Genetic parameters and correlations in growth and wood density traits of *Balfourodendron riedelianum* based on provenance and progeny testing

Eduardo L. Longui1*, Israel L. de Lima[1], Letícia Paneque[1], José A. R. Machado[1], Miguel L.M. Freitas[1,2] and Alexandre M. Sebbenn[1,2]

[1] Instituto Florestal de São Paulo, CP 1322, São Paulo, State of São Paulo, 01059-970, Brazil.
[2] UNESP Faculty of Engineering of Ilha Solteira, Ilha Solteira Campus, State of São Paulo, 15385-000, Brazil.

*Corresponding author: Dr. Alexandre Magno Sebbenn, E-mail: alexandresebbenn@yahoo.com.br

Abstract

Balfourodendron riedelianum is an important timber species of South America used in civil construction and carpentry. Knowing the genetic variation, heritability and correlation between traits is an essential prerequisite for guiding selection of the best genotypes in tree improvement. In this study, growth (diameter and height) and wood density (mean, pith, middle and bark position) traits were investigated in 30-year-old trees planted in a *B. riedelianum* provenance and progeny test established in two sites, Luiz Antônio (LA) and Pederneiras (PE), in São Paulo State (Brazil). ANOVA results showed significant differences between sites for all traits, among provenances and families for wood density traits in the LA site and among families for growth traits in PE. Provenance x site and family x site interactions were significant for almost traits, and genetic correlation between sites was low for all traits (0.17–0.20). Genetic variation (CV_g) was higher (4.0–5.4 %) and mean family heritability (h^2_m) was lower for growth (0.12–0.20) compared to wood density (CV_g: 2.3–3.8 %, h^2_m: 0.31–0.59) traits. Genetic correlation was significantly positive and ranged from moderate to high between growth traits (0.47–0.68) and between wood density traits (0.42–0.83) and non-significant between growth and wood density (-0.22–0.30) traits. An analysis of different radial positions showed that heritability tended to increase from pith to the bark position. Our results show a lower environmental effect on wood density traits, allowing the possibility of selecting superior provenances and families with high wood quality in breeding programs in both sites.

Keywords: : *commercial wood, genotype by environment interaction, heritability, tree species, wood properties*

Introduction

The most important physical property of wood is its basic density and is directly associated with its quality and industrial use, such as quality and production of charcoal and cellulose, physical mechanical resistance of paper (Albino and Tomazello Filho, 1985). Because of this, and due it is an easily measured traits, the wood density has been used in the forestry industry as a variable indicating wood quality (Albino and Tomazello Filho, 1985; Bouffier et al., 2009).

Wood density is recognized as a heritable trait (Montes et al., 2006; Kien et al., 2010; Hong et al., 2014; Fukatsu et al., 2015; Masendra et al., 2023; Poupon et al., 2023) and may presents genetic variation between provenances (Moura et al., 1991; Nabais et al., 2018; Zhang et al., 2022), families (Montes et al., 2006; Tung et al. 2011; Riva al., 2020) and clones (Pliura et al., 2005, 2007; Kien et al., 2010) which can be exploited by selection in tree improvement programs. Studies have also generally observed low or non-significant genotype by environmental interaction (GxE) for wood density (Li and Wu, 2005; Kien et al., 2010; Hung et al., 2015; Soro et al., 2022; Poupon et al., 2023; but look Montes et al., 2006 for contrasting results) which indicates that selection can be carried out in one site and genetic improved genotypes can be used for commercial

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reforestation in different sites. Due to that, wood density has been the focus of genetic improvement programs for several tree species around the world to increase wood productivity and quality (Montes et al., 2006; Santos et al., 2010; Hung et al., 2015; Soro et al., 2022; Poupon et al., 2023).

Some studies have been found that growth traits have low or absence of genetic correlation with wood density traits (Gerendiain et al., 2009; Kien et al., 2010; Tung et al., 2011; Fukatsu et al., 2015), indicating that selection in growth traits will not have adverse effects on wood density. In contrast, some studies have been reported significant negative correlation between growth and wood density traits (Li and Wu, 2005; Pliura et al., 2005; Bouffier et al., 2009; Hong et al., 2014), where others have found significant positive correlation between growth and wood and density traits (Williams and Megraw, 1994; Tung et al., 2011; Hung et al., 2015). Due to these contrasting results, it is important to investigate the correlation between growth and wood density traits in breeding programs.

