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SECONDARY XYLEM OF STEM AND ROOT OF CERRADO WOODY PLANTS: ANATOMICAL AND FUNCTIONAL APPROACH

RAFAELLA EMANUELLE MONTEIRO DUTRA

Dissertação apresentada ao Instituto de Biociências, Campus de Botucatu, UNESP, para obtenção do título de Mestre em Ciências Biológicas (Botânica), Área de Concentração em Morfologia e Diversidade Vegetal.

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“Somewhere, something incredible is waiting to be known."

Dr. Carl Sagan

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CONTENT

Abstract

The plant's ability to invest in the wood tissue in different organs is crucial to its survival in terrestrial environments. Wood is a complex structural system linked to water transport, mechanical support, and storage of essential substances. However, the understanding of wood traits patterns between organs and the relationship between structural and functional traits is still limited. In this study, we investigated the structural and functional wood patterns between the root and stem system across 15 woody species of the Cerrado domain (Brazilian savannah), also exploring the relationships among the wood traits across species. For that, we measured in both organs in all species the structural wood traits, theoretical hydraulic conductivity, wood density, and non-structural carbohydrates. Our results revealed a similar wood structure, estimation of theoretical hydraulic conductivity, and wood density when compared root and stem, but high content of non-structural carbohydrate in the root. Plant height had a positive effect on wood structure when combined ray width with vessel element length and ray density. Wood density was explained by rays features, while non-structural carbohydrates content was not related to the structural traits. We also identified a positive relationship between theoretical hydraulic conductivity and pits size. The structural and functional wood traits patterns observed provide a more integrated knowledge of wood function, and highlight that storage traits and function are prioritized in Brazilian savanna woody plants.

Keywords: non-structural carbohydrates, vessel-ray pit, wood density, carbon allocation, neotropical savanna.

Introduction

Wood (i.e., secondary xylem) is considered a key factor of evolutionary success linked to the growth and survival of plant species in terrestrial environments (Lucas *et al*. 2013). As part of a complex vascular system, wood forms a continuum throughout the plant body, and plays the functions of water transport, mechanical support, and storage (Evert 2006). At organ level, in the root, the wood is mainly related to water and nutrient storage and conduction functions (Evert & Eichhorn 2013). On the other hand, in the stem, it is mainly related to mechanical support and conduction functions (Evert & Eichhorn 2013). Based on this functional complexity, wood has different cell types to perform these multiple functions. In angiosperms, vessels (a set of superposed vessel elements) provide water transport, wherein the axial direction the conduction occurs by their perforation plates, and in the radial direction by the pits of their walls (Evert 2006); fibers provide mechanical support (Carlquist 2001); and axial parenchyma cells, rays, and living fibers stores carbohydrates, secondary compounds, minerals, and water (Plavcová & Jansen 2015; Morris *et al*. 2016). In this sense, structural traits can also explain some traits linked to hydraulic conductivity (Bittencourt *et al*. 2016), wood density (Chave *et al*. 2009), and energetic stock capacity (e.g., non-structural carbohydrates content) of the wood (Pratt & Jacobsen 2017; Plavcová *et al*. 2019). Nevertheless, to understand how wood traits differ between organs and which are the relationship among wood traits is important to take into those the structural and functional aspects of the plants. However, these issues remain a challenge.

Wood traits relationships allows the understanding into the functions and properties tissue (Chave *et al.* 2009; Zanne *et al*. 2010; Pratt & Jacobsen 2017). Concerning hydraulic aspects, traits are generally interpreted in the perspective of increased embolism (i.e., bubbles inside the conduits) resistance and conductive efficiency (Choat *et al*. 2012). For example, according to the West, Brown, and Enquist model (WBE model, West *et al*. 1999), vessel diameter tends to decrease in the root-leaf direction to counterbalance the higher resistance imposed on narrower vessels at the top of the tree (West *et al*. 1999). As a consequence, wider conduit cells are often observed in the root (Ewers *et al*. 1997; Choat *et al*. 2010) and are associated with higher hydraulic conductivity, since the flow rate increases proportionally to vessel diameter to the fourth power (Ewers *et al.* 1990; Tyree & Zimmermann 2002). On the other hand, although never observed experimentally, smaller cell dimensions (e.g., narrow vessels and narrower intervessel and vessel-ray pits), and higher cell wall thickness and fiber fraction are also considered important for promoting resistance to vessel implosion (Pratt *et al*. 2007; Lens *et al*. 2011; Pratt & Jacobsen 2017), and also contribute to higher wood density (Jacobsen *et al*. 2007; Pratt & Jacobsen 2017). This relationship is observed mainly in the stem

(Ziemińska *et al*. 2013; Janssen *et al*. 2020) since the combination of these traits is associated mainly to mechanical support demands (Chave *et al*. 2009; Plavcova *et al*. 2019). In addition, a higher size of fiber lumen diameter or amount of axial parenchyma, rays, and living fibers (Chen *et al.* 2020; Herrera-Ramírez *et al*. 2021) can lead to higher investment in non-structural carbohydrate storage (Chapotin *et al*. 1990; Herrera-Ramírez *et al*. 2021). These traits are found mainly in the roots than stem (Pratt *et al*. 2007; Jin *et al*. 2018), given its primary function of storage (Evert *et al*. 2006). Investment in storage traits might promote higher carbon storage (Chapotin 1990; Jacobsen *et al*. 2018), which can be crucial for regrowth, as evidenced in plants from post-fire environments such as savanna (Hoffmann *et al.* 2003; Clarke *et al.*2013; Simon & Pennington 2012).

The Cerrado domain (Brazilian neotropical savanna) is the most floristically diverse savanna among other savannas (Forzza *et al*. 2012), and its vegetation is shaped by fire dynamics, soil fertility, luminosity, and water seasonality (Oliveira-Filho & Ratter 2002). Additionally, the Brazilian savanna are considered mesic savannas (Franco *et al*. 2014), due the average annual rainfall greater than 1,000 mm (Coutinho 2000). In the Cerrado, plants show particular traits, such as thick bark and deeper roots which allow higher investment in carbohydrates reserves in the underground organs, used mainly in post-fire physiological processes such as regrowth and flowering (Simon & Pennington 2012).

Previous few works associate wood trait patterns of Cerrado species with different factors. Firstly, in general, wood structure differs when contrasted root and stem (Machado *et al*. 1997, 2007; Marcati *et al*. 2014). In the root, vessel element size and ray width might be larger than in the stem as observed in *Styrax camporum* (Styracaceae) (Machado *et al*. 1997). On the other hand, vessels and fiber with a smaller caliber tend to be observed only in the stem (Machado *et al*. 2007, Goulart & Marcati 2008). These structural differences have been associated with hydraulic function, suggesting that root has a water conduction efficiency, while stem tends to prioritize "safety" water transport (Machado *et al*. 2007). Despite the observed pattern, some traits linked to radial wood aspects (e.g., rays fraction, and vessel-ray pits diameter) tend not to differ between organs, as found on the similarity of the root and stem in *Citharexylum myrianthum* (Verbenaceae) (Marcati *et al*. 2014). Second, despite the higher proportion of belowground biomass compared to aboveground for most Cerrado plants (see ref. Durigan *et al*. 2012), similarities can also be found in wood density and non-structural carbohydrate content when compared root to stem, as observed in *Miconia pohliana* (Melastomataceae) and *Guapira noxia* (Nyctaginaceae) (Hoffmann *et al*. 2003). Generally, these patterns are linked to regrowth strategy, mainly because of fire disturbance (Hoffmann *et al*. 2003).

Here, we investigated the structural and functional (theoretical hydraulic conductivity, wood density, and content of non-structural carbohydrates) wood traits based on 15 Cerrado species to verify if structural and functional wood patterns differ between root and stem and explore the relationships among wood traits. We hypothesize that roots invest more in reserve and water transport and less in mechanical support than stem in the Cerrado. Specifically, we expect (a) an increase in vessel and parenchyma cells size, reflecting a higher hydraulic conductivity and non-structural carbohydrates content in the roots compared to stems; and (b) higher investment in cell wall thickness, fiber, and wood density in stems compared to roots. Additionally, we hypothesize that wood density and non-structural carbohydrates content are related to structural xylem traits. Specifically, we expect that (a) wood density is positively related to fiber traits (e.g., fiber wall thickness, fiber fraction), whereas (b) non-structural carbohydrates content is positively related to parenchyma traits (e.g., size and fraction). Furthermore, we also investigated the relationships between axial and radial hydraulic traits, and we expect theoretical hydraulic conductivity to be positively related to vessel-ray pit size.

