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Changes in rainfall patterns enhance the interrelationships between climate and wood traits of eucalyptus

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ABSTRACT

The intensity of climate changes demands studies on the adaptability of the most planted eucalyptus genetic materials in the world, such as *E. urophylla* and *E. grandis* × *E. camaldulensis* which were evaluated in this study. The objective of this work was to evaluate wood traits and to relate it to the meteorological variables for each year of growth of the trees that grew in four sites with different climatic conditions and 33% rainfall exclusion. The wood traits evaluated were: wood density, vessel density, diameter and area, vessel wall thickness, total vessel wall thickness between adjacent cells, theoretical hydraulic conductivity, potential hydraulic conductivity, lumen conductivity area, vessel composition within space, vessel implosion resistance and vulnerability index to drought. Pearson's correlations between the evaluated variables were estimated and the results expressed graphically through the correlation network. Multiple regression analysis with adjustment by the Exhaustive Search method was used to estimate the vessel wall thickness in order to isolate this characteristic and identify the explanation intensity of the meteorological variables. Pearson's correlations between meteorological factors and wood traits show different interactions in the behavior of the clones and in the water availability conditions. Air temperature was present in all the vessel wall thickness estimation equations. The 33% rainfall exclusion provided the best equation adjustments with meteorological variables, explaining up to 84% of the variation in the vessel wall thickness. The rainfall exclusion intensified the effects of the interrelations between climate and hydraulic architecture in *E. grandis* × *E. camaldulensis*, with implosion resistance and vessel wall thickness having a strong relationship between climate and wood. The results of rain reduction in the dynamics between wood and climate have implications for indirect selection in breeding programs.

1. Introduction

The interaction between genotype and the environment is considered complex because it involves factors at the local and temporal level (De Micco et al., 2019). The geographical distribution of vegetation on the planet is mainly governed by climatic factors (Wieczynski et al., 2018), with precipitation and air temperature being elements of primary influence. The variation in time occurs according to the seasons, defining seasonal periods of precipitation, temperature and solar radiation (Cuny and Rathgeber, 2016; De Micco et al., 2019; Gárate-Escamilla et al., 2020; Kuželová and Treml, 2020).

The availability of water in the soil is a determining and limiting factor for the *Eucalyptus* genus and is related to the negative impacts on biomass productivity (Elli et al., 2019), while temperature proves to be a barrier to adaptability of this genus (Araujo et al., 2019; Binkley et al., 2020). Thus, the interaction between climatic elements occurs in a complex way in the formation of the phenotype, also depending on interannual variation, since eucalyptus trees express climatic seasonality (Campoe et al., 2016).

The genetic changes acquired in the process of natural selection or

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artificially modified (Anderson et al., 2011) make it possible for plants to adapt to different environments. However, climate change influences this adaptation (Pritzkow et al., 2020). In the secondary xylem, climatic effects are responsible for changes in their anatomical structures and consequently in the vulnerability to collapse in the water conduits (Rita et al., 2015; Nola et al., 2020). There are plants which adapt to environmental changes under these conditions with a reinforcing mechanism in the hydraulic design with fiber and axial parenchyma (Janssen et al., 2019; Morris et al., 2018), increasing drought resistance.

Temperature and precipitation have a strong relationship with the vital functions of the plant, such as transpiration and photosynthesis (Gárate-Escamilla et al., 2020; Le Gall et al., 2015; Massmann et al., 2019). These metabolic functions are closely related to the conduction of water, which is inferred by the potential conductivity of the xylem (Kotowska et al., 2015). The water transport by vessel elements may or may not be continuous depending on the source-drain conditions (He et al., 2019). There is a probability of failure in the water column due to cavitation or implosion of a stem, being predicted by the xylem's vulnerability (Hacke et al., 2001; Koepke and Kolb, 2013).

There is a relationship between xylem traits and climate (Almeida et al., 2020; Arnaud et al., 2019; Barbosa et al., 2019; Chauvin et al., 2019). However, it is necessary to expand studies at the multi-species level (Fernández et al., 2019) and in different environmental conditions to clarify the character of adaptability for species. The hypothesis questioned by us is that rainfall exclusion can intensify the interrelationships between climate and hydraulic architecture in the wood of eucalyptus clones. Therefore, the objective of this research work was to evaluate the relationship between climatic variables and xylem traits; and identify and predict the xylem trait that best reflects the change in rainfall patterns. It is worth mentioning that this approach of several meteorological factors and wood traits in the sites considered most productive in Brazil, includes the evaluation of the most planted clone in the country: *E. urophylla* (A1), being the first to explore the relationship of transport structures of water and rainfall exclusion.

2. Material and methods

2.1. Experiment and wood sampling

Field experiments were carried out between the years 2012 and 2018 with clonal materials from *E. urophylla* (A1) and *E. grandis* × *E. camaldulensis* (C3), described in detail by Binkley et al. (2017). The selection of these clones was due to their high representativeness in plantations around the world (Stanturf et al., 2013), in addition to having adaptive features to the environmental diversities of much of the Brazilian territory. *E. urophylla* (A1) was developed to maximize productivity and *E. grandis* × *E. camaldulensis* (C3) was developed to survive drought (Binkley et al., 2017).

The plantations were carried out in 3 × 3 m spacing in the Brazilian municipalities of the Neotropical region: 04 Belo Oriente and 30 Bocaiúva (state of Minas Gerais), 07 Rio Verde (state of Goiás) and 20 Mogi Guaçu (state of São Paulo) (Fig. 1). Thus, the term municipality will be equivalent to a site and will be accompanied by the number corresponding to its identification, maintaining the same numbering presented by Binkley et al (2017). All plots were fertilized intensively during the first year (70 kg N ha^{-1}, 45 kg P ha^{-1}, 85 kg K ha^{-1}, 500 kg Ca ha^{-1}, 90 kg Mg ha^{-1}, 40 kg S ha^{-1} 3 kg B ha^{-1}, 1 kg Cu ha^{-1} e 1 kg Zn ha^{-1}) to reduce any nutrient limitations. The fertilizer application schedule varied between sites, with total application divided between 2 and 4 applications from pre-planting to 12 months. Herbicides were used to keep the plots free of weeds. See Binkley et al. (2017) for additional silvicultural details applied to the experiments.

