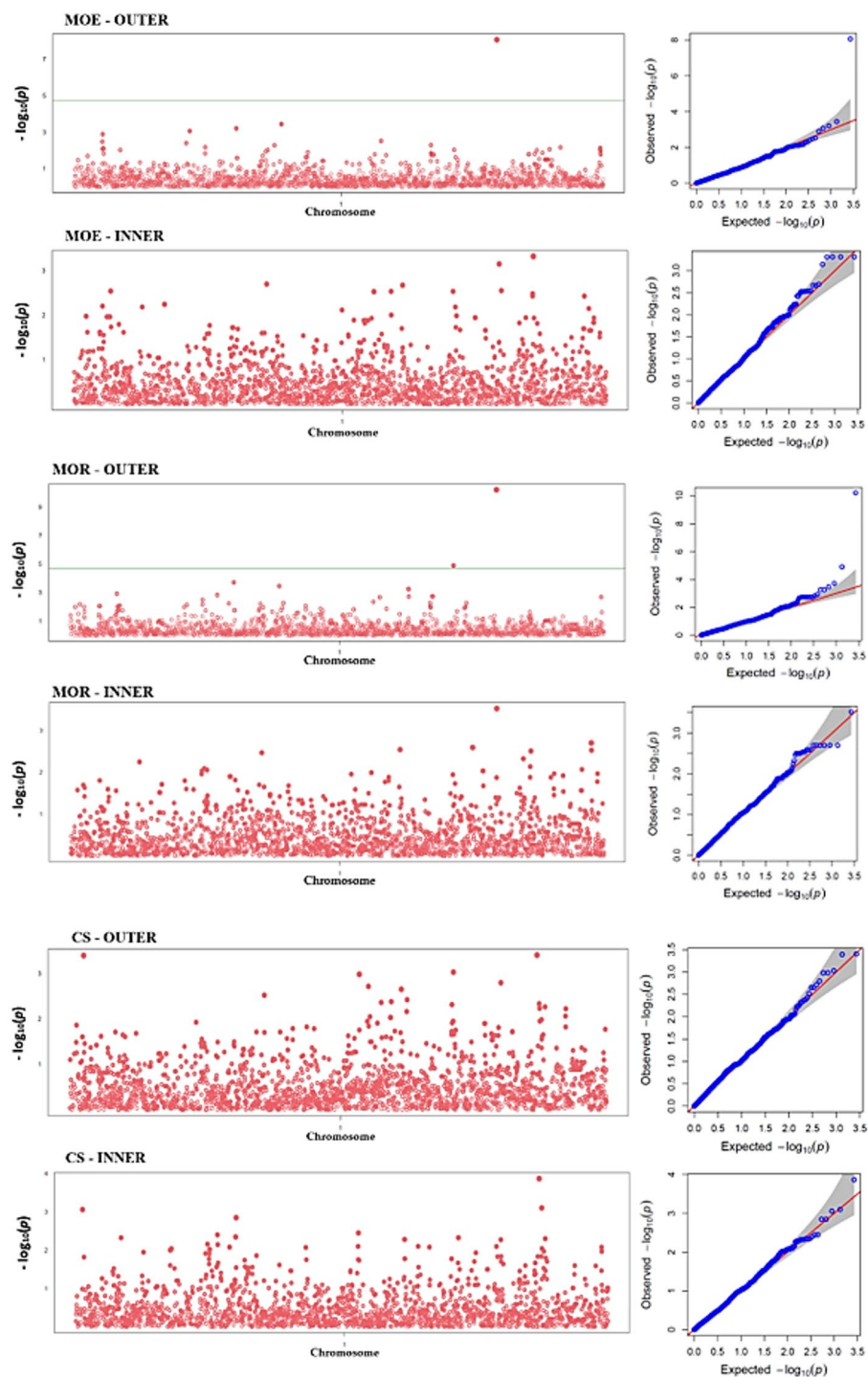


Fig. 7 Manhattan (left) and quantile-quantile (QQ) plots (right) showing SNP associations with modulus of elasticity (MOE), modulus of rupture (MOR), and CS in the outer and inner positions