Provenance tests allow us to determine which source populations of seeds or clones are most suitable for specific environments or economic purposes (Schaberg et al., 2022). Progeny trials are established using collected seed from many trees which displays the traits of interest and then planted in one or across a number of sites in order to evaluate the performance of each seed-tree through assessing its progeny (or family). These two genetic trials can also be combined into a single trial, called provenance and progeny test, which allows us to test both differences among seed sources (provenances) and the individual performance of seed-trees of seed origin (Wright, 1976). Furthermore, provenance and progeny tests, when planted simultaneously in more than one experimental site, allow evaluating the provenance x site and family x site interactions (GxE). The GxE interaction is one of the most important types of information in genetic improvement (Schaberg et al., 2022). GxE interaction occurs when the performance of a given genotype is dependent on the environment conditions of the site where it is evaluated, which may imply in a change in ranking performance between genotypes in different environments (Huang et al., 2020). The ex-situ conservation of populations using provenance and progeny tests allows saving the genetic variability of threatened or commercial species, the estimation of genetic parameters (coefficients of genetic variation and heritabilities) and monitoring genetic variation for quantitative and qualitative traits during tree growth (Sebbenn et al., 2007; Aguiar et al., 2019).

Balfourodendron riedelianum (Engler) Engler wood (Rutaceae) is an economically valuable timber species of South America with geographic distribution in midwestern, southeastern and southern Brazil, as well as the Cerrado and Atlantic Forest (Carvalho, 2003). The species also occurs in Argentina and Paraguay (Farias et al., 1995). It mainly inhabits the Submontane Semideciduous Seasonal Forest, Deciduous Seasonal Forest and the Mixed Ombrophilous Forest. It is classified as late secondary with a monopodial growth habit in the young phase, even in full sun, with a well-defined stem (Carvalho, 2003). Although its wood has high commercial value, the species remains at risk of extinction (SNIF, 2024). In adulthood, *B. riedelianum* can reach a height that ranges from 20–35 m, 40–100 cm in diameter at breast height (DBH), with a bole up to 15 m, presenting a straight and cylindrical trunk. Its wood is light with a smooth, moderately glossy surface. It is finely textured with generally regular grain and moderately heavy with wood density varying from 0.8–0.9 g.cm^{-3} (Carvalho, 2003). Its wood is used in civil construction and carpentry to make fine furniture, as well as frames, decorative laminates, shoe lasts, tacos, model airplane propellers, and paneling (Carvalho, 2003). Furthermore, the tree is used for ornamental purposes and in the reforestation of degraded areas (Durigan et al., 2002). It, however, presents low resistance to rotting and attack by xylophagous organisms (Lima et al., 2011).

Although *B. riedelianum* wood has economic value for the forestry sector and wood density is an indicator of wood quality, there are no studies for the trait on genotype by environment interaction, genetic control and correlations with growth traits of the species. Here we demonstrate that genetic selection can be explored through wood density traits of *B. riedelianum*. Thus, in addition to DBH, which is more commonly used in genetic selection, this gives forestry management an additional tool by the use of wood density, which is a predictor of mechanical properties, to select the best progenies to improve plantations of the species and, hence, reduce the impact on native forests. Based on that premise, this study aimed to estimate genetic parameters for both growth traits and mean and radial variation in wood density, as measured in the pith, middle and near the bark of 30-year-old trees planted in a *B. riedelianum* provenance and progeny tests established in two sites to evaluate the effects of genetic variability against the influence of the local environment. We also estimated genetic correlations between growth and wood density traits, as well as genetic correlations among the three radial positions of the trunk.

