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Influence of clone-site interaction on basic wood density of *Eucalyptus* clones in brazilian tropical zones

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TECHNOLOGY OF FOREST PRODUCTS

ABSTRACT

Background: Contrasting edaphoclimatic differences will influence the development of *Eucalyptus* forests, resulting in varying responses according to the clone. This study aimed to evaluate the impact of clone x site interaction on the wood density (WD) of *Eucalyptus* planted in tropical environments in Brazil. *Eucalyptus* clones (R9: *E. urophylla*, B2: *E. urophylla* x *E. grandis*, H8, and D4: *E. grandis* x *E. urophylla*) were analyzed 4 years after planting at 10 sites. A total of 120 trees were sampled, and the WD was determined. The relationship between WD, mean annual increment, and climate variables (temperature, precipitation, vapor pressure deficit and soil water deficit) was assessed for each clone.

Results: The site effect and clone x site interaction were significant. Clones H8 and R9 showed the most consistent WD across sites, with density differences of 18 % and 14 %, respectively, and H8 exhibited a similar mean in 80 % of the sites. B2 and D4 were the most influenced by local growth with density variations of 28 and 22 %, respectively, indicating that WD is affected by the interaction of genotype and growth environment. Only B2 showed significant correlations between density and all environmental variables, while density in R9 did not correlate with any variable.

Conclusion: Clones are similarly affected by climate across the tropical gradient of Brazil. However, the magnitude of responses differs among clones at a single site. The effects of climate conditions on density are more evident when contrasting situations are compared.

Keywords: tropical forestry, climate conditions, phenotypic plasticity, wood quality.

HIGHLIGHTS

Wood density is altered by clone x site interaction.
Genetic factors may be predominant, keeping density values constant.
Differences in wood density are more evident in extreme situations of soil water deficit.
The combined assessment of wood density, mean annual increment, and biomass improves the selection process.
Combined assessment of density, MAI, and biomass improves selection

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INTRODUCTION

Identifying suitable genotypes for specific environmental conditions is a key challenge for the expansion of *Eucalyptus* forests in Brazil (Binkley et al., 2020). In 2024, 10.52 million hectares were planted, reflecting an increase of 2.8% compared to 2023 (IBÁ, 2025). While increasing wood volumetric production has been a primary focus of breeding programs, wood quality is equally important for ensuring suitability for various end uses (Vidaurre et al., 2020). Wood formation is a dynamic and continuous process (Zhang et al., 2014), influenced by genetic factors, climate, and management practices (Costa et al., 2020; Elissetche et al., 2024).

Cultivating species in environments for which they have not been genetically improved can significantly affect tree growth and xylem cell development (Zhang et al., 2014). Therefore, understanding the variation in wood properties of different *Eucalyptus* clones across diverse environments is critical in preliminary trials (Elissetche et al., 2024; dos Santos et al., 2024), based on these responses, managers can consider incorporating these characteristics into the selection process.

Wood density is considered one of the key properties for predicting wood quality, as it is closely related to industrial processes and yields (Boakye et al., 2023). It can vary between species and within the same species, influencing the selection of materials - pure species, clones, and hybrids - as well as the implementation of clonal tests, forest management strategies, industrial process adjustments, and improvements in wood classification (Boschetti et al., 2020).

Climatic variables can serve as useful indexes for wood quality prediction (Zhang et al., 2014). Neotropical species typically exhibit a positive relationship between drought resistance and wood density (Janssen et al., 2020; Serra-Maluquer et al., 2022). Precipitation and air temperature are the most used meteorological variables to characterize the interaction between climate and *Eucalyptus* wood density (Rocha et al., 2020; Almeida et al., 2023), with higher wood density often observed in drier regions (Rocha et al., 2020). The highest density values of wood produced in drier sites are associated with its cells having thicker walls or smaller diameters. In hardwoods, this increase in density may also be associated with a lower vessel frequency (Pfautsch et al., 2016).

Research linking genotype performance to environmental conditions provides a scientific basis for recommending specific clones for deployment at particular sites. Soil and climate differences among sites are commonly considered determining factors in species selection (Scolforo et al., 2019). With the expansion of forest frontiers, selected clones tend to decrease their ideal phenotypic expression due to the occupation of areas with different conditions from the original ones. Climate forecasts for the next 20 years indicate changes in rainfall patterns, increase in temperatures and duration and severity of droughts (Elli et al., 2020; IPCC, 2023), further emphasizing the importance of studying wood characteristics in different clones.

In this context, the use of adapted clones will benefit not only expansion areas but also the traditional sites of each forestry enterprise. An alternative to mitigate these impacts is to select clones that are more adaptable to environmental variability or to develop new clones specifically suited to different conditions. Genotypes can be classified as specialists, generalists, or plastic according to their responses to environmental variation. Specialist genotypes exhibit high performance under specific conditions, whereas generalists maintain moderate and more stable performance across environments, and plastic genotypes adjust their phenotype in response to environmental gradients, enhancing adaptation to variable conditions (Fritsche-Neto; Borém, 2011).