The clones and sites were obtained from the Cooperative Program of Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses (TECHS) that belongs to the Institute of Forestry Research and Studies (Instituto de Pesquisas e Estudos Florestais – IPEF), as detailed in Binkley

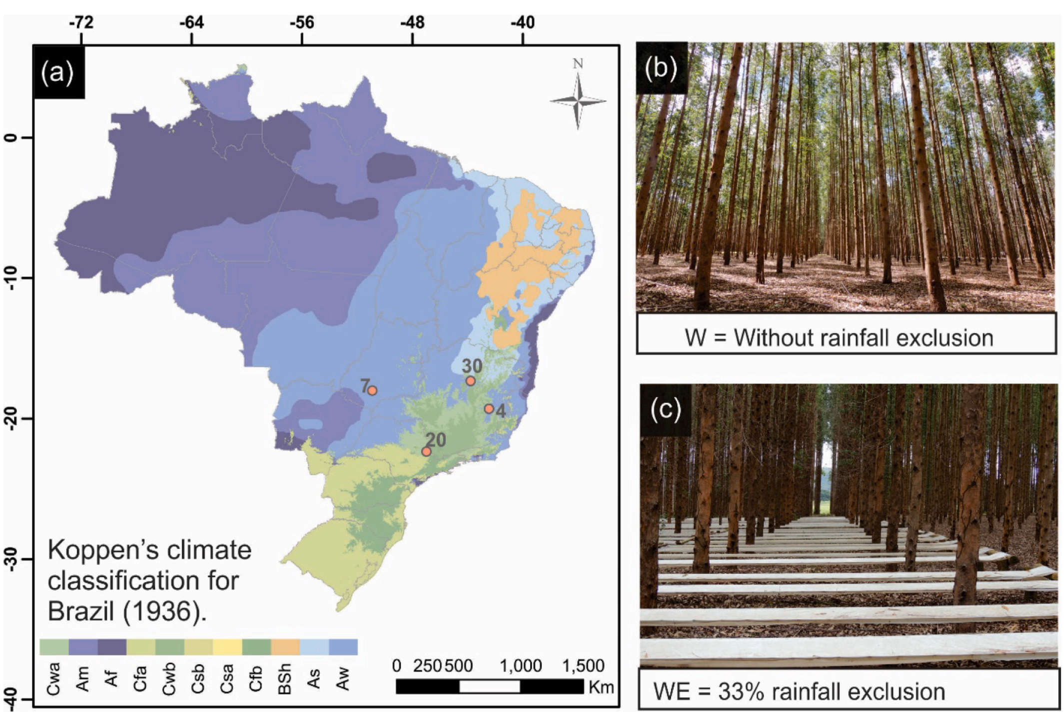


Fig. 1. Location of sites and experimental conditions evaluated in *Eucalyptus*. (a) Plantation installation sites, the red circles of which indicate the corresponding site. (b and c) Field photos of six-year-old *Eucalyptus* trees. (c) Standard arrangement of the gutters in the 33% rainfall exclusion condition (WE). Both experimental conditions were installed at the 4 sites. Cwa: Humid subtropical with hot and rainy summer; Am: Tropical monsoon; Af: Tropical equatorial;; Cfa: Subtropical hot summer sea; Cwb: Subtropical temperate and summer rains; Csb: Mediterranean climate with cool summer; Csa: Mediterranean climate with hot summer; Cfb: Subtropical oceanic temperate summer; BSh: Dry and hot semi-arid; As: Tropical with dry season of summer and rains of winter; Aw: Tropical with dry season and summer rains. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al. (2017). The project TECHS was launched in 2011 for the investigation of the development of eucalyptus in Uruguay and Brazil in the field of objective investigation into the development of eucalyptus in different climatic conditions. The four sites used in this study are defined as "tropical sites" for the TECHS project.

Each site had two water availability conditions: W - without rainfall exclusion with 100% of local rainfall, and WE – 33% rainfall exclusion (Fig. 1). The plot area (24 × 45 m) for the WE condition was equipped with 0.5 m wide polyethylene gutters, arranged between the plantation rows. The gutters were installed about one year after planting (year 2013 in the rainy season) and covered the surface below the canopy on a slope of 1 m in height in order to cover 33% of the soil area under the treetops. That is, 33% exclusion is for through rainfall, considering a canopy interception and stem flow, the exclusion percentage in gross rainfall should be lower.

Seven trees of each clone in each water availability conditions: W and WE (33% rainfall exclusion) were sampled, for a total of 28 trees at each site (112 trees across 4 sites). One tree being harvested per diameter class to ensure that trees of all diameters were represented in the study (Arnaud et al., 2019). The selection of the seven trees was according to the DBH distribution (diameter at breast height, measured at 1.30 m from the ground) amplitude of the plot in seven classes. The classes were separated based on the forest inventory carried out at 6 years.

The wood was sampled in disks and collected at 1.30 m from the ground for measuring wood microdensity and for anatomical analyzes. Wood traits were analyzed annually, totaling six years of growth, evaluated by tree. The identification of annual periods was performed using data from spreadsheets generated from semiannual forest inventories, with measurements at 1.30 m from the ground, and confirmed by macroscopic analysis using a stereoscope with a 10-fold magnification.

2.2. Meteorological data and analysis

Meteorological data were obtained from the National Institute of Meteorology - INMET (www.inmet.gov.br) of Brazil, from automatic surface stations located close to the experimental municipalities, except for the Belo Oriente, MG site, whose data were obtained locally. Seven monthly meteorological variables obtained from the planting date and covering the period 2012–2018 were used: maximum temperature (T_{mx}), minimum temperature (T_{mn}) and average temperature (T_{ave}) of the air, average relative humidity, wind speed at 2 m, overall solar radiation and precipitation. The missing data were filled in by other meteorological bases according to the fault filling methodology used by Elli et al. (2019).

The soil water deficit (SWD) was characterized from the sequential climatological water balance on a monthly scale based on the method of Thornthwaite and Mather (de Camargo, 1962). A 33% reduction in the total precipitation volume was applied for the WE condition. The annual SWD was obtained by adding the monthly water deficits. The annual temperature values (T) were calculated by the arithmetic mean of the monthly average temperature and the annual precipitation (P) was calculated by the sum of the accumulated precipitation in each month

