



UNIVERSITY OF BRASILIA
FACULTY OF TECHNOLOGY
DEPARTMENT OF FORESTRY ENGINEERING

**WOOD ANATOMY AND ITS CORRELATION WITH DENSITY,
SHRINKAGE AND ANISOTROPY OF NINETEEN SPECIES
COMMERCIALIZED IN MATO GROSSO**

REBECA DE OLIVEIRA MONTEIRO

Brasília – Distrito Federal

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Final project presented to the Department of Forest Engineering of the University of Brasília, as part of the requirements for obtaining the title of Forest Engineer.

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ABSTRACT: Wood anatomy is directly linked with the technological properties of wood, especially physical properties. The proportion of tissues, arrangement and size of cells may result in variation between wood density, shrinkage and anisotropy, but most studies are focused on fiber dimensions. For this reason, the relationship between wood anatomy and physical properties was investigated in nineteen species commonly found in lumberyards in the State of Mato Grosso. The basic density, shrinkage, transverse anisotropy was obtained from Ribeiro (2017). New measurements for the quantitative characteristics were done. The proportion of vessel wall, vessel lumen, fibers, rays and axial parenchyma was defined, as well as thirty measurements of the diameter and density of the vessels per mm², and dimensions of the rays (width and height) and distribution per millimeter were obtained using Image Pro-Plus software. Statistical analyses were performed using R software, applying Principal Component Analysis (PCA), Pearson correlation test and regression analysis with Linear Mixed Effect Models (Lmer). Both regression and correlation analysis showed that species with vessels of small diameter, although they occur in greater quantity per mm², contributed to an increase on wood density, which may indicate a trade-off between mechanical resistance and safety for the conductive system. The greater presence of the axial parenchyma, which has thin and weak walls was observed in low wood density species. The rays, in turn, increased wood density of the species, especially when they occur in high proportion, but with reduced dimensions. Most high wood density species also had the presence of extractives, which can raise the values of physical property. The shrinkage was higher for species with higher and wider rays when compared with low ones; also, the regression models reiterated the relationships between ray height, which may result from the fact that these cells are more susceptible to moisture changes. These models for shrinkage also included the diameter of the vessel, with an inverse relationship between these two. Anisotropy presented a negative relation with the number of rays/mm, but your variation among species was not capable of being explained through regression models. Thus, knowing how the wood will behavior according to its anatomical features, may be used to predict some physical properties, specifically wood density and shrinkage, and therefore its uses.

Key-words: Amazon wood species, commercial woods, dimensional stability, extractives, tissue proportion.

RESUMO: A anatomia da madeira está diretamente relacionada às propriedades tecnológicas da madeira, especialmente as propriedades físicas. A proporção de tecidos, arranjo e tamanho das células pode resultar em variação entre a massa específica da madeira, retratibilidade e anisotropia, mas a maioria dos estudos são focados em dimensões das fibras. Por essa razão, a relação entre anatomia da madeira e propriedades físicas foi investigada em dezenove espécies comumente encontradas em madeiras no Estado de Mato Grosso. A massa específica, a retratibilidade e a anisotropia transversal foram obtidas a partir de Ribeiro (2017). Para as características quantitativas, foram realizadas novas mensurações, além de novas descrições anatômicas. Foi definida a proporção de parede de vasos, lume de vaso, fibras, raios e parênquima axial, bem como trinta medições do diâmetro e densidade dos vasos por mm², e dimensões dos raios (largura e altura) e distribuição por milímetro, obtidas utilizando o software Image Pro-Plus. As análises estatísticas foram realizadas com o software R, aplicando a Análise de Componentes Principais (ACP), teste de correlação de Pearson e análise de regressão com Modelos Lineares de Efeito Misto (Lmer). Tanto a análise de regressão quanto a de correlação mostraram que espécies com vasos de pequeno diâmetro, embora estes ocorram em maior quantidade por mm², contribuíram para um aumento na densidade da madeira, o que pode indicar um *trade-off* entre resistência mecânica e segurança para o sistema condutor. A maior presença do parênquima axial foi observada em espécies de baixa densidade de madeira. Os raios, por sua vez, aumentaram a massa específica da madeira das espécies, especialmente quando ocorrem em alta proporção, mas com dimensões reduzidas. A maioria das espécies de alta densidade de madeira também tiveram alta presença de extrativos, o que pode elevar os valores da propriedade física. A retratibilidade foi maior para espécies com raios maiores e mais largos quando comparados com os menores; também os modelos de regressão reiteraram as relações entre a altura dos raios, o que pode resultar do fato de que essas células são mais suscetíveis às alterações de umidade. Estes modelos de retratibilidade também incluíram o diâmetro do vaso, com uma relação inversa entre esses dois. A anisotropia apresentou uma relação negativa com o número de raios/mm, mas sua variação entre as espécies não foi capaz de ser explicada através de modelos de regressão. Dessa maneira, saber como a madeira se comportará de acordo com suas características anatômicas, pode ser usado para prever algumas propriedades físicas, especificamente densidade e retração da madeira e, portanto, seus usos.

Palavras-chave: estabilidade dimensional, extrativos, madeiras comerciais, madeiras da Amazônia, proporção de tecidos.

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1 INTRODUCTION

In order to make proper use of wood pieces, it is necessary to know its quality, what, according to Gonçalves *et al.* (2006) means, being able of satisfying minimum requirements for fabricating a certain product. Therefore, research on wood properties have the goal of verifying the potential of a species as well as knowing its characteristics through anatomical, physics and mechanical analysis (VALENTE *et al.*, 2013; MOTTA *et al.*, 2014).

According to Florsheim *et al.* (2020), wood anatomy is a branch from botanical sciences focused on the cells present in xylem, its functions, organization, and its relationship with the biological activity of the plant. The tissues present in wood have different structural characteristics and their relative proportions can influence many technological properties, such as wood density and shrinkage (ZIEMINSKA *et al.*, 2013; BEECKMAN, 2016).

Density is commonly used to determine wood quality, since it is easier to measure, has a direct correlation with cellular composition and also can influence other physical properties (BATISTA *et al.*, 2010). This attribute is generally affected by fibers dimension, cell-wall thickness, volume and area of vessels and parenchyma, proportion of late and early wood, arrangement of cellular elements, and variation of mass and volume (FOELKEL *et al.*, 1971; PRESTON *et al.*, 2006).

Shrinkage variations happen in wood due to the exit of hygroscopic water, affecting the use of a determined species for a certain product, since it can cause defects during drying (GALVÃO and JANKOWSKY, 1985; DIAS *et al.*, 2018). This physical property is normally linked to proportions of cell-walls or increase of the cells (OLIVEIRA and SILVA, 2003; POUBEL *et al.*, 2011). Shrinkage also provides information whether a species is stable or not for use, according to the transverse anisotropic coefficient, defined by the ratio between tangential and radial shrinkage (ALVES *et al.*, 2017).

Currently, some studies try to find the correlation of these properties with the wood anatomy. However, most works only aim to characterize one or more species without considering the correlation the physical properties might have with wood anatomy.

2 OBJECTIVE

2.1 GENERAL OBJECTIVE

Evaluate how tissue proportion and macroscopic anatomical characteristics can be correlated with physical properties on nineteen commonly commercialized species in Mato Grosso state.

2.2 SPECIFIC OBJECTIVE

To study the correlations between tissue proportion (vessels - vessel wall and lumen, axial parenchyma, rays and fibers) and anatomical characteristics (vessel diameter, area and density, ray height, width and frequency) with wood density, shrinkage and transverse anisotropy in nineteen species marketed by Mato Grosso state, through macroscopic images, measurements of anatomical features and statistical analysis.

3 BIBLIOGRAPHIC REVIEW

3.1 WOOD ANATOMY

Wood is a very heterogeneous material, originated from secondary growth of higher plants (ZIEMINSKA *et al.*, 2013; COUTO, 2014). It can be applied in different ways, such as for extraction of cellulose, panels, flooring, structural components, etc. (COUTO, 2014). For this reason, there are many areas, such as wood chemistry and physiology (MAI *et al.*, 2022) that investigate this material. One of these areas is the wood anatomy.

The anatomical structure contains ecological information, being a helpful tool to identify a species or genus; also, this structure can aid in the knowledge and utilization of a new timber, or even pre-determine other physical and some mechanical properties (FONTI *et al.*, 2010). And, since these properties vary from one species to another, the understanding of wood cellular constitution is essential for understanding technological behavior of the wood as well (ALMEIDA, 2022).

At cell and tissue level, xylem is composed of three main cell types (SLUPIANEK *et al.*, 2021). For conifers or softwoods, there are tracheids, that can provide mechanical support and conduction, a small number of rays, and axial parenchyma present sometimes for some genres (EVERT, 2006). Angiosperms or hardwoods are composed by vessels, fibers and parenchyma cells, and their different volume fractions can variate within species (CHEN *et al.*, 2020; SLUPIANEK *et al.*, 2021). In addition, xylem architecture can also answer about how trees can adapt through trade-offs, allocations, morphology and adjustments to several factors

in the environment (FONTI *et al.*, 2010; LACHENBRUCH and MCCULLOH, 2014). Wider conduits, for an example, can be more efficient for water conduction, while leaving more space for supporting fibers (CHAVE *et al.*, 2009).

Therefore, prior to fabricating and designing wooden materials, it is fundamental to understand the relationship between the structure and properties of wood (CHEN *et al.*, 2020). Since wood density and shrinkage can be explained through this anatomical structure, and not only cells individually, but also their relative proportions, which can influence both physical properties (POUBEL *et al.*, 2011; ZIEMINSKA *et al.*, 2013; FORTUNEL *et al.*, 2014).

3.2 WOOD PHYSICAL PROPERTIES

3.2.1 Wood density

Wood density is one of wood physical properties. It can be defined as the weight or mass of wood divided by the volume at a certain moisture content, with value expressed in kilograms per cubic meter or grams per cubic centimeter, and the moisture content must be given when density is reported (WIEDENHOEFT and EBERHARDT, 2013). This property is very important for the tree, because it can affect the plant biomechanics, resistance to drought periods and decay resistance, as well as it is related to ecosystem processes and used to estimate biomass (HIETZ *et al.*, 2013).

Lachenbruch and McCulloh (2014) consider density a good example of a proxy measure, for being strongly correlated with many other measures and easy to determine, resulting in a lot of data available. There are some methods that can be used to verify the density of a species. One of the most used is called basic density, and it is defined by the ratio between the weight of dry wood at 0% of humidity and its green volume (MELO, 2002). However, it is also possible to calculate with dry weight over dry volume (dry density), green weight over green volume, or even with weight and volume at a defined humidity percentage (12% or 15%), named apparent wood density (ZOBEL and JETT, 1995; MELO, 2002).

The density of a determined species can be influenced by chemical traits, genetic components, major changes in the environment and anatomical structure (ZOBEL and JETT, 1995; LACHENBRUCH and MCCULLOH, 2014). For example, rapid volumetric growth can generate lower density woods. Also, in tropical wood species, extractives may constitute 20% of the dry weight of normal wood (PETTERSEN, 1984).

