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To cite this version:

Andry Clarel Raobelina, Jean Michel Leban, Caroline Christina Jaozandry, Tahiana Ramananantoandro. Wood density of 38 Dalbergia and 29 Diospyros malagasy species and its relationship with climate and tree diameter. 2024. hal-04676071

HAL Id: hal-04676071

https://hal.inrae.fr/hal-04676071v1

Preprint submitted on 23 Aug 2024

Wood density of 38 Dalbergia and 29 Diospyros malagasy species and its relationship with climate and tree diameter

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Research Article

Keywords: Dalbergia, Diospyros, Madagascar, X-ray computed tomography, Wood density, Wood radial density profile

Posted Date: April 4th, 2024

DOI: https://doi.org/10.21203/rs.3.rs-4129894/v1

Additional Declarations: No competing interests reported.

Abstract

Several Malagasy *Dalbergia* and *Diospyros* species are highly valued, especially in the furniture industry due to their desirable wood properties. However, there remains a lack of understanding regarding the wood technological properties of many species within these genera, hindering their effective utilization. This study aimed to adress this gap by assessing the wood density of 38 *Dalbergia* and 29 *Diospyros* species, their radial wood density variation, and the influence of climate and tree size. Wood density measurements were conducted on 297 wood cores using X-ray computed tomography. One-way analysis of variance was used to evaluate between-genus, between-species, and between-trees density variations. To compare the radial density profile of cores of different length, each analyzed core was divided into 10 segments of equal length. For species that show significant differences in mean density along the segments, the radial density trend was evaluated through correlation tests between the average density of each segment and its distance from the pith. Correlation test was also conducted to evaluate the relationship between tree diameter, climatic data, and density. *Diospyros* genus (1.070 ± 0.165 g∙cm^{-3}) have significantly denser heartwood compared to *Dalbergia* (0.961 ± 0.142 g∙cm^{-3}). Furthermore, eleven groups of *Dalbergia* and seven groups of *Diospyros*, each with significantly different heartwood density value ranges, were identified. While the radial wood density profile varied among species, a decreasing trend was observed in most analyzed species. Wood density increases with rising temperature and decreasing precipitation at the tree's growth site. Tree diameter does not influence the wood density.

1. Introduction

Wood density has long been considered as one of the most important properties for assessing wood quality. It is an easily measurable parameter that is correlated with the mechanical properties of wood (Izekor et al. 2010) and other properties such as dimensional stability (Almeida et al. 2017). It is also a parameter used in allometric equations to calculate carbon stocks stored in forests (Flores and Coomes 2011). However, wood density varies within different trees of the same species and between different species (Chowdhury et al. 2013; Sungpalee et al. 2009) due to environmental, genetic, and physiological factors that affect the anatomical structure of wood (Zobel and Buijtenen 1989). Wood density also varies within the same tree, radially from the pith to the bark (Sofia et al. 2007), and longitudinally along the main axis of the trunk (Kimberley et al. 2017).

Numerous authors carried out studies on wood density and its radial variation for tropical species. Among others, we selected references that illustrate the main different sources and patterns of wood density variations, within the same species, between species, and across geographic distributions. Nock et al. (2009) investigated the relationship between wood density and shade tolerance, as well as the effects of age and annual growth on radial density gradients in six tropical forest species. They found the presence of radial density gradients (from pith to bark), ranging from an approximately 70% increase in *Melia azedarach*, which is shade-intolerant, down to 13% decrease in *Neolitsea obtusifolia*, which is shade-tolerant. Nock et al. (2009) also found that, for *Melia azedarach*, radial increase of wood density is mainly due to tree size rather than tree age and annual growth. Gaitán-alvarez and Roque (2019) studied the variations in wood density profiles between two annual rings of *Tectona grandis* trees from plantations in five different regions of Costa Rica and found different profiles of radial wood density depending on the age of the tree. Hietz et al. (2013) examined the relationship between tree growth, size, mortality rate, wood density, and its radial variation in 453 tree species in a Panamanian rainforest and 687 species in an Ecuadorian rainforest. For heavier woods, they found a constant or decreasing radial trend in wood density, while for lighter woods, they observed an increasing radial trend from pith to bark.

