CBAB JOURNAL

ARTICLE

Inheritance and genetic correlations of *Corymbia citriodora* wood property traits

Crop Breeding and Applied Biotechnology
25(3): e519725313, 2025
Brazilian Society of Plant Breeding.
Printed in Brazil
http://dx.doi.org/10.1590/1984-70332025v25n3a43

Eduardo Luiz Longui[1*], Israel Luiz de Lima[1], Willyam de Lima Vieira[2], Maurício Ranzini[1], José Arimateia Rabelo Machado[1], Miguel Luiz Menezes Freitas[1,3], Adriano Wagner Ballarin[3] and Alexandre Magno Sebbenn[1,3]

Abstract: *Physical and mechanical properties of wood, such as basic density (ρ_{bas}), volumetric shrinkage (β_v), compressive strength (f_{c0}), modulus of elasticity (MOE) and modulus of rupture (MOR) were evaluated in near-pith (PI), intermediate (MI) and near-bark (BA) planks from a 33-year-old Corymbia citriodora progeny test, planted in Luiz Antônio, São Paulo, Brazil. These properties were assessed to support simultaneous breeding of multiple traits. All wood properties increased radially from PI to BA. Genetic variation among families was observed for ρ_{bas} at the averaged and BA radial positions. Moderate positive additive genetic correlations were found between $\rho_{bas} \times f_{c0}$, ρ_{bas} × MOE, ρ_{bas} × MOR, $\beta_v \times f_{c0}$, β_v × MOE, β_v × MOR, f_{c0} × MOE, f_{c0} × MOR, and MOE × MOR. These findings indicate the potential for simultaneous genetic improvement of multiple traits, with ρ_{bas} serving as a key trait for direct selection to achieve indirect genetic gains in other properties.*

Keywords: *Quantitative genetics, tree breeding, wood quality, physical properties, mechanical properties*

INTRODUCTION

Species of the genus *Corymbia* (syn. *Eucalyptus*, Nicolle 2024) are of significant interest to forestry companies. In Brazil, *Corymbia citriodora* (Hook) K.D. Hill & LAS Johnson is the most widely planted species of the genus due to its rapid growth, adaptability to poor and rocky soils, resistance to pests and diseases, and high-quality wood suitable for diverse applications (Moraes et al. 2010, Silva et al. 2022). The primary uses of *C. citriodora* include essential oil extraction from leaves for the perfumery and pharmaceutical industries and wood utilization in construction and furniture production (Oliveira and Pinto Júnior 2021). To enhance wood quality concurrently with other traits, new insights into genetic control and correlations among wood properties are essential (Souza et al. 2020, Ziegler and Tambarussi 2022).

Growth traits such as diameter at breast height (DBH), tree height (H), and volume are commonly used in breeding programs due to their direct relevance for timber yield and ease of measurement. However, wood quality traits are critical for industrial applications, as they determine suitability for specific uses (Zhang et al. 2022, Sousa Júnior et al. 2025). Key wood properties include basic density (ρ_{bas}), volumetric shrinkage (β_v), compressive strength (f_{c0}), modulus

***Corresponding author:**
E-mail: elongui@sp.gov.br

Received: 17 January 2025
Accepted: 30 August 2025
Published: 08 September 2025

[1] Instituto Florestal, Rua do Horto, 931, Horto Florestal, 01059-970, São Paulo, SP, Brazil
[2] Universidade Estadual Paulista, Avenida 24 A, s/n, Botucatu Campus, 13506-900, Rio Claro, SP, Brazil
[3] Faculdade de Engenharia de Ilha Solteira, Brasil Sul, 56, Ilha Solteira Campus, 15385-000, Ilha Solteira, SP, Brazil

of elasticity (MOE), and modulus of rupture (MOR). The traits ρ_{bas} and β_v reflect wood quality and durability, guiding appropriate industrial applications, while f_{c0}, MOE and MOR are used to classify wood into strength classes, indicating suitability for structural purposes (Fukatsu et al. 2015). Research indicates that these traits are genetically controlled and amenable to improvement by selection for various industrial purposes (Li et al. 2017, Fundova et al. 2020, Zhang et al. 2022, Fadwati et al. 2023, Takahashi et al. 2023). Notably, wood properties may vary radially across the trunk, from pith to heartwood and sapwood. For genetic breeding, it is crucial to assess these differences in wood quality between early and mature growth stages (Fukatsu et al. 2015, Tanabe et al. 2018).