Considering only the wood anatomy, most studies are focus on fiber tissue. It is known that variations in density are caused mainly by variations in fiber wall fractions (DE MIL *et al.*, 2018), for example high-density species have thick-walled fibers compared to low-density ones (CHAVE *et al.*, 2009). However, vessel area and vessel density per square millimeter also contribute to the wood density, since these aspects determine the amount of lumen space in wood (PRESTON *et al.*, 2006). The axial parenchyma is able to influence wood density too, as well as ray volume (FUJIWARA *et al.*, 1991; DE MIL *et al.*, 2018). Therefore, the main tissues (vessels, fibers and parenchyma) and their proportions and structure, can affect wood density (HACKE *et al.*, 2001; SWENSON and ENQUIST, 2008; ZIEMINSKA *et al.*, 2013).

These variations in wood anatomy related to its density are also linked to the changes in hydraulic properties (LACHENBRUCH and MCCULLOH, 2014). According to Baas and Wheeler (2011) and Poorter *et al.*, (2009), wide vessels are more efficient but can be more vulnerable to cavitation and reduce wood density, whilst narrower vessels are safer but result in low conductivity.

Despite of its importance, there are still few studies on the correlation between wood anatomy and its density, such as Rahman *et al.* (2004), investigating how wood density can be affected by tissue proportions in *Tectona grandis*, as well as Zieminska *et al.* (2013) with 24 Australian species, De Mil *et al.* (2018) with tropical trees from Congo and Dória *et al.* (2022) with Cerrado species. Poubel *et al.* (2011) and Uetimane Jr. and Ali (2011) also studied this relation but considering variations on the dimensions in the cells instead of the tissue proportions.

3.2.2 Shrinkage and anisotropy

Dimensional changes in wood are caused by the shrinking of the cells, as water leaves the cells walls at 25 to 30% of moisture content, that is, the fiber saturation point, in which all water present in the lumen has already left (PECK, 1957; SIMPSON, 1991), and it may cause cracks and warps (SIMPSON, 1991). Therefore, shrinkage is an important physical property of the wood, considering that it is a phenomenon that can determine the material usage time as well as predict their behavior during drying (JANKOWSKY and GALVÃO, 1979; ELAIEB *et al.*, 2019).

Shrinkage can differ widely between species, among tangential, radial and longitudinal direction and even between same species or from material cut from the same tree (PECK, 1957; ELAIEB *et al.*, 2019). The chemical composition and wood structure at ultrastructure,

microscopic or macroscopic levels can influence this property too (JANKOWSKA and REBROWSKA, 2018). Furthermore, some authors report that species with high density have greater shrinkage (SIMPSON, 1991; POUBEL *et al.*, 2011).

It is known that wood shrinks from 1.5 to 2 times more in tangential direction than radial, being the longitudinal shrinkage the lowest of all (SIMPSON, 1991). This is caused by a property intrinsic to wood, called transverse anisotropy or simply anisotropy (ELAIEB *et al.*, 2019). Luis Christoforo *et al.* (2016) affirm that anisotropy is very important to characterize wood and it is related to its moisture content. The same authors also explain that the anisotropy coefficient, that is, ratio between tangential and radial shrinkage, is a vital parameter used to indicate the best application of a species, given its drying quality.

There are two main theories that explain anisotropy, the first one being ray restraint theory, in which these cells are responsible to limit the radial movement of other xylem elements, and the second being the earlywood-latewood theory, applicable for conifers only, in which thick-walled cells in latewood forces thin-walled cells in earlywood shrink to a greater extent (SKAAR, 1988; GU *et al.*, 2001).

The majority of studies focus on the influence of rays on shrinkage (WIJESINGHE, 1959; DE LA PAZ *et al.*, 2005; POUBEL *et al.*, 2011; XUE *et al.*, 2018; ELAIEB *et al.*, 2019). However, recent papers are focusing on other anatomical characteristics as well, such as vessels, fibers and axial parenchyma, as done by Poubel *et al.* (2011) with *Eucalyptus pellita*; Moya *et al.* (2012) with *Vochysia guatemalensis*; Valente *et al.* (2013) with *Anadenanthera peregrina*; Toong *et al.* (2014) with many Malaysian timbers and Jankowska and Rebkowska (2018) on several tropical and subtropical species. Works involving anisotropy and wood anatomy, on the other side, are scarce. However, Elaieb *et al.* (2019) discuss anisotropy can be positively related to ray size and how the proportion of these cells can be a factor to improve predictions of physical properties, such as shrinkage.

4 MATERIALS AND METHODS

For this study 19 commonly commercialized species from Mato Grosso state were utilized: *Hymenolobium petraeum* Ducke, *Dipteryx odorata* (Aubl.) Forsyth f., *Hymenaea courbaril* L., *Apuleia leiocarpa* (Vogel) J.F.Macbr., *Lonchocarpus cultratus* (Vell.) A.M.G.Azevedo & H.C.Lima, *Cedrelinga cateniformis* (Ducke) Ducke and *Dinizia excelsa* Ducke (Fabaceae), *Qualea brevipedicellata* Stafleu, *Erismia uncinatum* Warm. and *Vochysia maxima* Ducke (Vochysiaceae), *Couratari oblongifolia* Ducke & Kunth (Lecythidaceae),

Pouteria egregia Sandwith and *Manilkara elata* (Allemão ex Miq.) Monach. (Sapotaceae), *Euplassa pinnata* (Lam.) I.M.Johnst. (Proteaceae), *Simarouba amara* Aubl. (Simaroubaceae), *Handroanthus serratifolius* (Vahl) S.Grose (Bignoniaceae), *Protium altissimum* (Aubl.) Marchand (Burseraceae), *Goupia glabra* Aubl. (Goupiaceae) and *Mezilaurus itauba* (Meisn.) Taub. ex Mez (Lauraceae).

Only the samples for these species as well as the data for wood density, shrinkage and anisotropy were obtained from Ribeiro (2017) study. For the present study, the wood density classes were classified in low (below 0.5 g/cm³), medium (0.5-0.72 g/cm³) and high basic density (above 0.72 g/cm³) according to Melo (2002). The anisotropy coefficient was classified following Moreschi (2014), in which 1.2-1.5 are high quality woods, 1.6-1.9 are regular woods and more than 2.0 are low quality woods.

New descriptions and measurements for macroscopic characters were realized. Three samples of each species were used for that. Samples were polished in transverse and tangential section with sandpaper grit 40, 180 and 320 and water sandpaper grit 600 and 1200, until the anatomical features were seen on naked eye or through stereoscope with 20x magnification. The measurements were based on COPANT norm (1973), Florsheim et al. (2020) and IAWA Committee (1989).

The macroscopic anatomical characters were photographed in tangential and transverse section, using a digital camera Olympus model DP25, attached in a stereoscope microscope SZX7 Olympus, and then were analyzed using the program Image-Pro Plus. Thirty measurements were taken for each quantitative anatomical feature, from each sample, as it follows: diameter (μm) and density of vessels per millimeter square; length of rays (μm) (tangential section); width (μm) and ray density per millimeter (transverse section). The tissue proportion was obtained for axial parenchyma, fibers, rays and vessels wall and lumen, using a grid composed of 240 squares and five images per species. Where there was an intersection of the grid lines the lumen and wall (only for vessels) or the cell was counted.

For statistical analysis, the software R version 4.1.3 was used with the packages car, vegan, ggplot2, lme4 and standardize. The Principal Component Analysis (PCA) was applied to verify the general relationship between the variables, together with Pearson correlation test, to check which ones were the most significant. Additionally, linear mixed effect models (Lmer) were used to analyze which anatomical features were able to explain wood density, shrinkage and anisotropy considering a variance inflation factor (VIF) under 2.

5 RESULTS

5.1 WOOD ANATOMY DESCRIPTION AND MEASUREMENTS

The anatomical description for each species is shown on Table 1, alongside with pictures of the transverse section (Fig. 1-2).

Table 1. Anatomical characterization of the species.

Species	Anatomical description
<i>Apuleia leiocarpa</i>	Growth rings distinct, marked by fiber zones and marginal parenchyma; wood diffuse-porous, vessels predominantly solitary and visible with hand lens, obstructed by yellowish substances and little tyloses occasionally; axial parenchyma visible with hand lens, winged-aliform forming short and long bands, sometimes marginal lines; rays visible with hand lens on transverse section and tangential section, short and medium width, storied; pleasant odor.
<i>Cedrelinga cateniformis</i>	Growth rings distinct, marked by fiber zones and very little by darkened lines; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with naked eye; axial parenchyma visible only with hand lens, vasicentric and lozenge-aliform; rays not visible on transverse and tangential section, short and narrow, irregularly storied.
<i>Couratari oblongifolia</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with naked eye; axial parenchyma visible with hand lens, reticulate; rays visible on transverse section with naked eye and with hand lens on tangential section, short and medium width, non-storied.
<i>Dinizia excelsa</i>	Growth rings distinct, marked by fiber zones and narrow lines of marginal parenchyma; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, completely obstructed by whitish, orangish and darkish substances; axial parenchyma visible with naked eye, short confluent and lozenge-aliform, sometimes in marginal lines; rays visible with hand lens on transverse section and only hand lens on tangential section, short and medium width, non-storied; unpleasant odor.
<i>Dipteryx odorata</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens; axial parenchyma visible with naked eye, short lozenge-aliform and confluent, sometimes unilateral; rays indistinct on both sections, short and medium width, storied.
<i>Erisma uncinatum</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, obstructed by tyloses; axial parenchyma visible with naked eye, forming bands, with included phloem; rays visible on transverse section and tangential section with hand lens, short and medium width, non-storied.
<i>Euplassa pinnata</i>	Growth rings indistinct; wood diffuse-porous, vessels solitary and multiple of 2, visible with hand lens; axial parenchyma visible with hand lens, scalariform; rays visible with hand lens on transverse section and with naked eye on tangential section, tall and wide, non-storied.
<i>Goupia glabra</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels predominantly solitary, visible with hand lens, partially obstructed by tyloses; axial parenchyma visible only with hand lens, apotracheal diffuse; rays visible with naked eye on transverse section and with hand lens on tangential section, short and medium width, non-storied; unpleasant odor.