Material and methods

Sites and experimental design

This study carried out provenance and progeny tests on 30-year-old *B. riedelianum* established in Luiz Antônio (LA; 21°40' S, 47°49' W, elevation 550 m) and Pederneiras (PE; 22°21' S, 48°46' W, elevation 500 m), São Paulo State, Brazil. Both sites have a dry season from May to September (rainfall ≤ 50 mm) and a hot and rainy season from November to March (Table 1). Mean annual precipitation, annual temperature, summer temperature, winter temperature, and soil type are also shown in Table 1. The trial was established using 57 open-pollinated families (19 families per population) collected in three natural populations of *B. riedelianum*, including Alvorada do Sul (AS) located in a semi-deciduous seasonal forest (22º46' S, 51º13' W) in the State of Paraná, Bauru (BA) located in an ecotone between semideciduous seasonal forest and Cerrado (22°18' S, 49°03' W) in the State of São Paulo and Gália (GA) located in a semi-deciduous seasonal forest (22º17' S and 49º33' W) in the State of São Paulo. Trees for provenance and progeny tests were planted in LA and PE in 1985, using the compact family

Table 1
Provenance and progeny test experimental sites and provenance characteristics. *Sebbenn et al. (2007); **Kubota et al. (2015).

Characteristics	Experimental site		Provenances		
	Luiz Antônio	Pederneiras	Alvorada do Sul	Gália	Bauru
State	São Paulo	São Paulo	Paraná	São Paulo	São Paulo
Latitude	21°40′ S	22°21′ S	22º46′ S	22º17′ S	22°18′ S
Longitude	47°49′ W	48°46′ W	51º13′ W	49º33′ W	49°03′ W
Altitude	550 m	500 m	373 m	561 m	526 m
Climate	Tropical, high altitude (Cwa)	Tropical with dry season (Aw)	Subtropical humid (Cfa)	Subtropical humid (Cfa)	Tropical, high altitude (Cwa)
Mean temperature					
Annual °C	23.5	27.0	19.5	21.0	22.6
Maximum annual °C	31.4	34.3	30.0	30.0	29.1
Minimum annual °C	11.9	14.0	14.0	14.0	16
Mean annual precipitation (mm)	1356	1361	1590	1325	1331
Type of soil features	Dark latosol with clay texture*	Sandy yellow latosol**	Cambisol latosol	Red-yellow latosol	Sandy yellow latosol

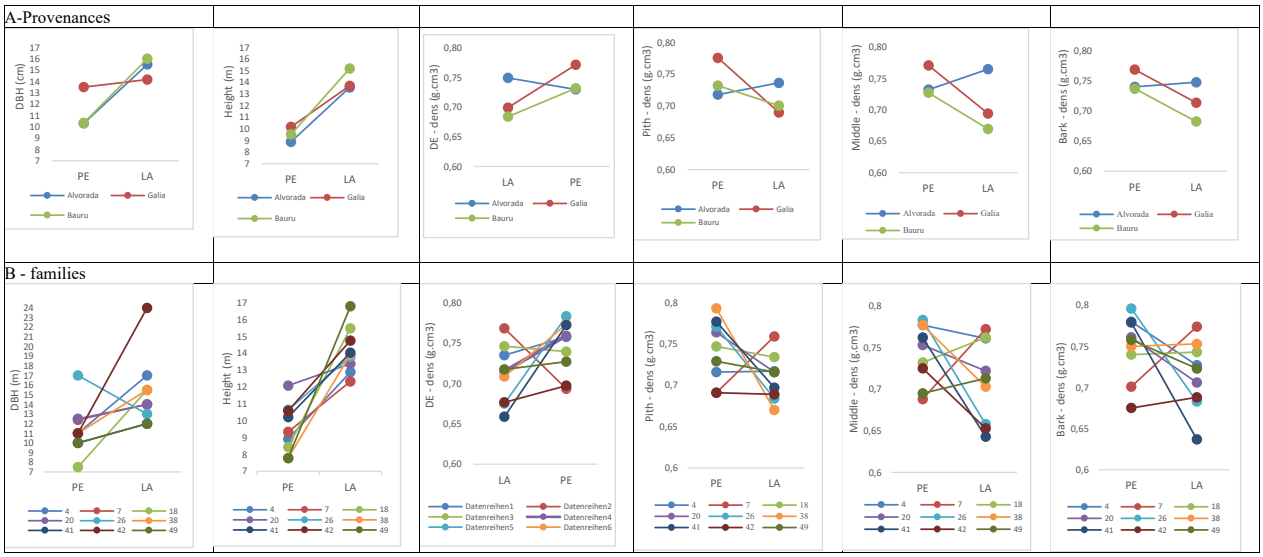

Figure 1
Mean growth (DBH, H) and wood density (DE, pith, middle, and bark) traits for provenances and families of *Balfourodendron riedelianum* in Pederneiras (PE) and Luiz Antônio (LA) sites.

block design (Wright, 1978), completely randomized within the blocks (six blocks per site). Provenances were established within plots (three plots per block), and families within provenances were allocated within subplots (19 subplots per provenance per block). To establish the trials, linear subplots of five plants each were used at a spacing of 3 x 3 m and a border outside the experiment with two rows, aiming to reduce environmental effects on the treatments.