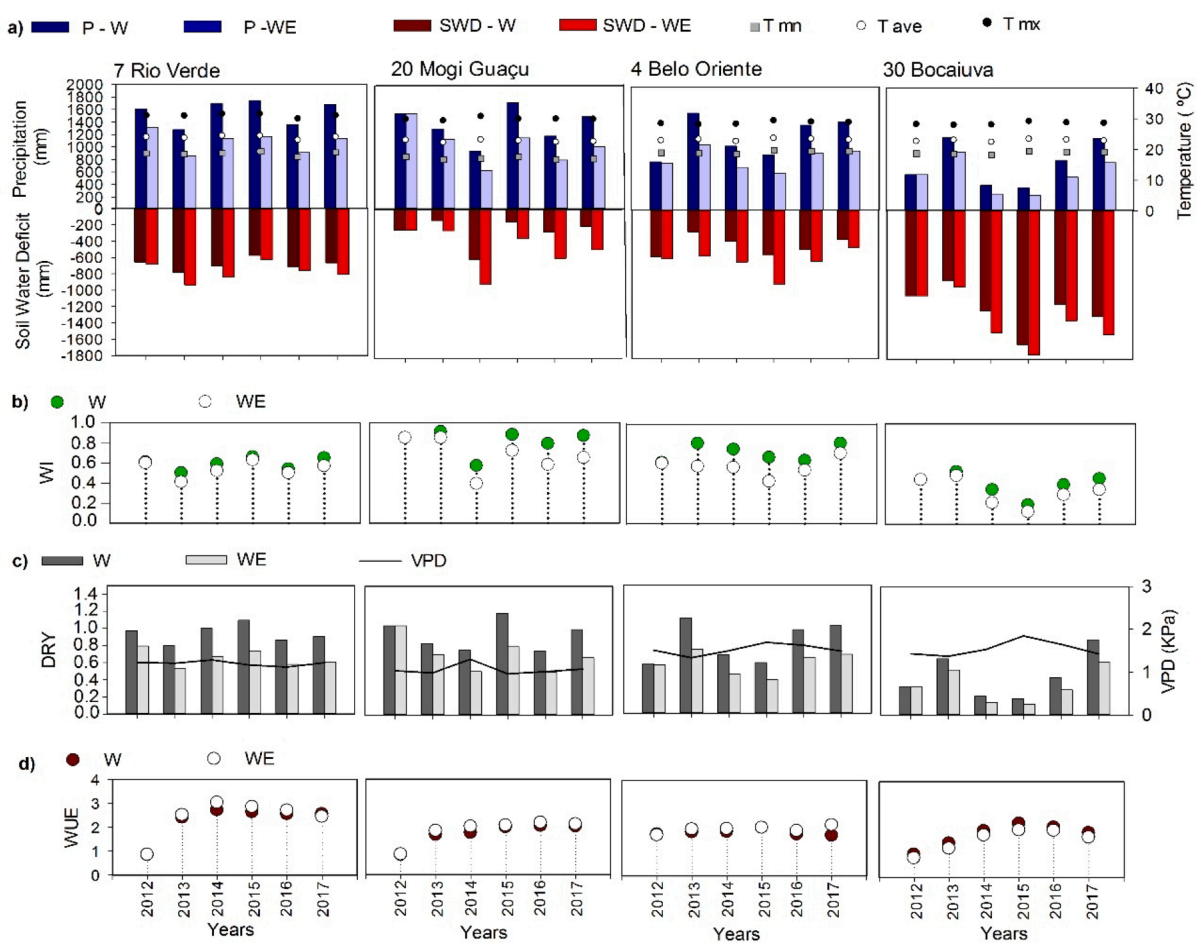


Fig. 2. Average annual temperature regime (Tmn, Tave, Tmx, minimum, average and maximum, respectively), precipitation (P), soil water deficit (SWD), water use index (WI), aridity index (DRY), maximum vapor pressure deficit (VPD) and water use efficiency (WUE) from four sites in Brazil. Where: W - without rainfall exclusion and WE – 33% rainfall exclusion.

(Fig. 2a). Potential evapotranspiration (PET) was calculated using the Penman-Monteith method (PM-FAO 56). The water storage capacity in the soil was calculated for two meters of effective depth and the water available in the soil (Menezes, 2005) from the silt and clay contents, the permanent wilting point (tension of 1500 kPa) and the field capacity (10 kPa voltage).

The maximum vapor pressure deficit (VPD) was calculated in an adapted way using the equation proposed by Tetens (Alvarenga et al., 2014) with the average temperature replaced with the maximum temperature of the day in the calculation of the saturation vapor pressure, and the annual VPD being the average of the monthly average VPD. The annual water use index (WI) was calculated by the ratio of actual evapotranspiration (ETA) to potential evaporation (PE) for the same growth period obtained from the water balance calculations (Fig. 2b).

The aridity index (DRY) is the ratio between precipitation and potential evapotranspiration (Fig. 2c), representing the dry conditions in the planting years (Sahin, 2012). Water use efficiency in (WUE) is expressed by the wood production by the amount of water transpired (Stape et al., 2004), and was determined by the ratio between the biomass of the live trees in the plot (kg) by the ETA (converted for m^3), both calculated annually (Fig. 2d).

2.3. Determination of wood apparent density and microscopy

The wood apparent density (WD) was determined as described by Dobner Júnior et al. (2018), with the humidity of the samples stabilized at 12%. The average wood apparent density (g cm^3) was measured every 80 μm by scanning the wood samples using a direct X-ray microdensitometer (QTRS01X, Quintek Measurement Systems Inc. Knoxville, TN) integrated with a computer analysis system. Two strips from the same disk were used for calculating annual density profiles.

The apparent density peaks (fibrous zone) obtained in X-ray densitometry and the wood porosity (observed in a 20x magnification in a stereo stereomicroscope (SZT, BEL Photonics)) contributed to delimit the annual periods of six years of growth (Fig. 3).

Histological sections of 20 μm in thickness were performed annually in a slide microtome (SM2000R, Leica), dehydrated in increasing concentrations of ethanol (10 to 100%) and photomicrographed by software coupled to an automated digital microscope (Zeiss Axio Scope.A1, software Axio Vision SE64) to determine the wood density, traits and indexes (Table 1).

Table 1
List of wood traits evaluated, their abbreviations and respective methodologies.

Traits	Abbreviation	Author
Vessel diameter	VD	Scholz et al. (2013)
Vessel density	VDn	
Vessel area	VA	
Vessel wall thickness	VWT	Hacke et al. (2001)
Total vessel wall thickness between adjacent cells	t	
Theoretical hydraulic conductivity	K_{th}	Fichot et al. (2010)
Potential hydraulic conductivity	K_S	Santini et al. (2018)
Lumen conductivity area	LCA	Zanne et al. (2010)
Vessel composition within space	S	
Vessel implosion resistance	IR	Hacke et al. (2001))
Vulnerability index to drought	VI	Carlquist (1977)
Wood density	WD	Dobner Júnior et al. (2018)

2.4. Data analysis

Pearson correlations between meteorological factors and wood traits were performed. The correlation was performed separately for the clones and the water availability conditions. The sites were used as replicates, with meteorological and wood data plotted annually (24 replicates, 4 sites and 6 years of growth). The objective of using sites as repetitions was to generate a greater variation in the database to have one or more wood traits that were more correlated with the meteorological conditions of the sites and the years of growth. Two-dimensional network correlation was used to graphically express the functional relationship between estimates of the correlation coefficients between the traits and to detect complex phenotypic patterns. Trait pairs were estimated according to Eq. (1):

$$r\frac{COV_{(xy)}}{\sqrt{\hat{\sigma}_x^2 x \hat{\sigma}_y^2}} \tag{1}$$

where $COV_{(XY)}$ is the covariance between the X and Y traits, $\hat{\sigma}_x^2$ is the variation of the variable X and $\hat{\sigma}_y^2$ is the variation of the variable Y.