Therefore, this study aimed to evaluate the influence of clone × site interaction on wood density in four *Eucalyptus* clones across a broad climatic gradient in tropical regions of Brazil, addressing the following research questions: (i) Which climatic variables most strongly drive the variation in wood density across contrasting sites? (ii) Which *Eucalyptus* clones show the greatest differences in phenotypic responses to site conditions?

MATERIAL AND METHODS

Characterization of the study area

The material used in this study was supplied by the TECHS Project (Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses; www.ipef.br/techs), a large-scale experimental network designed to evaluate the responses of *Eucalyptus* clones to climatic variability, particularly temperature and water availability. The project comprises 36 experimental sites distributed along a geographic gradient of more than 3,500 km, extending from the Amazon region to southern Brazil and Uruguay, and encompassing tropical and subtropical environments with contrasting climatic conditions.

TECHS integrates 18 genetically distinct and commercially relevant *Eucalyptus* clones, including broadly adapted ("plastic") genotypes and region-specific materials, representing the diversity currently deployed in intensive forest plantations. At each site, clonal trials were established using standardized experimental plots composed of 8 rows × 15 trees (120 trees per plot), with dimensions of 24 × 90 m, ensuring robust representation of stand structure and growth and enabling consistent evaluation of genotype × environment interactions at regional to continental scales (Binkley et al., 2017).

In this study, four *Eucalyptus* clones were specifically selected for analysis based on their broad deployment in commercial plantations and their contrasting genetic backgrounds. These clones were planted in commercial areas belonging to different Brazilian forestry companies and were derived from selection programs conducted under tropical environmental conditions. The evaluated materials included R9 (*Eucalyptus urophylla*), B2 (*E. urophylla* × *E. grandis*), and H8 and D4 (*E. grandis* × *E.*

urophylla), representing genotypes widely used in intensive forest production systems.

The clones were cultivated between 2012 and 2015 (4 years) at 10 sites distributed across Brazil, covering a wide geographic range (Figure 1a, Table 1). Each clone was planted in a single plot per site with 3 × 3 m spacing. During the first year after planting, all plots received standardized intensive fertilization to avoid nutrient limitations, totaling 70 kg ha^{-1} N, 45 kg ha^{-1} P, 85 kg ha^{-1} K, 500 kg ha^{-1} Ca, 90 kg ha^{-1} Mg, and 40 kg ha^{-1} S, with micronutrient supplementation (3 kg ha^{-1} B, 1 kg ha^{-1} Cu, and 1 kg ha^{-1} Zn). Fertilization was applied in two to four split applications from pre-planting to 12 months after planting, and herbicides were used for weed control during stand establishment.