Sampling

We measured two growth traits: DBH and tree height (H). We collected samples from the trunk at DBH of 36 trees at each site, 12 trees from each provenance and from three families randomly selected within each provenance so that the same nine families were sampled in both sites. In each family, samples were collected from four trees, one individual per subplot (four blocks). From each tree sampled, we cut a DBH disc 10 cm in thickness, and from these discs, we cut three specimens in radial positions to measure wood density traits, i.e., the part nearest trunk center, designated as pith (PI), a middle position (MI), a position close to the bark, designated as bark (BA), and mean wood density (DE). Then, we determined the wood density in 108 samples per site, totaling 216 samples for both sites. Wood basic density was determined by the method of maximum moisture content (ABNT, 2003). Samples of 2 x 2 x 3 cm were saturated in a vacuum system for 72 h to obtain the saturated volume of wood. In sequence, samples were dried in a laboratory kiln to determine the oven-dried mass at 103 ± 2 °C.

Data analyses

To determine significant differences in traits among and between sites, provenances, families and genotype in the context of environment interaction, SAS software was used (SAS, 1999). The Tukey test was used to determine differences in traits between sites and provenances, also using SAS software (SAS, 1999). Estimates of variance components and genetic parameters for each site and joint sites were obtained using the restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) method and SELEGEN-REML/BLUP software (Resende, 2016). Variance components and genetic parameters were estimated by grouping families from each of three provenances since only three families from each provenance were evaluated. Ignoring the effect of provenance, individual analysis at site level was calculated as:

$$y = Xr + Za + e, \quad (1)$$

where *y* is the data vector, *r* is the vector of blocks (fixed effect) added to the general mean, a is the vector of family (random) additive genetic effects, and e is the vector of (random) errors or residuals. Uppercase letters represent the incidence matrices for the aforementioned effects. Again, ignoring the effect of provenance, individual analysis at joint site level was calculated as:

$$y = Xr + Za + Ti + e, \quad (2)$$

where *y* is the data vector, *r* is the vector of block effects (fixed) added to the overall mean, *a* is the vector of individual additive genetic effects (random), *e* is the vector of the random effects of genotype by environment (GxE) interaction, and *e* is the random effect of error or residual vector. Uppercase letters represent incidence matrices for the aforementioned effects. The following variance components were estimated: σ_f^2 = genetic variance among families; σ_e^2 = variance owing to family and replication interaction effects; $\sigma_{e(l)}^2$ = variance owing to interaction between families and replications within sites; σ_{ge}^2 = variance interaction between families and sites (GxE). Mean heritability among families (h_f^2) was estimated for each site and joint sites, respectively, as:

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_e^2}{b}} \quad (3)$$

$$\text{and } h_{f(l)}^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_{ge}^2}{l} + \frac{\sigma_e^2}{bl}}, \quad (4)$$

where *l* and *b* are the number of sites and blocks, respectively. We also calculated the coefficients of genetic variation among families as:

$$(CV_g(\%) = 100(\sqrt{\sigma_f^2}/x) \quad (5)$$

where *x* is the mean of the trait under study, and the relative correlation coefficient (Vencovsky and Barriga, 1992) was calculated as:

$$CV_r = CV_g(\%)/CV_e(\%), \quad (6)$$

where $CV_e(\%)$ is the coefficient of environmental variation,

$$CV_e(\%) = 100(\sqrt{\sigma_e^2}/x). \quad (7)$$

Genetic correlations between sites (r_{gloc}) and genetic correlations between pairs of traits (r_g) were calculated, respectively, as:

$$r_{gloc} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{ge}^2}, \quad (8)$$

$$\text{and } r_g = \frac{Cov_{f(x,y)}}{\sqrt{\sigma_{fx}^2 \sigma_{fy}^2}}, \quad (9)$$

respectively, where $Cov_{f(x,y)}$ is the genetic covariance between trait x and y, respectively.