The proximity between the nodes (traits) was proportional to the absolute value of the correlation between these nodes. The thickness of the edges was controlled by applying a cut-off value of 0.70, which represents the significance by the *t*-test, whose edges were highlighted. The positive correlations were presented in green, while the negative correlations were presented in red scale.

Multiple regression analysis with adjustment by the Exhaustive

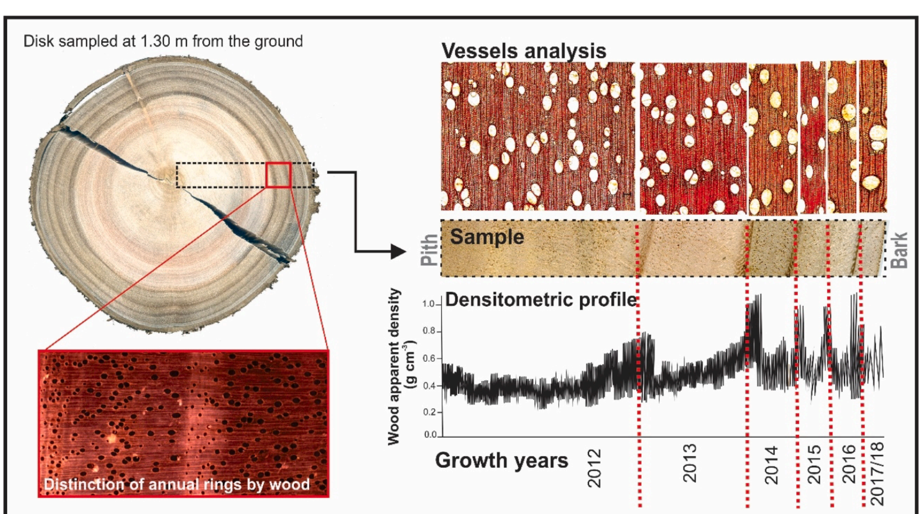


Fig. 3. Annual sampling of the wood (anatomy and wood apparent density).

Search method was used to estimate VWT, as the characteristic is strongly related to meteorological factors. All variable combinations were tested and provided the one which best estimates the dependent variable (Miller, 2002).

The averages of the six cultivation years of the variables T_{mn}, T_{ave}, T_{mx}, P, SWD, VPD, WI, DRY and WUE were used as independent variables by genetic material and water availability condition. The obtained combinations were compared and the best models were selected. The betas of the equation were presented in percentage, to represent the contribution of the independent variable in the estimation of the equation. The relative degree of the independent variable was scaled in terms of the ratio between the standard deviation of the criterion and the standard deviation of the *j*th predictor (s_{Xj}/s_Y), considering the beta of the criterion. The percentage was determined by the sum of the scaled betas (Kelley and Maxwell, 2003). All statistical analyzes were performed using the R statistical software program (R Core Team, 2014). The network correlation procedure was performed with the "qgraph" package (Epskamp et al., 2012), while the multiple regression analyzes were performed with the Leaps package.