Material and methods

Study site

The study was conducted in Estancia Santa Catarina Private Reserve, Botucatu, São Paulo state, Brazil (22º54’51”S, 48º30’13”W). The local area is characterized by a mean annual temperature of 21ºC, and seasonal precipitation, averaging 1507 mm/year in the rainy season (September-April) and 50 mm/year in the dry season (May-August). Climatic data were collected during 2005-2015 from the Meteorological Station of the Faculdade de Ciências Agronômicas, UNESP (Botucatu), São Paulo, Brazil. The soil is sandy, acidic, with low organic matter and high aluminium content. The site is covered by cerrado *sensu stricto* (*i.e*., Brazilian savanna), with vegetation composed of herbaceous and short and sparse woody species (Ribeiro & Walter 2008).

Plant material

We selected the 15 most dominant woody species in the study site, comprising different habits (shrubs, tree), taxonomic orders and large phylogenetic diversity (Table 1). All species are diffuse-porous wood, except for the semi-ring-porous of *Aegiphila verticillata*. We collected plant samples for structural and wood density analysis during the dry season (June-July 2015), when the vascular cambium is dormant (Marcati et al. 2016). We resampled the same individuals during the beginning of the growing season (October 2015) for non-structural carbohydrates (NSC) measurements, not compromising the analysis of the relationship with structural wood traits. Plant habit criteria defined the sampling to avoid structural damage or loss of individual due to the plant size (Table 1). We sampled stem (main trunk for trees, or the most developed branch for shrubs) and root (main for trees, or secondary for shrubs) from three mature individuals per species. Stem samples were collected at 60 cm aboveground and roots at a depth of 15 - 30 cm belowground (distal from root collar). We collected the twigs' entire disk, 10 cm of secondary root blocks for shrubs, and 50 – 100 cm^2 stem and root blocks for trees. After collection, we carefully washed the roots to remove the soil and the bark and reduced each sample to 1 cm^3 for the material analysis.

Structural wood analysis

Samples were cut in transversal and longitudinal (tangential and radial) sections of 15-22 μm thick with a sliding microtome. Sections were stained in 1% aqueous safranin (Bukatsch 1972) and 1% aqueous astra blue (Roeser 1972) (1:9), dehydrated in increasing ethanol series and mounted on permanent slides with synthetic resin. To visualize individual cellular elements, woody blocks were reduced to small fragments, placed in closed vials with hydrogen peroxide and glacial acetic acid (1:1) and put in an oven at 60°C for 24h. After, the material was stained in 1% safranin in 50% ethanol and mounted on semi-permanent slides with 50% glycerin. Slide analyses were performed using light microscopy and measurements in ImageJ 2.0 software (https://imagej.nih.gov/ij/). All structural traits measured are presented in Table 2, and according to IAWA Committee (1989) and Scholz *et al*. (2013) recommendations.

The hydraulic diameter of vessels (Dh) was calculated based on a formula by Tyree & Zimmerman (2002): $(\Sigma dv^4/n)^{1/4}$, where dv refers to vessel diameter, and n to vessel number. Considering that the vessels are not perfect circles in cross section, vessel diameter (dv) was calculated according to the area of the vessel lumen, by the formula: $dv = \sqrt{4A/\pi}$, where *dv* is vessel diameter, and *A* is vessel lumen area. We used this formula to consider the mean diameter of all vessels in the sample (Scholz *et al.* 2013), independent of the species wood porosity. Additionally, fiber wall thickness was determined by following the formula: ((fd – fld) /2), where fd is fiber diameter, and fld is fiber lumen diameter.

To quantify the cell fractions (vessels, fibers, axial parenchyma, and rays), we selected one area of 1 mm^2 from a cross-sectional image of each sample. Measurements were carried out using a digitizing table, Photoshop CS6 (Adobe Systems Inc) and Colour count plugin (at ImageJ 2.0), following Ziemińska *et al*. (2013) recommendations.

Theoretical hydraulic conductivity and sapwood density

Theoretical hydraulic conductivity (K_{TH}) was estimated following the formula (Fichot *et al*. 2010):

$$K_{\text{TH}} = \frac{Dh^4\pi}{128\,\eta} \text{ x } Dv$$

where *Dh* represents the hydraulic vessel diameter, η represents the viscosity of water at 20°C (1.002 × 10-9, MPa s), and *Dv* is the vessel density.

To calculate a wood density (WD, *i.e*., basic specific gravity), samples were submerged in water and weighed on an analytical balance to obtains the fresh volume (water displacement method). After samples were dried in an oven at 80°C until the constant weight and the dry mass was measured. Wood density was calculated by the ratio between dry mass and fresh volume.

Non-structural carbohydrates measurement

Immediately after collection, samples were oven dried at 60 to 65°C until constant weight. After drying, the samples were ground using a mini-mill (Thomas Scientific, Swedesboro, New Jersey) and sieved on a #60 mesh. Soluble sugars were extracted in 80% ethanol (Chow & Landhausser 2004) and starch in 1.1% hydrochloric acid (Chapotin *et al.* 2006). The anthropometric method performed two measurements per sample in 80% sulfuric acid (Bauer, Schulze & Mund 1997), and absorbances were read in a spectrophotometer at a wavelength of 630 nm. NSC content was determined by the sum of soluble sugars and starch content. Results are given in mg/g (mg glucose/g dry wood).

Data analysis

We tested all datasets for normality assumptions with a visual inspection. Due to the non-normality of most structural traits, some traits were transformed a priori to meet the normality, according to suggestions of package "bestNormalize" (Peterson RA, Cavanaugh JE, 2019) (Table 2). A Principal Component Analysis (PCA) was performed to summarize the variation of the structural traits (Legendre & Legendre 2012) with the package "vegan" (Oksanen et al. 2019). To minimize the multicollinearity, vessel lumen area and diameter were not used, and fiber diameter and lumen diameter. The scores of the two most explanatory PCA axes were used as structural wood proxies, allowing us to understand better the simultaneous combination of cell traits in the following analyses.

Linear mixed models (LMM) were conducted to compare the wood structure (PC1 and PC2 scores) and functional traits (K_{TH}, wood density, and NSC content; response variables) between organs. We also run mixed models to testing the effect of plant size effect (height and organ diameter size; fixed factors) on wood structure (PC scores; response variable). In this case, when any effect was detected, we included the factor as covariate in the next analyses. To test the relationships between structural and functional traits, we perform LMM. First, we tested the relationship between wood density or NSC (responses variables) and PC scores (PC1, PC2; fixed factors). Second, we evaluated the relationship between K_{TH} (response variable) and pit traits (diameter, aperture; fixed factors). In all models, organs were included as a fixed categorical factor (two levels: root and stem), and individuals nested in species were considered as a random variable. The models were compared by the likelihood ratio test. The R^2 values were calculated according to Nakagawa & Schielzeth (2013), and the R^2 marginal (R^2m) refers to the variance explained by the fixed factors, and R^2 conductional (R^2c) refers to the variance explained by fixed and random factors. Normality and homoscedasticity of the residuals were checked by visual inspection (Zuur *et al*. 2010). We used the R packages "lme4" (Bates *et al.* 2015) and "nmle" (Pinheiros *et al*. 2020) to perform the LMM.

All analyses were performed in R v.4.0.5 (R Development Core Team 2021).

Results

Wood structure

The structural wood pattern of root and stem was summarized by PCA (Figure 1A). The PCA revealed that the first two components axes explained 68% and 15% of observed data variance, respectively (Figure 1A). The PC1 was mainly described by ray height and ray width (Table S2), while the PC2 was described by ray density, vessel element length, and ray width (Table S2). In general, PC1 represented only ray features, and PC2 represented ray and vessel features. The overlapping points on the multivariate space suggested no structural wood distinction between organs (Figure 1A), as confirmed by mixed models (Table S2, Figure 1B).

Overall, only plant height had a positive effect on wood structure when summarized by PC2 (combination of higher ray width (positive values), with higher vessel element length and ray density (negative values)) (Table S4, Figure S2, $p<0.001$). However, despite mixed models suggest the effect of organ diameter also on PC2 ($p <0.01$), the estimate was low (Estimate = -0.01); thus, we conclude that organ diameter did not explain the wood cells variation summarized by PC2.