Table 2
Mean values and Pvalues of ANOVA F test for three 30-year-old *Balfourodendron riedelianum* provenances for growth (DBH, H) and wood density measured at mean trunk (DE), pith (PI), middle (MI), and close to bark (BA) of trees in Luiz Antônio, Pederneiras, and joint sites. *P< 0.05 and **P< 0.01; r_{gloc} is the genetic correlation between sites; Numbers followed by different uppercase letters indicate significant difference between sites for the mean traits, and numbers followed by lowercase letters indicate significant difference among provenances for the Tukey test at the 5 % probability level.

Site/provenance	DBH (cm)	H (m)	DE (g.cm^{-3})	PI (g.cm^{-3})	MI (g.cm^{-3})	BA (g.cm^{-3})
Luiz Antônio						
Alvorada do Sul	14.21a	13.56a	0.75a	0.74a	0.76a	0.75a
Gália	13.04a	13.70a	0.70b	0.69b	0.69b	0.71b
Bauru	15.58a	15.18a	0.68b	0.70b	0.67b	0.68b
Mean provenances	14.28A	14.15A	0.71**A	0.71**A	0.71**A	0.72**A
Provenance: Pvalue	0.18	0.37	<0.01	<0.01	<0.01	<0.01
Family: Pvalue	0.23	0.63	0.01	0.02	0.01	0.02
Pederneiras						
Alvorada do Sul	10.58a	8.89a	0.73a	0.72a	0.73a	0.74a
Gália	12.50a	10.17a	0.77a	0.78a	0.77a	0.77a
Bauru	12.08a	9.52a	0.73a	0.73a	0.73a	0.74a
Mean provenances	11.72B	9.53B	0.74B	0.74B	0.74B	0.75B
Provenance: Pvalue	0.08	0.25	0.05	0.14	0.19	0.29
Family: Pvalue	<0.01	0.03	0.07	0.62	0.33	0.06
Joint sites						
Alvorada do Sul	12.40a	11.20a	0.74a	0.73a	0.75a	0.74a
Gália	12.80a	11.90a	0.74a	0.73a	0.73a	0.74a
Bauru	13.83a	12.30a	0.71b	0.72a	0.70b	0.71b
Mean provenances	13.00	11.80	0.73**	0.73	0.73**	0.73*
Sites: Pvalue	<0.01	<0.01	<0.01	0.04	<0.01	<0.01
Provenance: Pvalue	0.23	0.40	0.01	0.68	<0.01	0.03
Prov. x sites: Pvalue	0.14	0.45	<0.01	0.03	<0.01	0.04
Family: Pvalue	0.23	0.66	0.05	0.09	0.01	0.02
Family x sites: Pvalue	0.01	0.05	<0.01	<0.01	0.03	<0.01
r_{gloc}	0.18	0.20	0.17	0.20	0.17	0.17

Results

Genetic variation

The joint analysis of variance detected significant differences between sites for all traits (P-value ranging from <0.01–0.04; Table 2). The Tukey test showed that mean growth in DBH and tree height was significantly greater in Luiz Antônio (DBH= 14.28 cm, H= 14.15 m) than in Pederneiras (DBH= 11.72 cm, H= 9.53 m), whereas the exact opposite was detected for the wood density traits at Luiz Antônio (ranging from 0.71–0.72 g.cm^{-3}) and Pederneiras (ranging from 0.74–0.75 g.cm^{-3}). The growth in DBH and H was 17.9 and 32.7 %, respectively, higher in Luiz Antônio compared to Pederneiras, whereas wood density traits were 4.4 to 4.6 % higher in Pederneiras compared to Luiz Antônio. Joint site analysis also showed that mean (DE), middle (MI) and bark (BA) traits were statistically different among the provenances. The Tukey test showed that DE, MI and BA traits were statistically significantly higher (4.3–6.8 %) for Alvorada do Sul (0.74–0.75 g.cm^{-3}) compared to Bauru (0.70–0.71 g.cm^{-3}).

Within sites, significant differences were detected in Luiz Antônio among provenances and among families for all wood density traits. The Tukey test shows that mean DE, PI, MI, and BA traits were significantly higher (4.5–9.3 %) for Alvorada do Sul (0.74–0.76 g.cm^{-3}) compared to Gália (0.69–0.71 g.cm^{-3}), as well as significantly higher (5.0–12.4 %) for Alvorada do Sul (5.0–12.4 %) compared to Bauru (0.67–0.70 g.cm^{-3}). In Pederneiras, significant differences were detected among families for mean DBH and H.