Species	Anatomical description
<i>Handroabthus serratifolius</i>	Growth rings distinct, marked by fiber zones and occasionally by marginal parenchyma, with more accumulation of vessels over fiber zones; wood diffuse-porous, vessels predominantly solitary, visible with hand lens, obstructed by naphthoquinone; axial parenchyma visible only hand lens, winged-aliform, vasicentric and sometimes forming marginal lines; rays visible only with hand lens on both sections, short and medium width, storied.
<i>Hymenaea courbaril</i>	Growth rings distinct, marked by marginal parenchyma; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, obstructed by darkish to orangish substances; axial parenchyma visible with naked eye, lozenge-aliform, marginal bands and sometimes short confluent; rays visible with naked eye on transverse section and with hand lens on tangential section, short and medium width, non-storied.
<i>Hymenolobium petraeum</i>	Growth rings a little distinct, marked by fiber zones and marginal parenchyma; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with naked eye; axial parenchyma visible with naked eye, confluent and forming irregular bands, lozenge-aliform and marginal lines; rays visible with naked eye on both sections, short and medium width, storied.
<i>Lonchocarpus cultratus</i>	Growth rings indistinct to distinct, marked by some fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, a little obstructed by whitish deposits; axial parenchyma visible with naked eye, forming bands; rays visible with naked eye on transverse section and with hand lens on tangential section, short and medium width, non-storied.
<i>Manilkara elata</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible only with hand lens, completely obstructed by whitish substances, arranged in radial pattern; axial parenchyma visible with hand lens, forming regular narrow lines; rays visible with hand lens on both sections, short and medium width, non-storied.
<i>Mezililarus itauba</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiples of 2 and 3, visible with hand lens, arranged in radial pattern, obstructed by tyloses; axial parenchyma visible with hand lens, scanty paratracheal; rays visible with hand lens on both sections, short and medium width, non-storied.
<i>Pouteria egregia</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, partially obstructed by tyloses, with a tendency to diagonal pattern arrangement; axial parenchyma visible with naked eye, forming sinuous lines and bands; rays visible with hand lens on both sections, short and medium width, non-storied.
<i>Protium altissimum</i>	Growth rings barely distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, obstructed by tyloses; axial parenchyma visible with naked eye, scanty paratracheal; rays visible with hand lens on both sections, short and medium width, non-storied, radial canals present.
<i>Qualea brevipedicellata</i>	Growth rings indistinct; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with naked eye, obstructed by whitish deposits; axial parenchyma visible with hand lens, winged-aliform and short to long confluent; rays visible with naked eye on transverse section and with hand lens on tangential section, medium width and short, non-storied; traumatic canals present.
<i>Simarouba amara</i>	Growth rings distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with hand lens, obstructed by tyloses; axial parenchyma forming lines; rays visible with hand lens on both sections, medium width and short., storied; traumatic canals present.
<i>Voxhysia maxima</i>	Growth rings barely distinct, marked by fiber zones; wood diffuse-porous, vessels solitary and multiple of 2 and 3, visible with naked eye, partially obstructed; axial parenchyma visible with naked eye, winged-aliform, sometimes forming lines; rays visible with naked eye on transverse and tangential section, wide and tall; traumatic canals present, obstructed by darkish substances.

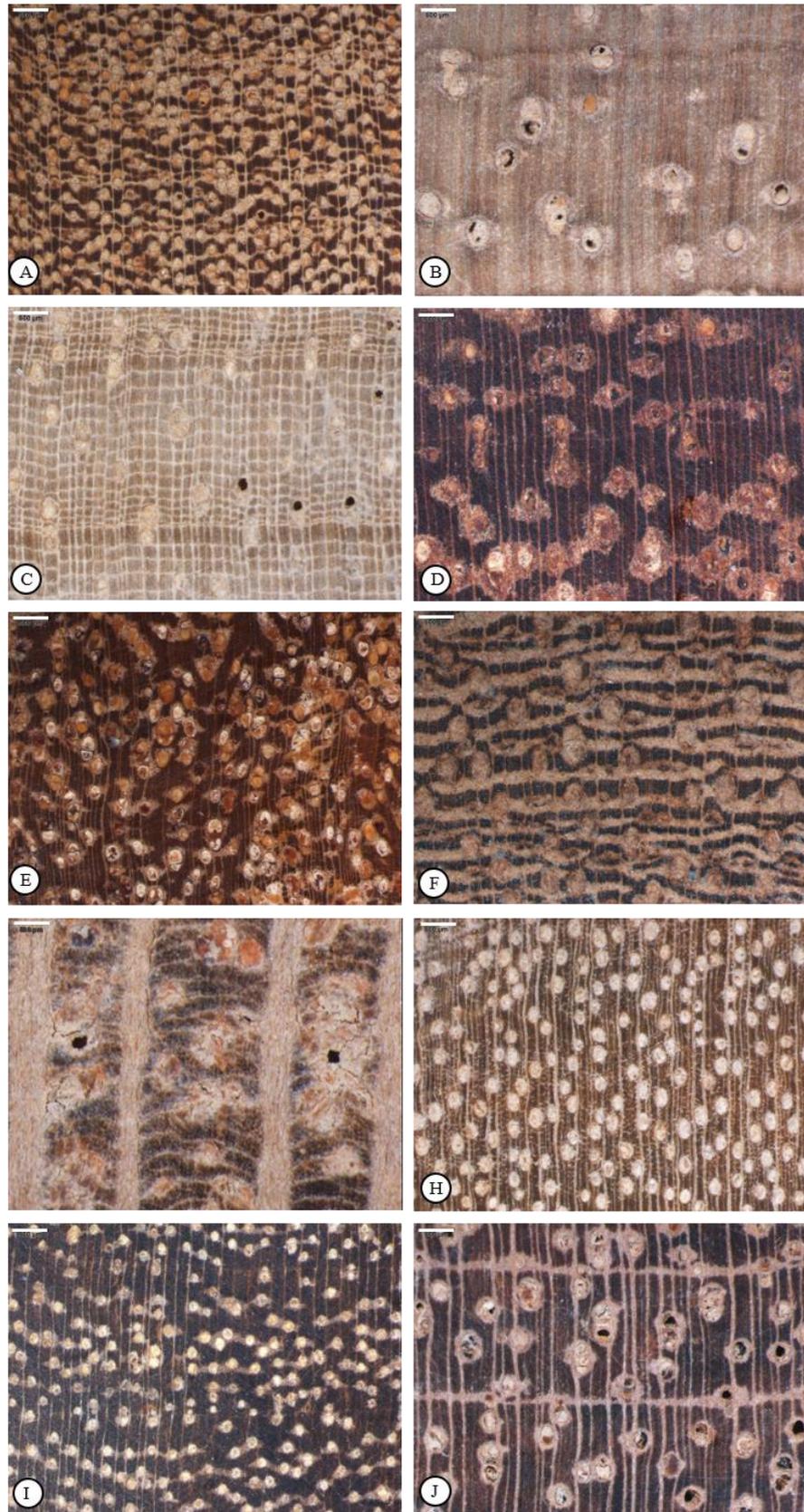


Figure 1. Transverse sections. A – *Apuleia leiocarpa*; B – *Cedrelinga cateniformis*; C – *Couratari oblongifolia*; D – *Dinizia excelsa*; E – *Dipteryx odorata*; F – *Erisma uncinatum*; G – *Euplassa pinnata*; H – *Goupia glabra*; I – *Handroanthus serratifolius*; J – *Hymenaea courbaril*. Bars = 500 µm.

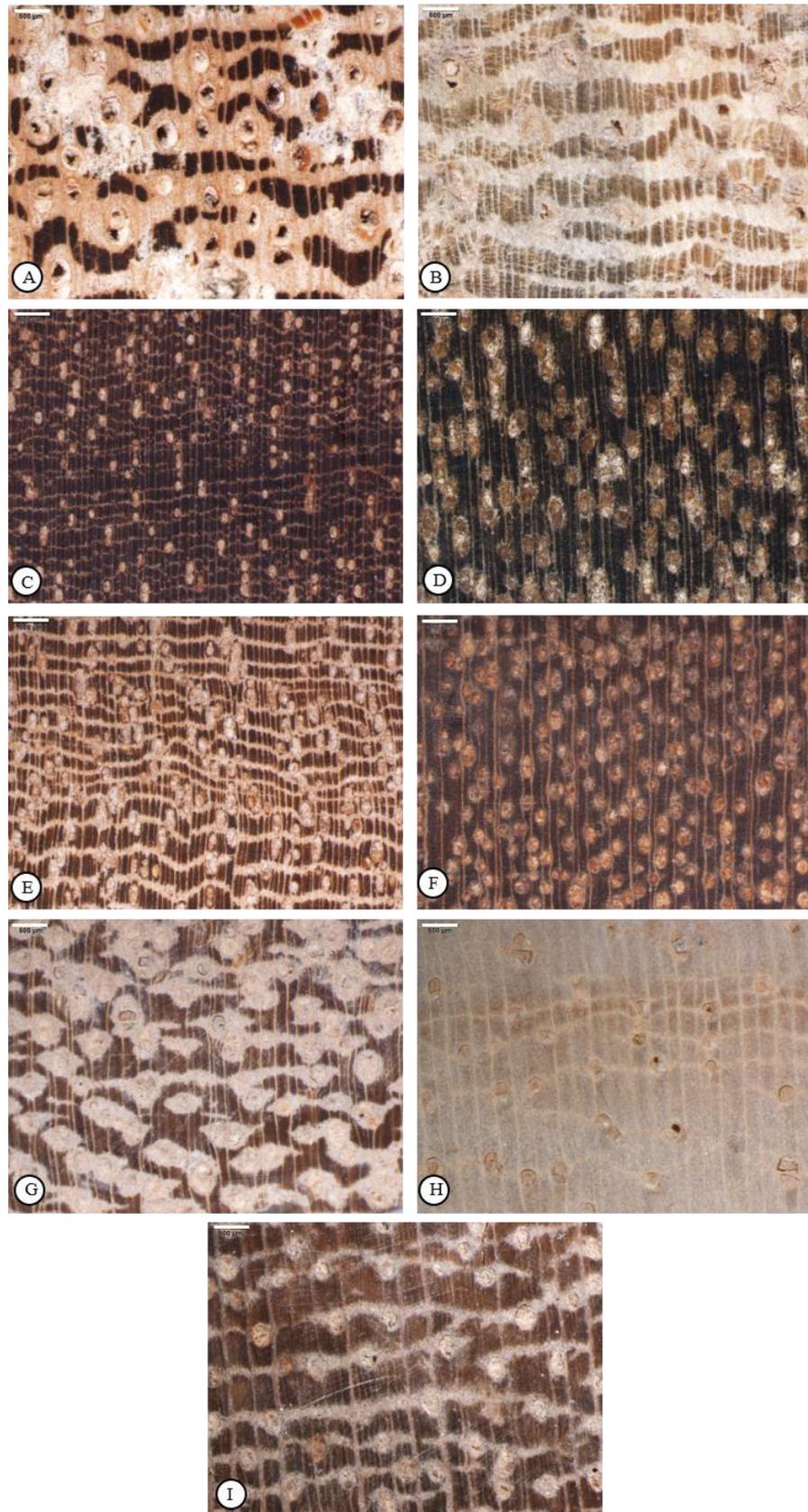


Figure 2. Transverse sections. A – *Hymenolobium petraeum*; B – *Lonchocarpus cultratus*; C – *Manilkara elata*; D – *Mezilaurus itauba*; E – *Pouteria egregia*; F – *Protium altissimum*; G – *Qualea brevipedicellata*; H – *Simarouba amara*; I – *Vochysia maxima*. Bars = 500 µm.

The measurements for quantitative wood characteristics are presented in Table 2. Vessels were small and in high density/mm² for the species *Apuleia leiocarpa*, *Dipteryx odorata*, *Goupia glabra*, *Handroanthus serratifolius*, *Manilkara elata*, *Mezilaurus itauba*, *Pouteria egregia* and *Protium altissimum*. While, the species *Euplassa pinnata* and *Vochysia maxima* had large and tall rays. Rays had a low frequency/mm in *Euplassa pinnata*, *Hymenolobium petraeum*, *Protium altissimum*, *Simarouba amara* and *Vochysia maxima*.

Table 2. Measurements for quantitative wood anatomical characters. VDi = vessel diameter; R/mm = rays per millimeter; VDe = vessel density/mm²; RH = ray height; RW = ray width.