Functional traits

Theoretical hydraulic conductivity estimates had large variation across organs (Table S1), with root varying from 0.06 to 464.10 Kg s^{-1} m^{-1} Mpa^{-1}, and stem from 5.56 to 84.72 Kg s^{-1} m^{-1} Mpa^{-1}. Wood density varied from 0.21 to 0.79 g/cm^3 and from 0.33 to 0.74 g/cm^3 in the root and stem, respectively (Table S1). Despite the variation, both traits were similar, on average, when compared root to stem (Table S1, S3, Figure 2).

The starch content varied from 27.45 to 476.90 mg/g in the root and from 15.59 to 371.24 mg/g in the stem (Table S1, Figure 3). Soluble sugar varied from 11.57 to 186.03 mg/g in the root and from 13.96 to 175.62 mg/g in the stem. The total non-structural carbohydrates content (starch + soluble sugar) was higher in the root (224.85 ± 16.74) than stem (156.20 ± 14.02), as expected ($p<0.0001$, Figure 2).

Relationships between wood structure and functional traits

No relationships were detected between structural traits summarized by PC1 (combination of higher ray height and width (positive values), with higher ray density (negative values)) and wood density (Table 3). Although it was observed that wood density was negatively related with PC2 (combination of higher ray width (positive values) and higher vessel element length and ray density (negative values)) (Figure 4; $p = 0.03$), the PC2 estimate value was low (Estimate = -0.02). Non-structural carbohydrates content was not related to PC1 or PC2 (Table 3).

In contrast, theoretical hydraulic conductivity was positively related to vessel-ray pit traits, as hypothesized (Figure 5; $p<0.001$).

Discussion

In this study, we investigated the structural and functional wood traits pattern between root and stem and the relationships among wood traits based on 15 species from Cerrado (Brazilian savanna). Our results demonstrated that the plants, at least concerning the sampled portions, exhibited similar wood structure, theoretical hydraulic conductivity estimates, and wood density between root and stem, but higher non-structural carbohydrates content in the root. Deeper root system and greater root: stem are key woody traits of savanna plants (Durigan *et al*. 2012; Zhou *et al*. 2020), and can potentially explain the similarities, as well as the higher reserve in carbohydrates (Shultz *et al*. 2009) in our samples. However, while ray width was related to wood density, structural wood traits did not explain the non-structural carbohydrates content, non supporting our expectations. Large cells with thin wall might reduce the space allocated for other wood cell, whereas non-structural carbohydrates content can be explained by another storage cell, such as living fibers. We also confirmed our expectation about positive link between vessel-ray pit traits and theoretical hydraulic conductivity, suggesting the influence of water availability in the environment can be associated to the processes of cell expansion (Lin & Soh 1997; Abe *et al*. 2003), favoring wider conduits and pits, as well as higher theoretical hydraulic conductivity in the species studied.

Structural and functional wood traits patterns between root and stem of cerrado plants

Our results show that cerrado woody plants have a similar wood structure and theoretical hydraulic conductivity (estimated from vessel traits) when compared root to stem. These findings diverge from previous studies reporting structural wood differences between root and stem in some cerrado species (Machado *et al*. 1997, 2007; Marcati *et al*. 2014). Plants from the cerrado, compared to other environments, tend to invest in a deeper root system (greater root: stem) (Schutz *et al*. 2009; Durigan *et al*. 2012), as in several species analyzed here (Rawitscher 1948). In this sense, a plausible explanation is that considering that our sampling was performed at 30cm depth, plants with deeper roots potentially might tissues with similar cell sizes in the portions sampled in this study. Additionally, similar traits in species of different ancestry that share the same environmental selective pressures are also important because can be interpreted as adaptations to a particular environment (Olson & Arroyo-Santos 2015). Indeed, fire has been the main natural disturbance shaping the dynamics of cerrado vegetation (Simon *et al*. 2009; Durigan *et al.* 2020), mainly by making plants susceptible to topkill disturbance (Miranda & Sato 2005; Hoffmann *et al*. 2009). Hence greater investment in secondary tissue (Larjavaara & Muller-Landau 2010), and for maintaining the woody functionalities of belowground organs, that may be damaged or lost, impose high costs to the plant (Schutz *et al*. 2009; Clark *et al*. 2013). In this sense, the similarities observed also can be explained in terms of plants' energetic demands. Thus, species that have a similar structural investment in root and stem can maintain a minimum structure necessary to sustain the aboveground vegetative and reproductive parts and for the acquisition of energy resources (via photosynthesis) while remaining in the environment.

Despite no difference in wood structure between root and stem discussed above, the plant height of studied plants scales with higher PC2 values (summarizing mainly wider rays). Our result is in line with previous studies concerning the dynamics of plant growth and development (Niklas 1994; Poorter *et al*. 2006; Rosell *et al*. 2017). However, works related to patterns of scaling of structural wood traits with plant size provide more evidence on the hydraulic perspective and at global scale (e.g., Rosell *et al*. 2017; Olson *et al*. 2018). On the other hand, the observed pattern in cerrado plants is linked to the rays, since the investment in storage cells is accentuated for savanna than forest species (Outer & van Veenendaal 1976; Simon & Pennington 2012). In addition to storage, rays also play the radial translocation function (Evert 2006; Carlquist 2018). This could favor the radial storage capacity and the transport over longer distances of sugar, water, or minerals (Morris *et al*. 2018) for taller plants.

Wood density was also similar between stem and root. Wood density is a key attribute linked to species survival (Hacke *et al*. 2001, Chave *et al*. 2009). While denser wood may facilitate more resistance to mechanical damage and pathogens (McCarthy-Neumann & Kobe, 2008; Chave *et al*. 2009), this investment is energetically costly (Chave *et al*. 2009). Furthermore, wood density is linked to the carbon stock of the plant (Brown *et al*. 1997; Chave *et al*. 2009), also given the relationship between lignin content and carbon content (Thomas & Malczew-ski 2007). Concerning that, lignin is an important organic polymer (composed of carbon) linked to secondary cell wall formation and rigidity (Schuetz *et al*. 2014; Liu *et al*. 2018). In this sense, lower wood density might minimize the energy costs, as mentioned before, and carbon allocation for wood structure. As consequence, in these species it is possible that the pattern reflects in carbon economy and allocation for use during periods of post-fire regrowth, or to supply any other physiological demands.

Compared to the stem, root had a higher content of non-structural carbohydrates, as expected for plants from fire-prone environments (Simon & Pennington 2012; Diaz-Toribio & Putz 2021; Ramirez *et al*. 2021). This result supports the allocation strategy in underground storage of savanna plants, since deep root systems might lead to higher reserve capacity that enable faster aboveground recuperation regrowth (Chapotin 1990; Schultz *et al*. 2009; Clarke *et al*. 2013). Nonetheless, our finding is different from those observed by Hofmann *et al*. (2003), who reported similar contents of non-structural carbohydrates in the stem and root of cerrado species. This may be explained by the season of sampling. The non-structural carbohydrates content is a sensitive trait to seasonal dynamics (Jin *et al*. 2018). In this sense, while we collected samples at the beginning of the rainy season (October), Hoffmann *et al*. (2003) collected at the peak of this same season (December - January). Given this, we suggest that non-structural carbohydrates content in our samples had not yet been actively utilized for growth demands because of the favorable period. On the other hand, our studies provide evidence that wood is an important tissue for carbon storage for cerrado plants.

Relationships among wood traits

We observed a decrease in wood density with higher values of PC2 (i.e., wider rays) (Figure 5). Our result diverges from expected patterns between wood density and structural traits, wherein the wood density is associated with fibers properties (Jacobsen *et al*. 2005, 2007) and cell wall thickness and lumen size (Pratt *et al*. 2007; Ziemińska *et al*. 2013). Overall, these links consider mainly stem than root, as well as species from diverse environments not just from savanna (e.g., Martínez-Cabrera *et al*. 2009; Ziemińska *et al*. 2013; Dória *et al*. 2019). Nevertheless, the negative relationship between wood density and rays features agrees with Ziemińska *et al*. (2013), who detected this relationship with ray area and suggested that this link is explained by drier environmental conditions. Here we interpreted that since rays are also parenchymatic cells mainly involved with storage function, this investment tends to be accentuated for species in savanna environment (Simon & Pennington 2012). Consequently, wider rays reduce the space allocated for other wood cells. In addition, rays are living cells, and investment in the secondary cell wall, compared to the other wood cells, is not prioritized (Evert 2006; Carlquist 2018).