Genetic parameters

The coefficient of experimental variation (CV_e) was higher for growth traits (ranging from 20.0–29.4 %) than for wood density traits (5.2–9.4 %) in both sites and joint analysis (Table 3). The coefficient of genetic variation (CV_g) was also higher for growth traits (4.0–5.4 %) than for wood density traits (2.3–3.8 %), especially in Pederneiras (Table 3). In contrast, the coefficient of relative variation (CV_r) was lower for growth traits (0.18–0.25) than for wood density traits (0.30–0.62) in both sites and in joint site analysis, indicating a high possibility for genetic breeding by selection among families () for wood density traits, especially in Luiz Antônio where the highest values were observed. Mean heritability among families (h_m^2) was also lower for DBH and H traits (0.12–0.20) compared to wood density traits (0.31–0.59) in both sites and in joint site analysis, indicating that wood density traits were more affected by genetic effects than growth traits. Mean h_m^2 was higher for growth

traits in Pederneiras than in Luiz Antônio where the opposite was observed for wood density traits. The results also showed a tendency for h_m^2 to increase from PI (0.31–0.42) to BA (0.43–0.59).

Genetic correlation between traits

Genetic correlation (r_g) was significantly higher than zero and ranged from moderate to high between DBH and H growth traits (0.47–0.68) and among wood density traits (0.42–0.83) (Table 4). In contrast, r_g was low and not statistically different than zero between growth (DBH and H) and wood density (-0.22–0.30) traits.

Discussion

Genetic variation

This study investigated genetic variation and heritability of growth and basic wood density traits in a 30-year-old *B. riedelianum* provenance and progeny test established at two sites, as well as the genetic correlation between traits. Our results showed significant differences between sites for all traits, where the highest growth for DBH (17.9 %) and H (32.7 %) were observed in Luiz Antônio and substantially high values for all wood density traits were observed in Pederneiras (4.4–4.6 %). Higher growth in DBH and H in Luiz Antônio than in Pederneiras has also been observed at 4 to 11 years of age in a previous analysis of our *B. riedelianum* provenance and progeny test (Siqueira et al., 2000), as well as in another *B. riedelianum* provenance and progeny test (Sebbenn et al., 1999) and in a *Cariniana legalis* provenance and progeny test (Sebbenn et al., 2002). Based on our results and those of others, it can be concluded that the environmental characteristics of Luiz Antônio favor tree growth and result in lower wood density. Sites where trees grow the most are the same places that have the lowest wood density (Land et al., 1983; Albino and Tomazello Filho, 1985). For example, *Eucalyptus citriodora*, *E. cloeziana*, *E. grandis*, *E. pilularis*, *E. saligna*, and *E. urophylla* all showed lower growth in plantations where wood density was high (Albino and Tomazello Filho, 1985).

ANOVA joint site analysis showed genetic differences among provenances, families, provenance x site interaction for most wood density traits, and family x site interaction for all traits. ANOVA individual site analysis found genetic variation among provenances and families within Luiz Antônio for wood density traits and among families within Pederneiras for DBH and H traits. These genetic variation for most traits can be exploited by selection among and within provenance (families) in breeding programs. However, we found that phenotypic variation for wood density traits mostly occurred in provenance x site and family x site interaction (GxE) with otherwise low genetic correlation between sites (r_{gloc}) for all traits, showing that GxE interaction is complex in the context of different genotypic performance rankings between sites for traits. This implies that selection for traits must be carried out from individuals within sites. Another study carried out in Luiz Antônio and Pederneiras based on different provenances and progenies of *B. riedelianum* from those studied here, also found significant differences among provenances, families and GxE interaction for DBH and H traits in trees with ages ranging from four to 11 years (Sebbenn et al., 1999). Genetic variation for wood density among provenances has also been reported among other tree species, such us *Pinus oocarpa*, *P. caribaea* var. *bahamensis*, and *P. caribaea* var. *hondurensis* (Moura et al., 1991) and among provenances and families for *Calycophyllum spruceanum* (Montes et al., 2006). In contrast, non-significant, or low GxE interaction, has typically been reported for wood density traits (Li and Wu, 2005; Hung et al., 2015; Soro et al., 2022; Poupon et al., 2023).