Table 12 Identified single nucleotide Polymorphisms (SNPs) associated with modulus of elasticity (MOE), modulus of rupture (MOR) and compressive strength (CS) in the inner and outer positions

SNP	Traits	Alleles	Pos	P-value	MAF	Allelic effect	Nearest Gene
SNP4096	MOE_Outer	A/G	4096	0.000**	0.245	-1452.797	<i>Eucgr.A00211</i>
	MOR_Outer	A/G	4096	0.000**	0.245	-16.202	
	MOR_Inner	A/G	4096	0.000**	0.209	-15.821	
SNP3683	MOR_Outer	G/A	3683	0.000**	0.091	15.830	
SNP1573	MOE_Outer	T/G	1573	0.001*	0.227	742.738	
	MOR_Outer	T/G	1573	0.000**	0.227	6.780	
SNP4462	CS_Inner	G/A	4462	0.000**	0.372	-8.475	
	CS_Outer	G/A	4462	0.000**	0.327	-5.040	
SNP4423	MOE_Inner	C/A	4423	0.000**	0.477	-1603.125	
SNP4424		G/C	4424	0.000**	0.477	-1603.125	
SNP4426		T/A	4426	0.000**	0.477	-1603.125	
SNP134	CS_Outer	C/A	134	0.000**	0.155	-5.450	
SNP3664		C/T	3664	0.001*	0.091	6.907	

All SNPs are located on Chromosome 1

** $p < 0.001$, * $p < 0.01$, Chr: chromosomes; Pos: SNP position in the population structure; MAF: minor allele frequency

CS) were located in the intergenic region upstream of *Eucgr.A00211* (Table 12), a gene on the *Eucalyptus grandis* reference genome available in the Phytozome database. *Eucgr.A00211* encodes a lipase-containing protein related to the CGI-141 family. Although its function in *Eucalyptus* is uncharacterised, CGI-141-like proteins are involved in lipid metabolism, membrane remodelling, and stress signalling. The SNPs were annotated with MODIFIER impact, indicating likely regulatory effects. Notably, the minor allele of SNP4096 had negative effects on MOE and MOR, while SNP3683, a rare variant, had a positive effect on MOR_outer, suggesting functional variation influencing gene expression and wood strength. Lipids and lipid-modifying enzymes have increasingly been implicated in xylem differentiation and secondary cell wall formation (Xie et al. 2021). These processes are tightly linked to wood mechanical performance through their influence on fibre structure, lignin deposition, and cell wall integrity (Herrera-Ramírez et al. 2021). Given this, the proximity of mechanical trait-associated SNPs to *Eucgr.A00211* points to a potential role in regulating wood strength via lipid-mediated pathways. The clustering of SNPs associated with multiple traits in the same genomic region also suggests pleiotropic effects or co-regulation, making *Eucgr.A00211* a promising target for further investigation.

Despite the small sample size, the detection of meaningful associations aligns with findings from previous SNP-trait studies in *Eucalyptus* using limited populations (Valenzuela et al. 2021; Ashwath et al. 2023). These results demonstrate the utility of association mapping for dissecting complex traits and identifying markers for early-generation selection. Additionally, combining phenotypic and genomic data in early-generation selection can also improve precision and support the production of high-quality structural timber (Marco de Lima et al. 2019; Wang et al. 2023a). Functional validation through gene expression analysis or promoter activity assays is recommended to confirm the role of *Eucgr.A00211* in mechanical trait variation. Overall, these findings highlight *Eucgr.A00211* as a strong candidate gene for struc-

tural wood quality improvement in *E. pellita*. Its upstream regulatory region may be harnessed for marker-assisted selection to enhance mechanical performance in breeding programs.