Some studies have shown relationships between non-structural carbohydrates content and parenchymatic cells (Chapotin 1990; Chen *et al*. 2020; Herrera-Ramirez 2021). In this study, we did not highlight any relationship between non-structural carbohydrate content and structural traits. Overall, rays not only storage non-structural carbohydrates but also water, minerals, and chemical compounds (Plavcová & Jansen 2015). Additionally, although the living fibers are observed in cerrado species (Sonsin *et al*. 2014; Herrera-Ramirez *et al*. 2021) and is a key trait linked to the storage strategy (Herrera-Ramírez *et al*. 2021), we did not measure the amount of living fibers separately. Thus, future studies should investigate whether the variation in the non-structural carbohydrate content of cerrado plants can be explained by living fibers.

The estimated theoretical hydraulic conductivity shows a positive relationship with vessel-ray pits sizes. First, pit size is related to vessel dimensions, specifically cell wall expansion during maturation (Hacke *et al*. 2017). Second, water availability reflects in the processes of cell expansion (Lin & Soh 1997; Abe *et al*. 2003). Thus, wider vessels and large pits that are in contact with the rays might be favored by water availability, given that this one is not a limiting factor for cerrado plants (Ferri et al. 1979). Since the theoretical hydraulic conductivity estimate is based on vessel diameter, the flow rate should increase proportionally to the fourth power of the vessel diameter (Tyree & Zimmermann 2002). In this perspective, higher estimates of the theoretical hydraulic conductivity are increased by larger diameters of the pits and indicate water transport efficiency. However, we point out that relationships with traits related to water transport should also consider the pit membrane features due to effect on water transport over long distances (Sperry *et al*. 2006; Rosell *et al*. 2017); and still need to be more evaluated in cerrado plants.

We would like to emphasize that although this study provides the first evidence regarding the patterns of structural and functional wood traits and its relationships based on 15 species, these species are frequent (Flora 2020) and represent the most important families of the Cerrado flora (Heringer *et al*. 1977; Cavassan 2002). However, also represents less than 1% of the total of cerrado species (Forzza *et al*. 2012). Thus, the patterns found at the local scale represents only part of the pattern that can be distinct for other species of the cerrado to what is here described. Furthermore, it is important to note that here we only evaluated traits linked to wood, a part of the vascular system, but that other traits linked to bark should also not be excluded for understanding adaptations of the vascular system of cerrado plants.

Conclusion

Comparing stem and root of 15 species from the cerrado, we show similar data concerning wood structure, theoretical hydraulic conductivity, and wood density between organs, but a higher carbon content in the root than stem. Moreover, we found a negative relationship between wider rays and lower wood density, while structural traits did not explain the non-structural carbohydrates content. Our findings provide a more integrated knowledge of storage wood traits and function, highlighting those traits linked to hydraulic demands and support not seem to be prioritized in a specific organ, since storage traits are directly involved in the survival strategy of savanna plants (Simon & Pennington 2012). Futures investigations along the axial axis, as well as considering wood and bark traits simultaneous, should provide a better understanding of the mechanisms linked to the dynamics of structural and functional wood aspects of plants from Brazilian Neotropical savanna.

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Table 1. Information on Cerrado plants sampled. Values represent means ± SD (n = 3). *: diameter at 60 cm aboveground; **: diameter at 15 – 30 cm belowground.

Species	Family	Order	Habit	Height (m)	Stem diameter (cm)*	Root diameter (cm)**
Aegiphila verticillata Vell.	Lamiaceae	Lamiales	Tree	4.3 ± 1.2	14.7 ± 6.8	3.6 ± 2.2
Annona crassiflora Mart.	Annonaceae	Magnoliales	Tree	3.8 ± 1.0	15.7 ± 4.0	8.8 ± 1.3
Caryocar brasiliensis Cambess.	Caryocaraceae	Malpighiales	Shrub	1.8 ± 0.3	5.7 ± 4.0	12.4 ± 3.5
Casearia silvestrys Sw.	Salicaceae	Malpighiales	Shrub	2.3 ± 0.2	4.7 ± 3.4	1.5 ± 0.4
Couepia grandiflora (Mart. & Zucc.) Benth.	Chrysobalanaceae	Malpighiales	Tree	3.1 ± 0.8	12.5 ± 1.8	11.9 ± 0.7
Diospyros lasiocalyx (Mart.) B. Walln.	Ebanaceae	Ericales	Tree	2.7 ± 0.3	9.2 ± 0.8	7.5 ± 0.8
Eriotheca gracilipes (K.Schum.) A.Robyns	Malvaceae	Malvales	Tree	4.6 ± 1.4	19.3 ± 4.1	13.6 ± 1.6
Erythroxylum buxos Peyr.	Erythroxylaceae	Malpighiales	Shrub	2.2 ± 0.7	2.7 ± 0.5	2.2 ± 0.3
Erythroxylum suberosum A.St.-Hil.	Erythroxylaceae	Malpighiales	Tree	2.7 ± 0.8	9.7 ± 2.7	2.7 ± 1.6
Leptolobium elegans Vogel	Leguminosae	Fabales	Tree	4.5 ± 1.8	13.3 ± 3.1	2.8 ± 1.1
Myrcia bella Cambess.	Myrtaceae	Myrtales	Tree	4.5 ± 0.9	11.9 ± 0.9	5.7 ± 4.4
Myrcia guianensis (Aubl.) DC.	Myrtaceae	Myrtales	Shrub	2.1 ± 0.1	2.9 ± 0.3	1.8 ± 0.5
Piptocarpha rotundifolia (Less.) Baker	Asteraceae	Asterales	Tree	3.0 ± 0.5	14.6 ± 6.1	7.5 ± 5.6
Qualea grandiflora Mart.	Vochysiaceae	Myrtales	Tree	5.8 ± 1.3	26.7 ± 8.1	13.5 ± 16
Roupala montana Aubl.	Proteaceae	Proteales	Tree	3.0 ± 0.9	6.3 ± 2.6	6.6 ± 4.5

Table 2. List of the wood cell traits measured with their respective units, and type of data transformation applied (according to R package "bestNormalize").

Wood cell trait	Unit	Data transformation
Vessel element length	µm	Square root
Vessel lumen área	μm^2	-
Hydraulic vessel diameter	µm	Log+1
Vessel grouping	nº /vessel group	Box-cox
Vessel density	nº mm^2	Log+1
Intervessel pit diameter	µm	Square root
Intervessel pit aperture	µm	Square root
Vessel-ray pit diameter	µm	Square root
Vessel-ray pit aperture	µm	Square root
Vessel fraction	-	Square root
Fiber length	µm	Box-cox
Fiber diameter	µm	-
Fiber lumen diameter	µm	-
Fiber wall thickness	µm	-
Fiber fraction	-	-
Ray height	µm	Square root
Ray width	µm	Square root
Ray density	nº mm^{-1}	-
Ray fraction	-	-
Axial parenchyma fraction	-	Square root

Table 3. Summary of linear mixed models examining the relationships between functional traits (wood density and non-structural carbohydrates) and structural wood traits (represented by the two axes of the PCA), between organs (root, stem) of plants from Cerrado. Plant height was included when had significative effect on PC axes. The estimate, standard error (SE), t-value and p-value of fixed factors are show. Individual nested within species were considered as random factor. R^2_m = variance explained by the fixed factors, R^2_c = variance explained by fixed and random factors of the models.