Species	VDi (µm)	R/mm	VDe (mm ²)	RH (µm)	RW (µm)
<i>Apuleia leiocarpa</i>	92.74	6.74	13.94	173.16	13.71
<i>Cedrelinga cateniformis</i>	248.19	7.56	2.89	135.15	13.56
<i>Couratari oblongifolia</i>	142.11	7.23	2.96	371.33	29.90
<i>Dinizia excelsa</i>	143.90	5.93	3.89	233.24	27.82
<i>Dipteryx odorata</i>	121.60	9.36	8.78	148.06	13.95
<i>Erisma uncinatum</i>	167.04	5.81	4.13	282.97	26.95
<i>Euplassa pinnata</i>	133.00	1.70	4.01	5398.30	178.12
<i>Goupia glabra</i>	109.83	9.53	7.97	210.69	26.46
<i>Handroanthus serratifolius</i>	71.94	6.38	9.91	226.71	14.24
<i>Hymenaea courbaril</i>	159.54	5.16	4.44	295.55	32.69
<i>Hymenolobium petraeum</i>	191.76	4.57	3.09	234.06	29.36
<i>Lonchocarpus cultratus</i>	160.37	6.36	3.51	276.79	24.55
<i>Manilkara elata</i>	74.69	8.33	11.19	235.24	13.93
<i>Mezilaurus itauba</i>	112.01	6.00	9.56	282.17	21.93
<i>Pouteria egregia</i>	108.08	9.17	12.22	222.52	16.60
<i>Protium altissimum</i>	100.75	4.99	9.82	221.69	21.99
<i>Qualea brevipedicellata</i>	126.43	5.14	5.13	313.93	19.21
<i>Simarouba amara</i>	161.05	3.56	3.13	372.08	28.08
<i>Vochysia maxima</i>	155.67	4.64	3.30	699.97	43.65

The fraction tissues are in Table 3. In Figure 3 and 4 it is possible to observe the proportions of vessel lumen, vessel wall, fibers, rays and axial parenchyma for each species, related to the density and volumetric shrinkage, respectively. Vessel wall and lumen proportion were low for all species. Half of the species had axial parenchyma as the most predominant tissue, whilst the other half had fiber wall proportion. *G. glabra* presented more ray proportion.

Table 3. Tissue fraction mensuration. SVP = solitary vessels proportion; MVP = multiple vessels proportion; VL = vessel lumen proportion; VW = vessel wall proportion; FP = fiber proportion; RP = ray proportion; AP = axial parenchyma proportion.

Species	SVP	MVP	VL	VW	FP	RP	AP
<i>Apuleia leiocarpa</i>	0.59	0.40	0.19	0.21	0.15	0.12	0.34
<i>Cedrelinga cateniformis</i>	0.43	0.56	0.05	0.07	0.45	0.25	0.18
<i>Couratari oblongifolia</i>	0.35	0.64	0.06	0.07	0.35	0.21	0.30
<i>Dinizia excelsa</i>	0.42	0.57	0.11	0.12	0.26	0.22	0.30
<i>Dipteryx odorata</i>	0.54	0.46	0.11	0.13	0.33	0.18	0.25
<i>Erisma uncinatum</i>	0.37	0.63	0.08	0.13	0.16	0.12	0.52
<i>Euplassa pinnata</i>	0.48	0.52	0.15	0.16	0.20	0.17	0.32
<i>Goupia glabra</i>	0.80	0.19	0.12	0.21	0.14	0.34	0.18
<i>Handroanthus serratifolius</i>	0.66	0.33	0.07	0.16	0.47	0.16	0.15
<i>Hymenaea courbaril</i>	0.58	0.40	0.08	0.12	0.32	0.18	0.30
<i>Hymenolobium petraeum</i>	0.37	0.60	0.09	0.11	0.16	0.13	0.51
<i>Lonchocarpus cultratus</i>	0.38	0.62	0.08	0.08	0.18	0.20	0.46
<i>Manilkara elata</i>	0.38	0.61	0.07	0.16	0.22	0.23	0.32
<i>Mezilaurus itauba</i>	0.26	0.73	0.16	0.17	0.25	0.22	0.21
<i>Pouteria egregia</i>	0.36	0.64	0.11	0.15	0.16	0.23	0.23
<i>Protium altissimum</i>	0.52	0.48	0.12	0.20	0.24	0.23	0.21
<i>Qualea brevipedicellata</i>	0.35	0.64	0.12	0.18	0.25	0.23	0.23
<i>Simarouba amara</i>	0.36	0.62	0.06	0.09	0.45	0.18	0.22
<i>Vochysia maxima</i>	0.57	0.42	0.09	0.15	0.27	0.16	0.33

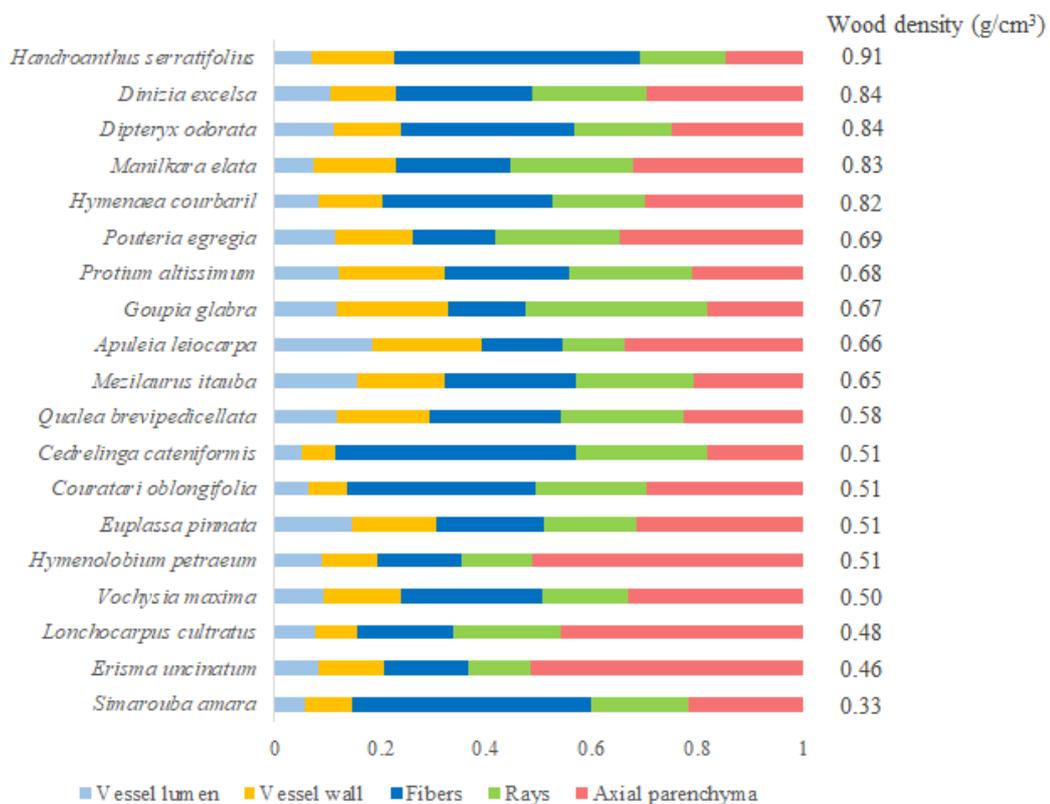


Figure 3. Wood density and tissue proportions for each species.

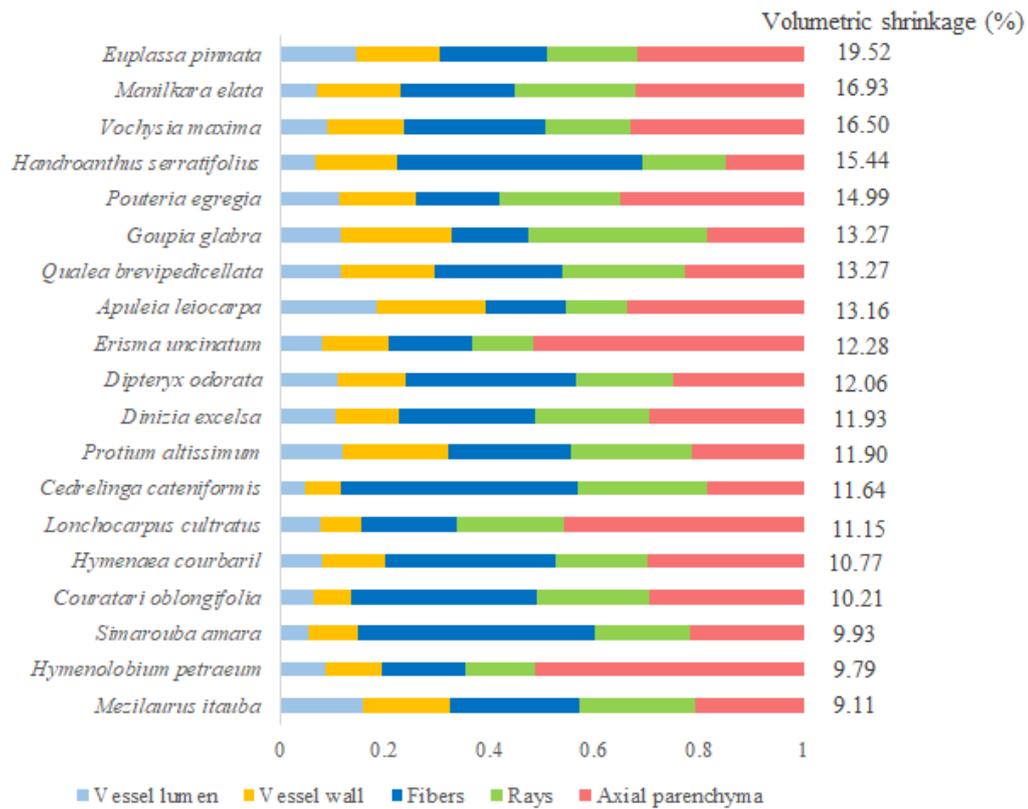


Figure 4. Volumetric shrinkage and tissue proportion for each species.

5.2 PHYSICAL PROPERTIES MEASUREMENTS

Table 4 summarizes Ribeiro (2017) results of the physical properties (density, shrinkage and anisotropy). Most species had volumetric shrinkage around 9 to 13%, except for *Euplassa pinnata*, *Handroanthus serratifolius*, *Manilkara elata*, *Pouteria egregia* and *Vochysia maxima*, that had volumetric shrinkage above 14%. Thus, the woods had medium to high shrinkage.

Table 4. Physical properties. WD = wood density (g/cm^3); RS = radial shrinkage (%); TgS = tangential shrinkage; VS = volumetric shrinkage (%); TgS/RS = transverse anisotropy. Med. = Medium. Adapted from Ribeiro (2017).