Among tropical wood genera, *Dalbergia* L.f. (Fabaceae) and *Diospyros* L. (Ebenaceae) are widely known. These genera are distributed across numerous countries and encompass a considerable diversity of species. There are approximately 273 accepted species of *Dalbergia* and 778 accepted species of *Diospyros* worldwide (POWO 2023a; POWO 2023b), of which 84 and 255 respectively exist in Madagascar (Phillipson and Crameri 2018). *Dalbergia* and *Diospyros* species found in Madagascar are highly prixed for their good technological properties and are unfortunately exploited to meet the demand in the illicit wood furniture market. Nevertheless, there is a lack of knowledge in the existing literature regarding their technological properties. Among the six references found on the wood density of Malagasy *Dalbergia* and *Diospyros*, two provide an average wood density value for *Dalbergia* spp and *Diospyros* spp (Rakotovao et al. 2012; Richter and Dallwitz 2019). At the species level, wood density values are only available for 7 species of *Dalbergia* and 2 species of *Diospyros* (Richter and Dallwitz 2019; Louppe et al. 2008; Rakotovao et al. 2012; Gerard et al. 2016; Lisan nd; Cooke et al. 2008). Furthermore, the wood density values currently available are average density, without any information regarding the intra tree radial variation.

Knowledge of wood density is crucial both for effective utilization as a proxy of wood physical and mechanical properties and for accurate wood species identification. However, the conventional sampling technique to measure wood density entails felling trees and cutting discs samples from tree sections at breast height, which is 1.3 meters above the tree base (Kuyah et al. 2015). This method is accurate but destructive, costly, laborious, and may not be applicable when it is not allowed to harvest trees. For Malagasy species, researchers have characterized the radial variation of wood density by non-destructively sampling wood cores and cutting sections at 1 cm intervals (Ramananantoandro et al. 2013). In the frame of the Xylodensmap project, (Leban et al. 2020) a faster and nondestructive method was developed at INRAE Champenoux France. This method allows the measurement of the wood density all along each core with a radial resolution of 0.625 mm (Freyburger et al. 2009; Jacquin et al. 2017, 2019). The main advantage is that wood cores remain intact after the wood density measurement and can be stored intact in one xylotheque and further used for other analyses.

Therefore, the aim of this study was to measure the radial variations of wood density in 297 wood cores from 38 species of *Dalbergia* and 29 species of *Diospyros* species using X-ray tomography. Three research questions were addressed in this study: (i) Can groups of *Dalbergia* and *Diospyros* species be identified by analyzing the average density per species, (ii) Does wood density vary from pith to bark in these species, and (iii) Does climate and tree size influence the average wood density?

2. Materials And Methods

2.1. Wood cores sampling

A total of 297 wood core samples (one core per tree) belonging to 38 *Dalbergia* species and 29 *Diospyros* species were collected from 2018 to 2021, inside and/or outside several forest protected areas in Madagascar (Table 1, Fig. 1). The number of cores varied among species due to their different abundance in the forest. Each wood core had a diameter of 5 mm (Fig. 2a) and was sampled at breast height (1.3 m from the ground) using a Pressler auger. For each tree, a voucher specimen was prepared in the field and stored between two sheets of newspaper. They were later sent to taxonomists at the Missouri Botanical Garden Madagascar (MBG) and the Muséum National d'Histoire Naturelle in Paris (MNHN) to assist in the accurate identification of species that had not been precisely identified in the field.

2.2. Laboratory works

2.2.1. Samples preparation

Laboratory works were carried out at the French National Research Institute for Agriculture, Food and Environment (INRAe) in Champenoux, Nancy. The wood cores were firstly conditioned at 12% humidity in a climatic chamber set at a temperature of 20° C and a relative humidity of 65% for a period of two weeks. Stabilized cores were put into alveolar polycarbonate transparent boxes of 235 mm × 105 mm × 10 mm (length × width × thickness; Fig. 2a). One box had a row of 9 alveolar and can therefore contain 9 cores, but the first and the last rows were left empty to allow box rows referencing during density data extraction. For cores cut into several pieces, a sponge of around 10 mm × 10 mm × 10 mm was placed between the cores pieces to prevent them from overlapping. The sponge was used because it has a very low density (0.1 g•cm^{-3}) compared to wood density (higher than 0.4 g•cm^{-3}). It allows the detection of the density profiles of each wooden core segment and by concatenation, the wood density profile all along the initial core.