	Wood density					**Non-structural carbohydrates content**				
	Estimate	SE	t-value	p-value	R^2_m / R^2_c	Estimate	SE	t-value	p-value	R^2_m / R^2_c
PC1 + organ										
Organ [stem]	-0.024	0.015	-1.655	0.106	0.01 / 0.64	-71.178	11.588	-6.142	<0.0001	0.12 / 0.76
PC1	-0.000	0.010	-0.020	0.984		8.315	8.943	0.93	0.355	
PC2 + organ + plant_height										
Organ [stem]	-0.018	0.015	-1.236	0.2231		-73.721	11.677	-6.313	<0.0001	
PC2	-0.024	0.011	-2.099	0.038	0.06 / 0.63	4.534	10.205	0.444	0.658	0.11 / 0.76
Plant_height	0.019	0.012	1.563	0.123		-0.603	11.808	-0.051	0.959	

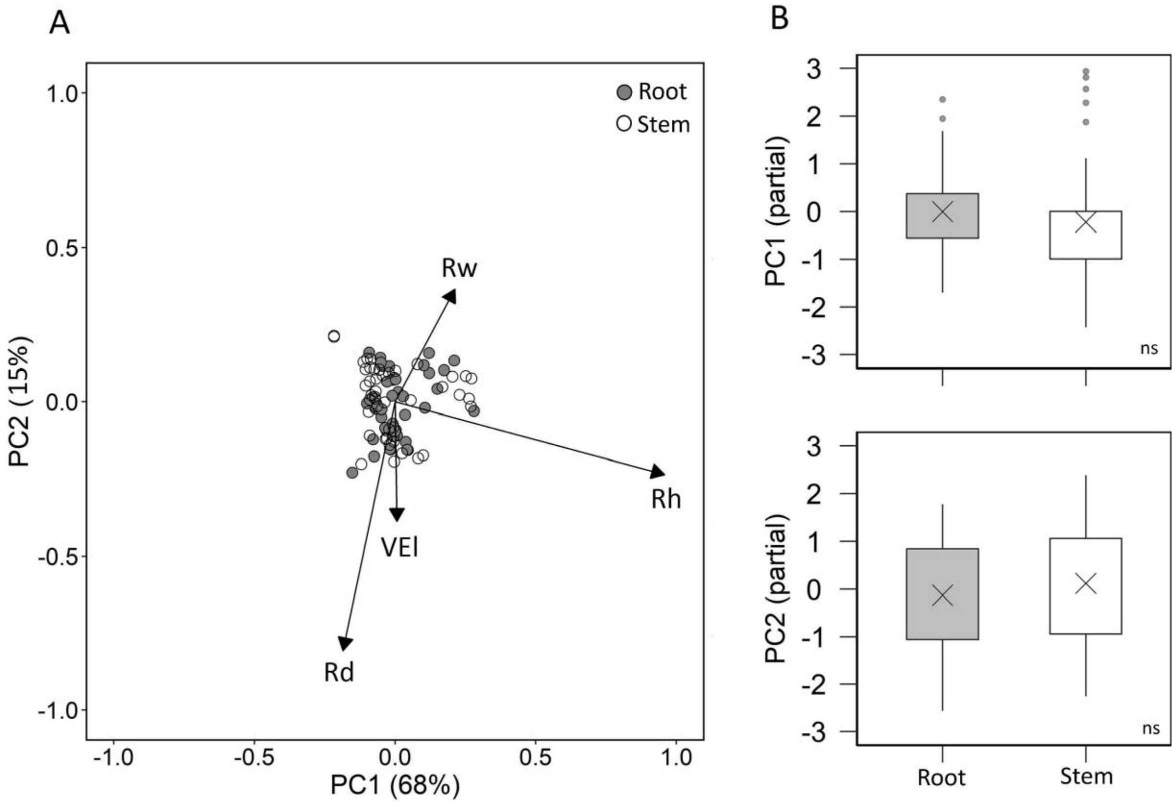

Figure 1. Structural wood traits in root (grey) and stem (white) of plants from Cerrado *sensu stricto*. (A) Principal component analysis. Circles refer to organs. Only loadings > 0.15 were plotted for each axis. VEl: vessel element length; Rd: ray density; Rh: ray height; Rw: ray width. (B) Comparison of wood structure summarized by the scores of PCA components between organs. PC1 refers to combination of ray height, width, and density; PC2 refers to combination of ray width, vessel element length, and ray density. Cross represent mean values; lower and upper box limits represent the 25th and 75th percentiles; the vertical line represents the minimum and maximum values; and dots represent outliers. Non-significative (ns) differences were detected according to linear mixed models with random factor as species nested with individuals (see Table S3 for statistical details).

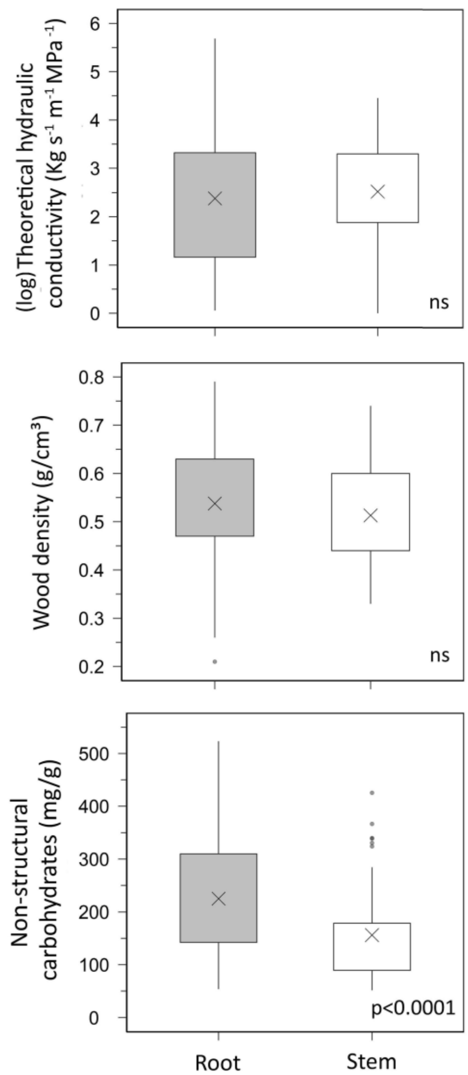

Figure 2. Comparison of functional wood traits between organs of Cerrado plants. Colors refer to root (grey) and stem (white). Cross represent mean values; lower and upper box limits represent the 25th and 75th percentiles, and the vertical line represents the minimum and maximum values; dots represent outliers. Significant differences are shown according to linear mixed models with random factor species nested with individuals. ns: non-significative.

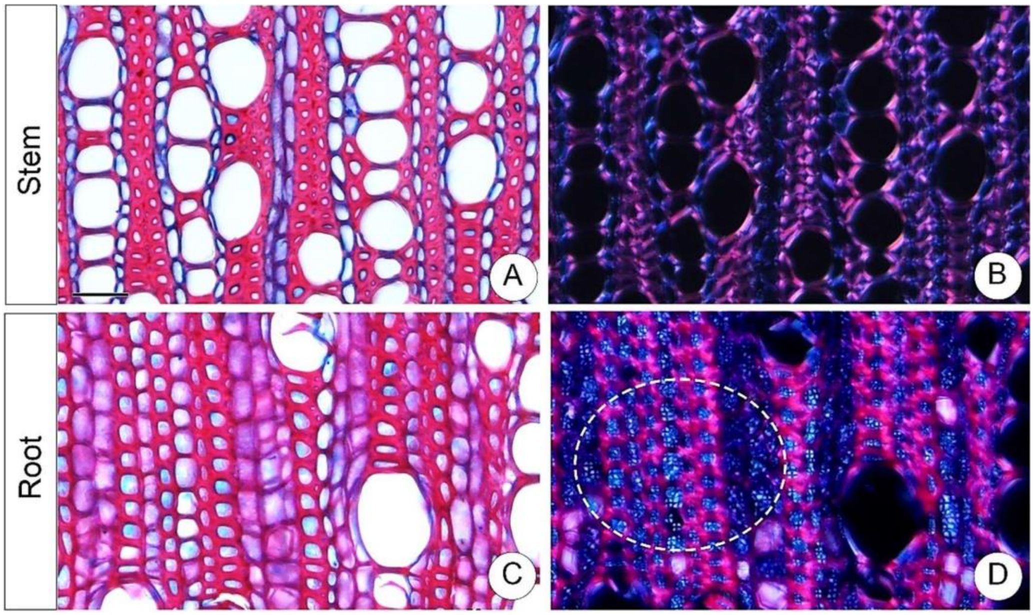

Figure 3. Starch storage contrast in light microscopy (A, C) and polarized light (B, D) in root and stem wood in *Casearia sylvestris* from Cerrado. Starch grains are present in axial parenchyma, rays, and living fibers cells, but with higher amounts in the root (dashed area in D). Scale bar = 50 μm (A, B, C, D).