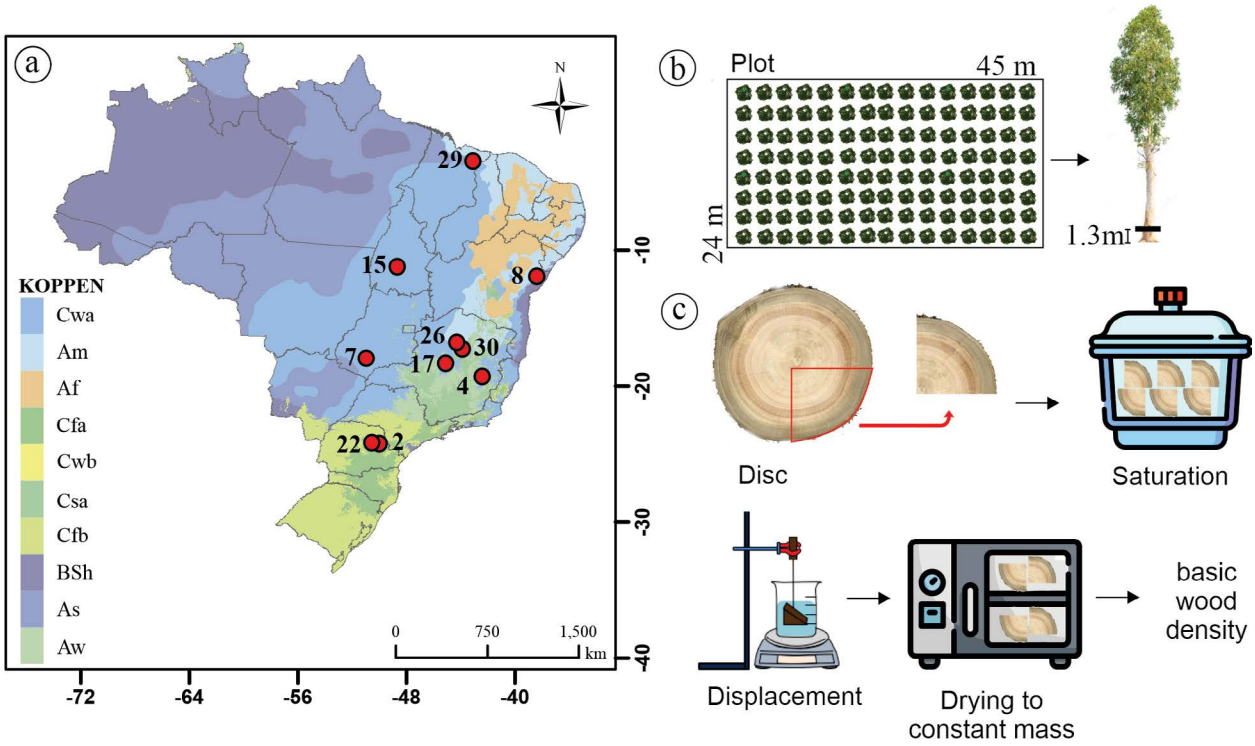

Figure 1: (a) Geographic location for the 10 growing sites of the four *Eucalyptus* clones in the period from 2012 to 2015. For site identification, the same numbering originally adopted by the TECHS program was used. Köppen climate classification (adapted from Alvares et al., 2013). (b) Sample collection. (c) Wood density analysis.

Table 1: Location of 10 evaluated TECHS sites.

Site[1]	Nearest city (City/State)	Lat[2] °	Long[3] °	Altitude m	T[4] °C	P[5] mm year^{-1}	SWD[6] mm year^{-1}	VPD[7] kPa	Climate[8]
2	Arapoti/Paraná	24.2	50.0	770	18.1	1671	69.0	1.0	Wet
4	Belo Oriente/Minas Gerais	19.3	42.4	243	22.9	961	470.9	1.7	Sub-humid
7	Rio Verde/Goiás	18.0	50.9	681	23.1	1572	693.2	1.2	Sub-humid
8	Inhambupe/Bahia	11.9	38.4	218	24.6	687	922.3	0.9	Sub-humid
15	Brejinho do Nazaré/Tocantins	11.2	48.6	255	26.1	1341	796.5	1.3	Sub-humid
17	Três Marias/Minas Gerais	18.3	45.1	806	22.2	1026	962.5	1.1	Sub-humid
22	Telêmaco Borba/Paraná	24.2	50.5	888	18.1	1677	97.1	0.6	Wet
26	Coração de Jesus/Minas Gerais	16.8	44.3	926	24.2	652	1158.4	1.5	Dry
29	Urbano Santos/Maranhão	3.4	43.1	81	27.4	1214	1017.0	1.3	Sub-humid
30	Bocaiúva/Minas Gerais	17.3	43.8	848	24.2	667	1143.8	1.5	Dry

[1] The same numbering adopted by the TECHS program was used for site numbers. [2]Lat: latitude; [3]Long: longitude; [4]T: temperature; [5]P: precipitation; [6]SWD: Soil water deficit; [7]VPD: Vapor pressure deficit. [8]Site classification was obtained from Binkley *et al*. 2017.

Climatic, growth and density database

Meteorological data of mean air temperature, mean relative humidity, 10-meter wind speed, global solar radiation, and precipitation from 2012 to 2015 were obtained from the Brazilian National Institute of Meteorology (INMET, 2025) and missing data were interpolated.

Annual temperature (T) was calculated as the arithmetic mean of the monthly average temperature. Precipitation (P) was determined as the sum of the accumulated monthly precipitation. Vapor pressure deficit (VPD) was calculated using a modified version of the equation proposed by Tetens in 1930 (Alvarenga et al., 2014), where the daily maximum temperature replaced the mean temperature in the saturation vapor pressure calculation, and the annual VPD was computed as the average of the monthly VPD values (Equation 1). Based on relative humidity and the saturation vapor pressure of water vapor in the air, the partial water vapor pressure in the air was determined (Equation 2). The difference between saturation vapor pressure and the partial water vapor pressure in the air allowed the calculation of the vapor pressure deficit, which represents the amount of water vapor required for the air to reach saturation (Equation 3).

$$e_s = 0.6108 exp\ exp\left[\frac{7.5 \times T}{237.5 + T}\right] \quad (1)$$

Where,
e_s = Water vapor saturation pressure in the air (kPa) and T = air temperature (ºC).

$$e_a = \frac{RH \times es}{100} \quad (2)$$

Where,
e_a = Partial water vapor pressure (kPa); RH = relative air humidity (%).

$$VPD = e_s - e_a \quad (3)$$

Where,
VPD = vapor pressure deficit of the air (kPa).