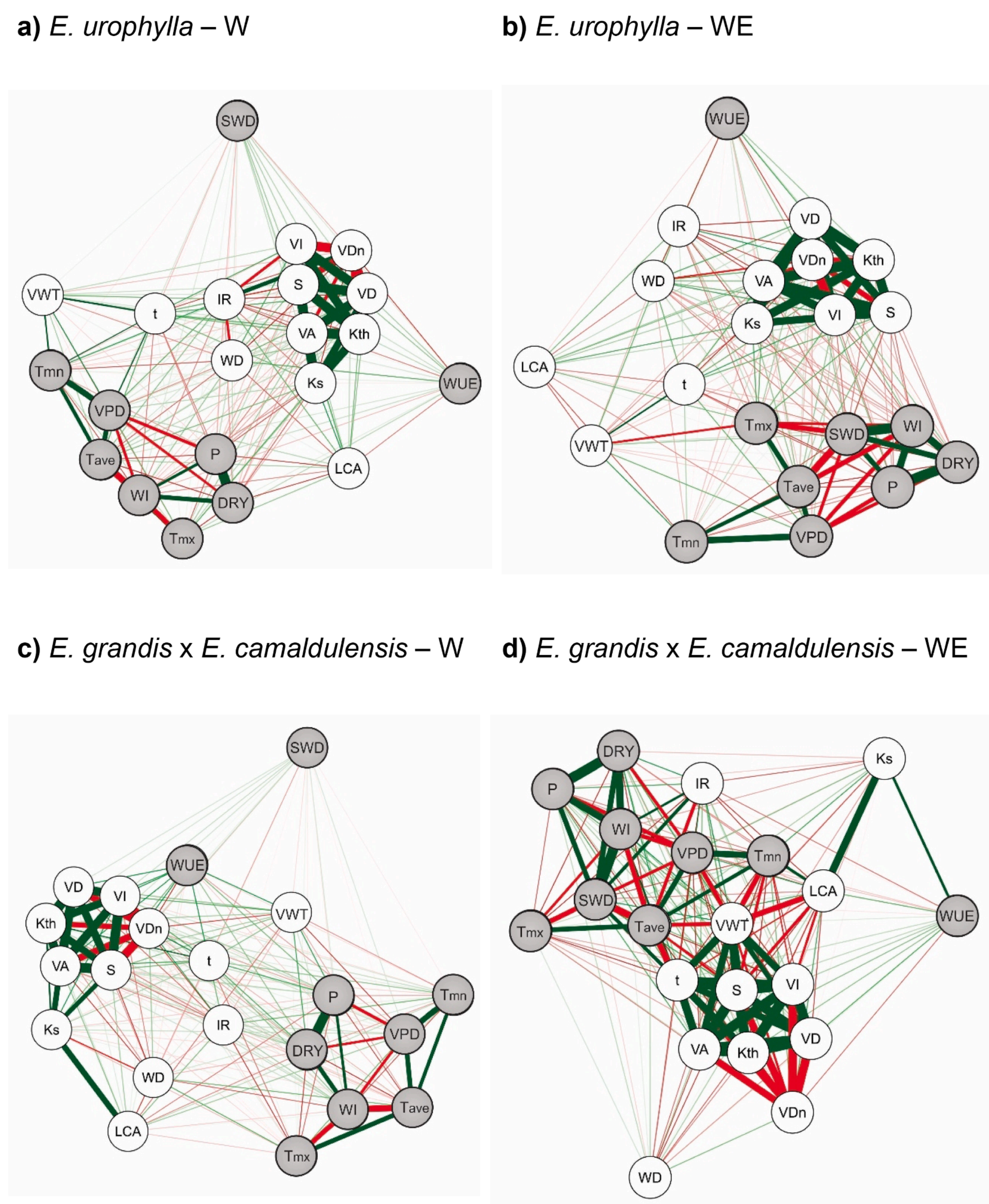


Fig. 4. Correlation of network between meteorological factors and wood traits evaluated in *Eucalyptus* cultivated in four sites in Brazil under two water availability conditions: W - without rainfall exclusion and WE – 33% rainfall exclusion. The positive correlations were presented in green, while the negative correlations were presented in red scale. Meteorological factors: maximum (T_{mx}), minimum (T_{mn}) and average (T_{ave}) temperatures, precipitation (P), soil water deficit (SWD), annual water use index (WI), maximum vapor pressure deficit (VPD), aridity index (DRY), water use efficiency (WUE). Wood traits: wood density (WD), vessel diameter (VD), vessel density (VDn), vessel area (VA), vessel wall thickness (VWT), total vessel wall thickness between adjacent cells (t), theoretical hydraulic conductivity (Kth), potential hydraulic conductivity (Ks), lumen conductivity area (LCA), vessel composition within space (S), vessel implosion resistance (IR) and vulnerability index to drought (VI). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Climate-wood correlations

A Pearson's correlation network was constructed between meteorological variables and wood traits (Fig. 4). There is evidence of different interactions with clones and water (W and WE). Differences in the combination strategies and climate-wood intensity were observed for the most productive clone (*E. urophylla*) and the drought tolerant clone (*E. grandis* × *E. camaldulensis*).

Even though the wood density was evaluated annually, it did not show significant correlation with the meteorological variables for the two clones. However, the density in *E. urophylla* wood in W and WE occurs in a more connected way, with correlations with the wood traits.

SWD and WUE in the W condition presented weak connectivity between the nodes for both clones, meaning that there is a low relation in the no rainfall exclusion condition between the wood traits and meteorological variables. *E. grandis* × *E. camaldulensis* – WE, SWD showed greater proximity between xylem traits and meteorological variables, indicating the greatest correlations. The annual meteorological averages at the four sites had little influence on the wood traits of *E. urophylla* – W (Fig. 4a), except for VWT, t and IR, which had a positive correlation (0.626; 0.605 and 0.492, respectively), with T_{mn}. VPD was related to moderate intensity with VWT and t, while DRY had a negative correlation with LCA.

The 33% rainfall exclusion resulted in a greater number of climate-wood correlations for *E. urophylla* (Fig. 4b). The most correlated meteorological variables were T_{mn}, T_{mx}, P, SWD and WUE. T_{mx} positively correlated with VA and Ks, and negatively with VWT. Higher T_{mn} results in an increase in VWT. The largest WUE promoted a decrease in the vessel density (VDn) and vessel implosion resistance (IR). Increases in precipitation and soil water deficits decreased the vessel double-walls (t) and composition within space (S), respectively. Wood density related to WUE in a positive way.

Weak relationships were found for *E. grandis* × *E. camaldulensis* – W, although significant (Fig. 4c). There was an influence of T_{mx}, P, VPD and WUE. T_{mx} had a positive effect on IR and a negative effect on WD. Increases in precipitation promote increases in VWT and t. WUE also positively correlated with VWT, t, S, VI and Kth. VWT represents a strongly connected node in the evaluated variables module in *E. grandis* × *E. camaldulensis* – WE, and correlates with five meteorological variables: T_{mn}, T_{ave}, SWD, WI and VPD (Fig. 4d). Six strong correlations were established between meteorological variables and wood traits: T_{mn} × VWT (-0.773), T_{ave} × VWT (-0.725), T_{ave} × t (-0.807), T_{ave} × IR (-0.704), SWD × t (0.708) and VPD × VWT (-0.738).

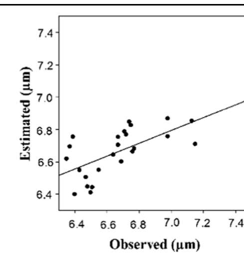
The WE condition enabled different links of the clones, including for the SWD effect, meaning that the wood traits are more altered in lower water supply conditions. The correlations between meteorological variables and wood traits showed that VWT was strongly correlated regardless of the clone and the water availability condition, being the

Table 2
Multiple linear regression equations and precision statistics for the vessel wall thickness (VWT) prediction of *Eucalyptus urophylla* and *E. grandis* × *E. camaldulensis* in two water availability conditions: W - without rainfall exclusion and WE − 33% rainfall exclusion due to meteorological variables in 4 sites in Brazil.

E. urophylla – W

$\mathbf{VWT} = 8.0480 - 0.1025{*}\mathbf{T_{mx}} + 0.0002{*}\mathbf{P} + 1.0118{*}\mathbf{VPD}$
r^2_{aj}: 0.66
RMSE: 1.83%

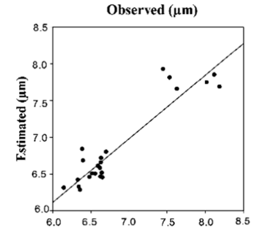
Coefficients:	Betas	Std. Error	t value	Pr (>| t |)
Intercept		8.688e-1	9.263	1.13e-8*
T_{mx}	1.7%	2.756e-2	−3.720	0.00135*
P	0.3%	9.684e-5	2.672	0.01465*
VPD	98%	1.629e-1	6.211	4.56e-6*



E. urophylla – WE

$\mathbf{VWT} = 19.2679 - 0.4998{*}\mathbf{T_{mx}} + 1.8095{*}\mathbf{VPD}$
r^2_{aj}: 0.84
RMSE: 3.34%

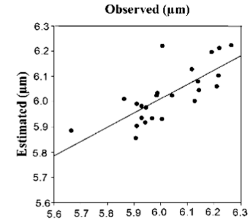
Coefficients:	Betas	Std. Error	t value	Pr (>| t |)
Intercept		1.3833	13.93	4.45e-12*
T_{mx}	5.6%	0.0493	−10.13	1.54e-9*
VPD	94.4%	0.2294	7.89	1.03e-7*



E. grandis × *E. camaldulensis* – W

$\mathbf{VWT} = 8.4870 - 0.1014{*}\mathbf{T_{ave}} + 0.0003{*}\mathbf{P} - 0.8498{*}\mathbf{WI}$
r^2_{aj}: 0.43
RMSE: 1.64%