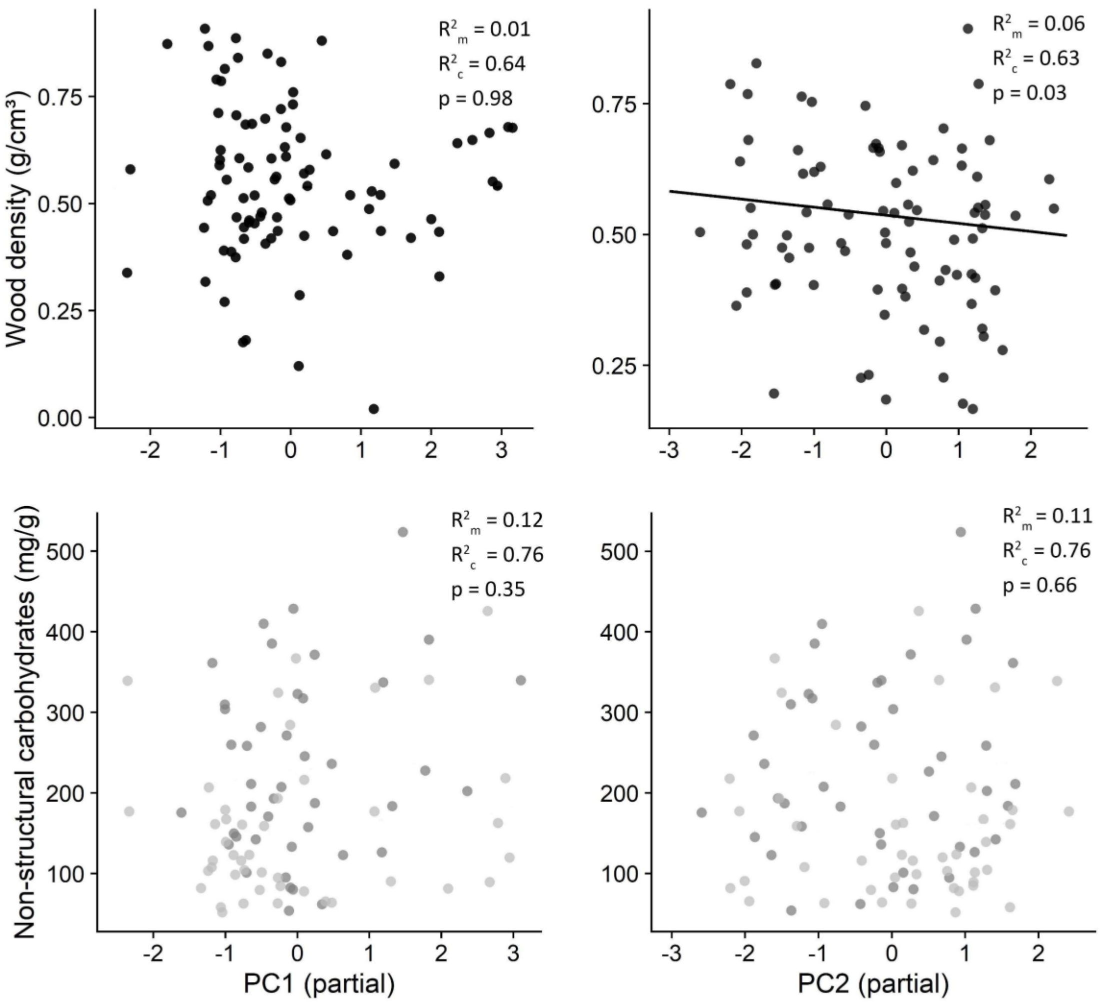

Figure 4. Relationships between structural wood traits (described by the first and second scores of PCA axes) and functional traits (wood density and non-structural carbohydrates content) between root and stem. PC1 refers to combination of higher ray height and width (positive values), with higher ray density (negative values); PC2 refers to combination of higher ray width (positive values), with higher vessel element length and ray density (negative values). Grey points (light: stem; dark: root) refer to significant differences between organs ($p < 0.0001$). Individuals nested within species were considered as random factor of the mixed models. R^2_m (variance explained by the fixed factors), R^2_c (variance explained by fixed + random factors), and p-value of each model are shown (see Table 3 for statistical details).

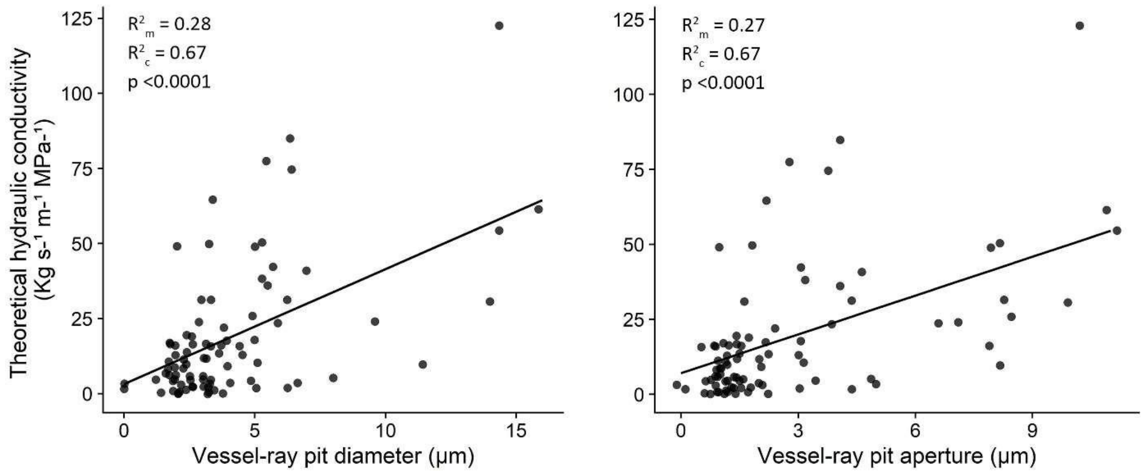

Figure 5. Relationships between theoretical hydraulic conductive and vessel-ray pit traits. Points refer to woody samples (root, stem) from Cerrado plants. Individuals nested within species were considered as random factor of the mixed models. R^2_m (variance explained by the fixed factors), R^2_c (variance explained by fixed + random factors), and p-value of each model are shown. Data from 15 species with three replicates per organ were include, except from root samples of *Aegiphila verticillata* and *Casearia silvestrys* due higher values of theoretical hydraulic conductivity.

SUPPLEMENTARY MATERIAL

Table S1. Structural and functional wood traits measured of stem and root from 15 Cerrado species (n= 3 individuals per species). SE= standard error; Min = minimum value; Max = maximum values.

Wood traits	Root			Stem		
	Mean ± SE	**Min.**	**Max.**	**Mean ± SE**	**Min.**	**Max.**
Structural						
Vessel element length (µm)	385.42 ± 18.68	195.20	695.10	388.82 ± 17.31	195.10	640.5
Vessel lumen área (µm^2)	9989.80 ± 1486.44	869.10	43643.30	9525.10 ± 1230.63	227.10	34424.40
Hydraulic vessel diameter (µm)	76.32 ± 6.25	25.26	182.03	76.55 ± 5.39	13.28	161.21
Vessel grouping (nº /vessel group)	5.07 ± 0.59	0.30	17.20	5.84 ± 0.72	0.25	23.20
Vessel density (nº mm^2)	34.63 ± 6.44	1.70	193.63	35.32 ± 6.32	3.00	164.70
Intervessel pit diameter (µm)	3.38 ± 0.32	1.99	11.05	3.67 ± 0.30	1.37	10.28
Intervessel pit aperture (µm)	2.05 ± 0.30	0.91	9.27	2.26 ± 0.30	0.65	9.12
Vessel-ray pit diameter (µm)	4.22 ± 0.50	2.21	15.83	4.27 ± 0.44	1.25	14.42
Vessel-ray pit aperture (µm)	2.81 ± 0.42	0.99	10.93	3.03 ± 0.40	0.62	11.04
Vessel fraction	0.16 ± 0.02	0.05	0.67	0.15 ± 0.02	0.11	0.31
Fiber length (µm)	1041.40 ± 59.01	395.90	2133.50	1065.80 ± 51.51	658.90	2147.80
Fiber diameter (µm)	24.15 ± 0.82	16.42	43.97	23.71 ± 0.77	15.23	38.39
Fiber lumen diameter (µm)	9.70 ± 0.74	6.42	28.90	9.64 ± 0.68	5.17	22.36
Fiber wall thickness (µm)	6.71 ± 0.24	3.01	9.94	6.49 ± 0.21	3.47	9.71
Fiber fraction	0.30 ± 0.02	0.01	0.65	0.37 ± 0.02	0.30	0.67
Ray height (µm)	814.0 ± 135.42	122.20	5214.80	662.20 ± 107.51	198.10	2567.10
Ray width (µm)	101.79 ± 16.86	11.06	486.04	132.18 ± 34.09	27.69	1511.74
Ray density (nº mm^{-1})	9.26 ± 0.77	1.80	24.57	8.66 ± 0.74	4.10	21.17
Ray fraction	0.36 ± 0.02	0.09	0.61	0.28 ± 0.01	0.22	0.47
Axial parenchyma fraction	0.22 ± 0.02	0.10	0.66	0.17 ± 0.01	0.11	0.40

Table S1. Continued.

