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ORIGINAL ARTICLE

Genotype influences hydraulic architecture and drought resilience in seedlings of seven clones of *Eucalyptus* spp. under two water regimes

O genótipo influencia a arquitetura hidráulica e a resiliência à seca em mudas de sete clones de *Eucalyptus* spp. sob dois regimes hídricos

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ABSTRACT

Droughts have increased tree mortality globally in recent years, compromising the productivity of commercial *Eucalyptus* spp. We investigated stomatal biometric characters, stem anatomical features and hydraulic conductivity in seedlings of *Eucalyptus* spp. under two water regimes in a greenhouse in order to associate them with water deficit tolerance. We concluded that genotypes show a reduction in stomatal pore width, vessel diameter and hydraulic conductivity under conditions of lower water availability. Stomatal density decreases under lower water availability, reinforcing the notion that stomatal cells act to prevent water loss. The vessels are predominantly solitary and rarely geminated. The G1 genotype (*E. urophylla*), with a proportionally smaller reduction in hydraulic conductivity, proved to be more stable to the reduction in water availability, which gives it greater hydraulic safety and, consequently, makes it more suitable for planting in areas prone to water deficiency. Cell percentage in xylem showed little variation between water regimes and/or among genotypes, suggesting that these characteristics are little influenced by the environment. The predominant occurrence of solitary vessels, surrounded by other types of cells, such as parenchyma and vasicentric tracheid, probably helps in conductivity and hydraulic safety.

Keywords: *Embolism; Forest improvement; Hydraulic stress; Water deficit.*

RESUMO

As secas têm aumentado, globalmente, a mortalidade de árvores nos últimos anos, comprometendo a produtividade de *Eucalyptus* spp. comerciais. Investigamos caracteres biométricos estomáticos, características anatômicas do caule e condutividade hidráulica em mudas de *Eucalyptus* spp. sob dois regimes hídricos em casa de vegetação e para associá-los à tolerância ao déficit hídrico. Concluímos que os genótipos apresentam redução na largura dos poros estomáticos, diâmetro dos vasos e condutividade hidráulica sob condições de menor disponibilidade hídrica. A densidade estomática diminui sob menor disponibilidade hídrica, demonstrando que as células estomáticas atuam para evitar a perda de água. Os vasos são predominantemente solitários e raramente geminados. O genótipo G1 (*E. urophylla*), com redução proporcionalmente menor na condutividade hidráulica, mostrou-se mais estável à redução na disponibilidade hídrica, o que lhe confere maior segurança hidráulica e, por conseguinte, mais adequação para plantios em áreas sujeitas à deficiência hídrica. A porcentagem de células no xilema apresentou pouca variação entre os regimes hídricos e/ou entre os genótipos, sugerindo que essas características são pouco influenciadas pelo ambiente. A ocorrência predominante de vasos solitários, cercados por outros tipos de células, como parênquima e traqueídes vasicêntricas, provavelmente auxilia na condutividade e segurança hidráulica.

Palavras-chave: *Embolia; Melhoramento florestal; Estresse hidráulico; Déficit hídrico.*

1. INTRODUCTION

Climatic variations have limited plant water availability (Pfautsch, 2016), influencing the balance of water supply in several parts of the world. Changes have been observed in rainfall distribution and an increase in temperature and evaporation, providing a greater frequency of extreme drought events (Basu et al., 2016).

As with any plant culture, low water availability seriously impairs the survival and productivity of *Eucalyptus* forests (Stape et al., 2010). In Brazil, in 2024, plantations of *Eucalyptus* spp. occupied 8.1 million hectares, representing 77% of total planted forest area in the country (Indústria Brasileira de Árvores, 2025).

Recently, extreme drought events have become more frequent in Brazil because of 1) the expansion of agriculture with serious water and nutritional limitations and 2) climatic instability with irregular and less rainfall observed, even in areas where forestry is already well established (Gonçalves et al., 2013). Several physiological, biochemical, anatomical, and molecular aspects are related to plant tolerance to drought, all acting together when a plant is under water deficit (Isah, 2019; Paula et al., 2012). Water deficit can cause loss of leaf turgor, reduction in relative water content and water potential and stomatal closure with reduction in xylem hydraulic conductivity (Maguire & Kobe, 2015).

Eucalyptus spp. wood anatomy has unique features, such as solitary vessels, vasicentric tracheids and fibro-tracheids, among others, determining a correspondingly unique functionality (Barotto et al., 2016). In this context, studying wood anatomical variations, especially in vessels (diameter and density, number of vessels/area), which are the water-conducting cells in the vertical direction, is particularly useful when seeking plant-water data in each environment (Zanne et al., 2010).

During a severe drought, larger vessel diameter is more vulnerable to drought-induced branch death (Zanne et al., 2010), while smaller vessels provide greater safety against hydraulic failure (Ewers et al., 2007). Gleason et al. (2016) reported that the effects of climate and environment can alter hydraulic efficiency or safety in woody plants, but they do not necessarily alter anatomical properties of the xylem. According to these last authors, this higher hydraulic safety allows plants to operate with greater xylem tension and less carbon-capturing obstruction inside vessels at a given tension. This, in turn, allows plants to reduce root mass and to grow in soils with less water availability, or transpire for longer periods of the day or year (Gleason et al., 2016).

Plants from dry regions with smaller vessel diameters are, in general, better able to manage cavitation because they withstand higher xylem stresses (lower water potential) than plants adapted to humid regions with larger vessel diameters (Bourne et al., 2017). Vessel cavitation reduces xylem hydraulic conductivity and total plant water supply to the photosynthetic surface (Meinzer et al., 2001).

Xylem hydraulic efficiency and vulnerability to cavitation-induced embolism are correlated with several anatomical features, including vessel dimensions and arrangement (Lens et al., 2013). Xylem hydraulic architecture reflects the efficiency and safety of water transport and is regulated, in part, by vessel anatomical features and pits of the conducting cells (Hacke et al., 2006).

We investigated hydraulic characteristics in seedlings of seven clones of *Eucalyptus* spp. under two water regimes in a greenhouse and associated them with water deficit tolerance. We hypothesized that both genotype and environment influence the hydraulic architecture in a similar way. To test this hypothesis our goal was to evaluate stomatal biometric characters, stem anatomical features and hydraulic conductivity in seedlings of *Eucalyptus* spp. under two water regimes in a greenhouse and to associate them with water deficit tolerance.

2. MATERIAL AND METHODS

2.1. Experimental design and sampling

This study was carried out with 90-day-old seedlings of seven clones of *Eucalyptus* spp. donated by Suzano S.A. (Table 1). They were propagated by minicutting, which consists of rooting shoots of vegetatively propagated seedlings (Xavier et al., 2013). In this study, the genotypes were named G1, G2, G3, G4, G5, G6 and G7.

The experiment was carried out in a greenhouse covered with a transparent plastic tarp (150 μm), laterally coated with screens with 30% capacity to intercept daily sunlight, a ceiling height of 3 m and total height of 5 m, located in the municipality of Jaboticabal, State of São Paulo, Brazil (21°14′33′′S, 48°17′55′′W, elevation 616 m). The experiment was carried out for 90 days, between August 6 and November 4, 2020. During the experiment, temperature inside the greenhouse varied from a minimum of 8.1 ºC and a maximum of 45.2 ºC and the relative humidity from a minimum of 8.6% and a maximum of 97%.

Table 1. Species/hybrid and seedling provenances of seven 90-day-old *Eucalyptus* spp. genotypes propagated via minicutting.

Genotypes	Species/Hybrid	Provenance
G1	*E. urophylla*	Turmalina, MG
G2	*E. grandis x E. urophylla*	São Simão, SP
G3	*E. grandis x E. urophylla*	São Simão, SP
G4	*E. grandis x E. urophylla*	Unknown
G5	*E. grandis x E. urophylla*	Unknown
G6	*E. grandis x E. urophylla*	Unknown
G7	*E. grandis x E. urophylla*	Santa Branca, SP

The 90-day-old seedlings were planted in black plastic pots filled with 7 kg of a typical eutroferric Red Latosol sample, clayey, moderate A, kaolinitic-oxidic (LVef) (Centurion & Andrioli, 2000). The soil was previously sieved and fertilized based on fertility analysis of samples sent to a specialized laboratory. Fertilization, per dm^3 of soil, was made with 0.05 g of magnesium carbonate, 0.20 g of calcium carbonate and 1.00 g of simple superphosphate.

Irrigation was performed based on percentages of field/pot capacity and considered as the maximum soil water retention capacity in the pots, as previously determined in laboratory tests. For this procedure, soil samples (500 g) were used and transferred to a funnel lined with a paper filter attached to a beaker, and, later, 200 ml of water were added. After drainage of excess water, the remaining soil material in the beaker was quantified. Three replications were performed, and soil water-holding capacity was determined by average volume of water retained in the soil sample (measured by the difference between volume of added and filtered water) and soil mass (500 g). Soon after, seedlings were planted in pots and irrigated to 100% of field capacity to ensure initial survival.

The experiment was implemented in a randomized block design with one plant per plot (pot) and ten replications. This was a split-plot scheme with two water regimes in the plot and seven *Eucalyptus* genotypes in the subplot, totaling 14 treatments. Water regime 1, corresponding to 60% of field capacity, and water regime 2, corresponding to 30% of field capacity, were defined to verify the effect of water restriction on plant development.

To ensure the maintenance of water regimes, two blocks were weighed daily on a digital electronic scale, and, according to their averages, the necessary irrigation was calculated. In addition, every seven days, all pots were weighed, and water regimes were corrected. Thus, water variation in the water regimes was approximately 50-60% of the field/pot capacity for regime 1 and 20-30% for regime 2.

2.2. Stomatal characteristics

An impression of the epidermis on leaf abaxial surfaces was removed with universal instant adhesive on a glass slide. The leaf region of interest was pressed onto the slide for approximately 10 seconds, the time required for the adhesive to spread and dry sufficiently, allowing impression of the epidermis. The slides obtained were observed and photographed under an optical microscope, using a 40x objective, coupled to a digital camera. Subsequently, to obtain data, images were analyzed, quantifying stomatal pore width, length, width, as well as stomatal density (number of stomata.mm^{-2}), using Image J® software version 1.53m.

2.3. Anatomical stem features

Stem fragments (5 cm) from the base were cut with a scalpel and stored in an FAA solution (50 ml of 95% ethyl alcohol, 5 ml of glacial acetic acid, 10 ml of 30-40% formaldehyde and 35 ml of distilled water) (Johansen, 1940) for sample conservation until slide preparation.

Anatomical analysis followed the recommendations of the International Association of Wood Anatomists (1989). Samples (1.5 cm^3 blocks) were softened in boiling water and glycerin (4:1) for approximately 30 minutes. Transverse sections 15 µm in thickness were cut using a sliding microtome (Johansen, 1940). Vessel diameter and density were evaluated from images captured from the slides, using a camera attached to a Zeiss® light microscope, and measurements were made using the Image Pro Plus 6.0® program.

Percentages of fibers and vessels, as well as axial and radial parenchyma, were also obtained, counting the different types of cells, using the Grid Mask program, where 25 points marked in 15 1 mm^2 sectors of the transverse plane were taken randomly in the photo field.

2.4. Potential hydraulic conductivity

From the values of vessel diameter and vessel density, we calculated potential hydraulic conductivity (Equation 1) by the Hagen Poiseuille equation, as described by Sterck et al. (2008) and Poorter et al. (2010). We used two equations as follows:

$$Kp = \left(\frac{\pi \, p_w}{128n}\right) \times VD \times Dh^4 \quad (1)$$

where *Kp* is potential hydraulic conductivity (in kg m MPa-1 s^{-1}), ρw is water density at 20 °C (998.2 kg m^{-3}), η is the viscosity index of water (1.002 x 10^{-3} MPa x s^{-1} at 20°C), *VD* is vessel density (cells / m^{-2}), and *Dh* is hydraulically weighted vessel diameter (mm).

Diameter of hydraulically weighted vessels (*Dh*) was then obtained by the expression:

$$Dh = \left(\frac{\sum d^4}{N}\right)^{0.25} \quad (2)$$

where *d* is equivalent vessel diameter (mm), and *N* is the number of vessels measured.

2.5. Data analyses

The data were analyzed according to a randomized block design, in a split-plot scheme, with two water regimes in the plot (water regime 1 and 2, respectively, of 60% and 30% of field capacity), and seven eucalyptus genotypes in the subplot (G1 to G7), totaling 14 treatments. The water regimes were defined to evaluate the effect of water restriction on plant development without, however, impairing survival under lower water availability.

Data were analyzed for normality using the Shapiro-Wilk test and the Levene test for homoscedasticity at 5% probability. When one of the assumptions for the Analysis of Variance was not met, data transformation and verification of compliance with the assumptions were carried out. The characters transformed by Box-Cox were stomatal width, vessel density, hydraulic conductivity, fiber percentages, axial parenchyma, radial parenchyma, and total parenchyma. Analyses of variance were performed using the AgroEstat program (Barbosa & Maldonado Júnior, 2015), and means were compared using the Tukey test at 5% probability.

3. RESULTS

3.1. Stomata

Stomatal length differed only between water regimes, being 2.3% smaller in the more restrictive water regime for plants (WR2). For stomatal width and density, differences were observed between water regimes and among genotypes. The WR2 provided a reduction of 10.2% and 13,1% in stomatal width and density, respectively. Among genotypes, when considering the average across both water regimes, G7 presented wider stomata than G2 (14.2%), G4 (8.4%) and G6 (10.3%), and G1 presented wider stomata than G2 (13.3%) and G6 (8.4%). G5 stood out with high stomatal density, but with no difference in relation to G6, but superior to the other genotypes (Figures 1a-c and 2).

All genotypes showed a reduction in stomatal pore width under lower water availability (WR2), ranging from 73.9% in G1 to 142.9% in G7. In the regime of greater water availability (WR1), genotype 7 (G7) presented wider stomatal pores than G1 (27.5%), G2 (21.4%) and G4 (18.6%), and G5 also presented wider stomatal pores than G1 (17.5%), but under water limitation, no difference occurred among genotypes (Figures 1d and 2).

3.2. Stem anatomy and hydraulic conductivity

Genotypes showed different behavior in the two water regimes for vessel diameter and density and potential hydraulic conductivity (Kp). All genotypes showed a reduction in vessel diameter and hydraulic conductivity under lower water availability (WR2). Without water limitation (WR1), genotypes G5, G6 and G7 had wider vessels than G2, and under lower water availability, G1 had wider vessels than G2 and G4 with no differences among the other genotypes (Figures 3 and 4).

Differences in vessel density between water regimes were observed for G5, which showed lower vessel density under lower water availability, and for G1 and G2, showed higher vessel density in this condition. Only G2 and G5 differed from each other, with higher vessel density observed in G2. Under greater water availability, G5 presented greater vessel density than others; G7 also had higher vessel density than G1 (Figure 3b).

In WR1, G5 showed higher potential hydraulic conductivity than G1 and G2. In WR2, G1 showed higher potential hydraulic conductivity than G2, G4 and G7 with no differences among the other genotypes (Figure 3).

Reductions in vessel diameter and hydraulic conductivity under lower water availability occurred differently, as observed in all genotypes. In this sense, G1 showed the smallest reduction in vessel diameter (10.7%) and hydraulic conductivity (27.1%), while G4, G5, G6 and G7 showed similar reductions, ranging from 24.5% to 28.9% in vessel diameter and from 69.8% to 74% in hydraulic conductivity. The variations observed in vessel density were smaller than those observed in vessel diameter and hydraulic conductivity and did not

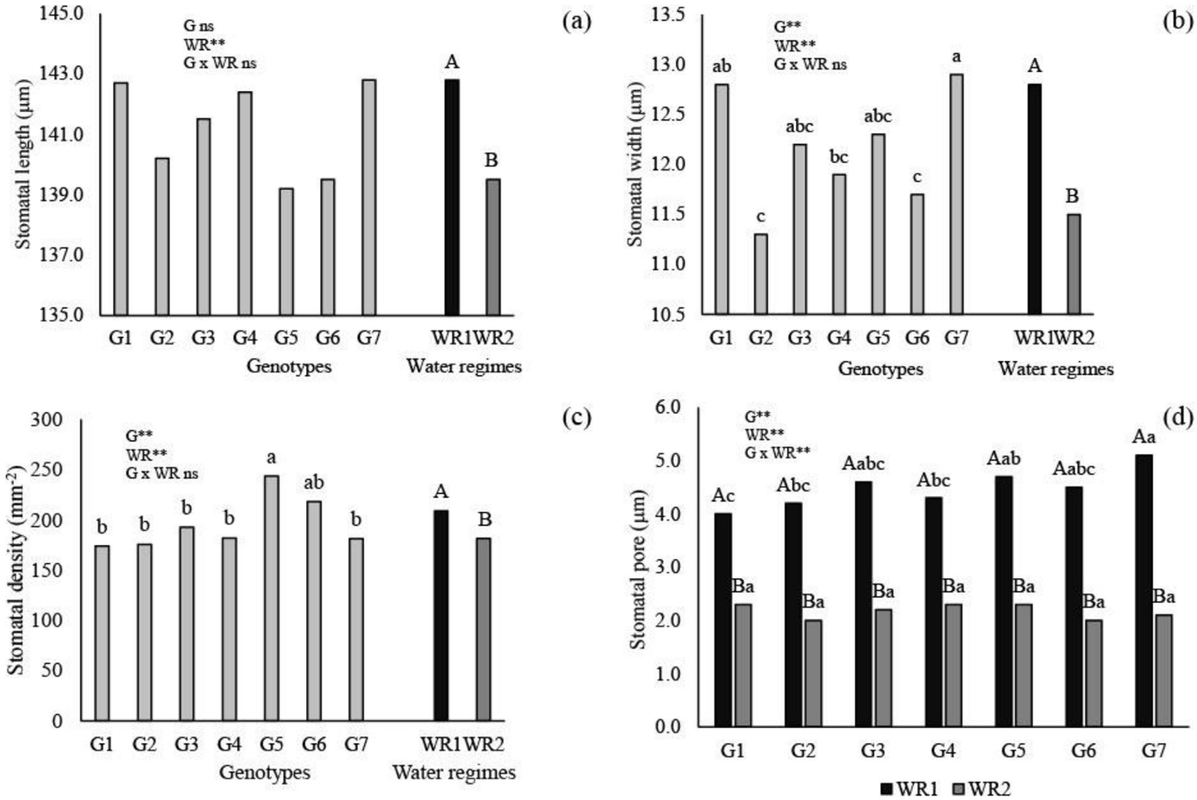

Figure 1. Means of length (a), width (b), density (c) and stomatal pore width (d) of the seven genotypes of *Eucalyptus* spp. cultivated under two water regimes (WR1 and WR2 – respectively, 60% and 30% of the soil's maximum water retention capacity). *, **, ns - significant effect at 5%, 1% and non-significant at 5% by the F test. G – Genotypes; WR – Water Regimes. Means followed by the same lowercase letters compare genotypes, and uppercase letters compare water regimes; they do not differ by Tukey's test at 5% probability.

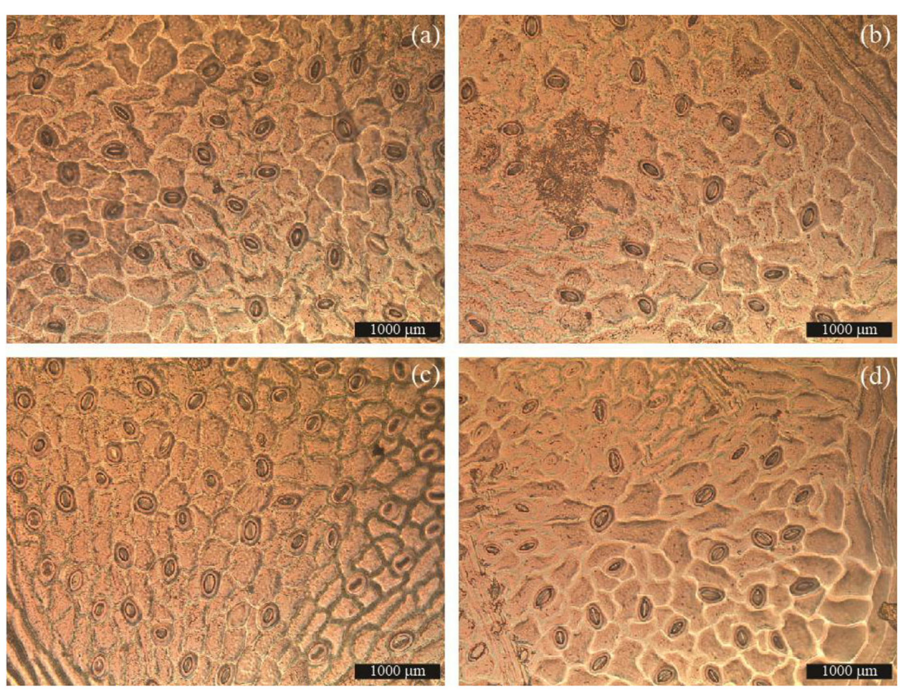

Figure 2. Aspects of stomata in abaxial epidermis of *Eucalyptus* leaf. Genotype 1 in WR1 (a). Genotype 1 in WR2 (b). Genotype 7 in WR1 (c). Genotype 7 in WR2 (d). WR1 and WR2 – respectively, 60% and 30% of the soil's maximum water holding capacity.

occur in the same direction. G1 and G2 increased vessel density in WR2 by 8.7% and 11.2%, respectively, and G5 showed a reduction of 18.8%; for the other genotypes, the variation in this characteristic was not significant.

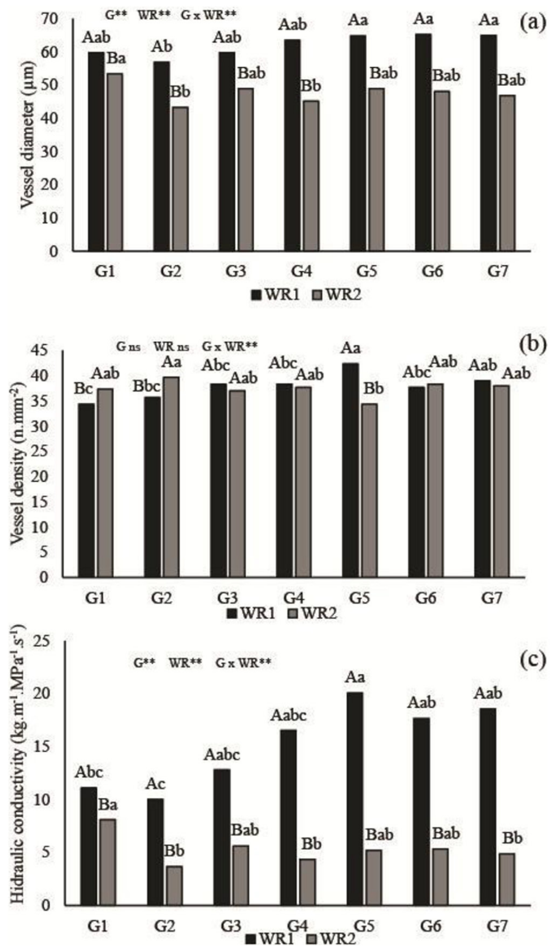

Figure 3. Vessel diameter (a), vessel density (b) and hydraulic conductivity (c) of the seven genotypes of *Eucalyptus* spp. cultivated under two water regimes (WR1 and WR2 – respectively, 60% and 30% of the soil's maximum water retention capacity). **, ns - significant ($p<0.05$) effect, respectively, by the F test G – Genotypes; WR – Water Regimes. Means followed by the same uppercase letters compare water regimes for each clone, and lowercase letters compare clones in each water regime; they do not differ from each other by Tukey's test at 5% probability.

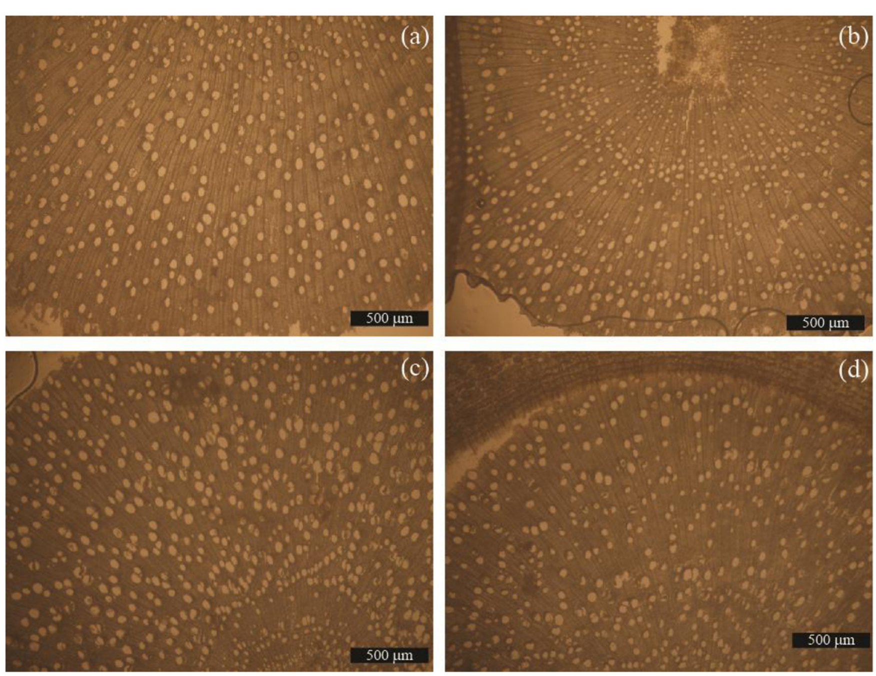

Figure 4. Transverse section of *Eucalyptus* stem. Genotype 1 in WR1 (a). Genotype 1 in WR2 (b). Genotype 5 in WR1 (c). Genotype 5 in WR2 (d). WR1 and WR2 – respectively, 60% and 30% of the soil's maximum water holding capacity.

It was observed that vessels are predominantly solitary, rarely geminated, and had a mean diameter of 62 µm in WR1 and 47 µm in WR2 but mean vessel density did not change between the two water regimes (37-38 vessels mm^{-2}) (Figures 3 and 4).

The proportion of fibers, vessels, and parenchyma showed little variation depending on the factors evaluated (Figure 5). The genotype by water regime interaction and the isolated effect of water regimes were not significant ($p>0.05$) for these characteristics, but there were differences among genotypes for the percentage of axial, radial, and total parenchyma and vessel. On average, between the water regimes, the variation among genotypes ranged from 38.4% to 43.1% for fiber percentage, 16.6% to 23.8% for vessel percentage, 7.5% to 15.9% for axial parenchyma, 23.5% to 30.7% for radial parenchyma, and 33.7% to 41.6% for total parenchyma. This variation was small between water regimes, reinforcing that these characteristics are little influenced by the environment. Genotype G3 showed a higher percentage of axial parenchyma in relation to G5, G6 and G7; G6 and G7 had a higher percentage of radial parenchyma than G5, and for percentage of total parenchyma, G5 also had the lowest mean value, differing, however, only from G3 (Figure 5).

4. DISCUSSION

The results demonstrate that genotypes presented reductions in stomatal pore width, length and width, vessel diameter and hydraulic conductivity under lower water availability. Stomatal density was reduced in low water availability. In WR2, genotypes G1 and G2 increased in vessel density, but decreased in diameter, compared to

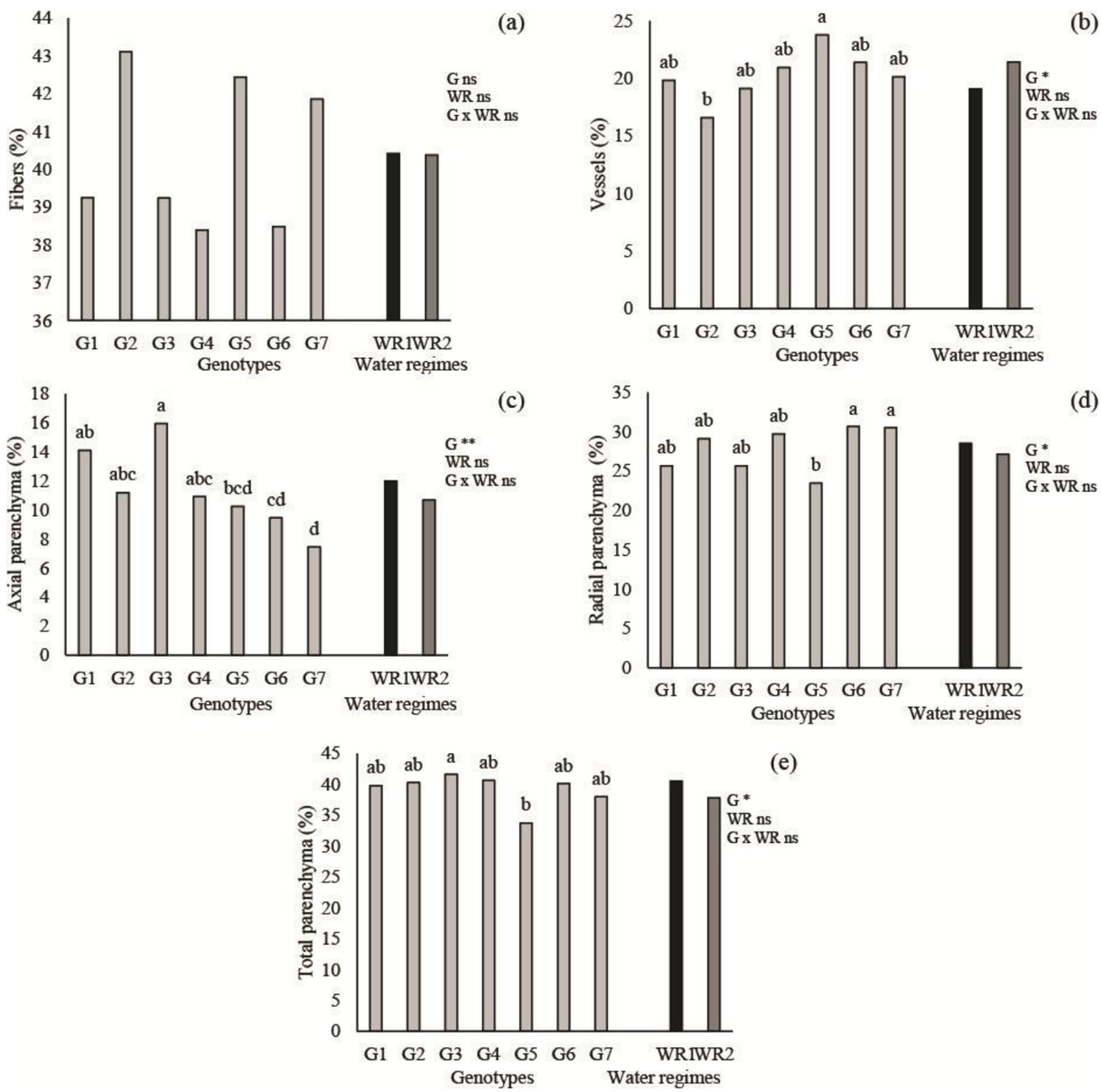

Figure 5. Means of percentage of fibers (a), vessels (b), axial parenchyma (c), radial parenchyma (d) and total parenchyma (e) of seven genotypes of *Eucalyptus* spp. cultivated under two water regimes (WR1 and WR2 – respectively, 60% and 30% of the soil's maximum water retention capacity). ** - significant effect; ns – not significant ($P<0.01$) by the F test. G – Genotypes; WR – Water regimes; Means followed by the same letter do not differ from each other by the Tukey test at 5%.

the regime with less water limitation. However, in contrast to G2, we highlight that G1 presented wider vessels and higher hydraulic conductivity under water limitation. The cell percentage in xylem was not influenced by water regimes, but parenchyma percentage varied among genotypes.

4.1. Stomata

The stomatal density of G5 was 40% higher than G1, 38% higher than G2, 34% higher than G4 and G7, and 26% higher than G3. Although stomatal density was 15% lower in water regime 2, the genotypes were similarly affected by the reduction in water availability. The higher stomatal density displayed in G5, in relation to the other genotypes, except G6, may indicate that this genotype has lower hydraulic stability under low water availability since higher stomatal density results in greater water loss. On the other hand, changes in stomatal density in response to water deficit vary among species and are dependent on the severity of stress with a reduction in stomatal density being more common under more severe stress (Hamanishi et al., 2012).

In conditions of low water availability, reduction in stomatal density, as observed in WR2, is a protective mechanism that contributes to a reduction of leaf transpiration (Hamanishi et al., 2012). The behavior of stomata can be affected by environmental factors, such as water deficit, vapor pressure deficit, temperature, CO_2 concentrations and light (Laanemets et al., 2013; Šigut et al., 2015). In addition, short-term responses can occur, such as stomatal closure, which, in this study, is represented by stomatal pore width, or long-term responses affecting size, e.g., stomatal length and density because of environmental changes. However, these changes are genotype-dependent (Haworth et al., 2013; DaMatta et al., 2016), like the results obtained here. Also, alteration in the functioning of stomata can constitute a physiological compromise because when it is opened, they allow carbon dioxide assimilation, but when closed, they decrease the transpiration rate, conserving water and reducing the risk of plant dehydration (Matthews et al., 2017). This is one of the most important defense mechanisms of plants against excessive water loss and eventual death by desiccation (Larcher, 2004). On the other hand, reducing transpiration by closing the stomata is a strategy to avoid dehydration (Buckley, 2019), not necessarily a characteristic of drought tolerance.

Most *Eucalyptus* species in operational plantations have a high-water consumption when it is easily available (Correia et al., 2014). However, as water availability decreases, transpiration is significantly controlled, causing partial or total stomatal closure (Stape et al., 2010). This could result in reduced forest productivity (Larcher, 2004; Stape et al., 2010).

4.2. Stem anatomy and hydraulic conductivity

Our study evaluated one aspect not commonly explored in *Eucalyptus* spp. culture: xylem hydraulic conductivity, which is mainly determined by the diameter and density of vessels (Poorter, 2008; Zanne et al., 2010). For example, in places with high water availability, it is well known that hydraulic capacity is increased by decreasing the resistance of water flow in the xylem, as characterized by wider vessels. However, under conditions of water scarcity, large, hydraulically efficient vessels are more likely to have hydraulic failures (Jacobsen et al., 2005) or drought-induced cavitation (Brodribb et al., 2016). Therefore, understanding the effects of water deficit on plants is vital for improving agricultural and forestry management and practices (Rampino et al., 2006), and one of the alternatives to mitigate its effects is the selection and use of genotypes with characteristics of tolerance to water deficit for implantation in programs of genetic improvement, which, currently, is one of the biggest challenges in forest management.

Higher resistance to cavitation is often associated with narrower vessels, as well as higher vessel density, for a given conduction area (Lens et al., 2011). Under lower water availability, G1 had wider vessels than G2 and G4. In the same condition, G2 showed higher vessel density than G5 with no differences among other genotypes.

Thus, G2 compensates, at least in part, for narrower by higher vessel density under lower water availability. Under greater water availability, G5, G6 and G7 had wider vessels than G2; G5, with vessel density like G7, had higher vessel density than other genotypes, indicating that they are genotypes with potential for conditions without water limitation. In this condition, G1 also presented the lowest vessel density. In another condition, in WR2, G5 showed intermediate vessel diameter and the lowest vessel density among the genotypes, demonstrating the ability to adjust to low water availability, opposite to what occurred with the stomata. However, the reduction in vessel density can be a factor that compromises productivity in conditions of water limitation.

Wider vessels are more efficient in carrying water since they offer less friction on the sides of the walls and carry a greater amount of liquid (Baas et al., 2004). As a result, species subject to lower water availability tend to have narrower vessels, while vessel density tends to increase to compensate for efficiency in water transport and avoid embolism (Baas et al., 1983).

Xylem hydraulic conductivity is highly variable among species (Maherali et al., 2004), and variations within species may also occur in different environments (Cornwell et al., 2007), as observed in our study. In certain situations, plants may exhibit characteristics related to hydraulic safety, such as narrower vessels and higher density, to avoid interruption of water conduction owing to the formation of gas bubbles inside the xylem (embolism), or related to hydraulic efficiency, such as wider vessels, which, on the other hand, can increase the risk of embolism (Hacke et al., 2006; Gleason et al., 2016).

According to Pfautsch (2016), it is possible to investigate climate adaptation by studying the characteristics of axial conducting cells in *Eucalyptus* because this genus has a long evolutionary history under a wide diversity of environments. In a study using wood from 28 *Eucalyptus* species from a wide xeric gradient across Australia, these authors reported that hydraulic architecture reflects the adaptive variation of *Eucalyptus* spp. in response to climate variation. Under conditions of limited water, the selection of plant materials should favor genotypes that develop hydraulically safer characteristics, such as those mentioned above, reducing the risk of embolism and cavitation in the xylem (Gleason et al., 2016).

In WR2, genotypes G1 and G2 presented an increase in density and a decrease in vessel diameter, compared to the regime without water limitation, which could at first demonstrate hydraulic security under lower water availability. However, in contrast to G2, G1 presented wider vessels and higher potential hydraulic conductivity under water limitation (WR2), indicating that they are genotypes with different behaviors and strategies in the face of water deficit.

In a study with *E. camaldulensis* plants subjected to water stress for 70 days, Barigah et al. (2021) verified that narrower vessels were more vulnerable to cavitation. This observation, however, contradicted the well-founded paradigm that wider vessels are more prone to cavitation than narrower vessels for most species. Although *Eucalyptus* presents predominantly solitary vessels, an explanation for these results may be related to the presence of cells that surround vessels, such as libriform fibers, fibro-tracheids, vasicentric tracheids and living parenchyma (Barigah et al., 2021). These cells can contribute to xylem efficiency by increasing connectivity between vessels and/or hydraulic safety by reducing the propagation of embolism through the xylem (Barotto et al., 2016).

In *E. grandis*, for example, it was observed that narrower vessels have wider pits and thinner membranes than wider vessels, making the former more vulnerable to cavitation and, thus, breaking with such paradigm (Fernández et al., 2019; Barigah et al., 2021). This, however, is not well documented and needs further study.

The smaller percentage reduction in potential hydraulic conductivity that occurred in WR2 for G1 indicates that this genotype is more stable to the reduction in water availability and, therefore, possesses greater water security. This likely results from the smaller reduction in vessel diameter observed in this genotype in that condition, being a very important factor for potential hydraulic conductivity, and the low value of potential hydraulic conductivity in WR1, notably in relation to G5. In WR1, G5 showed higher potential hydraulic conductivity than G1 and G2, and G6 and G7 also had higher potential hydraulic conductivity than G2. G1 presented good performance in several evaluated characters, and, in this sense, it may present greater hydraulic safety. This genotype seems to have a strategy that allows it to maintain its metabolic activity and, hence, survive in environments of low water availability (high tension in the xylem). This characteristic may be related to the genotype species, since *E. urophylla* is known to have greater stability. It seems to handle some gas bubbles inside xylem cells in a given tension, i.e., withstand the effect of embolism at a higher level (Gleason, et al., 2016).

Theoretically, the presence of vasicentric tracheids contributes to water conduction. Specifically, they are less vulnerable to cavitation than vessels, and a certain degree of isolation exists between them, preventing air from entering a cavitated vessel. Thus, wood with a higher proportion of vasicentric tracheids would be more resistant to xylem cavitation than one with a lower proportion of this type of cell, even when both have similar characteristics. Vasicentric tracheids could also act as water reservoirs, increasing hydraulic conductivity (Carrasco et al., 2015; Pfautsch, 2016). The presence of vasicentric tracheids can be considered a strategy associated with other wood features with the objective of increasing safety in water transport. In a study on the flora of southern California and similar areas, Carlquist (1985) found a greater presence of vasicentric tracheids in the wood of several species in areas with low water availability. Thus, the presence of these cells in *Eucalyptus* spp. can be considered a strategy to assist in water transport.

In *Eucalyptus* spp., vessels are predominantly solitary, and the presence of vasicentric tracheids, as also observed in other angiosperm species, is essential for cell communication (Carlquist, 2012), increasing the connection among xylem cells (Loepfe et al., 2007; Martínez-Vilalta et al., 2012). Furthermore, it was proposed by Carlquist (1985) that vasicentric tracheids could constitute a subsidiary water conduction system when vessels are cavitated.

The proportion of fibers, vessels and parenchyma showed little variation as a function of the factors evaluated, and differences were only observed among the genotypes for percentage of axial, radial and total parenchyma, suggesting that these characteristics do not undergo major changes along cultivation conditions and are relatively stable among genotypes. On average, 40.40% of transverse section of stem is occupied with fibers, 20.24% with vessels, 11.34% with axial parenchyma and 27.83% with radial parenchyma. Higher percentages of axial parenchyma were observed in G3 in relation to G5, G6 and G7, in G1 in relation to G6 and G7 and in G2 and G4 in relation to G7. The radial parenchyma had less variation with differences only in the G6 and G7 genotypes, each having higher percentages in relation to G5. For percentage of total parenchyma, G5 also had the lowest mean value, differing, however, only from G3 (Figure 5).

Axial and radial parenchyma are part of xylem tissue and influence water relationships in plants (Klock et al., 2005). They are involved in water storage and carbohydrates and their mobilization in wood, in addition to their importance in defending against mechanical damage (Alves and Angyalossy-Alfonso, 2002). These two types of parenchyma constitute accessory tissues to the conducting elements, giving rise to greater osmotic force within the vessels through the mobilization of osmotically active substances, increasing sap flow in the vessels (Braun, 1984). Available information indicates that storage of reserved metabolites such as starch in the parenchyma cells may be helpful in removal embolism and increase in pulling of water in vessels (Longui et al., 2018). According to Mooney & Gartner (1991) and Carlquist (2001) starch is hydrolyzed in sugar and if that sugar is transported into vessels, it increases the osmotic potential. This mechanism may pull water and help in recovery of air embolism (Longui et al., 2018).

In addition to vessels and fibers, the presence of parenchyma can aid in water storage. If parenchyma cells are adjacent to the vessel and have good hydraulic connections, they can contribute to the repair of embolism, and because they are lignified, they help to prevent deformation of xylem elements (Holbrook, 1995).

In the case of *Eucalyptus* spp. wood, vasicentric tracheids can play an auxiliary role in water transport, especially when vessels are compromised by embolism, as demonstrated in the study by Barotto et al. (2016). These authors, studying commercial genotypes of three *Eucalyptus* species, reported that cells adjacent to vessels showed correlations with functional variables, suggesting that they contribute to increasing connectivity between vessels and to the efficiency of xylem conduction, decreasing the probability of propagation of the embolism in the tissue, thus providing greater hydraulic safety.

In a study with *E. camaldulensis* seedlings subjected to water stress for 70 days, Barigah et al. (2021) concluded that the cells surrounding vessels contribute to water transport from xylem by increasing the connectivity between different cell types and increasing hydraulic safety by preventing embolism propagation when a vessel is embolized. Therefore, the cells around vessels may be involved in this phenomenon as they are correlated, and these results may provide new insights into the relationships between wood anatomy and its hydraulic capacity.

5. CONCLUSIONS

We concluded that genotypes show a reduction in stomatal pore width, vessel diameter and hydraulic conductivity under conditions of lower water availability. Stomatal density decreases under lower water availability, demonstrating that stomatal cells act to prevent water loss. The vessels are predominantly solitary and rarely geminated. The G1 genotype (*E. urophylla*), with a proportionally smaller reduction in hydraulic conductivity, proved to be more stable to the reduction in water availability, which gives it greater hydraulic safety and makes it more suitable for planting in areas prone to water deficiency. Cell percentage in xylem showed little variation between water regimes and/or among genotypes, suggesting that these characteristics are little influenced by the environment. The predominant occurrence of solitary vessels, surrounded by other types of cells, such as parenchyma and vasicentric tracheid, probably helps in conductivity and hydraulic safety.

The G5 and G7 genotypes, which were most affected by reduced water availability, should preferably be allocated to areas not subject to water stress, while the more stable G1 and G2 genotypes can be used as sources of drought tolerance in breeding programs. Field experiments should be encouraged and conducted to certify the results obtained here in pots.

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AUTHOR CONTRIBUTIONS

BZ and RCP: Conceptualization, Data curation and Formal analysis; BZ, RCP, ELL, DCD and ICGS: Methodology, Writing – review & editing.