Simultaneous breeding for multiple traits is highly desirable for the timber industry. Such forest breeding programs can produce propagules (seeds or clones) that combine enhanced productivity with high-quality timber, meeting the demands of the forestry sector. This is feasible for traits that are heritable and genetically correlated. For example, pairs of traits with high, positive genetic correlations allow direct selection on one trait with indirect improvement of the other. Thus, understanding genetic correlations among traits is crucial for simultaneous multi-trait improvement (Zhang et al. 2022, Lima et al. 2024, Longui et al. 2024).

This study aimed to evaluate genetic variability, family-mean heritability (h^2_m) and genetic correlations for wood properties in a 33-year-old open-pollinated progeny test of *C. citriodora*, in Luiz Antônio, São Paulo, Brazil, for simultaneous multi-trait improvement. The specific objectives were: i) to assess genetic variation among families for wood properties (ρ_{bas}, β_v, f_{c0}, MOE, and MOR) at three radial trunk positions – near-pith (PI), middle (MI) and near-bark (BA) - and the mean across positions (PI, MI, and BA); and ii) to determine genetic correlations among wood properties and the expected indirect selection response from direct selection on another trait.

MATERIAL AND METHODS

Progeny test establishment and data collection

The progeny test was planted (1983) at three sites of the Experimental Station Luiz Antônio (lat 21° 34’ 12’’ S, long 47° 44’ 06’’ W, alt 550 m asl), of the São Paulo Forestry Institute, Brazil (Sebbenn et al. 2009). The sites differed in soil type: i) typical orthic Quartzarenic Neosol, with a moderate alic A horizon (QN), ii) typical dystrophic Red Latosol, with a medium-textured, moderate alic A horizon (RL), and iii) typical eutrophic Red Latosol, with clayey to very clayey texture and a moderate A horizon (CL). Due to their geographic proximity, the climatic conditions of all three sites were considered identical. The regional climate was classified as humid subtropical (Cwa), according to the Köppen–Geiger system, with two well-defined seasons - a rainy (January, February, and March) and a dry season (June, July, and August), with warm summer temperatures. The mean annual precipitation is 1433 mm and mean annual temperature 21.7 °C (Alvares et al. 2013). At each replication site, the progeny test included 56 open-pollinated families of *Corymbia citriodora* arranged in a 7 × 8 rectangular lattice design with three blocks, 10 plants per plot, 3 × 2 m spacing, and a single border row surrounding the trial. To investigate the genetic inheritance of wood properties, 54 trees from 18 families were selected (one tree per family per soil type), as wood property assessments required destructive sampling. At each site, one tree per family was randomly selected from among the three blocks. The selected trees were felled, and a 1-m log was extracted from immediately below the diameter at breast height (DBH) for wood property analysis. A 7-cm-thick central plank was sawn from each log (Figure 1). From these planks, 4 × 4 × 100 cm battens were extracted: one near the pith (PI), one from the mid- region (MI), and one near the bark (BA). These battens were used to determine physical and mechanical properties, with specific specimens prepared for each test. The evaluated physical and mechanical properties included basic density (ρ_{bas}), volumetric shrinkage (β_v>), compressive strength parallel to the grain (f_{c0}>), modulus of elasticity (MOE), and modulus of rupture (MOR). Basic

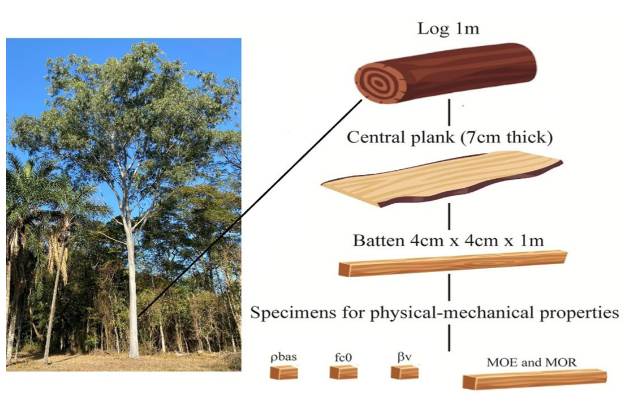

Figure 1. Schematic representation of sampling procedure to determine physical-mechanical properties of wood.