Wood traits	Root			Stem		
	Mean ± SE	**Min.**	**Max.**	**Mean ± SE**	**Min.**	**Max.**
Functional						
Theoretical hydraulic conductivity (Kg s^{-1} m^{-1} Mpa^{-1})	37.67 ± 12.25	0.06	464.10	18.51 ± 2.63	5.56	84.72
Wood density (g/cm^3)	0.54 ± 0.02	0.21	0.79	0.51 ± 0.01	0.33	0.74
Non-structural carbohydrates (mg/g)	224.85 ± 16.74	53.66	523.39	156.20 ± 14.02	51.46	425.42
Starch (mg/g)	173.00 ± 16.47	27.45	476.90	108.63 ± 13.66	15.59	371.24
Soluble sugar (mg/g)	52.05 ± 5.00	11.57	186.03	47.86 ± 4.83	13.96	175.62

Table S2. Principal component analysis (PCA) summary of structural wood traits. Values in bold indicate the variables more correlated with each principal component (loadings > 0.15).

	PC1	PC2
Eigenvalue	123.94	28.20
Variation explained (%)	68.70	15.63
Cumulative variance (%)	68.70	84.33
Loadings		
(sqrt) Vessel element length	0.0068	**-0.3868**
(log+1) Hydraulic vessel diameter	0.0093	0.0328
(sqrt) Intervessel pit diameter	0.0010	0.0111
(sqrt) Intervessel pit aperture	0.0121	0.0239
(sqrt) Vessel-ray pit diameter	-0.0006	-0.0127
(sqrt) Vessel-ray pit aperture	0.0095	-0.0049
(log+1) Vessel density	-0.0135	-0.0503
(box-cox) Vessel grouping	-0.0001	-0.0171
(sqrt) Vessel fraction	-0.0005	0.0005
(box-cox) Fiber length	0.0373	0.0441
Fiber wall thickness	0.0232	-0.0666
Fiber fraction	-0.0011	0.0003
(sqrt) Axial parenchyma fraction	-0.0023	0.0034
Ray fraction	0.0043	-0.0026
Ray density	**-0.1855**	**-0.8060**
(sqrt) Ray height	**0.9580**	-0.2359
(sqrt) Ray width	**0.2125**	**0.3658**

Table S3. Summary of linear mixed models testing structural (represented by the two axes of the PCA) and functional wood traits mean differences between organs (root, stem) of plants from Cerrado. The estimate, standard error (SE), t-value and p-value of fixed factors are show. Individual nested within species were considered as random factor.

Wood trait	**Fixed factor** [stem compared to root]		
	Estimate (CI – 95%)	t-value	p-value
Structural			
PC1	-0.1754 (-0.45– 0.10)	-1.267	0.205
PC2	0.24 (-0.03 – -0.51)	1.760	0.078
Functional			
(log+1)Theoretical hydraulic conductivity	0.06 (-0.36 – 0.48)	0.265	0.791
Wood density	-0.02 (-0.05 – 0.00)	-1.715	0.086
Non-structural carbohydrates content	-72.63 (-95.07 – -50.19)	-6.344	**<0.001**

Table S4. Summary of linear mixed models testing the effect of plant size (organ diameter, plant height) on wood structure (represented by the two PCA axes scores) of plants from Cerrado. In all models, organs were also included as fixed categorical factor (two levels: root and stem), and individuals nested in species were considered as a random variable. Individuals nested within species were considered as random factor. The estimate, standard error (SE), t-value and p-value of fixed factors are show. R^2_m = variance explained by the fixed factors, R^2_c = variance explained by fixed and random factors of the models.

	PC1					**PC2**				
	Estimate	SE	t-value	p-value	R^2_m / R^2_c	Estimate	SE	t-value	p-value	R^2_m/ R^2_c
Organ diameter										
organ [stem]	-0.164	0.154	-1.071	0.284	0.005 / 0.72	0.068	0.156	0.439	0.661	0.08 / 0.66
organ_diameter	-0.000	0.005	-0.154	0.877		0.014	0.005	2.681	<0.01	
Plant height										
organ [stem]	-0.174	0.138	-1.264	0.213	0.01 / 0.72	0.239	0.137	1.744	0.088	0.36 / 0.72
plant_height	-0.093	0.123	-0.764	0.449		0.527	0.092	5.688	<0.0001	

Figure S1. Stem and root wood, in transversal section, of Cerrado species studied. Scale bars= 200 μm.

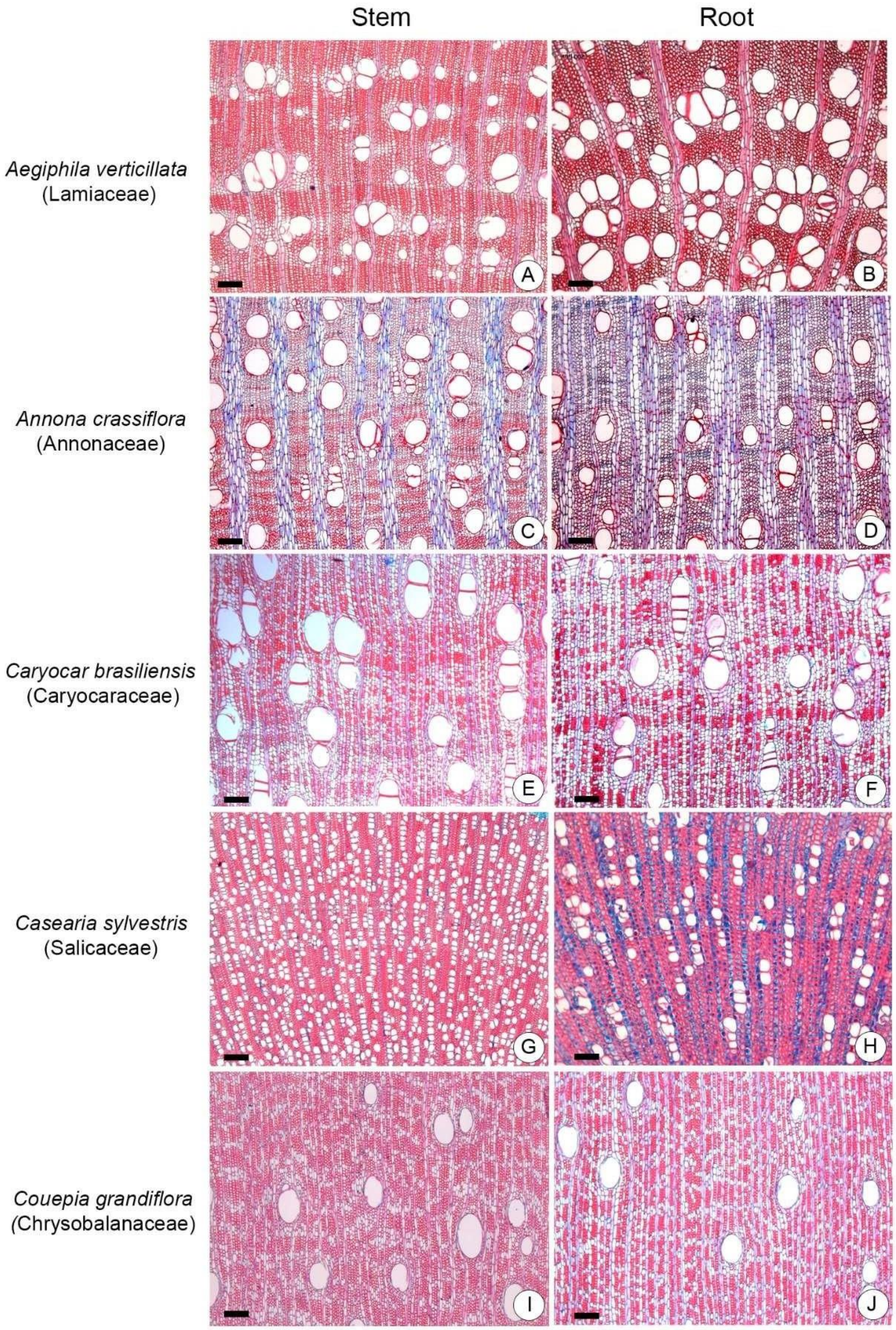

Figure S1. Continued.