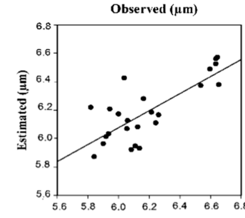
Coefficients:	Betas	Std. Error	t value	Pr (>| t |)
Intercept		1.1253	7.542	2.86e-7*
T_{ave}	1.87%	0.0438	−2.312	0.0315*
P	0.03%	0.0001	4.282	0.0004*
WI	98.1%	0.2747	−3.094	0.0005*



E. grandis × *E. camaldulensis* – WE

$\mathbf{VWT} = 9.1997 - 0.1812{*}\mathbf{T_{mn}} + 0.3931{*}\mathbf{DRY}$
r^2_{aj}: 0.65
RMSE: 2.49%

Coefficients:	Betas	Std. Error	t value	Pr (>| t |)
Intercept		0.6334	14.52	2.01e-12*
T_{mn}	8.4%	0.0336	−5.396	2.37e-5*
DRY	91.6%	0.1715	2.292	0.0323*



T_{mx}: maximum temperature; P: precipitation; VPD: maximum deficit vapor pressure; T_{ave}: average temperature; WI: water use index; DRY: aridity index. r^2_{aj}: adjusted determination coefficient, RMSE: root mean square error. The percentage was determined by the sum of the scaled betas (Kelley and Maxwell, 2003).

* Significant by the *t* test (α = 5%).

link between the nodes. Thus, multiple regressions were adjusted to isolate this characteristic and to identify the explanation intensity of the meteorological variables.

3.2. VWT estimates by meteorological variables

The air temperature was present in all equations of the VWT estimate (Table 2) under the W and WE conditions. The VWT variation of both clones studied in this work obtained the best adjustments in the rainfall exclusion condition (WE), with an explanation of 84% by meteorological variables, while it was necessary to use precipitation as the third variable in W condition to improve the equation.

T_{mx} and VPD explain VWT for *E. urophylla*, regardless of water condition. The WI variable explains 98% in *E. grandis* × *E. camaldulensis* - W, and the WE condition is explained 91.6% by DRY. Thus, it appears that *E. urophylla* was influenced by VPD and *E. grandis* × *E. camaldulensis* of variables linked to water, such as WI and DRY.

3.3. Annual VWT and IR influenced by lower precipitation and high air temperature

There was an annual variation of VWT and IR in the two clones among the four different growth sites of the trees, whose years of lower annual precipitation and higher annual average air temperature are highlighted in blue and orange, respectively (Fig. 5).

VWT showed little variation between the studied clones and evaluated water availability conditions, with site 4 having the greatest variation for *E. urophylla* – WE. Site 4 presents the highest seasonality of the soil water deficit. Year 1 and 3 were similar in relation to the soil water deficit, but year 2 had the highest precipitation, which may have influenced year 3. There was a reduction in IR in the two clones in two moments, in the two conditions and in all four sites: from the first to the second year and from the fifth to the sixth year of growth.

E. urophylla had a higher IR in all the years evaluated, except at site 20, with a lower soil water deficit. The IR showed a greater difference in W and WE at site 20 for the two clones. *E. grandis* × *E. camaldulensis* obtained a 62% increase in the vessel resistance of W to WE in the year with the lowest precipitation and the highest temperature (year 2014). The increase for *E. urophylla* was 43% from W to WE. The IR in *E. urophylla* - W increases in all sites in the year after the year with the highest temperature. The IR at site 20, with the lowest soil water deficit, did not differ between the clones for WE. IR is obtained by the relationship between two traits: the diameter of the vessels and the adjacent double walls. The vessel elements in the *Eucalyptus* genus are mostly

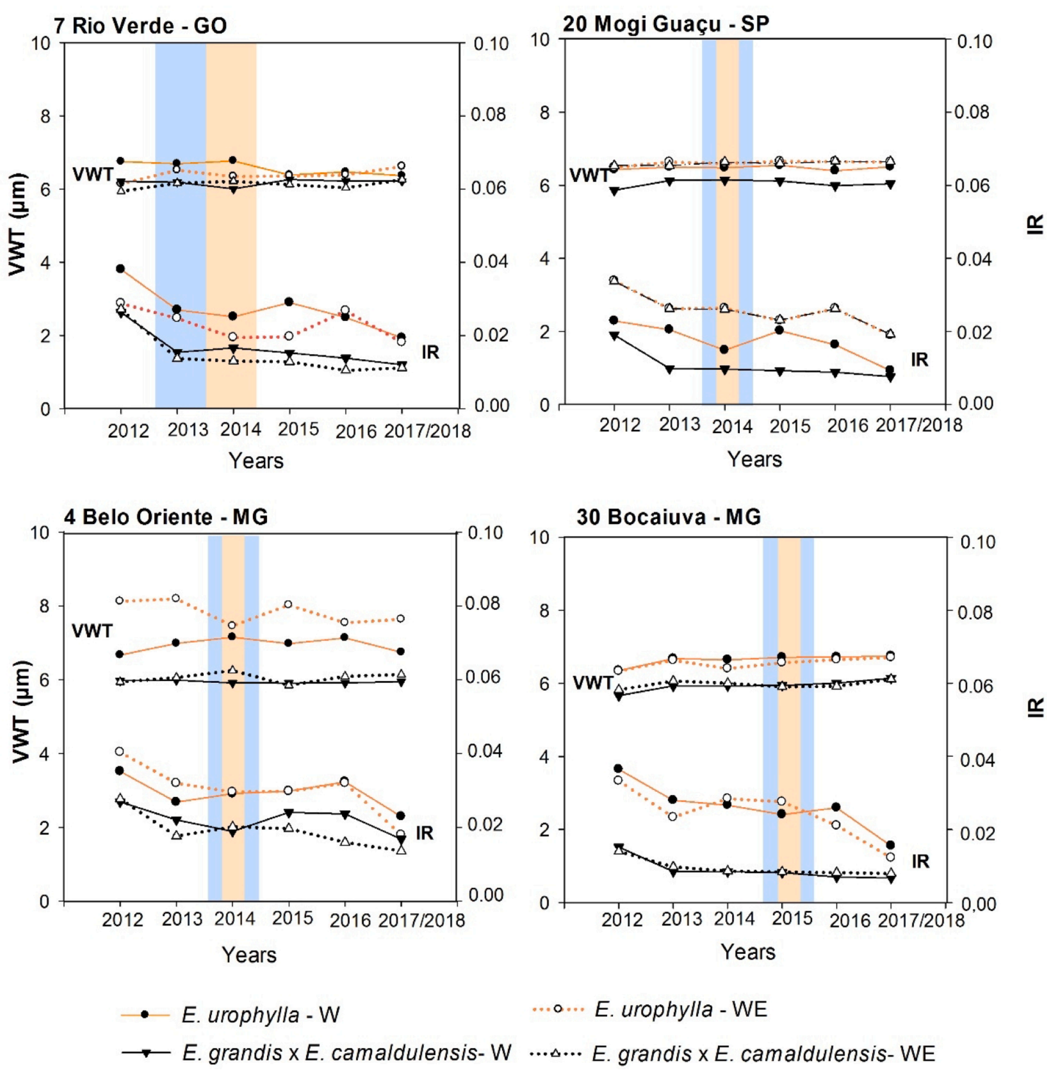


Fig. 5. Annual behavior of vessel wall thickness (VWT) and vessel implosion resistance (IR) of *E. urophylla* and *E. grandis* × *E. camaldulensis* cultivated in four sites in Brazil under two water availability conditions: W: without rainfall exclusion and WE: 33% rainfall exclusion. The blue and orange colors correspond to the years of lowest precipitation and highest temperature, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

solitary; thus, the responses of the annual variations in the IR correspond to the annual variability in the vessel diameters.

Vessel diameter accompanies the initial growth start of the eucalyptus (Fig. 6), and favors the intense conduction of water in an ascending manner in the initial years of all evaluated conditions (site, clone and water availability). The greatest variation in vessel size was determined by clones rather than water availability.

E. grandis × *E. camaldulensis* showed smaller vessel dimensions in the evaluated sites, with little variation except for site 20 with the lowest SWD, which presented larger vessels than in other sites. The variability of the vessels observed in *E. urophylla* – WE, corresponds to the variations which occurred in IR. The combination of precipitation and temperature did not show a clear trend in vessel size.

4. Discussion

4.1. Networks of wood-climate interactions

The intensity and significance with which the meteorological variables influence the development and growth of the species are different (Begum et al., 2012), as verified for the evaluated *Eucalyptus* materials. In general, precipitation and temperature directly influence physiology and xylogenesis (Ali et al., 2019; Quintilhan, 2019), although we did not observe the effect on wood traits of other dependent variables such as VPD, WI and DRY. The dynamics of yield in biomass production is a characteristic of improved materials for short-cycle forest plantations (Booth, 2013) in which adaptability and productive stability promote adaptation to different growing environments. This fact resulted in weak and non-significant correlations between wood traits and meteorological variables in W condition.

The strong correlations between meteorological variables and wood traits in the WE condition may be the result of the physiological control of the trees' water status which was impacted by the rainfall exclusion. The increase in atmospheric vapor pressure deficit has specifically resulted in transpiration rates which increase the water tension in the xylem, in turn favoring embolism and/or implosion of the vessel elements in response to the plant increasing the IR (Zwieniecki et al., 2001). Thus, the increase in VWT and t would be a safety and maintenance strategy for water transport.

The use of network correlation contributed to identify strong and weak connections between nodes; in addition, the positioning of variables indicates interaction connectivity (Langfelder and Horvath, 2008). It is important to note that this technique is a procedure for graphically visualizing a correlation matrix. It is not subject to multicollinearity problems, as it is not necessary to estimate the inverse of any matrix for its use. The efficiency of this innovative technique has already been reported by Silva et al. (2016) and Teodoro et al. (2018).