Each core has one unique ID defined by the box number and by the cell number. Each box is sealed with adhesive tape at both ends prior to scanning to prevent cores from falling and to minimize wood moisture fluctuations. Ten boxes were assembled together to form a packet (Fig. 2b). Therefore, 43 boxes were needed to store the 297 cores, corresponding to 5 packets.

2.2.2. Computed tomography scanning

Packets were placed parallel side by side in the direction of their length to perform the CT scanning. A GE brightspeed Excel 4 CT Scanner was used for the X-ray CT scanning (Fig. 3). A scan was carried out every 0.625 mm along each core (radial direction of the ligneous plane). The reconstructions were performed with a pixel size of 0.32 mm and a field of view of 16 cm × 16 cm. The pixel value is expressed in Hounsfield units (Razi et al. 2014) and converted in kg•m^{-3} by the mean of the calibration process (Jacquin et al. 2019). A stack of slice composed of around 400 CT images per packet was then used for reconstruction. The images were recorded in DICOM format.

2.3. Data processing

2.3.1. Radial density data extraction

The CardenQB plugin running under ImageJ software was used for density data extraction. The DICOM images obtained from the X-ray CT scanning were processed separately for each of the five packets while each packet corresponds to a sequence of approximately 400 images. The DICOM images were first converted to TIF format. The positions of cells on the transversal section of the packets TIF images sequence were automatically detected. Cells containing cores were then identified from empty ones. Manual corrections were carried out on the images in case any cells were not detected or if there was confusion between cells containing cores and empty ones. Then each pixel of the TIF image is converted into a density value based on the gray level of the pixel. The final result of this processing steps is one wood density profile at 12% moisture content for each core with a resolution of 0.625 mm.

2.3.2. Intergeneric, interspecific and intraspecific wood density variation

All statistical analysis was conducted on R v.4.1.2 software by using the R stats v.4.1.2 (R Core Team 2021) and agricolae packages v.1.3-5 (Felipe 2021). From the wood density profiles, we calculated the average wood density along the whole core (CWD), along the heartwood (HWD) and along the sapwood (SWD). The hypothesis on the normality of the data was evaluated graphically and by the Shapiro-Wilk test. Levenn test (R core Team 2021) was used to check the homogeneity of data variance. Comparison of the wood average density variance [between the (i) two genera, (ii) species for the two genera and (iii) trees for each species] were performed respectively for the CWD, HWD and SWD by using one-way Analysis of variance (ANOVA) and Kruskal-Wallis test. Tukey post-hoc tests were used to determine which species or groups of species are statistically different from the others in terms of wood density. Statistical significance of all tests was set at $P > 0.05$.

2.3.3. Radial variation analysis of wood density

The analysis was performed for species with at least two full cores, including both pith and bark. This resulted in a total of 52 cores from 8 species of *Dalbergia* and 9 species of *Diospyros*. To allow the comparison of radial wood density profiles among trees with varying diameter at breast height (Dbh), each individual tree radial wood density profile was divided into ten segments of equal length. Within each segment, an average wood density value was calculated.

The normality and the variance homogeneity of the data were then checked using Shapiro-wilk and Levenne test. At the genus and species level, the analysis of the pith to bark wood density variance were carried out using Anova and Kruskall Wallis test. Pearson and Spearman correlation tests were performed between the wood density values and the distance from the pith. The Pearson's (r) and Spearman's (rho) coefficient tests were used to evaluate the trend of the radial wood density and its strength. The tests were performed at a statistical significance $P > 0.05$.

2.3.4. Influence of tree diameter and climatic conditions of the selected forests on the average core density

Climate data for the years 1970-2000 were obtained from the Wordclim v2.1 database (Fick and Hijmans 2017). Temperature and precipitation values for the geographical coordinates of the sampled forests were extracted from this database using the R software with the raster v.3.5-15 package (Etten et al. 2023) and sp v.1.6-0 package (Hijmans et al. 2023). Based on the normality and homogeneity of variance of the data, one-way ANOVA tests or corresponding non-parametric tests were performed to assess the influence of the bioclimatic region of the growth sites on CWD, SWD, and HWD. For significant tests, pairwise multiple comparisons were conducted to identify the bioclimatic regions where wood density varies significantly.