The sequential monthly water balance proposed by Thornthwaite and Mather in 1955 was used to calculate the soil water deficit (SWD) (Camargo, 1962) (Equation 4). Potential evapotranspiration was estimated by the Penman-Monteith method, parameterized by FAO (PM-FAO 56) (Equation 5). Available water in the soil was calculated based on the equation proposed by Menezes (2005), using the silt and clay contents of the studied sites. The available water values were adjusted considering an effective soil exploration depth of two meters for the root system to estimate the soil water storage capacity (WSC). Annual SWD was obtained by summing the monthly deficits.

$$SWD = ETo - AET \quad (4)$$

Where,
ETo = evapotranspiration estimated by the Penman–Monteith method (mm day^{-1}) and AET = actual evapotranspiration (mm day^{-1}).

$$ETo = \frac{0.408\Delta\left(Rn - G\right) + \gamma \frac{900}{Tm + 273} u2\left(e_s - e_a\right)}{\Delta + \gamma\left(1 + 0.34 \cdot u2\right)} \quad (5)$$

Where,
ETo = evapotranspiration estimated by the Penman–Monteith method (mm day^{-1}); Rn = total net radiation (MJ m^{-2} day^{-1}); G = soil heat flux density (MJ m^{-2} day^{-1}); Tm = daily mean air temperature (°C); u_2 = daily mean wind speed at 2 m height (m s^{-1}); e_s = saturation vapor pressure (kPa); e_a = actual vapor pressure (kPa); $e_s - e_a$ = vapor pressure deficit (kPa); Δ = the slope of the vapor pressure curve at Tmean (kPa $°C^{-1}$); and γ = psychrometric constant (kPa $°C^{-1}$).

The diameter at breast height (DBH, 1.3 m above ground level) and total height (H) of all trees at each site were measured. Wood volume (WV / m^3 ha^{-1}) was calculated using equations provided by (Mattos et al., 2020), with the coefficients for each clone listed in Table 2. The mean annual increment (MAI / m^3 ha^{-1} $year^{-1}$) was calculated by dividing the accumulated plot wood volume by stand age, and the resulting values were then extrapolated to a per-hectare basis. The stem biomass (SB / ton) was calculated by multiplying the plot volume by the WD for each clone at each site.

Table 2: Coefficients of wood volume equations (ln volume = a + b (ln (DBH)) + c (ln (H)), volume in m^3, DBH in cm and H in m).

Clone	Coefficients		
	a	b	c
B2	-10.1944	1.6552	1.2800
D4	-10.1467	1.6552	1.2800
H8	-10.2234	1.6552	1.2800
R9	-10.2370	1.6552	1.2800

The sampled trees were selected based on DBH. The mean DBH of each clone was calculated from the measurements of all trees in the plot, and three trees of average size per plot were selected, excluding dead, crooked, damaged, or diseased trees, totalizando 120 trees (3 trees x 4 clones x 10 sites). A wood disc sample was collected from each tree at breast height (Figure 1b). Wood density (WD) was determined from one quarter of each

disc using the hydrostatic balance (immersion) method, as recommended by the Brazilian Regulatory Norm (ABNT, 2003) (Figure 1c).

Statistical analysis

A two-way ANOVA (factorial experimental design) was used to evaluate clone x site interaction in WD. Clone was the first factor with 4 levels, and site was the second factor with 10 fixed levels. The equality of variance (homoscedasticity) and data normality were verified by the Cochran and Shapiro-Wilk tests ($\alpha = 0.05$), respectively. The means of each treatment were compared using the Scott Knott test ($p < 0.05$). Sites were ranked from lower to higher SWD (mean of 2012 to 2015). The WD of the sites by clone was correlated with T, P, SWD, VPD, and MAI using Pearson's correlation ($\alpha = 10$ %, $n = 60$) in the R software (R CORE TEAM, 2024).

RESULTS

Soil water deficit (SWD) was the climatic variable that presented the largest variation between sites (51.7 %). The temperature ranged from 18.1 to 27.4 °C and precipitation from 500 to 2000 mm (Table 1). Sites further south of the country showed milder temperatures and lower water deficit values. Sites 26 - Coração de Jesus, 29 - Urbano Santos and 30 - Bocaiúva presented drier characteristics.

The two-way ANOVA revealed a significant effect of sites and a non-significant main effect of clones on WD, while the clone × site interaction was highly significant (Table 3). This result indicates that differences in WD among clones are not consistent across environments but rather depend on site-specific conditions. In addition, the site effect contributed more to the total variance in wood density than the clone effect indicating that environmental variation was the main driver of density differences. Given the non-significant overall clone effect combined with a significant clone × site interaction, the analysis was therefore focused on the factorial unfolding of sites within each clone, allowing a more appropriate interpretation of how environmental variation modulates clone-specific WD responses.

In Figure 2a, the factorial unfolding of sites within each clone is presented for WD. Letters on the horizontal axis indicate mean comparisons according to the Scott–Knott test at the 5% significance level. WD was lower in sites with lower SWD for clones B2 and D4, but not for H8 and R9, indicating that different clones respond differently to this variable (Figure 2a). This is evident in sites 2 (Arapoti) and 22 (Telêmaco Borba), which had an SWD of less than 100 mm year^{-1} (Table 1). The densities of B2 and D4 were more influenced by the higher water availability, ranging from 0.35 to 0.50 g.cm^{-3} and 0.40 to 0.52 g.cm^{-3}, respectively. In contrast, H8 and R9 showed density variations that did not follow the SWD gradient, ranging from 0.43 to 0.55 g.cm^{-3} and 0.46 to 0.55 g.cm^{-3}, respectively.