density of 3 × 2 × 5 cm samples was measured using the hydrostatic balance method, as determined by the Brazilian norm NBR 11941 (Associação Brasileira de Normas Técnicas - ABNT 2003) and calculated as $\rho_{bas} = M/V$ ($g.cm^{-3}$), where M is the oven-dry weight (g) and V the saturated volume (cm^3) at 12% moisture content. Volumetric shrinkage was determined using 3 × 2 × 5 cm samples (NBR 7190-1; ABNT 2022) and calculated as $\beta_v = (100[(V_s - V_d)/(V_d])$ (%), where V_s and V_d are saturated and oven-dry volumes, respectively. All mechanical tests were carried out with air-dried samples, conditioned to 12% moisture in a controlled environment, per NBR7190-1 (ABNT 2022). Compressive strength parallel to the grain (f_{c0}, MPa), was assessed using 54 specimens per batten (2 × 2 × 3 cm; longitudinal × radial × tangential) on a universal testing machine, following a modified NBR 7190-1 protocol (ABNT 2022). The f_{c0} was estimated by $f_{c0} = (F/S)0.01$ (MPa), where F is the rupture load (N) and S the cross-sectional area (2 × 2 cm= 4 cm^2). Modulus of elasticity (MOE) and modulus of rupture (MOR) in static bending were evaluated using 2 × 2 × 35 cm specimens prepared from each batten on a universal testing machine, with load increments of 10 MPa min^{-1}. Testing followed NBR 7190 (ABNT 1997) and NBR 7190-1 (ABNT 2022), with specimen sizes of 2 × 2 cm (width × height) and a 30-cm span (L), resulting in an L/h ratio of 15. Modulus of elasticity was calculated as $MOE = PL^3/4bLh^3\delta$ (MPa) and modulus of rupture as $MOR = 3PrL/2bh^2$ (MPa), where P is increment of applied force (N), P_r the rupture force (N), *L* the distance between supports (mm), *b* the width (mm), *h* the height (mm), and δ the vertical displacement due to incremental force (mm).

Statistical analysis

Variance components for each trait were estimated using restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) in mixed linear models using SELEGEN software (model 95; Resende 2016). Components of variance were estimated for each trait using the additive model $y = Xr + Za + e$, where: *y* is the data vector, *r* the vector of fixed repetition effects (added to the overall mean), *a* the vector of random individual additive genetic effects, and *e* the vector of random errors. *X* and *Z* are incidence matrices for these effects (Resende 2016). Estimated components of variance included: genetic variance among families (σ^2_g), additive genetic variance ($\sigma^2_a = 4\sigma^2_g$), residual variance (σ^2_e), and phenotypic variance (σ^2_p). The estimated parameters were: family-mean heritability ($h^2_m = (1/4)\sigma^2_a/[\sigma^2_g + (\sigma^2_e/J)]$, where *J* is the number of blocks (repetitions); coefficient of genetic variation among families, $CV_g\% = 100(\sqrt{\sigma^2_g}/m)$ coefficient of environmental variation, $CV_e\% = 100(\sqrt{\sigma^2_e}/m)$, where *m* is the overall mean of the target trait, and relative variation coefficient ($CV_r = CV_g\%/CV_e\%$). Additive genetic correlations (r_g) between wood properties at different radial positions (PI, MI, and BA) were estimated as $r_g = COV_a(x,y)/\sqrt{\sigma^2_{a(x)}\sigma^2_{a(y)}}$, where $COVa(x,y)$ is the additive genetic covariance between trait *x* and *y*, and $\sigma^2_{a(x)}$ and $\sigma^2_{a(y)}$ are additive genetic variances for *x* and *y*, respectively. The statistical significance of r_g was assessed by the *t*-test with *n*-2 degrees of freedom, $t = r_a/\sqrt{(1-r_a^2)/(n-2)}$, where *n* is the number of families (Cruz and Regazzi 1997). To illustrate the breeding potential of the population for multiple traits, direct and indirect predicted genetic gains were estimated by selecting three of the 18 sampled families (16.7%) for each trait (Falconer and Mackay 1996). Note that these gains illustrate simultaneous improvement across traits; in practice, selection would target 18 of the 56 progeny-test families (32.1%). The expected direct genetic gain ($PG_g\%$) was $PG_g\% = 100[(ih_{m(x)}\,\sigma_{a(x)})/x_{p(x)}]$, where *i* is the standardized selection differential at a selection intensity of 16.7% ($i = 1.5$, Falconer and Mackay 1996); $h_{m(y)}$ is the standard deviation of family-mean heritability of trait *x*; $\sigma_{a(y)}$ is the square root of additive genetic variance for trait *x;* and $x_{p(x)}$ is the population mean for trait *x*. The indirect genetic gain ($IPG_g\%$) for trait *y* under selection for *x* was estimated by $IPG_g\% = 100[(ih_{m(x)}\, r_a\, \sigma_{a(y)})/x_{p(y)}]$, where r_a is the additive genetic correlation between traits *x* and *y;* $\sigma_{a(y)}$ is the square root of additive genetic variance for *y;* and $x_{p(y)}$ is the population mean for *y*.