Genetic parameter

The coefficient of genetic variation (CV_g) was higher for growth traits than for wood density traits in both sites and in the joint analysis. In contrast, Riva et al. (2020) reported in *Myracrodruon urundeuva* progeny tests at 31-year-old lower CV_g values for DBH (3.9–4.4 %) and H (1.5–1.6 %) compared to wood density (8.3–8.9 %). The coefficient of relative variation (CV_r) was lower for growth than for wood density traits, indicating a higher possibility of genetic breeding by selection among families for wood density traits, especially in Luiz Antônio where the highest values were observed. Heritability among families (h_m^2) was average ($0.1 \leq h_m^2 \leq 0.3$) and lower for growth than for wood density traits ($h_m^2 \geq 0.3$) in both sites and in joint site analysis. However, mean h_m^2 was highest for growth traits in Pederneiras than in Luiz Antônio, whereas in Luiz Antônio, values were highest for wood density traits than in Pederneiras. These results indicate that wood density traits were mostly determined by mean genotypic effects of the families, whereas growth traits were mainly determined by environmental effects of the sites. These results were corroborated in a study reporting on *C. spruceanum* h_m^2, showing that wood density (0.48–0.60) was higher than DBH (0.27–0.31) and H (0.10–0.37) (Montes et al., 2006). However, some studies in the literature reported contradictory results for heritability of wood density traits, sometimes showing low and sometimes high heritability values. For example, the heritability in *Acacia mangium* for DBH and H traits has been reported to range from 0.0–0.44 and for wood density to range from 0.17–0.48 (Masendra et al., 2023). Additionally, in *Eucalyptus pellita* for DBH, the range was from 0.14–0.33 and for wood density ranged from 0.23–0.25, respectively (Hung et al., 2015), in *Larix decidua* for DBH and H ranged from 0.24–0.35 and for wood density ranged from 0.24–0.30, respectively (Poupon et al., 2023), and in *Larix kaempferi* from 0.22–0.55 for DBH and H and 0.57 for wood density (Fukatsu et al., 2015). In an *M. urundeuva* progeny test for DBH and H, h_m^2 values of 0.04 and 0.33, respectively, were found and a value of 0.81 for wood density (Riva et al., 2020), while in *Pinus sylvestris*, DBH and H values ranged from 0.24–0.27 and from 0.40–0.48 for wood density (Hong et al., 2014).

In the analyses of different radial positions, it is also noted that CV_g values oscillate from the PI to BA. For instance, in a 21-year-old *Eucalyptus camaldulensis* progeny test for wood density, CV_g values in PI, MI and BA were within the observed

Table 3
Genetic parameters for open-pollinated families of 30-year-old *Balfourodendron riedelianum* for growth traits (DBH, H) and wood density measured at mean trunk (DE), pith (PI), middle (MI), and close to bark (BA) in Luiz Antônio (LA), Pederneiras (PE), and joint sites.

Parameter	DBH	H	DE	PI	MI	BA
Genetic variation coefficient: CV_g (%)						
LA	4.9	4.6	3.0	3.5	3.2	3.5
PE	5.4	5.2	2.5	3.0	3.0	3.2
Joint	5.3	4.0	2.7	2.3	2.5	3.8
CV_r = CV_g (%) / CV_e (%)						
LA	0.19	0.19	0.58	0.42	0.46	0.55
PE	0.25	0.24	0.39	0.37	0.32	0.47
Joint	0.18	0.20	0.52	0.30	0.41	0.62
Mean heritability among family: h_m^2						
LA	0.16	0.13	0.56	0.42	0.46	0.55
PE	0.20	0.19	0.38	0.36	0.40	0.43
Joint	0.19	0.12	0.50	0.31	0.42	0.59

Table 4
Genetic (r_g) correlation among DBH, height (H), mean (DE), pith (PI), middle (MI), and close to the bark (BA) wood density in open-pollinated families of *Balfourodendron riedelianum*. **P< 0.01 according to t-test with 2 degrees of freedom.