The relationships between CWD and (i) tree diameter from which the wood core was taken, (ii) temperature, and (iii) precipitation were evaluated using Pearson correlation coefficients (r) for normal data and Spearman correlation coefficient (rho) for non-normal data. All tests were conducted at a significance level of $p > 0.05$.

3. Results

3.1. Intergeneric, interspecific and intraspecific wood density analysis

Among the different part of the wood, significance difference in wood mean density between the two genera is observed only on heartwood, as evaluated by Kruskall Wallis test ($p < 00001$). The mean HWD of *Dalbergia* and *Diospyros* genera are respectively 0.961 ± 0.142 g•cm^{-3} and 1.070 ± 0.165 g•cm^{-3}. This difference could be attributed to a higher content of extractives in the heartwood of *Diospyros*. However, some authors such as Zanne et al. (2009) found the opposite results, with higher wood density for *Dalbergia* compared to *Diospyros* genus. As summarize in table 2 for both genera, Malagasy species generally have denser wood compared to species of the same genus growing in other countries. The wood of Malagasy *Dalbergia* and *Diospyros* species is also denser than that of most native species. The average wood density of *Dalbergia* is similar to *Stephanostegia capuronii* Mark (WD = 0.975 g•cm^{-3}) and *Scolopia madagascariensis* Si (WD = 0.950 g•cm^{-3}), while the average wood density of *Diospyros* is similar to *Neobeguea mahafaliensis* Leroy (WD = 1.040 g•cm^{-3}) and *Cedrelopsis grevei* Baillon (WD = 1.000 g•cm^{-3}) (Blaser et al. 1993).

Between-species, wood mean density varies significantly either based on CWD, SPW or HWD for *Dalbergia* and *Diospyros* species. The wood mean density variation is however higher based on HWD, with coefficients of variation of 13.92% and 16.33% for *Dalbergia* and *Diospyros* species respectively. Mean HWD for *Dalbergia* species ranges from 0.655 ± 0.070 g•cm^{-3} (*Dalbergia baronii* Baker) to 1.299 g•cm^{-3} (*Dalbergia rakotovaoi*) while it ranges from 0.740 ± 0.072 g•cm^{-3} (*Diospyros subtrinervis* H. Perrier) to 1.273 ± 0.047 g•cm^{-3} (*Diospyros malandy* H.N. Rakouth, Randrianaivo, G.E. Schatz & Lowry) for *Diospyros* species. Intraspecific density variation ranges (between trees) are closely similar for both genera, with a Coefficient of Variation of 1.51% (*Dalbergia madagascariensis*) up to 26.68% (*Dalbergia ambongoensis*) for *Dalbergia* species, and 1.94% (*Diospyros crassifolia*) up to 22.51% (*Diospyros* sp.) for *Diospyros* species.

The Coefficient of Variation of the HWD seems to be the best proxy for defining wood density-based groups. HWD values show that the 35 *Dalbergia* (n = 150) species can be classified in eleven groups, as shown in Table 1 and Fig. 4. Among the different *Dalbergia* groups that exhibit significantly distinct HWD ranges, *Dalbergia rakotovaoi* and *Dalbergia baronii* stand out as distinct classes. The former has the highest HWD of 1.299 g•cm-3, while the latter has the lowest HWD of 0.655 ± 0.07 g•cm^{-3}. For the *Diospyros* species (n = 72), seven groups can be observed. *Diospyros malandy* has the highest HWD, while *Diospyros subtrinervis* has the lowest. This interspecific density variation can be attributed to the difference in anatomical characteristics between the species which affect its wood density. The comparison of our results to the published anatomical data of Malagasy *Dalbergia* and *Diospyros* species (Sandratriniaina et al. 2021; Ramanantsialonina et al. 2022) allow to understand that species with a larger tangential vessel diameter tend to have lower heartwood density. For example, this is the case with *Dalbergia baronii* (HWD = 0.655 g•cm^{-3}) and *Dalbergia davidii* (HWD = 1.172 g•cm^{-3}), whose wood is among the lighter and denser, respectively, based on HWD values, and they have mean TVD of 136 μm and 64 μm (Ramanantsialonina et al. 2022). In contrast, *Diospyros malandy* (HWD = 1.273 g•cm^{-3}) and *Diospyros lewisiae* (HWD = 0.780 g•cm^{-3}), which also differ significantly in terms of heartwood density values, have mean TVD of 43 μm and 73 μm, respectively (Sandratriniaina et al. 2021). This is supported by Fichtler et al. (2012), who assessed, across various tropical species, the relationships between wood anatomical variables and tree growth site conditions. They also found a negative correlation between vessel diameter and wood density (Fichtler et al. 2012). This can be explained by the fact that wood density is generally influenced by the proportion of solid material (cellulose, lignin, etc.) relative to the volume of empty spaces (vessels, cavities, etc.). The presence of larger vessels thus contributes more significantly to creating void spaces within the wood, resulting in a reduction of its density. Other factors for which data are not available, and whose effect on wood density could not be assessed for Malagasy *Dalbergia* and *Diospyros*, may also interact with these wood anatomical factors to determine wood density. These factors include for example genetic factors such as tree growth rate (Hietz et al. 2013), or environmental variables such as soil type.