RESULTS AND DISCUSSION

Deviation analysis detected significant differences between families only for ρ_{bas} at the mean and basal area (BA) positions (Table 1), indicating potential for selective breeding among families. All wood properties increased radially from pith-to-bark (PI to BA) positions (Table 1). Tukey's test confirmed significantly higher values for all wood properties at BA compared to PI, and ρ_{bas}, f_{c0}, MOE, and MOR were also significantly higher in the middle (MI) than PI position. This radial increase aligns with previous findings for ρ_{bas} and β_v in in 15-year-old *C. citriodora* (Lemos et al. 2012) and for ρ_{bas} and f_{c0} in 21-year-old *Eucalyptus camaldulensis* (Santos et al. 2010). Moreschi (2012) attributed this trend to differences in dry weight of heartwood (lower specific weight) versus green weight moisture content of sapwood (higher specific weight). Consequently, in heartwood, as the hardest and most rigid part of the trunk, ρbas, βv, fc0, and MOE ρ_{bas}, β_v, f_{c0}, and MOE tend to be lower (Moreschi 2012). Based on ABNT (2022) standards, the wood of the studied population has moderately high ρ_{bas}, f_{c0}, MOE, and MOR, indicating suitability for structural applications.

Genetic gains from selection for a given trait depend on the factors genetic variation, heritability, and selection intensity (Falconer and Mackay 1996). Genetic variation and heritability are trait-specific within a given population and environment, while selection intensity is breeder-determined (Falconer and Mackay 1996). Higher values of these factors enhance selection gains. The coefficient of genetic variation (CV_e%) was highest for MOR and lowest for β_v (Table 1), decreasing from PI to BA, indicating greater genetic variation in heartwood (PI) than sapwood (BA). The relative coefficient of variation CV_r for ρ_{bas} was moderate (0.46-0.5), according to Tung et al. (2010) (moderate: $0.25 < CV_r \leq 0.50$). The CV_r also showed minimal radial variation for wood properties (Table 1), suggesting that measurement position has little influence on selection success among families. Overall, the results indicate ρ_{bas} as the most suitable trait for direct selection, applicable across all radial positions.

In this study, heritability (h^2_m) was classified as low (≤ 0.15), moderate (>0.15 to ≤0.50), moderately high (>0.50 to ≤0.75), or high (>0.75). All traits exhibited moderate h^2_m, but with higher values of ρ_{bas} than of the other properties at the mean and radial positions (Table 1). Heritability varied little between radial positions, with ρ_{bas} under the strongest genetic control, confirming its suitability for direct selection among families.