A low correlation of SWD in *Eucalyptus urophylla* - W was observed in

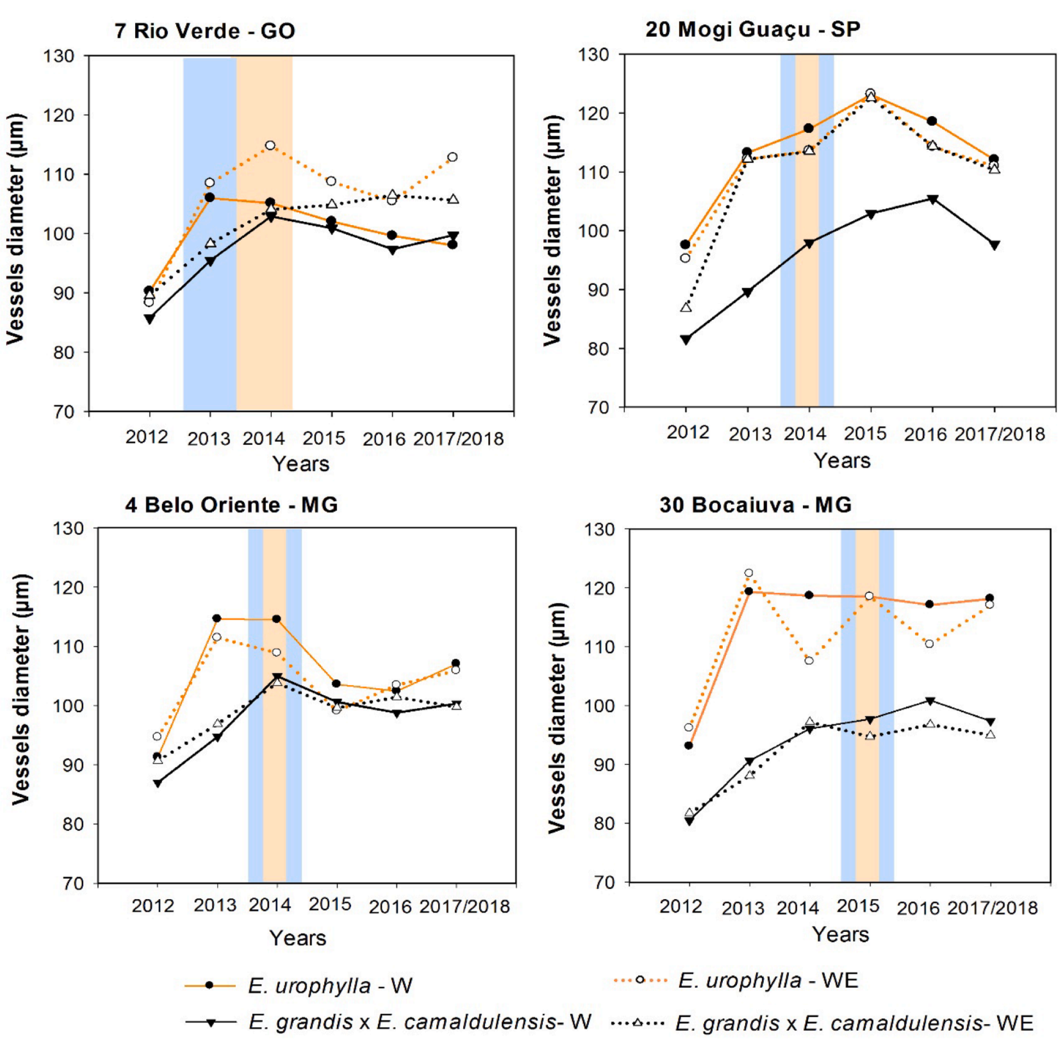


Fig. 6. Annual behavior vessel diameter of *E. urophylla* and *E. grandis* × *E. camaldulensis* cultivated in four sites in Brazil under two water availability conditions: W: without rainfall exclusion and WE: 33% rainfall exclusion. The blue and orange colors correspond to the years of lowest precipitation and highest temperature, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the wood traits, which favors the evaluation of this clone under soil water deficit conditions. However, greater effects on wood occur in situations with temperature changes. It was possible to select the wood trait most influenced by meteorological variables, since the central positioning in the module corresponds to the high interaction connectivity, as observed for VWT in *E. grandis* × *E. camaldulensis* – WE. The weak correlations of SWD and WUE may be related to the adaptation of plastic clones to the environment, constituting variables which are indirectly linked to water supply. Thus, the most pronounced correlations were in the WE condition for *E. grandis* × *E. camaldulensis*.

4.2. Meteorological variables explain *E. urophylla* and *E. grandis* × *E. camaldulensis* wood traits

The diversity and functioning of the ecosystem in tropical forests are regulated by climatic factors such as the average annual temperature and water availability (Araujo et al., 2019; Poorter et al., 2017). Photosynthesis and respiration rates increase exponentially with rising temperatures, so variations in temperature have distinct structural impacts on species, as evidenced by the equations' adjustments (Table 2). *E. urophylla* was sensitive to temperature variations, so this variable was related to VWT. However, the greatest impact on vessel thickening was VPD, whose relationship is exponential with the increase in air temperature (Yuan et al., 2019). This means the higher temperatures decrease the amount of water in the air and consequently the VPD (Massmann et al., 2019). The VPD had a marked effect on *E. urophylla* because it considers air humidity and temperature, indicating that this material is more sensitive to these factors.

VWT was explained by factors directly related to water (WI and DRY) in *E. grandis* × *E. camaldulensis*. This response is due to the intrinsic traits of *E. camaldulensis* which occurs in rainfall zones ranging from 250 to 1600 mm (Butcher and Southerton, 2007), its ability to access groundwater along drainage systems (Mensforth et al., 1994), and its adaptation to tropical and arid climatic zones.

4.3. Annual behavior of VWT, IR and vessels diameter under rainfall exclusion

The constant behavior of VWT over the years is in line with the intra-annual variation of the meteorological variables of the sites, except for site 4. The greater variation in VWT at site 4 (greater soil water deficit seasonality) over the years may have been influenced by the amplitude of WI values between the water availability conditions (Fig. 2b). This fact was confirmed in the equations' adjustment, in which WI explains about 98% of VWT in *E. grandis* × *E. camaldulensis* in the W condition (Table 2).

The drop in IR in the four sites follows a similar behavior to the increase in WUE (in the first years), meaning that there was a trade-off between safety and water use efficiency. This is because the production of photoassimilates used for conversion to biomass comes from the leaves (Yadav et al., 2017), which are also responsible for the negative pressure of water rising in the vessels (Rodriguez-Zaccaro and Groover, 2019). This result suggests that there were coordinated actions between wood traits and leaf traits (Bourne et al., 2017) with impacts on biomass production. However, species of the same genus or hybrids diverge in behavior, with the Eucalyptus genus having diverse traits determined by the climate (Pfautsch et al., 2016), thus increasing the importance of multi-species studies. The conditions of site 30 (lower P, WI and DRY and higher SWD and WUE) in this work demonstrated particular IR behaviors for the clones. *E. urophylla* had a higher IR compared to the extreme conditions of the site with the 33% rainfall exclusion.

Vessels in the xylem formed in the first year of tree growth are larger and numerous, and favor the greater hydraulic conductivity of the tree's wood and thus a high growth rate (Franco, 2018). Annual variability of vessels in *E. grandis* × *E. camaldulensis* – W subsequently occurs in a specific way with less growth and variations, regardless of environmental conditions, and characteristic of plants which have plasticity (Fritsche-Neto and Borém, 2011).

Wood formation does not happen simultaneously with the climatic effect (del Castillo et al., 2016), as we have seen for vessel implosion resistance in relation to the higher temperature of the growth period for *E. urophylla* – W. The carbon allocation process in tropical species occurs hierarchically, especially when there is marked seasonality, spreading hierarchically for breathing, leaves, roots, reserves and sapwood (Schippers et al., 2015). In this sense, the investment in carbon did not go directly to the vessels when there were the highest temperatures in the sites, showing strategies used by the trees (Way and Oren, 2010). However, climate change can increase critical periods and intensify the dynamics of essential elements intrinsic to the tree's survival and consequently increase seasonality.

5. Conclusions and implications

The rainfall exclusion potentiated interrelationships between climate and hydraulic architecture in *E. grandis* × *E. camaldulensis*. Despite the geoclimatic amplitudes of the evaluated sites, it is possible to distinguish a general correlation pattern between meteorological factors and wood traits, which is independent of the variable conditions of the site, having vessel implosion resistance and wall thickness, and a strong relationship between climate and wood.

Greater amplitudes in vessel implosion resistance occurred in the period with higher temperature and less precipitation at site 20. The vessel wall thickness was greater at site 4, with greater seasonality of soil water deficit.

The temperature had a significant influence on the vessel wall thickness estimates of both clones and water conditions, having a strong influence on *E. urophylla*. The water use and aridity index had a high influence on the *E. grandis* × *E. camaldulensis* wood traits.

The vessel wall thickness is important in adaptive studies on species facing climate change, since it correlates with different meteorological variables. The study shows that despite the edaphoclimatic differences between the sites, there are common relationships between climate and wood traits, and vary according to the genetic material. This information highlights the mechanisms and interactions with the climate that make the clones more productive and the other more tolerant to drought and provides insights into the knowledge of the dynamics of the wood in reducing rainfall, which has implications for the selection of promising breeding the facing climate change.

CRediT authorship contribution statement

Ana Paula Câmara: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Graziela Baptista Vidaurre:** Conceptualization, Methodology, Funding acquisition, Project administration, Supervision. **Jean Carlos Lopes Oliveira:** Conceptualization, Methodology, Writing - review & editing, Investigation. **Paulo Eduardo Teodoro:** Methodology, Writing - review & editing. **Maria Naruna Félix Almeida:** Writing - review & editing. **João Vitor Toledo:** Writing - review & editing. **Ananias Francisco Dias Júnior:** Writing - review & editing. **Gabriela Aguiar Amorim:** Writing - review & editing. **José Eduardo Macedo Pezzopane:** Conceptualization, Methodology. **Otávio Camargo Campoe:** Resources, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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