Conclusion

This study advances understanding of the mechanical properties and genetic drivers of wood quality in *Eucalyptus pellita* and its hybrids. It demonstrates that mechanical traits (MOE, MOR, and CS) are influenced by both structural variation along the stem and genetic background. The outer wood consistently exhibited superior mechanical performance, reaffirming its importance in structural applications, while the middle and upper stem sections also showed adequate strength, supporting broader utilisation of the log. Positive correlations with density, lignin, and extractives highlight the contribution of these physical and chemical traits to wood strength. A negative correlation between compressive strength and microfibril angle (MFA) further emphasises the importance of cell wall orientation in enhancing load-bearing capacity, making MFA a valuable trait for selection.

Despite a modest sample size, the SNP-based analysis identified genetic markers associated with key mechanical traits. All associated variants were located in the upstream region of *Eucgr.A00211*, a gene likely involved in lipid-related signalling and cell wall development. These findings highlight the possibility that regulatory variation at this locus may influence fibre structure and strength. The consistent association of this gene with multiple traits indicates its potential relevance for genomic selection. These findings are particularly relevant for *E. pellita* grown in the dry tropics, providing evidence that trees from this region can yield structurally suitable timber. By integrating phenotypic assessment with molecular insights, this study offers a practical framework for selecting superior genotypes. The results support breeding strategies aimed at improving structural performance and product recovery in tropical hardwood plantations, contributing to more sustainable and commercially viable forestry.

Future work should aim to validate these associations in larger and genetically diverse populations, explore the functional role of *Eucgr.A00211* in wood formation, and integrate mechanical properties into multi-trait selection models. In the interim, breeders may apply these insights to refine early selection strategies, while industry may consider hybrid deployment strategies that align wood properties with end-use requirements.

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Author contributions O.E.F., B.B., G.B., B.O., and A.S. contributed to the conceptualisation of the study. Methodology was developed by O.E.F. and B.B. Software was implemented by O.E.F. Validation was performed by O.E.F., B.B., B.O., G.B., and A.S. Formal analysis and investigation were conducted by O.E.F.

Resources were provided by B.B., B.O., A.S., and G.B. Data curation was carried out by O.E.F., L.M.D., U.I., J.F., and B.T. The original draft was written by O.E.F., and the manuscript was reviewed and edited by O.E.F., B.B., B.O., G.B., and A.S. Visualisation was prepared by O.E.F. Supervision was provided by B.B., A.S., B.O., and G.B. Project administration was managed by O.E.F., B.B., G.B., and A.S. Funding acquisition was secured by B.B., G.B., B.O., and A.S.

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Data availability Dataset available on request from the authors.

Declarations

Conflict of interest The authors declare no competing interests.

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Authors and Affiliations

Oluwatosin Esther Falade¹ · Antanas Spokevicius¹ · Barbara Ozarska¹ · Gerd Bossinger¹ · Listya Mustika Dewi¹ · Umar Ibrahim¹ · Johannes Fehrmann² · Bala Thumma³ · Benoit Belleville¹

✉ Oluwatosin Esther Falade
oluwatosin.falade@student.unimelb.edu.au

Antanas Spokevicius
avjs@unimelb.edu.au

Barbara Ozarska
bo@unimelb.edu.au

Gerd Bossinger
gerd@unimelb.edu.au

Listya Mustika Dewi
ldewi@student.unimelb.edu.au

Umar Ibrahim
umaribrahim.suliankatchisha@student.unimelb.edu.au

Johannes Fehrmann
johannes.fehrmann@unimelb.edu.au

Bala Thumma
balat@diversityarrays.com

Benoit Belleville
benoit.belleville@unimelb.edu.au

¹ School of Agriculture, Food and Ecosystem Sciences, Faculty of Science, The University of Melbourne, Parkville, VIC 3010, Australia

² Department of Infrastructure Engineering, The University of Melbourne, Parkville, VIC 3010, Australia

³ Diversity Arrays Technology Pty Ltd (DArT), University of Canberra, Monana Street, Bruce, ACT 2617, Australia