Consistent with these findings in open-pollinated families, moderate h^2_m was reported for ρ_{bas} (0.37–0.43) in 9-year-old *E. nitens* (Hamilton et al. 2009); ρ_{bas} (0.41) and MOE (0.37) in 13-year-old *E. nitens* (Blackburn et al. 2011); MOE (0.33) in 11-year-old *E. pellita* (Kien and Bien 2024); and MOE (0.36–0.51) in 10-year-old *E. pellita* (Hung et al. 2015), while low to moderate h^2_m values across radial positions were reported for ρ_{bas} (0.1–0.36) and β_v (0.02–0.41) of 21-year-old

Table 1. Mean and genetic parameters for wood property traits in the pith (PI), middle (MI), bark (BA), and average of the radial positions of the trunk

Statistics	PI	MI	BA	Average
Mean				
Wood basic density (ρ_{bas}, g.cm^{-3})	0.658a	0.741b	0.785c*	0.728*
Volumetric shrinkage (β_v, %)	14.4a	14.9a	16.6b	15.3
Compression strength (f_{c0}, MPa)	49.3a	62.0b	67.2c	59.5
Modulus of elasticity (MOE, MPa)	11436a	14361b	18492c	14763
Modulus of rupture (MOR, MPa)	87.1a	113.6b	134.05c	111.6
Genetic variation coefficient (CV_g%)				
Wood basic density (ρ_{bas})	3.9	2.9	2.5	2.7
Volumetric shrinkage (β_v)	2.0	1.6	1.9	1.4
Compression strength (f_{c0})	4.8	3.8	3.3	3.0
Modulus of elasticity (MOE)	5.9	4.8	3.5	3.2
Modulus of rupture (MOR)	6.2	4.7	3.5	4.5
Relative variation coefficient (CV_r)				
Wood basic density (ρ_{bas})	0.5	0.46	0.48	0.49
Volumetric shrinkage (β_v)	0.30	0.30	0.32	0.31
Compression strength (f_{c0})	0.32	0.31	0.31	0.31
Modulus of elasticity (MOE)	0.31	0.32	0.31	0.32
Modulus of rupture (MOR)	0.31	0.33	0.32	0.33
Family-mean heritability (h^2_m)				
Wood basic density (ρ_{bas})	0.428	0.391	0.425	0.417
Volumetric shrinkage (β_v)	0.209	0.217	0.231	0.226
Compression strength (f_{c0})	0.235	0.233	0.228	0.225
Modulus of elasticity (MOE)	0.228	0.232	0.226	0.231
Modulus of rupture (MOR)	0.223	0.244	0.233	0.249

* P< 0.05, with 0.5 degrees of freedom for likelihood ratio test (LRT), χ^2 deviance chi-square; Different letters (a, b, and c) indicate significant differences (P< 0.05) by Tukey's test between the radial positions PI, MI, and BA.

Table 2. Additive genetic correlation (r_a) between the average radial positions (PI, MI, and BA) of wood properties

	β_v	f_{c0}	MOE	MOR
ρ_{bas}	0.39	0.62**	0.65**	0.59**
β_v		0.51*	0.53*	0.61**
f_{c0}			0.63**	0.74**
MOE				0.75**

** P< 0.01 and * P< 0.05 by the t-test with 16 degrees of freedom; ρ_{bas}: wood basic density; β_v: volumetric shrinkage; f_{c0}: compression strength; MOE: modulus of elasticity; MOR: modulus of rupture.

E. camaldulensis (Santos et al. 2008, Santos et al. 2010). In contrast, lower h^2_m values were reported for ρ_{bas} (0.03), f_{c0} (0.03), MOE (0.1), and MOR (0.04) in 9.5-year-old *E. cloeziana* (Li et al. 2017).

Knowing the additive genetic correlation (r_a) between traits is important for genetic improvement, for predicting indirect responses from direct selection. Estimated r_a values for mean radial positions ranged from moderate to high (0.51–0.75) and were statistically significant for most trait pairs: $\beta_v \times f_{c0}$ and $\beta_v \times$ MOE at 5% significance; and $\rho_{bas} \times f_{c0}$, $\rho_{bas} \times$ MOE, $\rho_{bas} \times$ MOR, $\beta_v \times$ MOR, $f_{c0} \times$ MOE, $f_{c0} \times$ MOR, and MOE × MOR at 1% (Table 2). This suggests potential for simultaneous breeding of most traits, where direct selection for one trait indirectly enhances correlated traits. Genetic correlations arise from either gene linkage or pleiotropy (Falconer and Mackay 1996): linkage implies that genes located close together on chromosomes control two or more traits and is considered a transient cause of r_a, as it tends to decrease as crossing-over occurs. Pleiotropy is considered the main cause of r_a between traits, as it is permanent due to shared gene control of different traits (Falconer and Mackay 1996). Moderate to high r_a values likely indicate pleiotropy as the primary source, while low values suggest linkage (Tolfo et al. 2005). This suggests the occurrence of pleiotropy as the determinant factor of r_a. Comparable moderate to high r_a correlations between wood traits have been reported in related species for $\rho_{bas} \times$ MOE (r_a= 0.82) in *C. citriodora* (Hung et al. 2016); $\rho_{bas} \times f_{c0}$ (r_a= 0.75), $f_{c0} \times$ MOR (r_a= 0.64), and MOE × MOR (r_a= 0.8) in *E. cloeziana* (Li et al. 2017); $\rho_{bas} \times f_{c0}$ (r_g= 0.98) in *E. grandis* (Santos et al. 2004); $\rho_{bas} \times$ MOE (r_g= 0.62) in *E. nitens* (Blackburn et al. 2010); and $\rho_{bas} \times$ MOR (r_g= 0.58) and MOE × MOR (r_g= 0.83) in *E. pellita* (Kien and Bien 2024).