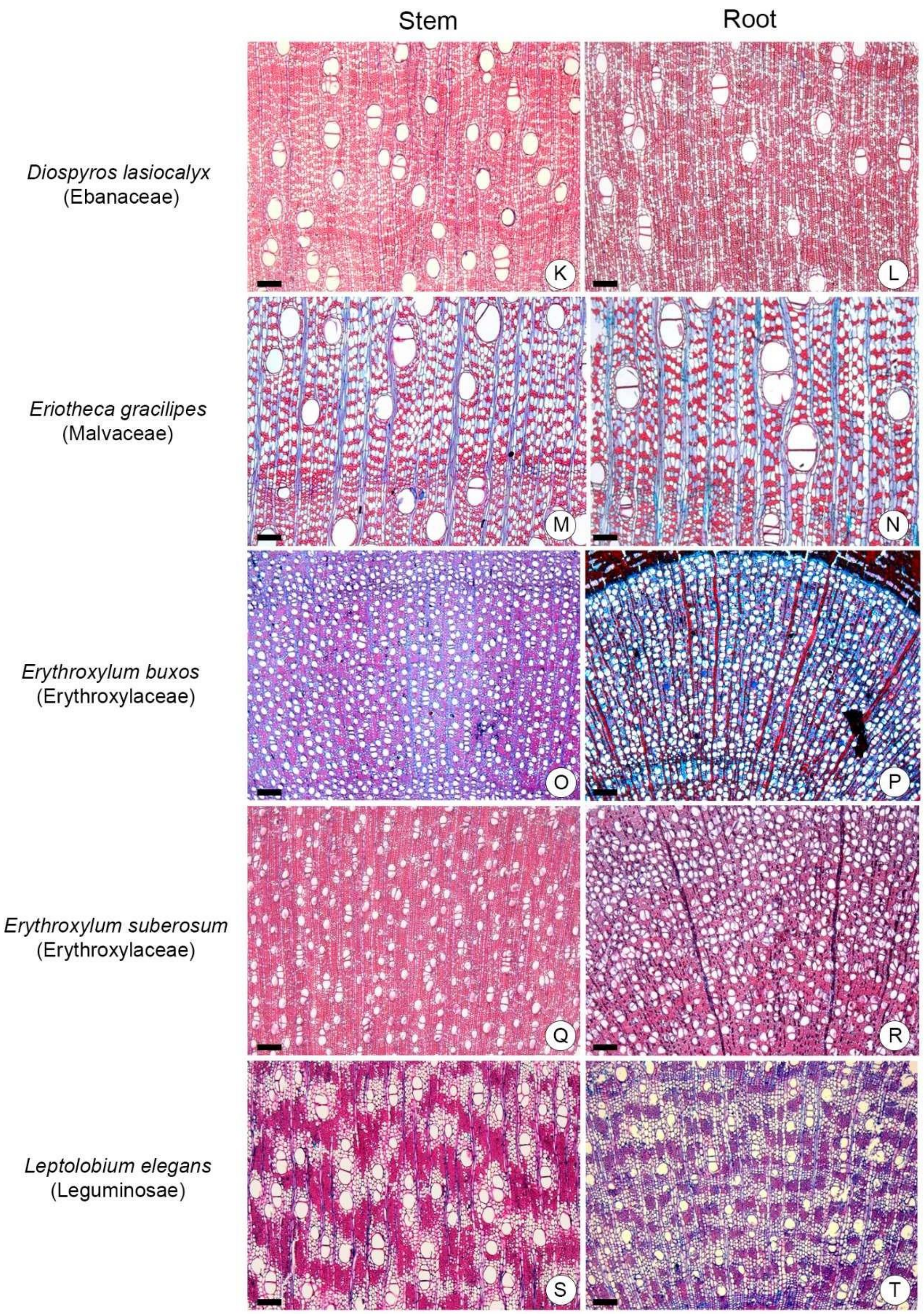

Figure S1. Continued.

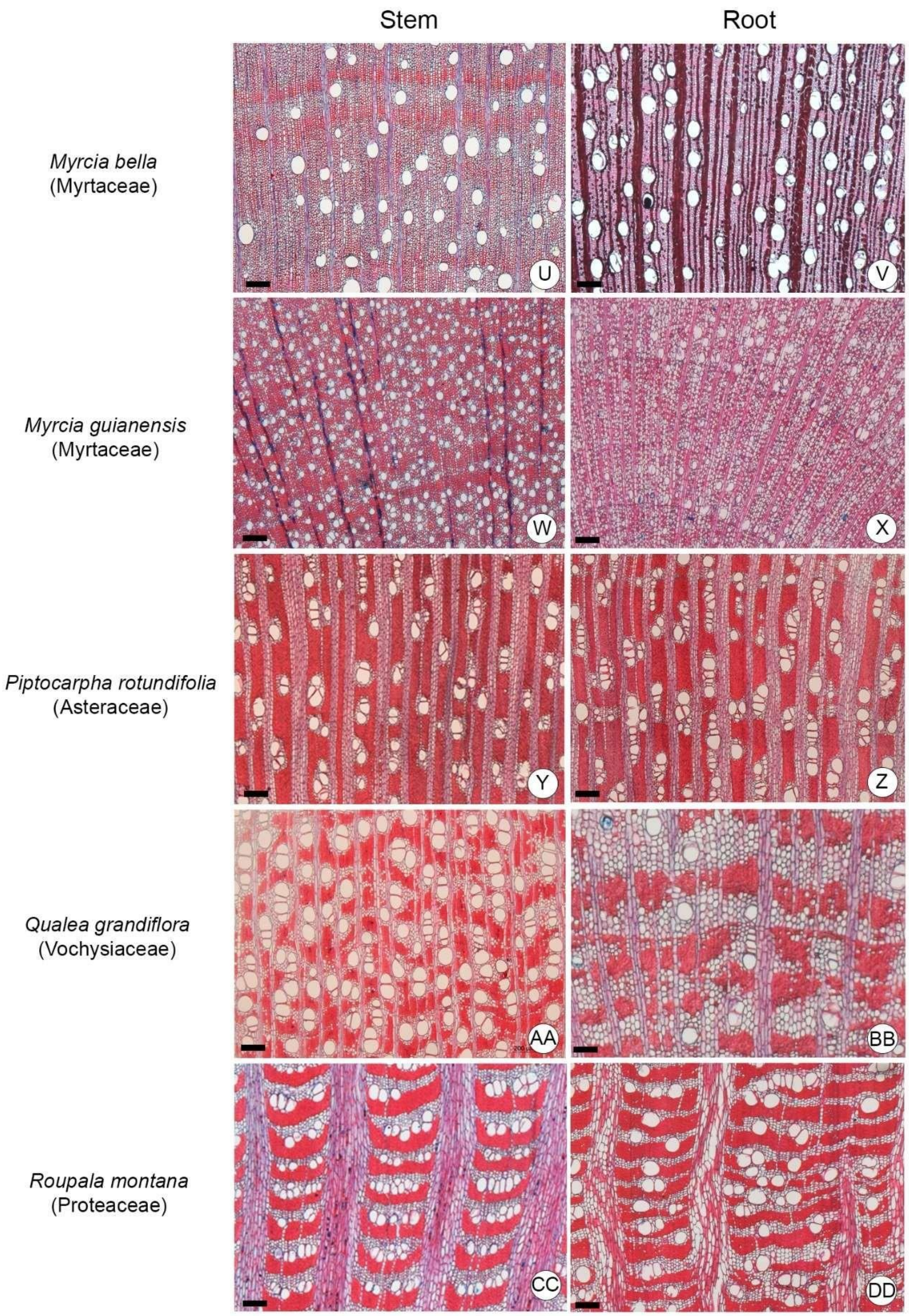

Figure S2. Relationship between plant height and PC2 scores (combination of higher ray width (positive values), with higher vessel element length and ray density (negative values)) of Cerrado plants. Organs were also included as fixed categorical factor (two levels: root and stem), and individuals nested in species were considered as a random variable. R^2_m (variance explained by the fixed factors), R^2_c (variance explained by fixed and random factors), and p-value are shown.