The same site was classified into different "density mean groups" for each clone, reinforcing the interaction effect on density. However, the sites at the extremes of evaluated meteorological conditions, 2 (Arapoti) and 30 (Bocaiuva), remained in the same groups of lower and higher density, respectively, for all the clones.

Figure 2b shows the variation in mean annual increment (MAI) across sites for each clone. Values represent site-level estimates calculated from trees within each plot; therefore, factorial analysis and mean comparison tests were not applicable. The B2, H8 and D4 clones showed a tendency to decrease MAI from the most humid to the driest sites, which was not observed for WD (Figure 2b). Site 2 was the most productive environment, among the high MAI values recorded there, B2 achieved the highest at 73.4 m^3 ha^{-1} year^{-1}, while R9 had the lowest at 44.4 m^3 ha^{-1} year^{-1}. The R9 clone was the least productive overall and, similar to its WD, showed no clear tendency for greater growth in either wetter or drier sites. For both clones H8 and D4, the highest MAI was recorded at site 22, with values of 65.8 and 68.3 m^3 ha^{-1} year^{-1}, respectively. On the other hand, the lowest MAI was observed at site 26, with values of 16.1 and 19.0 m^3 ha^{-1} year^{-1}, respectively. Sites classified as semi-humid and dry presented similar conditions, sometimes with wet sites, and sometimes with dry sites, with the differences between growth and WD being better demarcated in the extreme conditions of SWD.

Figure 2c presents stem biomass across sites for each clone. Values correspond to site-level estimates derived from trees within each plot, and no factorial analysis or mean comparison test was applied. B2, H8 and D4 clones showed similar tendencies to decrease stem biomass for the wet group to dry sites (Figure 2c). Among the high MAI values, the B2 clone achieved the highest biomass at 119.2

Table 3: Two-way ANOVA of WD (g cm^{-3}) for *Eucalyptus* sp. clones and sites in Brazil.

Source of variation	df	Sum of squares	Mean square	Fcal	p-value (%)
Clones (C)	3	0.0174	0.0058	2.93^{ns}	5.1832
Sites (S)	9	0.1117	0.0124	6.26**	0.0094
C x S	27	0.0536	0.0020	5.17**	0.0000
Residual	80	0.0307	0.0004		
Total	119	0.2134			

ns: not significant ($p > 0.05$); ** significant (5 % by F-test).
Parameters:
Residual coefficient of variation (CV): 4.1629 %
Overall mean: 0.4707 g cm^{-3}

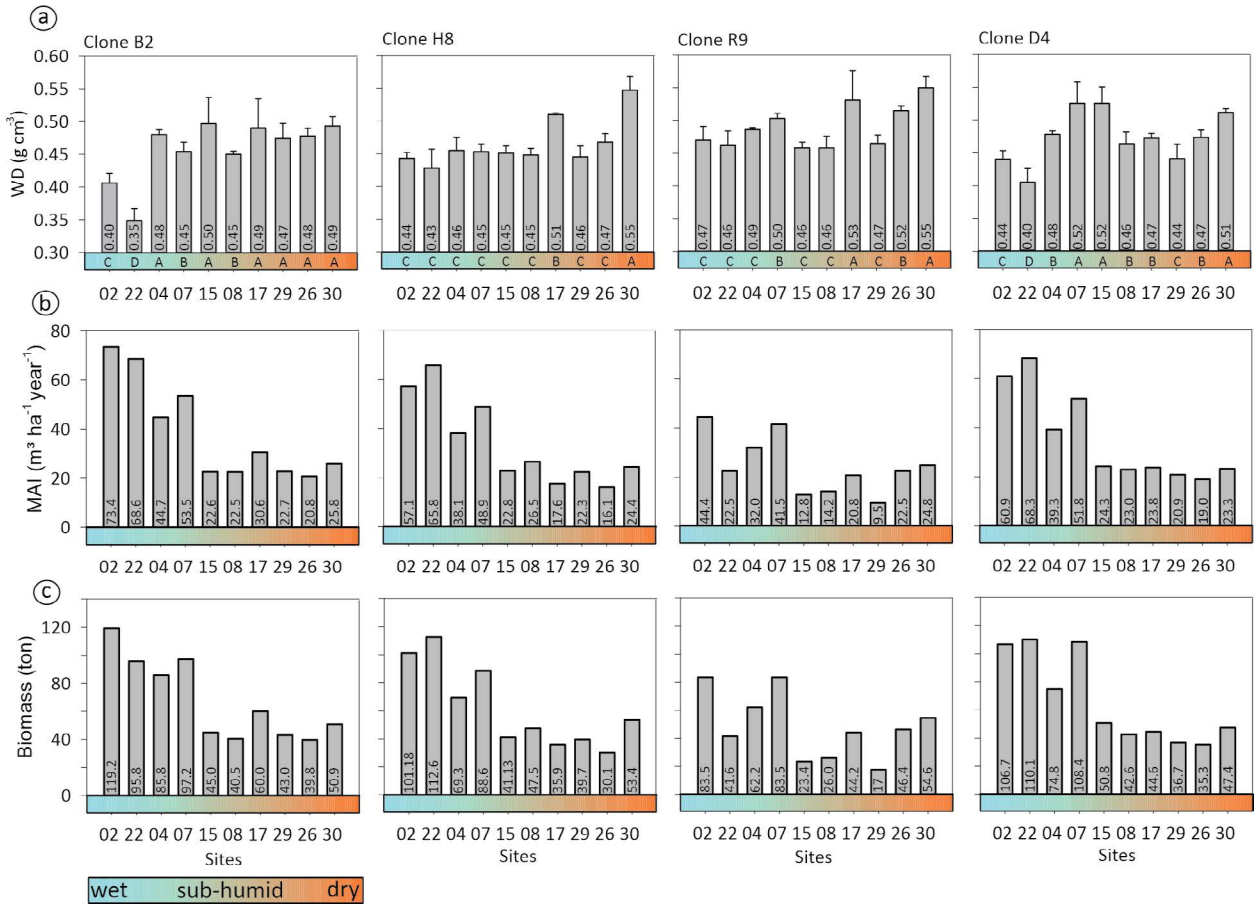

Figure 2: (a) Wood density (WD), (b) mean annual increment (MAI) and (c) stem biomass of 4 *Eucalyptus* clones at 4 years. Sites were organized from regions from lowest to highest SWD of 2012 to 2015. Equal letters in the WD graph indicate no statistical difference according to the Scott–Knott test at the 5% significance level (factorial decomposition of sites within each clone). MAI and biomass values refer to plot means.

tons, while R9 clone recorded the lowest at 83.5 tons. Sites 26 and 30 had higher biomass values than sub-humid sites, despite lower MAI values, which is associated with higher density values obtained at these sites. Among the lowest SB values, which ranged from 17.0 tons to 39.8 tons, the R9 clone had the lowest value. Furthermore, these values did not show a consistent trend between wetter and drier sites. Clones can be ranked in decreasing order of plasticity: B2 – *E. urophylla* x *E. grandis*, D4 – *E. grandis* x *E. urophylla*, H8 – *E. grandis* x *E. urophylla*, and R9 – *E. urophylla*.

Overall, the WD of clones varied in their response to climate and growth variables with some showing strong and significant correlations, while others showed no or non-significant ones (Figure 3). The B2 clone was the most strongly influenced by environmental variables, presenting significant correlations with all the variables studied, followed by H8, which showed correlations with P and SWD. D4 and R9 clones showed weaker or non-significant correlations, suggesting lower climate sensitivity. Precipitation may increase the growth rate by enlarging cell lumen, which in turn can reduce density. This can be seen by the generally negative correlation of P and MAI with WD.

The densities of clones ranged from 0.35 – 0.55 g.cm^{-3}. Figure 4 presents the distribution of sites in density ranges for each clone. The B2 and H8 clones had the lowest average densities, with most sites with densities up to 0.46 g cm^{-3}. On the other hand, R9 and D4 clones had densities from 0.462 g cm^{-3} at the majority of sites.

DISCUSSION

All clones showed less growth in the driest sites. Water deficit typically induces stomatal closure as a regulatory response to declining soil and atmospheric moisture availability, leading to reduced stomatal conductance (Flexas & Medrano, 2002; Taiz et al., 2015). The resulting decline in photosynthetic carbon assimilation constrains biomass accumulation, resulting in decreased tree growth under drought conditions (Rocha et al., 2020). In addition, prolonged water stress can exacerbate carbon limitations by increasing photorespiration and altering source–sink relationships, further impairing growth performance (Chaves et al., 2009).

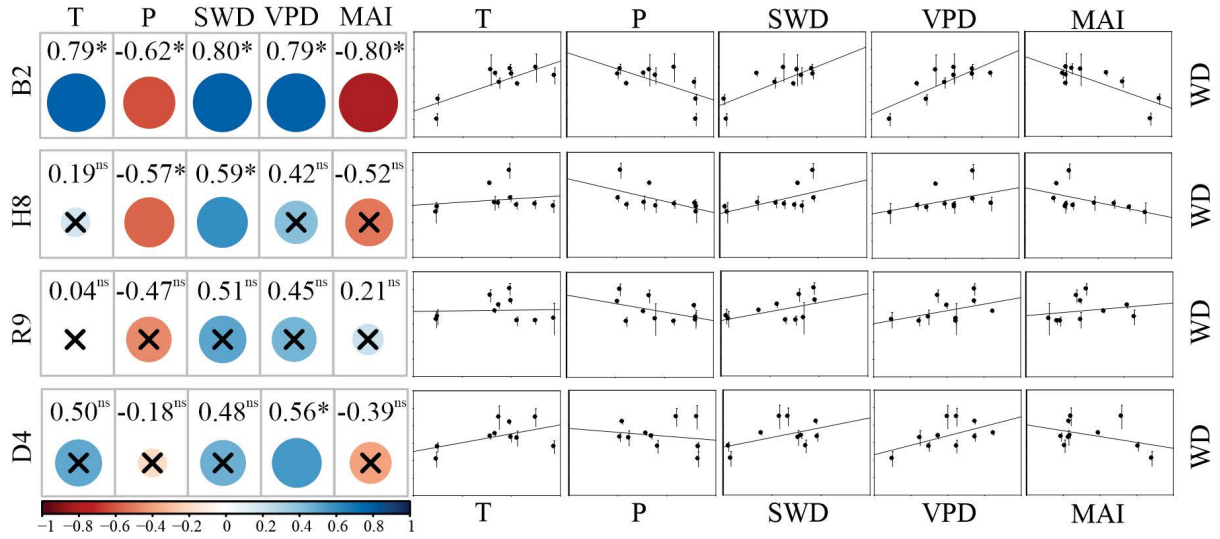

Figure 3: Pearson correlation matrix between wood density (WD) of clones and site climatic variables. Where: T: temperature; P: precipitation, SWD: soil water deficit, VPD: vapor pressure deficit, MAI: mean annual increment. *Significant correlations ($p < 0.1$) and ^{ns} non-significant correlations. Blue circles represent positive correlations and red circles indicate negative correlations. Circle size and color intensity represent the magnitude of correlation. Circles which contain an X indicate non-significant correlations.

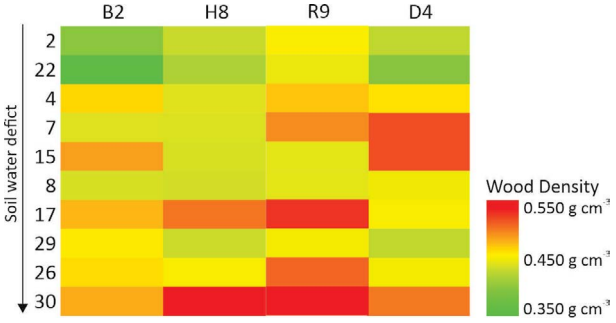

Figure 4: Site distribution at density ranges for each clone.

These physiological responses help explain the consistently lower growth observed across all clones under drier climatic conditions. An increased growth rate under favorable conditions is commonly associated with a decrease in WD (Rocha et al., 2020), as rapid cambial activity tends to promote the formation of cells with larger lumens and thinner cell walls, particularly in fibers and vessels (Downes et al., 1997; Zobel & van Buijtenen, 1989). This anatomical adjustment allows trees to sustain higher hydraulic efficiency and growth rates but results in lower mass per unit volume, thereby reducing WD. Such growth–density trade-offs are widely reported in fast-growing forest species and reflect physiological prioritization of resource acquisition over structural investment under favorable conditions.

In contrast to the responses observed under favorable water conditions, high soil water deficit promoted higher WD values in the clones grown at site 30 (Bocaiuva, dry site). This response can be explained by the maintenance of cambial activity under moderate water limitation, in which reduced cell expansion leads to the formation of smaller-diameter cells that still undergo normal secondary wall thickening during the maturation phase, resulting in denser wood (Rathgeber et al., 2016). Importantly, this pattern suggests that water deficit did not severely constrain photosynthetic capacity, indicating a degree of physiological tolerance to drought conditions.

Higher densities are associated with greater resistance to embolism, resulting in a trade-off between the xylem safety (its ability to resist embolism formation and spread) and xylem efficiency (its capacity to transport water) (Fajardo et al., 2022; Janssen et al., 2020). Species increase fiber wall thickness and vessel-vessel contact under high negative pressures as a hydraulic and mechanical strategy to reduce the risk of collapses, which enables an increase in WD (Liang al., 2021).

Different genetic materials adopt distinct physiological strategies and safety–efficiency trade-offs in response to environmental stress, resulting in contrasting phenotypic expressions, as observed in this study. Clones capable of maintaining carbon assimilation and wood formation under such conditions tend to modulate their phenotype toward increased density rather than growth suppression. In this study, this behavior was particularly evident for the B2 and D4 clones, which showed increased WD at drier sites while maintaining competitive levels of mean annual increment. In contrast, the H8 and R9 clones exhibited more stable WD across sites, with lower sensitivity to increasing water deficit, characterizing a more generalist response.

From a broader perspective, these contrasting strategies highlight the relevance of selecting either responsive or stable genotypes depending on management objectives. Clones such as B2 and D4 are promising candidates for deployment in water-limited environments

where increased WD is desirable, whereas H8 and R9 may be more suitable for regions with higher climatic variability, where stability of wood properties is a priority.

Consistent with these contrasting strategies, each clone showed different correlations between WD and meteorological variables, indicating the importance of genetic background in modulating WD responses to climatic conditions. Griebel et al. (2017) reported different relationships between water deficit, growth, and WD depending on Eucalyptus species and the environmental origin of each genetic material in temperate forests. In tropical clones, Rocha et al. (2020) observed, as a general trend, that WD tends to be higher in drier locations; however, this pattern becomes less predictable under humid conditions, as also observed in the present study.

Evaluating *Eucalyptus* clones under contrasting environmental conditions in Brazil (P7 – *Eucalyptus urophylla* × *Eucalyptus brassiana*; G7 – *Eucalyptus urophylla*; and E5 – *Eucalyptus urophylla*), Costa et al. (2020) reported that wood responses in terms of WD and mean annual increment are clone-specific. Their results further indicated that MAI is proportionally more sensitive to environmental variation than WD, reinforcing the differential responsiveness of growth and wood properties to climatic conditions. Furthermore, for *Eucalyptus urophylla*, the influence of climate on WD becomes more pronounced after the third year of growth, with WD showing significant correlations with temperature, precipitation, and soil water deficit (Almeida et al., 2023).

Humid sites favored tree growth and reduced density for B2 and D4 clones compared to values observed by dry sites. The R9 clone showed the lowest WD variation, with the changes in this feature being more associated with particular characteristics of the genetic material. This clone differs as the only pure species (*E. urophylla*), while the others are *E. urophylla* with *E. grandis* hybrids. The *E. grandis* parent in the hybrids is a drought-tolerant species (Seidel et al., 2024), being one of the adaptation strategies of this clone the increase in WD.

However, precipitation had very little effect on WD in the H8 clone, even though variation among sites was observed. This result suggests that precipitation alone is not a direct driver of WD but instead interacts in combination with other climatic factors that regulate water availability and physiological processes. Although higher precipitation increases soil water supply, its effects may be constrained under conditions of elevated temperatures and high vapor pressure deficit, which intensify atmospheric demand for water. Under such conditions, clones differ in their phenotypic modulation strategies: genotypes better adapted to sustain transpiration tend to maintain stomatal opening and carbon assimilation, whereas more hydraulically sensitive clones reduce stomatal conductance, limiting photosynthesis and, consequently, the availability of photoassimilates for allocation to growth and wood formation.

Sites with higher water availability and lower temperatures also showed higher stem biomass. Sites 04 and 07 (sub-humid) and 02 and 22 (wet), which presented the lowest soil water deficit (SWD), were grouped into a single cluster in terms of stem biomass. Despite this, an increase in WD of approximately 50 kg m^{-3} was observed from the wet sites to the sub-humid sites. This response is explained by the higher temperatures at sites 04 and 07, which, despite adequate water availability, increased atmospheric demand and constrained carbon assimilation, as previously discussed.

Brazil hosts a variety of climate zones, making the identification of optimal species for forest cultivation a significant challenge for the forestry industry (Rocha et al., 2020). The pulp industry has used materials ranging from 0.40 to 0.55 $g.cm^{-3}$ (Boschetti et al. 2020). This range is associated with productivity in the pulping process, as low-density wood leads to increased specific wood consumption. Conversely, high-density wood may present challenges for industrial chippers and require more drastic cooking (Boschetti et al., 2020). In this sense, almost all clones in all sites would fit this requirement, except for B2 and D4 at sites 2 and 22. This demonstrates the clones' consistency in wood quality, even in very contrasting conditions.

Density is also a benchmark for the energy industry. In the case of charcoal production, some authors recommend WD values above 0.50 g cm^{-3} (Protásio et al., 2021). The clones that came closest to this value were B2, H8 and D4 in humid sites. Therefore, in drier sites, what can be done is to wait for an increase in density until the cutting cycle (about 6 years) can supply this difference, once density tends to increase as trees age (Santos et al., 2021).

Although WD is relevant to several forest-based industries, these results should be interpreted cautiously in terms of end-use recommendations. The clones were evaluated at an early age (four years), and key wood quality traits required for other uses like panels and solid wood applications are strongly age-dependent.

Thus, the main contribution of this study is improve the understanding of clone-specific adaptive strategies and clone × site interactions that modulate WD under contrasting climatic conditions. Some clones are more affected than others, with the R9 clone exhibiting the greatest stability across climatic variables. Although all the clones come from selection programs in tropical environments, they showed specific trends for WD and volume in biomass, which reinforces the need to specifically study genetic traits of affinity of each clone in specific climates.

CONCLUSION

The influence of climate on wood density (WD) was confirmed, despite the strong hereditary control of this trait. Among the climatic variables, soil water deficit (SWD) and vapor pressure deficit (VPD) were the most relevant, as they integrate the combined effects of temperature, precipitation, and atmospheric demand, highlighting the importance of the microclimatic context as a whole.

For all clones, growth-related traits were more strongly influenced by climatic conditions than WD. Concerning density, the B2 and D4 clones were more responsive to climatic differences among sites, whereas the H8 and R9 clones exhibited greater stability, characterizing a more generalist behavior.

The joint evaluation of WD, mean annual increment, and stem biomass supports the selection of suitable clones for specific regions, contributing to improved productivity and feedstock quality under contrasting climatic conditions.

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AUTHORSHIP CONTRIBUTION

Project Idea: MNFA; GBV; JLPCL; JEMP;

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DATA AVAILABILITY

The datasets analyzed during the current study are available from the corresponding author upon reasonable request.

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