Table 3. Direct genetic gains (PG_g %) and indirect genetic gains (IPG_g %) based on direct selection for the three best families (16.7%) for wood basic density (ρ_{bas})

Traits	PG_g %	IPG_g %
Wood basic density (ρ_{bas})	5.2	-
Compression strength (f_{c0})	4.3	3.6
Modulus of elasticity (MOE)	4.7	4.1
Modulus of rupture (MOR)	6.8	5.2

For genetic improvement of *C. citriodora* in construction and furniture applications, the establishment of commercial plantations with improved clones or seeds with high ρ_{bas}, f_{c0}, MOE, and MOR is essential for greater mechanical strength (Scanavaca Junior and Garcia 2004). Based on CV_r and h^2_m, ρ_{bas} emerges as the most efficient selection criterion and r_g results suggest that selecting families with higher ρ_{bas} will indirectly increase f_{c0}, MOE, and MOR. Thus, selection for increased ρ_{bas} can indirectly enhance most wood quality traits.

To illustrate the potential for multi-trait improvement of the population, indirect genetic gains for f_{c0}, MOE, and MOR by direct selection of three of the 18 families based on ρ_{bas} were estimated (Table 3). Direct genetic gain (PG_g%) for ρ_{bas} was 5.2%, while gains for f_{c0}, MOE, and MOR ranged from 4.3 to 6.8%. In contrast, the expected indirect genetic gains (IPG_g%) for f_{c0}, MOE, and MOR from selection on ρ_{bas} were somewhat lower (3.6 - 5.2%) compared to direct selection on these traits. These results highlight the potential for indirect improvement of f_{c0}, MOE, and MOR traits through ρ_{bas} selection. Note that this example does not reflect the selection intensity that would be adopted in practice, which could involve, for instance, that a larger proportion (e.g., 32.1% or 18 of the 56 families) could be selected in progeny tests.

CONCLUSIONS

All wood properties increased radially from the pith (PI) toward the basal area (BA) of the trunk. The genetic variation among families for average ρ_{bas} at radial and BA positions indicates potential for genetic improvement by selection among families. Moderate heritability values for all traits, particularly the highest values observed for ρ_{bas}, indicated that the population can be improved by family selection. Moderate to high positive genetic correlations between trait pairs ($\rho_{bas} \times f_{c0}$, $\rho_{bas} \times$ MOE, $\rho_{bas} \times$ MOR, $\beta_v \times f_{c0}$, $\beta_v \times$ MOE, $\beta_v \times$ MOR, $f_{c0} \times$ MOE, $f_{c0} \times$ MOR, and MOE×MOR) demonstrated the feasibility of achieving indirect genetic gains via direct selection on either trait within these pairs. Therefore, the population can be genetically improved simultaneously for multiple wood property traits, using ρ_{bas} as an effective direct selection criterion to generate indirect gains in f_{c0}, MOE, and MOR.

ACKNOWLEDGMENTS

The authors thank the National Council for Scientific and Technological Development (CNPq) for granting a Research Productivity Scholarship to E.L.L. (Process 312145/2021-7), A.M.S. (Process 304650/2020-0), and M.L.M.F. (Process 313459/2021-5).

DATA AVAILABILITY

The datasets generated and/or analyzed in this study are available from the corresponding author upon reasonable request.

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