Species	WD	WD class	RS	TgS	VS	TgS/RS	TgS/RS class
<i>Apuleia leiocarpa</i>	0.66	Med.	5.41	7.70	13.16	1.44	Regular
<i>Cedrelinga cateniformis</i>	0.51	Med.	4.82	6.63	11.64	1.39	Regular
<i>Couratari oblongifolia</i>	0.51	Med.	4.02	5.80	10.21	1.49	Regular
<i>Dinizia excelsa</i>	0.84	High	4.78	7.09	11.93	1.50	Regular
<i>Dipteryx odorata</i>	0.84	High	4.59	6.95	12.06	1.57	Regular
<i>Erisma uncinatum</i>	0.46	Low	5.57	7.04	12.28	1.32	Regular
<i>Euplassa pinnata</i>	0.51	Med.	7.24	12.82	19.52	1.79	Regular
<i>Goupia glabra</i>	0.67	Med.	5.7	8.01	13.27	1.51	Regular
<i>Handroanthus serratifolius</i>	0.91	High	6.85	8.13	15.44	1.18	High quality
<i>Hymenaea courbaril</i>	0.82	High	3.73	6.45	10.77	1.76	Regular
<i>Hymenolobium petraeum</i>	0.51	Med.	3.92	5.57	9.79	1.42	Regular
<i>Lonchocarpus cultratus</i>	0.48	Low	4.38	6.52	11.15	1.50	Regular
<i>Manilkara elata</i>	0.83	High	7.05	10.26	16.93	1.48	Regular

Species	WD	WD class	RS	T _{gS}	VS	T _{gS} /RS	T _{gS} /RS class
<i>Mezilaurus itauba</i>	0.65	Med.	3.47	5.15	9.11	1.53	Regular
<i>Pouteria egregia</i>	0.69	Med.	6.53	8.44	14.99	1.31	Regular
<i>Protium altissimum</i>	0.68	Med.	3.91	7.78	11.90	2.01	Low quality
<i>Qualea brevipedicellata</i>	0.58	Med.	5.74	7.63	13.27	1.34	Regular
<i>Simarouba amara</i>	0.33	Low	3.59	6.13	9.93	1.80	Regular
<i>Vochysia maxima</i>	0.50	Med.	5.97	10.39	16.50	1.76	Regular

5.3 CORRELATIONS BETWEEN WOOD ANATOMY AND PHYSICAL PROPERTIES

It was observed that wood density had a negative relation to vessel diameter, axial parenchyma proportion, and multiple vessels proportions, and a positive relation to vessel density/mm², ray proportion, rays per millimeter, and proportion of solitary vessels (Fig. 5).

Shrinkage was positively related to ray width and height, proportion of vessel lumen and wall, and negatively related to fiber proportion (Fig. 5). Anisotropy had a positive relation to axial parenchyma proportion, vessel diameter, and multiple vessels proportion, and a negative relation to ray proportion, vessel density/mm², rays per millimeter, and solitary vessels proportion (Fig. 5). In order to test whether the correlations were significant or not, the Pearson correlation test was applied (Table 5).

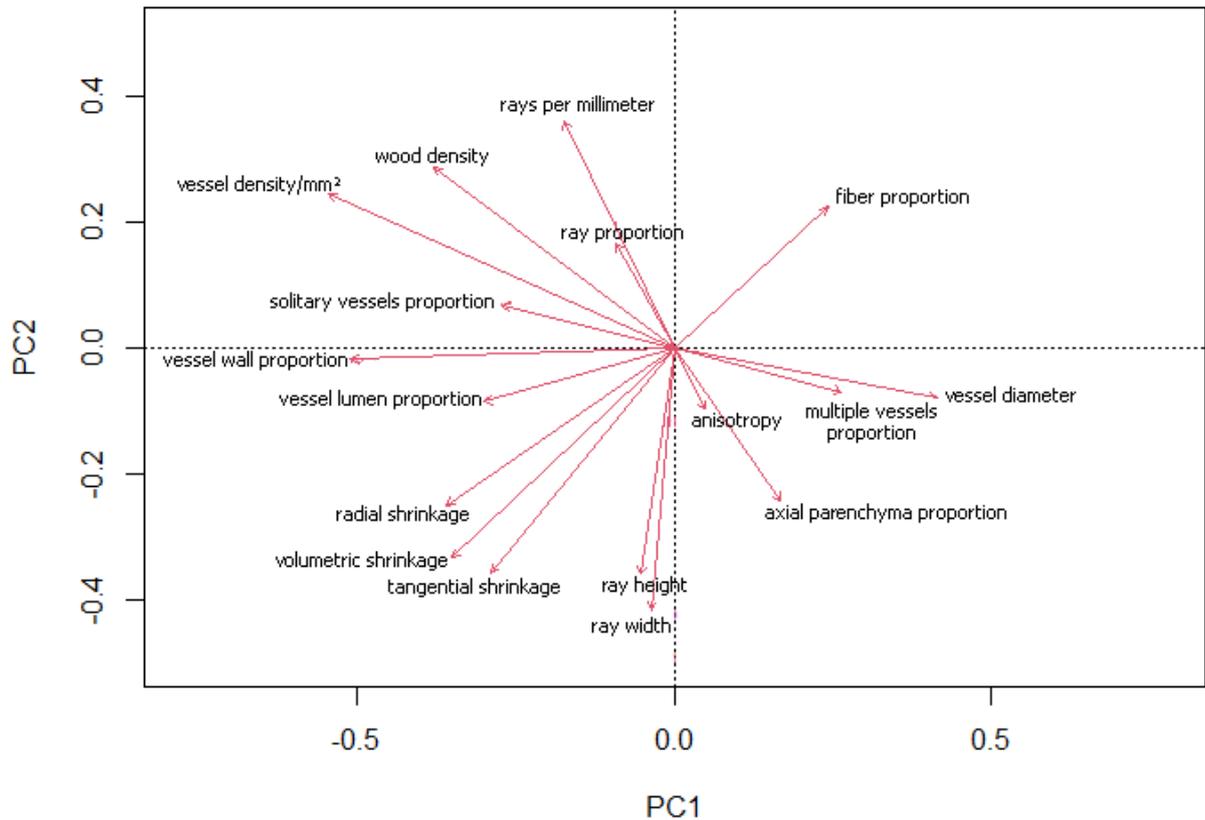


Figure 5. Principal Component Analysis (PCA) for wood anatomical characters, tissues fraction and physical properties.

Table 5. Pearson correlation test for anatomical and physical properties. VD = vessel diameter (μm); R/mm = rays per millimeter (mm); VDe = vessel density (mm^2); RH = ray height (μm); RW = ray width (μm); SVP = solitary vessels proportion; MVP = multiple vessels proportion; FW = fiber proportion; RP = ray proportion; VL = vessel lumen proportion; VW = vessel wall proportion; AP = axial parenchyma proportion. * $P < 0.05$ = significative correlation; ns: non-significative.; - = not correlated.

Physical properties/wood anatomical characters	Wood density	Volumetric shrinkage	Anisotropy
VD	-0.57*	0.03 ns	0.03 ns
R/mm	0.44*	-	-0.27*
VDe	0.57*	-	-0.11 ns
RH	-	0.54*	-
RW	-	0.49*	-
SVP	0.34*	0.23 ns	0.01 ns
MVP	-0.33*	-	-0.01 ns
FP	-	-0.16 ns	-
RP	0.14 ns	-	0.05 ns
VL	-	0.13 ns	-
VW	-	0.36 ns	-
AP	-0.33*	-	-0.09 ns

According to the linear mixed effects model (Lmer) for wood density, the main xylem character that was able to explain this property variation on the species was vessel diameter, (Table 6, Fig. 6).

Table 6. Coefficients of linear mixed effects model for wood density.

Anatomical characters	Coefficients	R ²
VD	-0.155*	0.970

VD = vessel diameter (μm). *P < 0.1 = significative correlation.

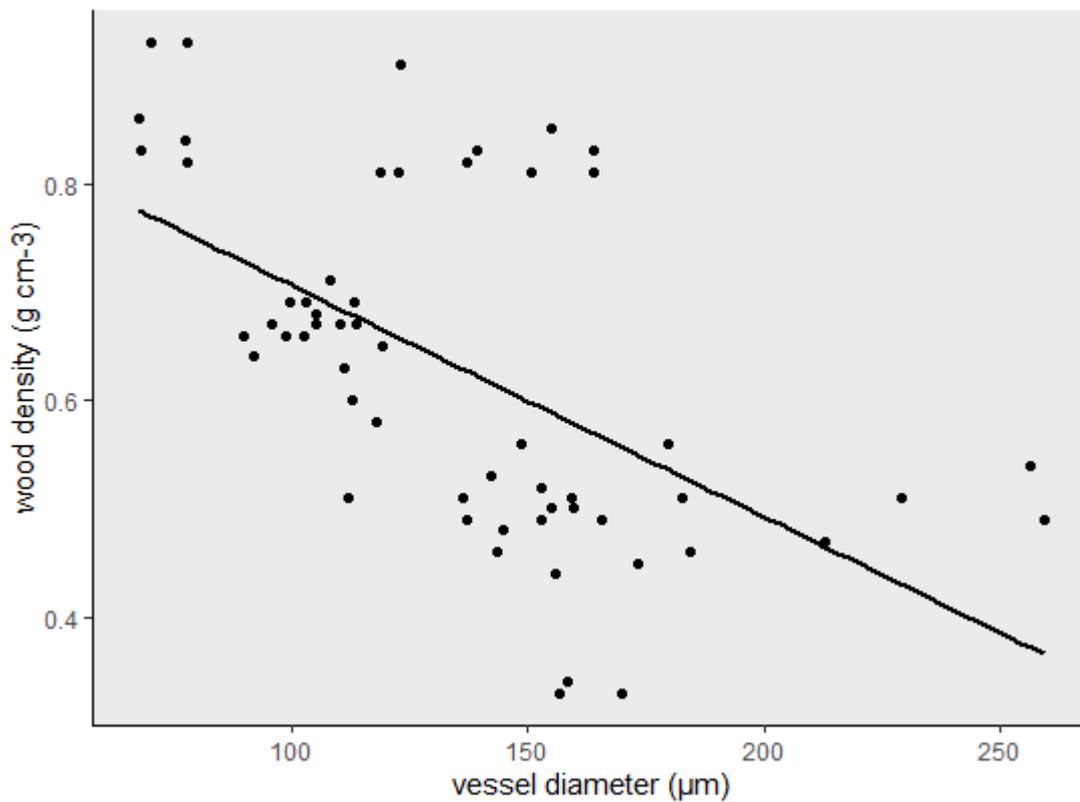


Figure 6. Correlation between vessel diameter of the linear mixed effects model, able to explain wood density variation.

The Lmer shows that the characters able to explain and predict shrinkage were ray height and vessel diameter (Figure 7). This last one was not observed on PCA, but it was correlated to shrinkage on the regression analysis (Table 7, Figure 7A). Ray height had its correlation drawn mostly by *E. pinnata* ray dimensions (Figure 7C). Once this model was applied without this species data, the same pattern between ray height and shrinkage was observed (Figure 7D).

Table 7. Coefficients for linear mixed effects model for shrinkage.

Anatomic feature	Coefficients	R ²
VD	-0.3519*	0.7758
RH	0.4746**	

VD = vessel density (μm); RH = ray height (μm). **P < 0.01 = significant correlation; *P < 0.05 = significant correlation.