Table 1 Mean values (± standard deviation) of wood density at 12% moisture content according to wood section (whole core, heartwood, sapwood) for the 38 Dalbergia and 29 Diospyros.

Botanical name (*Dalbergia*, n= 165)	**n**	**CWD**		**SWD**		**HWD**		**Class**
Dalbergia rakotovaoi	1	1.111		1.092		1.299		a
Dalbergia davidii Bosser & R. Rabev.	2	1.145	± 0.005	1.091		1.172	± 0.043	ab
Dalbergia chermezonii R. Vig.	2	1.132	± 0.039	1.091	± 0.040	1.154	± 0.054	abc
Dalbergia humbertii R. Vig.	5	1.090	± 0.076	1.006	± 0.019	1.140	± 0.111	abc
Dalbergia bemarivensis Phillipson & N. Wilding	8	1.119	± 0.059	1.062	± 0.083	1.138	± 0.105	abc
Dalbergia suaresensis Baill.	5	1.039	± 0.059	1.015	± 0.046	1.074	± 0.061	abc
Dalbergia lemurica Bosser & R. Rabev.	3	1.051	± 0.018	0.905	± 0.118	1.070	± 0.039	abcd
Dalbergia trichocarpa Baker	3	1.009	± 0.045	0.975	± 0.048	1.053	± 0.040	abcde
Dalbergia purpurascens Baill.	12	1.027	± 0.043	1.022	± 0.052	1.048	± 0.062	abcde
Dalbergia neoperrieri Bosser & R. Rabev.	1	0.977		0.857		1.040		abcdef
Dalbergia pseudobaronii R. Vig.	5	0.994	± 0.015	0.970	± 0.030	1.037	± 0.041	abcdef
Dalbergia obtusa Lecompte	7	0.994	± 0.057	0.952	± 0.044	1.018	± 0.070	abcdef
Dalbergia abrahamii Bosser & R. Rabev.	7	0.961	± 0.053	0.913	± 0.038	1.001	± 0.072	abcdef
Dalbergia tricolor Drake	6	0.947	± 0.061	0.925	± 0.057	0.993	± 0.125	abcdef
Dalbergia emirnensis Bosser & R. Rabev.	14	0.994	± 0.054	1.019	± 0.044	0.989	± 0.065	abcdef
Dalbergia aff. greveana Baill.	1	0.945		0.898		0.986		abcdef
Dalbergia chlorocarpa R. Vig.	1	0.964		0.940		0.977		abcdef
Dalbergia greveana Baill.	5	0.957	± 0.086	0.941	± 0.081	0.972	± 0.122	abcdef
Dalbergia densicoma Baill.	6	0.931	± 0.101	0.928	± 0.100	0.946	± 0.142	abcdef

Dalbergia aff. purpurascens Baill.	1	0.935		0.909		0.946		abcdef
Dalbergia occidentalis	4	0.932	± 0.057	0.914	± 0.054	0.942	± 0.084	abcdef
Dalbergia ambongoensis Baill.	2	0.912	± 0.133	0.916	± 0.115	0.933	± 0.249	abcdef
Dalbergia bathiei R. Vig.	5	0.845	± 0.052	0.819	± 0.039	0.911	± 0.070	abcdef
Dalbergia glaucocarpa Bosser & R. Rabev.	5	0.900	± 0.069	0.903	± 0.068	0.880	± 0.096	bcdef
Dalbergia antsirananae Phillipson, Crameri & N. Wilding	7	0.888	± 0.052	0.895	± 0.052	0.867	± 0.047	bcdef
Dalbergia leandrii	2	0.866	± 0.003	0.864	± 0.010	0.867	± 000	cdef
Dalbergia viguieri Bosser & R. Rabev.	4	0.912	± 0.069	0.906	± 0.078	0.862	± 0.027	cdef
Dalbergia madagascariensis (Baker) Bosser & R. Rabev.	4	0.884	± 0.050	0.891	± 0.066	0.858	± 0.013	cdef
Dalbergia normandii Bosser & R. Rabev.	6	0.842	± 0.119	0.828	± 0.119	0.841	± 0.215	cdef
Dalbergia cloiselii Drake	1	0.820		0.787		0.839		cdef
Dalbergia monticola Bosser & R. Rabev.	12	0.856	± 0.045	0.875	± 0.062	0.838	± 0.063	def
Dalbergia orientalis Bosser. & R. Rabev.	5	0.786	± 0.056	0.791	± 0.075	0.830	± 0.168	def
Dalbergia aff. chapelieri Baill.	4	0.815	± 0.110	0.842	± 0.100	0.781	± 0.116	ef
Dalbergia L. f.	1	0.755		0.790		0.721		ef
Dalbergia baronii Baker	5	0.743	± 0.082	0.757	± 0.075	0.655	± 0.070	f
Dalbergia chapelieri Baill.	1	0.711		0.711				-
Dalbergia manongarivensis Bosser & R. Rabev.	1	0.828		0.828				-
Dalbergia rajeryi	1	1.128		1.128				-
Botanical name (*Diospyros*, n= 132)	**n**	**CWD**		**SWD**		**HWD**		**Class**

Diospyros malandy H.N. Rakouth, Randrianaivo, G.E. Schatz & Lowry	4	1.018	± 0.044	0.976	± 0.042	1.273	± 0.047	a
Diospyros crassifolia A.G. Linan, G.E. Schatz & Lowry	5	1.089	± 0.037	1.006	± 0.038	1.232	± 0.024	ab
Diospyros torquata H. Perrier	3	1.008	± 0.030	0.983	± 0.046	1.225	± 0.095	abc
Diospyros obscurinerva A.G. Linan, G.E. Schatz & Lowry	5	1.087	± 0.049	1.024	± 0.059	1.211	± 0.039	abc
Diospyros analamerensis H. Perrier	5	1.054	± 0.022	1.012	± 0.037	1.180	± 0.023	abc
Diospyros chitoniophora Capuron ex A.G. Linan, G.E. Schatz & Lowry	6	1.044	± 0.032	0.988	± 0.016	1.166	± 0.073	abc
Diospyros humbertiana H. Perrier	4	1.123	± 0.021	1.035	± 0.124	1.152	± 0.054	abc
Diospyros platycalyx Hiern	5	0.998	± 0.041	0.927	± 0.042	1.149	± 0.046	abc
Diospyros clusiifolia (Hiern) G.E. Schatz & Lowry	6	0.935	± 0.053	0.911	± 0.074	1.059	± 0.098	bcd
Diospyros toxicaria Hiern	7	0.937	± 0.033	0.912	± 0.050	1.031	± 0.042	cd
Diospyros ferrea (WillDiospyros) Bakh.	4	1.032	± 0.033	1.030	± 0.041	1.020	± 0.023	cde
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	5	1.006	± 0.025	1.004	± 0.026	1.000		cde
Diospyros pubiramulis A.G. Linan, G.E. Schatz & Lowry	1	0.961		0.956		0.978		cde
Diospyros occlusa H. Perrier	6	0.874	± 0.084	0.836	± 0.035	0.973	± 0.162	cde
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	5	0.946	± 0.030	0.946	± 0.031	0.952		cde
Diospyros haplostylis Boivin ex Hiern	4	0.937	± 0.088	0.917	± 0.117	0.911		cde
Diospyros rubripetiolata G.E. Schatz & Lowry	4	0.917	± 0.018	0.924	± 0.011	0.894		cde
Diospyros baronii (H. Perrier) G.E. Schatz & Lowry	5	0.767	± 0.059	0.732	± 0.068	0.875	± 0.103	de
Diospyros sp. L.	4	0.929	±	0.927	±	0.866	±	de

			0.081		0.084		0.195	
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	5	0.864	± 0.033	0.864	± 0.033	0.860		de
Diospyros ultima G.E. Schatz & Lowry	4	0.816	± 0.065	0.811	± 0.073	0.835		de
Diospyros ramisonii G.E. Schatz & Lowry	1	0.861		0.861		0.796		de
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas	3	0.695	± 0.090	0.750	± 0.183	0.792		de
Diospyros lewisiae Mas, G.E. Schatz & Lowry	6	0.866	± 0.066	0.873	± 0.062	0.780		de
Diospyros subtrinervis H. Perrier	5	0.751	± 0.058	0.758	± 0.063	0.740	±0.072	e
Diospyros squamosa Bojer	6	1.006	± 0.040	1.006	± 0.040			-
Diospyros brevipedicellata G.E. Schatz, Lowry & Mas	5	0.818	± 0.037	0.817	± 0.037			-
Diospyros gracilipes Hiern	5	0.843	± 0.085	0.843	± 0.085			-
Diospyros sakalavarum H. Perrier	4	0.795	± 0.070	0.795	± 0.070			-

CWD: mean density of the whole core, SWD: mean density of the sapwood, HWD: mean density of the heartwood, n: number of cores (trees) per species. Species groups defined by different letters have significantly different HWD intervals at a threshold of $p > 0.05$

This study significantly enriches the density database for Malagasy *Dalbergia* and *Diospyros* species as wood density was previously measured for only seven species of *Dalbergia* and two species of *Diospyros* (Richter and Dallwitz 2019; Louppe Dominique 2008; Gerard et al. 2016; Lisan n.d). Among publised density data found in the literature, only those that provided density at 12% moisture content and infradensity, which were subsequently converted into density at 12% moisture content according to the equation defined by Vieilledent et al. (2018), were compared with the results of our study. Some authors provide one average wood density value for trees belonging to several *Dalbergia* spp or *Diospyros* spp species (Rakotovao et al. 2012).

Regarding the interspecific variation of wood density, our results show that density variation is more pronounced in the heartwood, allowing the distinction of 11 *Dalbergia* and 7 *Diospyros* groups with significantly different density value ranges.

Table 2 Comparison of the average wood density of Dalbergia and Diospyros species in the literature.

Genus	n	Average wood density (g•cm^{-3})	Countrys	References
Dalbergia	3	0.915 ± 0.02	India	Zanne et al. 2019
	1	0.990	Madagascar	Rakotovao et al. 2012
	2	0.857 ± 0.08	India	Reyes et al. 1992
	5	0.837 ± 0.148	Madagascar Africa	Louppe et al. 2008
	1	0.850	Madagascar	Lisan, n.d
	3	0906 ± 0.079	Madagascar	Cooke et al. 2008
	spp	0.995	Madagascar	Rakotovao et al. 2012
	38	0.961 ± 0.14	Madagascar	Current research
Diospyros	14	0.838 ± 0.01	India	Zanne et al. 2019
	10	0.857 ± 0.08	Tropical Asia Tropical Africa Tropical America	Reyes et al. 1992
	spp	0.990	Madagascar	Rakotovao et al. 2012
	1	1.000	Madagascar	Louppe et al. 2008
	29	1.070 ± 0.160	Madagascar	Current research

n : number of species, spp : several species whose list and number are not determined

3.2. Radial wood density variation

Kruskall Wallis test shows that there is no statistically significant difference in density values along the radial direction of the wood for the *Dalbergia* genus (p = 0.19). Mean density values of the core segments are nearly constant between the pith and the seventh segment (rho = -0,011), with an average value ranging from 0.982 ± 0.119 g•cm^{-3} to 1.014 ± 0.100 g•cm^{-3}. Density then decreases in the three last segments, with an average value of 0.941 ± 0.105 g•cm^{-3} to 0.982 ± 0.172 g•cm^{-3} (Fig. 5). The wood density for *Diospyros* genus however varies significantly (p < 0.001) from the pith to the bark. The mean density values for the core segments range from 0.852 ± 0.104 g•cm^{-3} to 1.010 ± 0.158 g•cm^{-3}. Table 3 shows the results of Spearman correlation test which reveals a decrease in wood density from the pith towards the bark, but the radial density trend is relatively weak (rho = -0,27).

Analysis of density variance at the species level shows a significant difference in radial wood density within the tree ($p < 0.05$) for *Dalbergia abrahamii* Bosser & R. