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Relationships between diameter growth and functional wood anatomy in *Eucalyptus globulus* clones

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Abstract

Aim of study: We aimed to 1) analyze the variability of wood hydraulic anatomical traits in 10 clones of *E. globulus* Labill. with different growth rates, and 2) determine whether the magnitude of diameter growth affects the relationships between anatomical variables and diameter at breast height (DBH).

Area of study: 25-year-old common garden trial in Balcarce, Buenos Aires, Argentina.

Material and methods: We measured vessel diameter and number per unit area in transverse histological sections of stem wood, and calculated the proportion of vessel lumens, vessel composition (S), and theoretical specific hydraulic conductivity (Ks) of 10 *E. globulus* clones of high (HG) and low (LG) mean growth rates (measured as DBH) under field conditions.

Main results: There was a difference in the range of variability in hydraulic anatomy between HG and LG clones, with LG clones showing a wider range. HG clones had wood with larger and fewer vessels and higher S compared to LG clones, with similar Ks between both growth groups. No clear or strong trends were observed between wood anatomy and DBH within the HG and LG groups, but across all clones a high correlation (Spearman coefficient r; $p<0.001$) was observed between vessel number – DBH (r= -0.68), and S – DBH (r= 0.74). These correlations were driven by contrasting mean values of both growth groups.

Research highlights: Commercial *E. globulus* clones present a relatively large variation in anatomical and hydraulic strategies. However, in contrast to what is postulated for various woody species, there was no clear relationship between theoretical hydraulic efficiency and individual diameter growth rate in the genotypes studied.

Additional keywords: xylem vessels; hydraulic conductivity; forest productivity; wood anatomy; xylem efficiency.

Abbreviations used: DBH (diameter at breast high); F (vessel lumen fractions); HG (high growth); Ks (xylem theoretical specific hydraulic conductivity); LG (low growth); S (vessel composition); VD (vessel diameter); VN (vessel number).

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Introduction

The resistance of xylem vessels to water movement depends primarily on their anatomical characteristics (vessel diameter - VD, and vessel number - VN, interconnection, and spatial arrangement). Larger (wider) vessels have lower resistance to water flow than narrow vessels, resulting in higher hydraulic conductivity (Ks), which is generally correlated with high stomatal conductance, carbon fixation, and growth in woody species (Santiago et al., 2004; Brodribb et al., 2005). However, it is recognized that there is a trade-off between the maximum capacity to move water over long distances within the xylem and its vulnerability to cavitation (Tyree & Zimmermann, 2002; Hacke et al., 2006). This implies a potential trade-off between growth and resistance to drought stress in plants. To adjust water requirements according to the growth environment, plants can alter wood properties in several ways, such as varying vessel diameter or number, varying the lumen fraction (F, the fraction of sapwood occupied by vessel lumens), varying vessel composition (S, a measure of vessel diameter distribution), and varying the total area of sapwood supplying water to a specific leaf area (Zanne et al., 2010). These variations depend in part on the genotype (genotypic variation) and in part on the ability to change in response to fluctuations in environmental factors (phenotypic variation or plasticity) (e.g. Pausftch et al., 2016).

The aforementioned relationships between functional wood anatomy, growth, and drought stress resistance have been extensively studied at the inter-specific level, exploring wide ranges of variation in wood traits (e.g., Wheeler et al., 2005; Hacke et al., 2006, 2009; Gleason et al., 2016). However, relationships at the intra-species or intra-genus level are scarcer, and at these levels, examples can be found that bypass the mentioned trade-offs between efficiency and safety of the conducting system (e.g., Lobo et al., 2018 at the intra-specific level in *Quercus petraea*; Fernández et al., 2019 at the inter-specific level in *Eucalyptus* spp). Nevertheless, given the generally positive relationship between vessel size and maximum xylem hydraulic conductivity (Ks_max, measured independently of anatomy), it is expected that the relationship between Ks_max and growth will also be positive at the intra-specific (or intra-genus) level.

Considering the relationships between wood anatomy and tree growth at the inter-specific level, comparative analyses of several tropical species have reported positive correlations between vessel diameter or area and growth –in terms of stem diameter, total height, and growth ring width– (Fichter & Worbes, 2012; Hietz et al., 2017). Principal component analyses in these studies indicated that between 34-50% of the observed variation reflected the positive relationship between growth and variables associated with water transport efficiency (vessel diameter and area, vessel composition – S – and vulnerability index) and a negative relationship with vessel frequency (Fichter & Worbes, 2012; Hietz et al., 2017). Furthermore, when individual tree size is included in the models, hydraulic conductivity scales positively with maximum tree size (Hietz et al., 2017). In contrast, no relationship was discovered between vessel diameter and tree size (measured as stem diameter) in interspecific comparisons conducted within the genus *Eucalyptus* in both a common garden and an environmental gradient, but a positive relationship with climate (aridity index) was apparent. These studies concluded that the hydraulic anatomy of these species is primarily determined by climate and genetics, rather than tree size (Pausftch et al., 2016; Bourne et al., 2017; Santos et al., 2021).

At the intra-specific level, some recent studies have shown variable relationships between anatomy and growth. For ring-porous species, positive correlations between tree ring width or stem diameter and hydraulic vessel diameter have been reported (Camarero et al., 2021 in *Fraxinus* sp; Hietz et al., 2022 in *Quercus* sp). These authors concluded that wood production and hydraulic conductivity are coordinated by the development of large vessels in earlywood, which allows for high growth rates. Tree size explained the highest percentage of the observed variation in vessel size, in contrast to the lesser influence of other factors studied in these species (site, provenance, and their interaction). Studies at the intra-specific level within the genus *Eucalyptus*, which presents diffuse-porous wood, show different behavior of xylem structural variables among commercial clones/hybrids in response to extreme environmental events (drought), resulting in different individual growth rates (Camara et al., 2020; Binkley et al., 2022; Chambi-Legoas et al., 2023). However, to our knowledge there are no publications quantifying these relationships at the intra-specific (and clone) level within the genus *Eucalyptus*.

The genus *Eucalyptus* comprises more than 700 species occupying a wide range of environmental conditions and developing a large variation in strategies for environmental stress tolerance (Pausftch et al., 2016). Among the species in this genus, *Eucalyptus globulus* Labill. stands out for its high industrial wood quality and extensive global commercial use, which indeed is geographically limited by its sensitivity to frost and high temperatures, but exhibits moderate drought tolerance. For this species and others of the same genus cultivated in temperate and subtropical areas of South-America, differences in wood anatomy and density have been demonstrated in different sites, suggesting the adaptive value of xylem anatomical changes in this genus (Barotto et al., 2016, 2017; Moreno et al., 2018; Fernández et al., 2019). According to previous studies, despite showing high stem growth rates in temperate areas (25-35 m^3 ha^{-1} $year^{-1}$), *E. globulus* is characterized by an anatomy of relatively small and not very numerous vessels, resulting in low theoretical hydraulic conductivity (Ks) compared to other *Eucalyptus* species, such as *E. grandis*. However, although vessel size is important in determining Ks, it has been shown for several species within the genus that the total lumen area measured by the F index has a higher relative influence than vessel composition (measured by the parameter S) (Barotto et al., 2017). Furthermore, F is more stable within and between species, while S shows higher variation, suggesting that it has a more plastic nature and/or is more susceptible to variations due to natural selection (genetic variation). An analysis of 3005 angiosperm species showed that F and S are not correlated with each other and can vary independently in response to different selection factors (Zanne et al., 2010).

In this context, the objectives of this study were to: 1) analyze the variability of hydraulic anatomical parameters in clones of *E. globulus* with different growth rates, and 2) determine if the mean magnitude of growth (measured as two growth groups) affects the relationships between anatomical variables and individual mean growth in *E. globulus* clones.

We expected that the correlations between functional anatomical variables and individual growth (measured as diameter at breast height – DBH – at a common age) to have different signs and/or magnitudes between the growth groups (high and low growth clones), driven by groups´ differences in the genotype × environment interaction.

Due to the variable antecedents in the genus (none of them at the level studied here) is not possible to anticipate the particular sign of these relationships within each group. However, we expect that these relationships do differ as a result of different wood anatomical responses to common environmental signals by the different clones, which largely explain their different growth rates.

Material and methods

Sampling was conducted in a clone productivity trial of *E. globulus* established in 1996 by the Instituto Nacional de Tecnología Agropecuaria (INTA) of Argentina. This trial is located at the Experimental Station of INTA in Balcarce, Buenos Aires Province (37°46' S; 58°18' W; 160 meters above sea level). At the time of the wood sampling, the trees in the trial were 25 years old. The genetic material examined in this study consisted of 10 clones selected and released by the Portuguese company Soporcel SA, 5 of high growth (HG) and 5 of low growth (LG) under the environmental conditions of the study area (Table 1). This classification was made after analyzing the growth patterns of the trees *in situ* based on the remeasurement of DBH. Based on this analysis (unpublished data), 3 clone groups, corresponding to high, low, and intermediate growth were defined, with the two extremes selected for the present study. In this regard, clones with mean DBH greater than 30 cm were selected as HG and those with mean DBH lower than 21 cm were selected as LG. In this study, the DBH at 25 years was taken as a proxy for mean growth of the clones since the plantation.

A core sample was taken from the stem of each selected tree at DBH with a 5.15 mm in diameter Pressler increment borer, from pith to bark, for further wood anatomical determinations.

Table 1. Identity of clones (origin: Soporcel SA) and classification by volume (dm^3) of trees at 4 years after planting and diameter at breast height (DBH, cm) at 25 years after planting of the 10 sampled clones of *Eucalyptus globulus*. HG and LG represent the clones with the highest and the lowest mean diameter growth of the trial. The number of sampled trees corresponds to the total number of live trees of the referenced clones in the trial at the sampling age.

Growth groups	Identity (n trees)	Volume[1] at 4 years	DBH at 25 years
HG	503 (3)	203	38.83
	504 (3)	170	34.06
	508 (3)	179	31.67
	513 (4)	179	33.50
	516 (5)	161	35.30
LG	501 (3)	103	19.90
	507 (5)	113	20.34
	512 (6)	141	19.86
	517 (3)	81	12.20
	520 (6)	101	18.17

[1] Volume without bark published in Gelid et al. (2001)

Wood anatomical parameters were estimated from serial transverse histologic sections taken at three radial positions proportional to the radius length in each wood core. These positions corresponded to inner wood (closest to the pith, between 70-55% of the radius length), middle wood (between 70-85% of the radius length), and outer wood (adjacent to the bark, between 100-85% of the radius length). The sections were stained with 1% toluidine blue, observed under a light microscope (Olympus CX31, Japan), and digital images were captured at 4x magnification for vessel measurement. The following measurements were taken for all vessels using Image Pro software (v 6.0, Media Cybernetics, USA): vessel diameter (VD, μm) and number of vessels per unit area (VN, $n \cdot mm^{-2}$). After that, we estimated the fraction of lumens (F) = VA·VN (VA = vessel area), the vessel composition (S) = VA/VN, and the theoretical specific hydraulic conductivity (Ks, $kg \cdot m^{-1} \cdot MPa^{-1} \cdot s^{-1}$).

The hydraulic conductivity kh was calculated using the Hagen-Poiseuille formula (Tyree & Ewers, 1991):

$$kh = \sum_i \left(\frac{d_i^4 \, \pi \rho}{128 \eta w} \right)$$

where kh is the xylem hydraulic conductivity, ρ is the density of water ($kg \cdot m^{-3}$), d is the diameter of the vessel lumen (m), and ηw is the viscosity of water (MPa·s). Ks is the specific hydraulic conductivity and it was estimated as Ks = kh / xylem area where vessels were measured.

Statistical analyses

As previously mentioned, clones were grouped into two groups of 5 clones each based on their mean diameter DBH (HG, high growth and LG, low growth). Trees were also grouped according to genotype (10 clones). Anatomical data were analyzed by averaging the measurements from the three sampled radial positions along each increment core within each tree. The effect of tree was not included in the analysis because we pooled the data from the entire core. Statistical comparisons of all variables between HG and LG groups and between clones were performed using non-parametric tests (Kruskal-Wallis, $p<0.05$) due to the lack of normality in some variables. The coefficient of variation was used as a measure of the variability or degree of plasticity of each variable (Valladares et al., 2006).

Spearman correlation analysis was applied to determine the relationships between the means of the anatomical-functional variables and the DBH of each individual tree, both within and between growth groups. All analyses were performed using Statistica 10 software.

Results

Variability between growth groups

Except for the variables F and Ks, significant differences ($p<0.05$) were observed between the HG and LG groups of *E. globulus* (Table 2). The DBH showed, as expected, a significantly higher value in HG than in LG trees, with the former trees having almost twice the DBH of those in the LG group (Table 2). The parameters that showed the highest variability (i.e. higher coefficient of variation, Table 2) were VN, F, S, and Ks, with higher variability in trees from the LG group than the HG group. VD showed similar variation in both groups (Table 2).

The studied *E. globulus* clones showed significant differences ($p<0.05$) in VD and VN, with HG trees having larger vessel diameter and fewer vessels per unit xylem area compared to trees in the LG group. In addition, HG trees showed a greater variation in S (Table 2 & Fig. 1). It was also observed that the most frequent values of vessel diameter in HG trees were around 105 µm, while in LG trees it ranged from 75 to 105 µm (Fig. 1). Nevertheless, these differences in vessel size and number were not reflected in the theoretical Ks, which did not differ between HG and LG trees ($p>0.05$).

Variability among clones within each growth group

Clones within each growth group showed different behavior for some anatomical variables (Table 2, Fig. 2). Regarding VD, only 3 clones within the HG group produced large vessels (clones 516, 513, 504), while the other 2 clones (508 and 503) formed vessels with significantly ($p<0.05$) smaller diameters (similar to the vessels of the LG clones, see Table S1 [suppl]). HG clones 516, 513 and 504 also showed the highest F values and the other 2 clones (508 and 503) the lowest. In the LG group, only clone 520 presented low F values, the remaining 4 clones were like the HG group. However, for VN and S, the behavior of the clones within each growth group was more homogeneous (Fig. 2, i.e. there were no significant differences between clones within the groups according to the non-parametric analysis, $p>0.05$, Table S1 [suppl]). In this regard, all clones in the HG group produced wood with fewer vessels per unit area and a wider diameter distribution (high S value) compared to clones in the LG group. Finally, Ks, as an integrative variable of the other parameters, showed a high variability among clones, with non-significant differences ($p>0.05$) between the HG and LG groups (Fig. 3, Table S1 [suppl]). Only two genotypes from the HG group showed significant differences with another genotype from the LG group (clones 504 and 513 vs. clone 512).

Table 2. Diameter at breast height (DBH), vessel functional anatomy (VD: vessel diameter, VN: number of vessels per xylem unit area, F: lumen fraction, S: vessel composition), and theoretical specific hydraulic conductivity (Ks) of 10 clones of *Eucalyptus globulus* grouped by growth rate: high growth (HG) and low growth (LG). Mean and coefficient of variation (%).

	DBH (cm)	VD (µm)	VN ($n^o \cdot mm^{-2}$)	F	S (mm^4)	Ks ($kg \cdot m^{-1} \cdot MPa^{-1} \cdot s^{-1}$)
HG, n=18	31.79b	87.87b	7.57a	0.0458a	0.00082b	22.47a
	14.22%	12.61%	15.91%	22.40%	30.68%	41.50%
LG, n=23	17.92a	77.38a	9.93b	0.0469a	0.00052a	18.94a
	25.78%	13.88%	29.02%	34.66%	39.50%	55.23%

n = number of sampled trees. Different letters indicate significant differences between HG and LG groups (Kruskal-Wallis non-parametric test, $p<0.05$).

Correlations between anatomical-functional variables and diameter growth

Table 3 shows the non-parametric correlations between anatomical-functional variables and DBH (as a surrogate for diameter growth) for the HG and LG groups and when considering all clones together. Within each group, significant correlations ($p<0.1$) were observed only in the LG group. In the LG clones, DBH was negatively correlated with vessel number and positively correlated with S. On the other hand, DBH was not correlated with individual Ks (Table 3). When analyzing the relationships without distinguishing between growth groups, we obtained new and stronger relationships (Table 3 All). Across all trees, those with larger vessel diameters but fewer vessels, and most importantly, with a wide diameter distribution (i.e. higher S), had higher DBH. However, even at this level, Ks did not show a significant relationship with the DBH of the trees (Table 3).

Discussion

The study's findings, which compared the HG and LG clone groups and examined genetically selected *E. globulus* clones planted in a common garden trial in the Argentine Pampa region, revealed differences in the degree of variability and the relationships between these variables and individual tree growth (measured here by the DBH of the trees at a common age). In fact, the moderate relationships observed within the LG group disappeared within the HG group, but reappeared when all trees were included in the analysis, suggesting that the large variation in values across all clones and individuals studied was responsible for the observed patterns.

The variability among clones within each growth group was high for some variables (VD, F) and low for others (S, Ks) (Figs. 2 and 3). Some authors have postulated that the low variability found in *Eucalyptus* hydraulic anatomy is due to a strong genetic limitation (Bourne et al., 2017; Santos et al., 2021). For instance, in an inter-specific study of 6 *Eucalyptus* species with different climatic adaptations (rainfall ranges), Bourne et al. (2017) showed that genetics still limits phenotypic plasticity in hydraulic anatomical traits when growing in the same environment (common garden). They also showed that other rapidly responsive physiological variables (water relations, stomatal closure) were positively related to growth, suggesting that different water use strategies among different genotypes (species in their study) led to higher productivity and growth. Similarly, Santos et al. (2021) found differences in hydraulic anatomy and growth in 4 interspecific hybrid clones of *Eucalyptus* growing in a common garden in Brazil. These authors indicated that trends in the relationships between anatomical parameters and growth depended on the clone evaluated. For example, vessel composition (S) was positively related to volume growth, meanwhile VD was related to DBH in some genotypes. These authors also concluded that high Ks did not necessarily imply higher growth rates. These results are consistent with what was observed in our study on *E. globulus,* although we cannot demonstrate genetic limitations of the selected clones.

In the present study, the relationships between anatomical-functional variables related to hydraulic efficiency and the DBH showed partially different behavior depending on the growth group. HG clones did not show significant correlations between hydraulic variables and DBH. In contrast, in the LG group, significant associations were found between two of the variables analyzed (VN and S) and diameter growth. Therefore, partial evidence was found in relation to our expectations, suggesting that the potential genetic differences among the clones and their interactions with the environment could influence this differential behavior within growth groups (e.g. Santos et al., 2021). The lack of significant relationships within the HG group suggests that the different clones achieved high growth through different hydraulic strategies. Unfortunately, due to the low number of replicates per clone, it was not possible to evaluate correlations within clones to elucidate alternative relationships between clones. On the other hand, when all trees were analyzed, regardless of the growth group, some significant trends were observed, including the relationship between the amplitude of xylem vessel size, measured here by the S parameter, and DBH. At the same time, our results suggest that xylem hydraulic efficiency, estimated as theoretical

Table 3. Correlations (Spearman coefficient) between diameter at breast height (DBH), vessel functional anatomy (VD: vessel diameter, VN: number of vessels per xylem unit area, F: lumen fraction, S: vessel composition), and theoretical specific hydraulic conductivity (Ks) of 10 clones of *Eucalyptus globulus* grouped by growth rate: high growth (HG) and low growth (LG).

Group	VD (µm)	VN ($n^o \cdot mm^{-2}$)	F	S (mm^4)	Ks ($kg \cdot m^{-1} \cdot MPa^{-1} \cdot s^{-1}$)
HG, n=18	-0.34	-0.15	-0.39	-0.02	-0.17
LG, n=23	0.19	-0.41*	-0.14	0.39*	0.01
All, n=41	0.42**	-0.68***	-0.10	0.74***	0.18

n = number of sampled trees. Grey shadows indicate significant correlations with ***p<0.001, **p<0.05, *p<0.1.

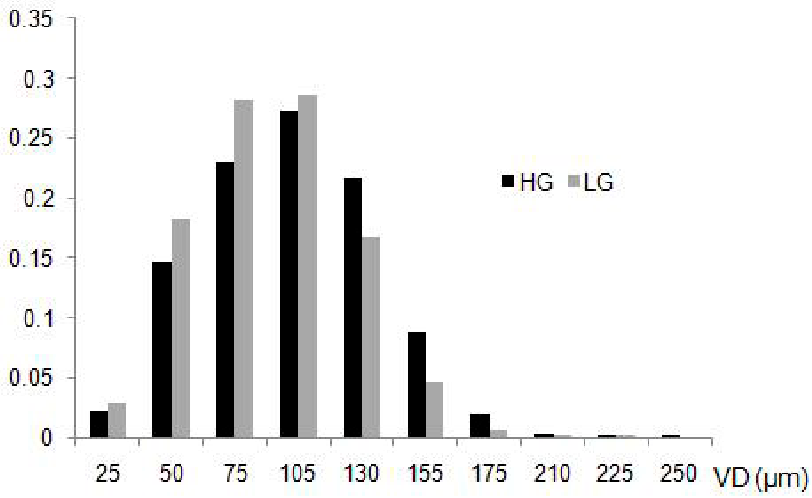

Figure 1. Frequency distribution (proportion of vessels of each size category in relation to all vessels) of vessel diameter (VD) for *E. globulus* categorized by diameter growth. HG = high mean growth; LG = low mean growth.

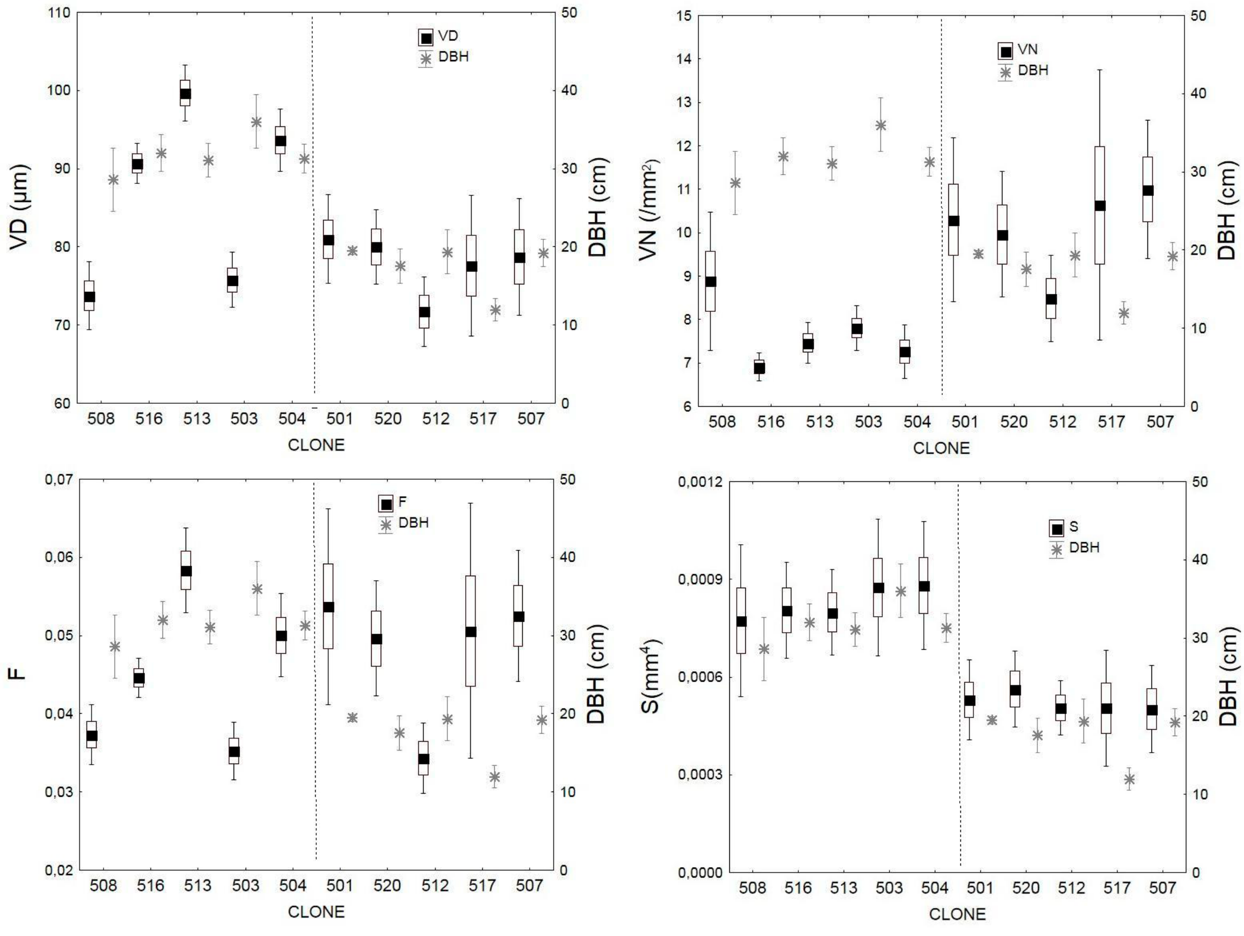

Figure 2. Variability in hydraulic anatomy between high-growth (HG: to the left of the dotted vertical line) and low-growth (LG: to the right of the dotted vertical line) clones (mean and confidence intervals, DBH values plotted in gray). VD: vessels diameter. VN: number of vessels per xylem unit area. F: fraction of lumens. S: vessels composition.

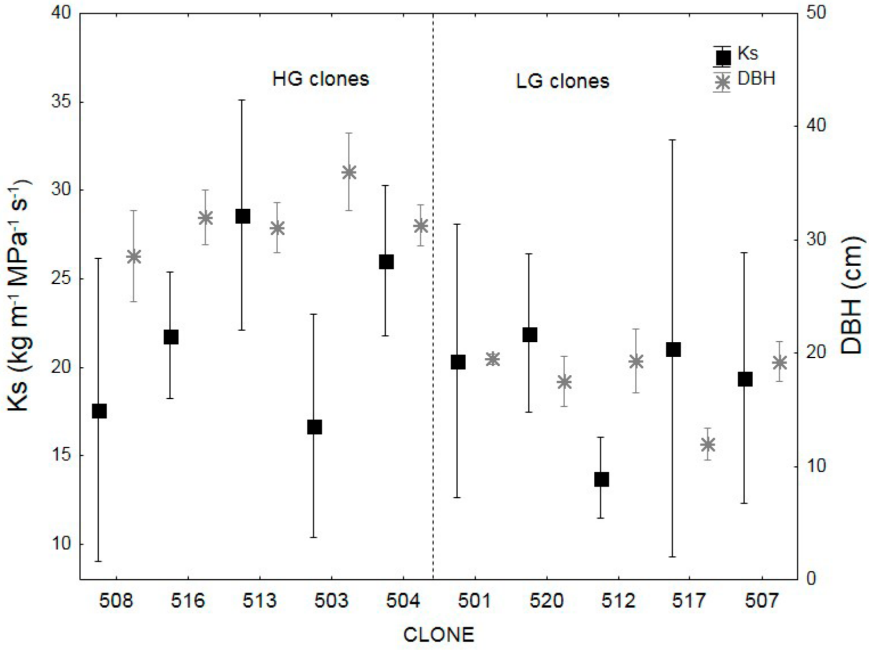

Figure 3. Variability in theoretical specific hydraulic conductivity (Ks) among high-growth (HG) and low-growth (LG) clones (mean and confidence intervals, DBH values plotted in gray).

Ks, does not have a significant effect on the DBH in *E. globulus*. This behavior is likely due to opposite changes in vessel size and number (Table 2) resulting in a similar area occupied by lumens (F), which has a greater impact on Ks than S (Barotto et al., 2017).

Vessel size amplitude (S) in branches has been correlated in *Eucalyptus* spp with the safety of the conductive system (larger diameter amplitude, lower vulnerability to cavitation) both at the inter-specific level (Barotto et al., 2016; Fernández et al., 2019) and within *E. globulus* (Fernández et al., 2019). In these studies, this variable was also associated with a high maximum Ks (measured hydraulically). In the present study, clones with high S, which also had the highest DBH, had theoretical Ks that were either high or low, decoupling the S-Ks association seen in the previously stated studies. In this regard, it appears that the amplitude of vessel diameter is more important in relation to growth than hydraulic efficiency itself. A possible explanation for this result could be that the growth was measured under field conditions, not as potential growth without resource and climatic constraint.

Conclusions

Studies of functional anatomy and its relationship to growth in commercial *Eucalyptus* clones are very recent, so it is important to expand the knowledge in these areas for use in genetic improvement programs. The different genotypes characterized by differential growth rates appear to have different hydraulic strategies. These different strategies are reflected in the differential variability in anatomical-functional variables observed between the HG and LG groups and among different clones. However, contrary to what has been postulated in various woody species, there is generally no clear relationship between theoretical xylem hydraulic efficiency (Ks) and growth (measured here as DBH) in the genotypes studied. Instead, a relationship was found between vessel size amplitude (S) and DBH. Consequently, studies are needed to elucidate the relationship between Ks and growth under non-limited (potential) growth conditions, as well as the impact of vascular system safety (vulnerability to cavitation) on maximum potential growth and under field conditions. This will contribute to the identification of key genetic selection traits for different environmental conditions in economically important forest species.

Supplementary material (Table S1) accompanies the paper on *Forest Systems*' website".

Data availability: The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Authors' contributions: Silvia Monteoliva: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Leonardo Sallesses:** Investigation, Methodology, Writing – original draft. **Adriana Quiñones Martorello:** Investigation, Methodology, Writing – original draft. **Karen Moreno:** Investigation, Methodology, Writing – original draft. **Javier Gyenge:** Formal analysis, Writing – review & editing. **María Elena Fernández:** Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

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