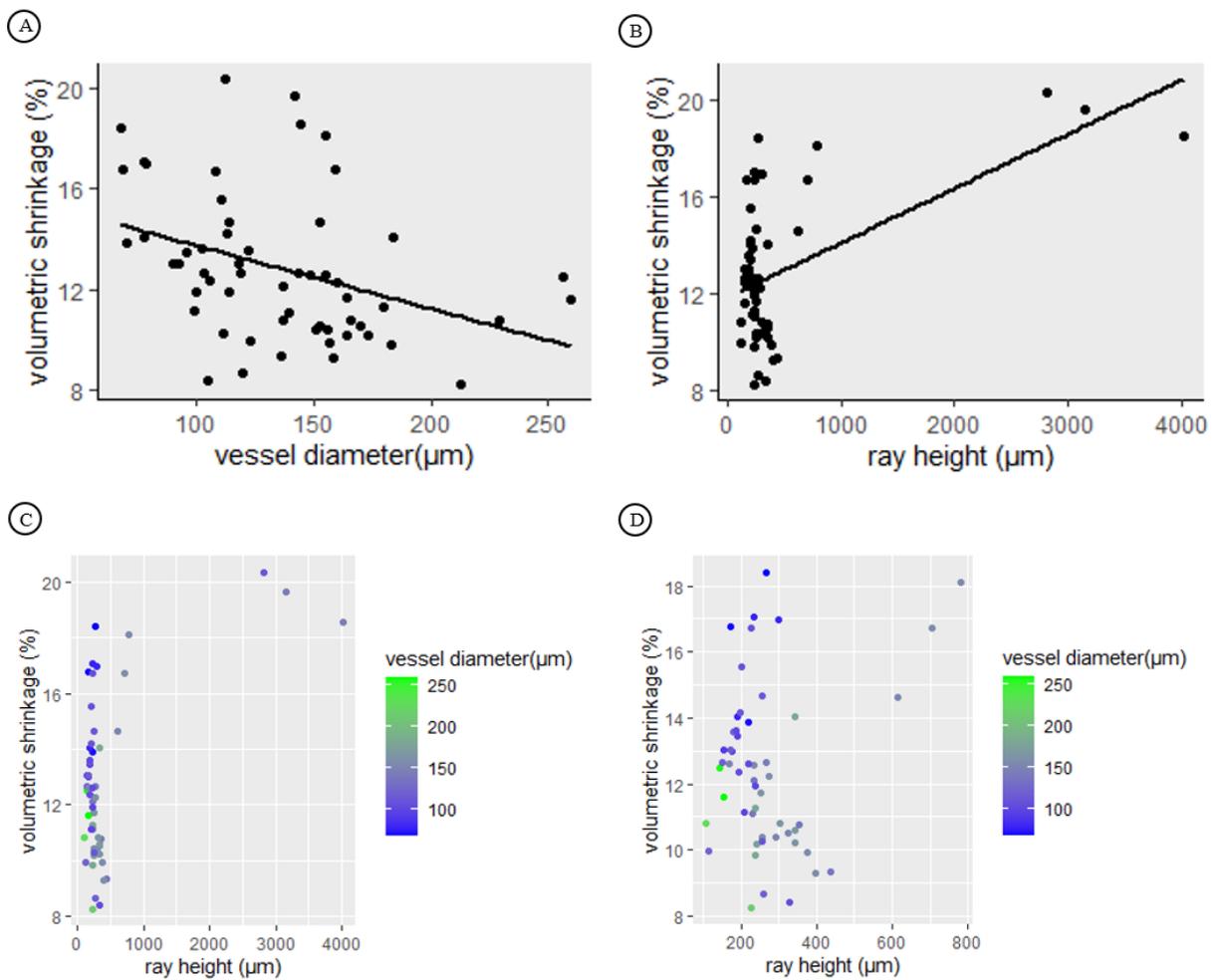


Figure 7. Volumetric shrinkage relationship with vessel diameter (A) and ray height (B). Relationship between volumetric shrinkage, ray height and vessel diameter, considering *Euplassa pinnata* data (C), and without *E. pinnata* data (D).

Anisotropy was the only property that none of the anatomical characters were able to explain this through regression models.

6 DISCUSSIONS

6.1 WOOD ANATOMICAL CHARACTERS, TISSUE PROPORTION AND PHYSICAL PROPERTIES

The anatomical description is in conformity for most species from what was found by Florsheim *et al.* (2020) and the website Inside Wood (2022). *Protium altissimum* had distinct growth rings, marked by fiber zones which is the only character that differs from Florsheim *et al.* (2020) description. As for the tissue proportion, Ziemska *et al.*, 2013, De Mil *et al.* (2018) and Dória *et al.* (2022) also found fibers and parenchyma as the most present tissues and an insignificant amount of vessel traits (wall and lumen). However, these authors observed more ray proportion than axial parenchyma.

All these results for physical properties are compatible with the available literature for the species (SILVA FILHO *et al.*, 1992; NAHUZ *et al.*, 2013; DIAS *et al.*, 2019; IPT, 2022; LPF, 2022), varying a little its values, perhaps for the difference between samples. The anisotropy was not higher than two for most species (Table 4). *Protium altissimum* presented a high anisotropy coefficient (2.01) indicating that this wood has a low stability, while *Handroanthus serratifolius* can be classified as a high quality species, for its low anisotropy (1.18).

6.2 DOES WOOD ANATOMY CAN EXPLAIN DENSITY?

It was found that wood density was not explained by the fiber proportion (see Fig. 5), which differs from many different authors findings, in which fiber wall cells are the main determinant of wood density, since these are lignified and have the primary function of support (EVERT, 2006; MARTÍNEZ-CABRERA *et al.*, 2011; DE MIL *et al.*, 2018). Yet, other types of anatomical characters related positively to wood density were observed, such as ray proportions, vessel density/mm², proportion of solitary vessels, and rays per millimeter, and negatively, such as axial parenchyma proportion, vessel diameter (see Fig. 5, Table 5). Therefore, is not only about fiber general proportion or wall thickness, but also, the quantity of empty spaces, quantity of cells with thin wall. So, this property is not automatically related to fiber cell wall in all cases because this measure also depends of vessels and parenchyma (NAIDOO *et al.*, 2006).

The species with the higher wood density in this study was *Handroanthus serratifolius*, mainly because of the small vessel diameter and low proportion of axial parenchyma (see Table 2 and 3, Table 4, Fig. 3). This negative relationship was also reported by Zheng and Martínez-

Cabrera (2013), Hietz *et al.* (2017) and Dória *et al.* (2022). Larger vessels diameters can lead to lower density in virtue of more presence of open spaces (ALVES and ANGYALOSSY, 2002; PRESTON *et al.*, 2006), and these open spaces can be even more reduced when the vessels are predominantly solitary, as was observed for *Handroanthus serratifolius*. The same pattern was also found for *Dipteryx odorata* and *Hymenaea courbaril* (see Table 2 and 3, Table 4, Fig. 3). These three species, especially *Handroanthus serratifolius* had a high amount of fiber proportion as well (see Table 3, Fig. 3), and though this tissue was not correlated to wood density (Table 5, see Fig. 5), it still can have an impact on the physical property, since fibers main function is increasement of mechanical support on trees (MARTÍNEZ-CABRERA *et al.*, 2009).

As for the others high wood density species (*Dinizia excelsa* and *Manilkara elata*), both had a greater amount of axial parenchyma and multiple vessels (Table 2 and 3). It is possible that *M. elata* had the wood density compensated by the presence of smaller vessels diameter, close to *H. serratifolius* (74.69 μm). Also, this species had an increase on vessel density/ mm^2 (11.19), which not only was positively correlated to wood density but, alongside with high axial parenchyma and narrower vessels, can lead to more efficiency and security for the conductive system (DÓRIA *et al.*, 2019; LOURENÇO *et al.*, 2022). *D. excelsa*, however, had larger vessels (143.90 μm), which can reduce wood density. So, the extractives in cells walls are probably interfering positively with its wood density, not only for this species but to the other high density ones as well, since these woods have darker color.

In medium wood density species, there were some specific factors that could have impacted wood density. Yet, in general, a greater proportion of axial parenchyma and multiple vessels ruled the variation between species. Axial parenchyma is known for its thin walls and wider lumen (NAIDOO *et al.*, 2006; MARTÍNEZ-CABRERA *et al.*, 2009), which can reduce wood density. Furthermore, it was observed that the increment of these cells is negatively correlated to wood density. However, it is positively correlated to conduction efficiency, embolism repair and resistance to drought periods (ZHENG AND MARTÍNEZ-CABRERA, 2013; JANSSEN *et al.*, 2020), which can be an ecological trade-off from these species between mechanical support and water and nutrients supply.

Apuleia leiocarpa (medium wood density), for example, had vessels of small diameter (92.74 μm), but these were mostly multiple, and this wood also had a high amount of axial parenchyma cells (0.34). Vessels of medium diameter and multiple together with an increment of axial parenchyma were observed for *Euplassa pinnata*, *Hymenolobium petraeum*, *Pouteria*

egregia and *Vochysia maxima*, which explains why these species had a decrease in wood density too (see Table 2 and 3, Table 4, Fig. 3). As for *Cedrelinga cateniformis*, *Couratari oblongifolia*, *Mezilaurus itauba*, *Protium altissimum* and *Qualea brevipedicellata*, the greater allocation for fiber tissue was not sufficient to increase wood density. The first one has the largest vessels in this study, and these are multiple, while the second, third and last ones have multiple vessels as well (see Table 2 and Table 3). *Protium altissimum*, on the other hand, showed more solitary vessels and they were predominantly obstructed by tiloses, so it can be considered that the lack of increase on wood density might be because the fraction of fiber tissue on this species is not very high (25%).

The amount of ray cells and solitary vessels on *Goupia glabra* (see Table 3, Fig. 3) could have increased its density, a pattern also found by Rahman *et al.* (2004), Uetimane Jr. and Ali (2011), Zheng and Martínez-Cabrera (2013) and Elaieb *et al.* (2019). There are evidences that rays can contribute to wood density positively because of the high proportion of this tissue, caused by the absence of large internal cell voids and the low existence of intercellular spaces, but this relationship is variable between species and can be considered tree specific, more frequent on thick walled and tightly packed cells (TAYLOR, 1969; RAHMAN, *et al.*, 2004). This could have happened to *Goupia glabra* or *Pouteria egregia* as well, since this species had a great amount of ray proportion (0.23), the same as the axial parenchyma proportion, and had 0.69 g/cm³ of wood density, despite not having many fibers (0.16) as *Dipteryx odorata*, *Hymenaea courbaril* and *Handroanthus serratifolius*.

Low wood density woods (see Table 4) have a high proportion of multiple vessels in common (Table 3, Fig. 3). However, *Simarouba amara*, that had the lowest wood density on this study, presented a greater amount of fibers, that can increase wood density (see Table 3 and 4, Fig. 3). In InsideWood website (2022), this species had in general very thin to thick-walled but, since this is feature was not directly correlated to wood density, the medium vessel diameter alongside with a lot of multiple vessels might have interfered strongly with this physical property as well. This species also has a very light color, which might because of a lack of extractives, that can elevate wood density. The other low density woods (*Erismia uncinatum* and *Lonchocarpus cultratus*) had a higher amount of axial parenchyma tissue, around 52% and 46% respectively, and many multiple vessels as well (0.63 and 0.62, respectively).

The Lmer models showed that the most relevant anatomical character which explained and differentiated wood density between these species was vessel diameter (see Table 6, Fig. 6). As explained previously, species with high density have small vessel diameter compared

with species with low density, which may implicate in a strategy prone to efficiency of water transport, with a high quantity of small conduits while maintaining mechanical support and securing against vessel implosion. Wood density is often considered related to these xylem components, since water transport efficiency depends on the amount of open conduits space (CHAVE *et al.*, 2009).

6.3 DOES WOOD ANATOMY EXPLAINS VARIATIONS IN SHRINKAGE AND ANISOTROPY?

Shrinkage was mainly affected by ray dimensions and vessel wall proportion (see Table 5, Fig. 5). Therefore, *Euplassa pinnata*, that had rays above 1 mm taller and very wide, had the greatest shrinkage (19.52%). The same was observed for *Vochysia maxima*, that also had tall and wide rays (16.5%). Such results were also pointed by De La Paz *et al.* (2005) and Toong *et al.* (2014), where ray height was correlated to shrinkage. Elaieb *et al.* (2019) found rays proportion related positively to tangential and radial shrinkage of wood. Rays are cells with little lignification and weak, and because of that, more susceptible to humidity variations, tending to dry faster, especially when they are in multiseriate arrangement and have larger cavities (SIMPSON, 1991; PANG, 2002; WU *et al.*, 2006). So, for these species with larger and taller portions of rays, it is expected that rays may show a tendency of increasing the shrinkage.

For woods with narrow rays, it is hypothesized by some authors that these cells can improve mechanical support of the tree, securing its inner structure and acting as stiff pins (BURGERT *et al.*, 1999; ZHENG and MARTÍNEZ-CABRERA, 2013; SLUPIANEK *et al.*, 2021). However, species like *Handroanthus serratifolius* and *Manilkara elata* still had higher shrinkage (15.44 and 16,93%, respectively) despite its short and narrow rays (see Table 2, Table 4). Then, the positive relationship between shrinkage and ray dimensions might not be maintained (see Fig. 7C, D). Another important characteristic about *M. elata* is the high proportion of axial parenchyma (Table 3, Fig. 4), which could have increased shrinkage, as this tissue has a weak structure.

Nevertheless, for the species above, the shrinkage can be explained with the Lmer model, which shows that as vessels reduce its diameter the shrinkage is increased (see Table 7, Fig. 7A). However, Moya *et al.* (2012) found an inverse relationship between vessel diameter and shrinkage, and according to Pang (2002) it is expected that greater vessels diameters might

be able to result in greater values of shrinkage because this physical property is also dependable of dimensional changes in lumen. There must be another factor interfering with the shrinkage for these two species, such as the presence of extractive substances, that can have a positive relation to shrinkage, as Nzokou and Kamdem (2004) and Jankowska *et al.* (2017) reported that the hygroscopic substances will be more susceptible to absorbing water and resulting in greater shrinkage values. Still, there are other authors that contradicts this hypothesis (CHOONG and ACHMADI, 1991; MOREIRA, 1999; ADAMAPOULOS and VOULGARIDIS, 2012; TEIXEIRA, 2015). Therefore, for the species which there is no simple correlation observed, there is a need to improve the studies and to do new evaluations to have a better comprehension of this complex relationship.

As for anisotropy, a negative relation with rays per millimeter was observed on the PCA (Fig. 5). The same was reported by Gonçalez (1993) *apud* Moreira (1999), whilst Elaieb *et al.* (2019) found a positive relation. So, in the present study, the presence of more ray cells may be causing a reduction on the difference between tangential and radial shrinkage. Thin rays (<0.05 μm) occurred for all species except for *Euplassa pinnata* and *Vochysia maxima* (see Table 2). As mentioned before, the thin rays could secure the inner structure of the wood, acting as stiff pins (BURGERT *et al.*, 1999; ZHENG and MARTÍNEZ-CABRERA, 2013; SLUPIANEK *et al.*, 2021), therefore, restraining the anisotropy between sections.

However, despite this hypothesis, in Lmer models, none of the anatomical characters were able to explain this property variation on the species. Perhaps, it could be affected by the microfibril angles, that is one of the reasons why it is not possible to check a clear relationship in a macro scale. As according to Yamamoto *et al.* (2001) the microfibril angle in the S2 layer of the cells wall is the most impactful factor related to anisotropy. Therefore, more studies are necessary on this sense to determine how transverse anisotropy can be affected by wood anatomy.

7 CONCLUSIONS

Wood density was correlated mainly with vessels characteristics, in which woods with narrower vessels occur in a great quantity, especially when it has a higher proportion of solitary ones. The increase on vessel per mm^2 also corroborates with a higher wood density when the vessels are narrower, which may indicate a trade-off between conductive efficiency and mechanical strength, since the increase on the quantity of vessels per mm^2 does not affects wood density as long as these elements have small diameter, concomitantly increasing wood density.

Most woods with higher proportion of axial parenchyma tissue had its density lowered. Rays, on the other hand, presented a positive relation to wood density, and these cells can interfere with wood density especially when they are narrow. Also, the high quantity of extractive substances also could have increased this physical property value.

Shrinkage was higher for species with tall and wide rays. However, this relationship can change when rays are narrow and short. The Lmer models also adds that one of the wood characters that are relevant to explain shrinkage variation is vessel diameter, in which narrow diameter vessels resulted in species with higher values of shrinkage. The high presence of extractives might be a factor to be considered as well, since species with high shrinkage values may have a higher amount of these substances on cell walls.

As for transverse anisotropy, its variations could not be explained through the anatomical characteristics measured on this work, but on the correlation tests. This property is negatively impacted by rays per millimeter. The regression models, however, could not find an anatomical character capable of explaining anisotropy variation, as this property is mainly related to microcellular structure, especially the disposition of S2 microfibril angle, so this could be one of the reasons a clear relation was not observed.

Therefore, studies analyzing the correlation between wood anatomy and its physical properties, especially wood density and shrinkage, may be able to provide tools to predict and provide further information about a species technological behavior through anatomical characters and tissue proportion.

REFERENCES

- ADAMOPOULOS, S.; VOULGARIDIS, E. Effect of hot-water extractives on water sorption and dimensional changes of black locust wood. **Wood Research**, v. 57, n. 1, p. 69–78, 2012.
- ALMEIDA, A. S. **Estimativa das propriedades físico-mecânicas de madeiras tropicais brasileiras através da análise de porosimetria por intrusão de mercúrio**. 101 f. Tese (Doutorado em Engenharia Civil) – Departamento de Engenharia Civil, Universidade Federal de São Carlos, São Carlos, 2022.
- ALVES, E. S.; ANGYALOSSY-ALFONSO, V. Ecological trends in the wood anatomy of some Brazilian species. 2. Axial parenchyma, rays and fibres. **IAWA Journal**, v. 23, n. 4, p. 391–418, 2002.
- ALVES, R. C.; OLIVEIRA, A. L. C.; CARRASCO, E. V. M. Propriedades físicas da madeira de *Eucalyptus cloeziana* F. Muell. **Floresta e Ambiente**, v. 24, p. 1–7, 2017.
- BATISTA, D. C.; KLITZKE, R. J.; SANTOS, C. V. T. Basic density and retractibility of wood clones of three. **Ciência Florestal**, v. 20, n. 4, p. 665–674, 2010.
- BAAS, P.; WHEELER, E.A. Wood anatomy and Climate Change. In: HOSKINSON, T.R.; JONES, M.B.; WALDREN, S.; PARNELL, J.A.N (ed.) **Climate Change, Ecology and Systematics**. Cambridge University Press, The Systematics Association, p. 141-155, 2011.
- BEECKMAN, H. WOOD ANATOMY and TRAIT-BASED ECOLOGY. **IAWA Journal**, v. 37, n. 2, p. 127–151, 2016.
- BURGERT, I.; BERNASCONI, A.; ECKSTEIN, D. Evidence for the strength function of rays in living trees. **Holz als Roh - und Werkstoff**, v. 57, n. 5, p. 397–399, 1999.
- CHAVE, J. *et al.* Towards a worldwide wood economics spectrum. **Ecology Letters**, v. 12, n. 4, p. 351–366, 2009.
- CHEN, C. *et al.* Structure–property–function relationships of natural and engineered wood. **Nature Reviews Materials**, v. 5, n. 9, p. 642–666, 2020.
- CHOONG, E. T.; ACHMADI, S. S. Effect of extractives on moisture sorption and shrinkage in tropical woods. **Wood And Fiber Science**, v. 23, n. 2, p. 185–196, 1991.
- COPANT – COMISSÃO PANAMERICANA DE NORMAS TÉCNICAS. Descrição geral macroscópica e microscópica da madeira, São Paulo, v. 30, p. 1-19. 1973.
- COUTO, A.M. **Influência das propriedades anatômicas, químicas e físicas da madeira de *Eucalyptus* e *Corymbia* na qualidade do carvão para uso siderúrgico**. 173 p. Tese (Doutorado), Universidade Federal de Lavras, Lavras, MG, 2014.
- DE LA PAZ PÉREZ OLVERA, C.; DÁVALOS SOTELO, R.; QUINTANAR ISAÍAS, P. A. Influencia de los radios en algunas propiedades físicas y mecánicas de la madera de ocho encinos (*Quercus*) de Durango, México. **Madera y Bosques**, v. 11, n. 2, p. 49–68, 2005.
- DE MIL, T. *et al.* Wood density profiles and their corresponding tissue fractions in tropical angiosperm trees. **Forests**, v. 9, n. 12, 2018.

DIAS, A. C. C. *et al.* Relação entre a densidade básica e as retrações em madeira de teca. **Revista Ciência da Madeira - RCM**, v. 9, n. 1, p. 37–44, 2018.

DIAS, F.M. *et al.* Influence of the apparent density on the shrinkage of 43 tropical species. **Acta Scientiarum**, v. 4, 2019.

DÓRIA, L. C. *et al.* Axial sampling height outperforms site as predictor of wood trait variation. **IAWA Journal**, v. 24, p. 1–24, 2019.

DÓRIA, L.C. *et al.* Functional trade-offs in volume allocation to xylem cell types in 75 species from the Brazilian savanna Cerrado. **Annals of Botany**, **22:mcac095**. 2022. doi: 10.1093/aob/mcac095.

ELAIEB, M. T. *et al.* Physical properties of four ring-porous hardwood species: Influence of wood rays on tangential and radial wood shrinkage. **Madera y Bosques**, v. 25, n. 2, p. 1–18, 2019.

EVERT, R.F. **Esau's Plant anatomy: meristems, cells and tissues of the plant body: their structure, function, and development**. 3rd ed. Rev. ed. of: Plant anatomy / Katherine Esau, John Wiley & Sons, Inc., Hoboken, New Jersey, 607 p. 2006.

FLORSHEIM, S.M.B. *et al.* **Identificação macroscópica de madeiras comerciais do Estado de São Paulo**. São Paulo: Instituto Florestal, 2020.

FOELKEL, C. E. B.; BRASIL, M. A. M.; BARRICHELO, L. E. G. Métodos para a determinação da Densidade Básica de cavacos para coníferas e folhosas. **IPEF**, n. 2/3, p. 65-73, 1971.

FONTI, P. *et al.* Studying global change through investigation of plastic responses of xylem anatomy in tree rings. **New Phytologist**, v. 185, n. 1, p. 42-53, 2010.

FORTUNEL, C. *et al.* Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients. **New Phytologist**, v. 202, n. 1, p. 79–94, 2014.

FUJIWARA, S. **Anatomy and properties of Japanese hardwoods II. Variation of dimensions of ray cells and their relation to basic density**. IAWA Bulletin, v. 13, p. 397-402, 1992.

GALVÃO, A.P.M.; JANKOWSKY, I.P. **Secagem racional da madeira**. São Paulo: Nobel, 1985.

GONÇALEZ, J.C. *et al.* Características tecnológicas das madeiras de *Eucalyptus grandis* W.Hill ex Maiden e *Eucalyptus cloeziana* F.Muell visando ao seu aproveitamento na indústria moveleira. **Ciência Florestal**, v. 16, n. 3, p. 329-341, 2006.

GU, H.; ZINK-SHARP, A.; SELL, J. Hypothesis on the role of cell wall structure in differential transverse shrinkage of wood. **Holz als Roh - und Werkstoff**, v. 59, n. 6, p. 436–442, 2001.

HACKE, U. G. *et al.* Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. **Oecologia**, v. 126, n. 4, p. 457–461, 2001.

HIETZ, P. *et al.* Wood traits related to size and life history of trees in a Panamanian rainforest. **New Phytologist**, v. 213, n. 1, p. 170–180, 2017.

HIETZ, P.; VALENCIA, R.; JOSEPH WRIGHT, S. Strong radial variation in wood density follows a uniform pattern in two neotropical rain forests. **Functional Ecology**, v. 27, n. 3, p. 684–692, 2013.

IAWA Committee. IAWA list of microscopic features for hardwood identification. WHEELER, E. A.; BAAS, P.; GASSON, P. (eds.). **IAWA Bulletin** 10: 219-332. 1989.

INSIDEWOOD. 2004-onwards. Published on the Internet. <http://insidewood.lib.ncsu.edu/search>. Acesso em 13 de agosto de 2022.

Instituto de Pesquisas Tecnológicas (IPT). **Informações sobre madeiras.** https://www.ipt.br/consultas_online/informacoes_sobre_madeira. Acesso em 13 de Agosto de 2022.

JANKOWSKA, A. *et al.* Effect of Extractives on the Equilibrium Moisture Content and Shrinkage of Selected Tropical Wood Species. **BioResources**, v. 12, n. 1, p. 597–607, 2017.

JANKOWSKA, A.; REBKOWSKI, B. The role of parenchyma content in dimensional stability of wood. **Annals of Warsaw University of Life Science**, Warsaw, Forestry and Wood Technology, p. 18-21, 2018.

JANKOWSKY, I.P.; GALVÃO, A.P.M. Influência do teor de extrativos na umidade de equilíbrio da madeira. **IPEF**, n.18, p.1-33, 1979.

JANSSEN, T. A. J. *et al.* Wood allocation trade-offs between fiber wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees. **Plant Cell and Environment**, v. 43, n. 4, p. 965–980, 2020.

Laboratório de Produtos Florestais (LPF). **Banco de dados de madeiras brasileiras.** Serviço Florestal Brasileiro (SFB). <https://lpf.florestal.gov.br/pt-br/madeiras-brasileiras>. Acesso em 13 de agosto de 2022.

LACHENBRUCH, B.; MCCULLOH, K. A. Traits, properties, and performance: How woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. **New Phytologist**, v. 204, n. 4, p. 747–764, 2014.

LOURENÇO, J. *et al.* Hydraulic tradeoffs underlie local variation in tropical forest functional diversity and sensitivity to drought. **New Phytologist**, v. 234, n. 1, p. 50–63, 2022.

LUIS CHRISTOFORO, A. *et al.* Shrinkage for Some Wood Species Estimated by Density. **International Journal of Materials Engineering**, v. 6, n. 2, p. 23–27, 2016.

MAI, C.; SCHMITT, U.; NIEMZ, P. A brief overview on the development of wood research. **Holzforschung**, v. 76, n. 2, p. 102–119, 2022.

MARTÍNEZ-CABRERA, H. I. *et al.* Wood anatomy and wood density in shrubs: Responses to varying aridity along transcontinental transects. **American Journal of Botany**, v. 96, n. 8, p. 1388–1398, 2009.

MARTÍNEZ-CABRERA, H. I. *et al.* Integration of vessel traits, wood density, and height in angiosperm shrubs and trees. **American Journal of Botany**, v. 98, n. 5, p. 915–922, 2011.

MELO, J.E. Madeira: características e aplicações. LPF, Brasília, 30 p. 2002.

MOREIRA, W. D. S. Relações entre propriedades físico-mecânicas e características anatômicas e químicas da madeira. Tese (Doctor Scientiae), Universidade Federal de Viçosa, MG, 1999.

MORESCHI, J.C. **Propriedades da Madeira**. Curitiba: Departamento de Engenharia e Tecnologia Florestal da UFPR, 2014.

MOTTA, J. P. *et al.* Caracterização da madeira de quatro espécies florestais. **Ciencia Rural**, v. 44, n. 12, p. 2186–2192, 2014.

MOYA, R.; TENORIO, C.; MEYER, Í. Influence of wood anatomy on moisture content, shrinkage and during defects in *Vochysia guatemalensis* Donn Sm. **Scientia Forestalis/Forest Sciences**, v. 40, n. 94, p. 249–258, 2012.

NAHUZ, M.A.R. *et al.* **Catálogo de madeiras brasileiras para a construção civil**. São Paulo: IPT, 104 p. 2013.

NAIDOO, S.; ZBOŇÁK, A.; AHMED, F. The effect of moisture availability on wood density and vessel characteristics of *Eucalyptus grandis* in the warm temperate region of South Africa. **Proceedings of the 5th International Symposium on Wood Structure and Properties**, p. 117–122, 2006.

NZOKOU, P.; KAMDEM, D. P. Influence of wood extractives on moisture sorption and wettability of red oak (*Quercus rubra*), black cherry (*Prunus serotina*), and red pine (*Pinus resinosa*). **Wood and Fiber Science**, v. 36, n. 4, p. 483–492, 2004.

OLIVEIRA, J. T. S.; SILVA, J.C. Variação Radial da Retratibilidade e Densidade Básica da madeira de *Eucalyptus saligna* Sm. **Revista Árvore**, v. 27, n. 3, p. 381–385, 2003.

PANG, S. Predicting anisotropic shrinkage of softwood Part 1: Theories. **Wood Science and Technology**, v. 36, n. 1, p. 75–91, 2002.

PECK, E. C. How Wood Shrinks and Swells. **Forest Products Journal**, v. 7, n. 7, p. 235–244, 1957.

PETTERSEN, R. C. The chemical composition of wood. *The Chemistry of Solid Wood*, 57–126. 1984. doi:10.1021/ba-1984-0207.ch002.

POORTER, L. *et al.* The importance of wood traits and hydraulic conductance for the performance and life story strategies of 42 rainforest tree species. **New Phytologist**, v. 2, n. 185, p. 481–492, 2009.

POUBEL, D. DA S. *et al.* Estrutura Anatômica e Propriedades Físicas da Madeira de *Eucalyptus pellita* F. Muell. **Floresta e Ambiente**, v. 18, n. 2, p. 117–126, 2011.

PRESTON, K. A.; CORNWELL, W. K.; DENOYER, J. L. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. **New Phytologist**, v. 170, n. 4, p. 807–818, 2006.

RAHMAN, MD. M. *et al.* Wood Density in Relation to Growth Rate and Tissue Proportions of Teak Grown in Bangladesh. **Journal of Forest Planning**, v. 10, n. 2, p. 53–57, 2004.

RIBEIRO, E.S. **Propriedades tecnológicas de vinte espécies de madeiras tropicais comercializadas pelo estado de Mato Grosso**. 2017. 183f. Tese (Doutorado em Ciências Florestais), Departamento de Engenharia Florestal, Universidade de Brasília, DF, 2017.

SILVA FILHO, D.F.S.; ROCHA, J.S.; MOURA, J.B. Influência da densidade na dureza Janka em oito espécies madeireiras da Amazônia Central. **Acta Amazonica**, v. 22, n. 2, p. 275-283, 1992.

SIMPSON, W. T. Dry kiln operator's manual (Introduction-Glosary). **Dry kiln operator's manual**, n. 188, 1991.

SKAAR, C. Wood-Water Relations. Springer-Verlag, Berlin, 263 p., 1988.

ŚLUPIANEK, A.; DOLZBLASZ, A.; SOKOŁOWSKA, K. Xylem parenchyma—role and relevance in wood functioning in trees. **Plants**, v. 10, n. 6, 2021.

SWENSON, N. G.; ENQUIST, B. J. The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. **American Journal of Botany**, v. 95, n. 4, p. 516–519, 2008.

TAYLOR, F. W. **The effect of ray tissue on the specific gravity of wood**. Wood and Fiber Science, v.1, n.2, p.p. 142-145. 1969.

TEIXEIRA, R.U. Efeito da produtividade florestal e permeabilidade da madeira de *Eucalyptus* spp. na velocidade de secagem. Tese – Magister Scientiae, Universidade Federal de Viçosa, MG, 47 f. 2015.

TOONG, W. *et al.* The prediction of wood properties from anatomical characteristics: The case of common commercial Malaysian timbers. **BioResources**, v. 9, n. 3, p. 5184–5197, 2014.

UETIMANE JUNIOR, E.; ALI, A. C. Relationship between mechanical properties and selected anatomical features of Ntholo (*Pseudolachnostylis maprounaefolia*). **Journal of Tropical Forest Science**, v. 23, n. 2, p. 166–176, 2019.

VALENTE, B.M.R.T. *et al.* Variabilidade radial e longitudinal das propriedades físicas e anatômicas da madeira de angico-vermelho. **Sci. For.**, v. 41, n. 100, p. 485-496, 2013.

WIEDENHOEFT, A.; EBERHARDT, T. Chapter 3: Structure and Function of Wood. In: **Wood Handbook – wood as an engineering material**. General Technical Report FPL-GTR-282. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, pp. 3.1-3.18. 2010.

WIJESINGHE, L.C.A.S. The shrinkage of rays and fibres in wood. **Forestry**, v. 32, n. 1, p. 31-38, 1959.

WU, Y. Q. et al. Relationships of anatomical characteristics versus shrinkage and collapse properties in plantation-grown eucalypt wood from China. **Journal of Wood Science**, v. 52, n. 3, p. 187–194, 2006.

XUE, Q. et al. Effects of wood rays on the shrinkage of wood during the drying process. **BioResources**, v. 13, n. 3, p. 7086–7095, 2019.

YAMAMOTO, H. et al. A model of anisotropic swelling and shrinking process of wood. **Wood Science and Technology**, v. 35, p. 167-181, 2001.

ZHENG, J.; MARTÍNEZ-CABRERA, H. I. Wood anatomical correlates with theoretical conductivity and wood density across China: Evolutionary evidence of the functional differentiation of axial and radial parenchyma. **Annals of Botany**, v. 112, n. 5, p. 927–935, 2013.

ZIEMIŃSKA, K. *et al.* Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. **AoB PLANTS**, v. 5, p. 1–14, 2013.

ZOBEL, B. J.; JETT, J. B. The Importance of Wood Density (Specific Gravity) and Its Component Parts. n. 1972, p. 78–97, 1995.