	H	DE	PI	MI	BA
Luiz Antônio					
DBH	0.68**	0.18	0.17	0.14	0.16
H		-0.19	-0.22	-0.22	-0.19
PI				0.78**	0.49**
MI					0.83**
Pederneiras					
DBH	0.57**	-0.26	-0.10	0.22	-0.05
H		0.10	0.03	-0.22	0.02
PI				0.67**	0.68**
MI					0.65**
Joint					
DBH	0.47**	0.12	0.01	0.30	-0.02
H		-0.11	-0.08	-0.04	-0.13
PI				0.48**	0.42**
MI					0.49**

pattern herein reported, ranging from 1.0–4.1 % (Santos et al., 2010), whereas in a 20-year-old *M. urundeuva* progeny test, CV_g values were higher than those we observed, ranging from 5.7–7.5 % (Tung et al., 2010). Our studies also showed that h^2_m tended to increase from PI to BA. However, the opposite was observed in a *E. camaldulensis* progeny test (Santos et al., 2010) in which h^2_m decreased from 0.64 and PI and MI decreased to 0.11 in BA, while in a *M. urundeuva* progeny test, h^2_m increased from 0.11 in PI to 0.36 in MI, but decreased to 0.11 in BA (Tung et al., 2010).

Genetic correlation between traits

Genetic correlation (r_g) was positive and ranged from moderate ($0.4 \geq r_g \leq 0.6$) to high ($r_g \geq 0.6$) between DBH and H growth traits and between pairwise wood density traits (PI and MI, PI and BA, and MI and BA) in both sites, and for joint site analysis. These results indicate that DBH and H, as well as wood density traits, are controlled by the same genes (pleiotropic genes) or are jointly inherited (genetic linkage), which is favorable to indirect selection between traits for tree improvement (Vencovsky and Barriga, 1992). In contrast, r_g was low and not statistically different than zero between growth and wood density traits, suggesting that growth and wood density traits are independently genetic controlled. These results indicate the possibility of simultaneous selection between DBH and H growth traits, as well as between wood density traits, and that growth and wood density traits can be independently selected. For growth traits, DBH is easier to measure and is therefore the most suitable variable for selection, where among wood density traits, BA is apparently the most suitable variable for selection due to the fact that it generally presented the greater r_g with the other two wood density traits. Furthermore, DBH and wood density for BA also presented the highest values of CV_g, CV_r, and h^2_m. Selection of families with higher DBH will result in greater H growth (genetic gain), while selection of families with higher mean wood density for BA will result in indirect genetic gains in wood density for PI and MI.

In tree species, the r_g between growth traits and wood density has been shown to be complex (Fukatsu et al., 2015), while for some species a positive and high genetic association has been reported, in other species a low or negative association has been observed. For example, moderated to high and positive r_g between DBH and H and between wood density traits (0.59–0.96), but low negative correlation between growth and wood density traits (-0.55–0.0) were reported for 19-year-old *Picea abies* var. *pendula* clones (Gerendiain et al., 2009), as well as for 40-year-old *P. sylvestris* open-pollinated progenies (DBH and H= 0.82; wood density traits: 0.76–0.93; DBH and H traits and wood density traits of -0.52 and -0.18, respectively) (Hong et al., 2014). Lowe r_g value between DBH and wood density (0.22) was also observed for *M. urundeuva* open-pollinated progenies (Tung et al., 2011). In contrast, high r_g between DBH and H growth traits (0.90), between wood density traits (0.98), and between growth and wood density (0.76–0.91) traits were reported for *L. kaempferi* (Fukatsu et al., 2015). This shows the importance of knowing the r_g between traits to determine the most appropriate selection strategy (direct or indirect selection) in tree improvement programs.

Conclusions

Significant differences were observed between sites for all traits, among and within provenances for wood density traits in Luiz Antônio and among families for growth traits in Pederneiras, as well as significant interactions among provenances and sites and families and sites for most traits and low genetic correlation between sites. Genetic variation was higher and mean heritability among families was lower for growth than wood density traits. Genetic correlation showed a positive correlation that ranged from moderately to high between growth traits and wood density traits, and low and non-significant between growth and wood density traits. Analyzing the different radial positions, heritability tended to increase from PI to BA. Wood density traits showed greatest genetic control and the possibility of obtaining genetic gains through the selection of superior provenances and families in genetic improvement programs. However, the GxE interaction was complex for all traits, implying that selection must be carried out individually within each sites.

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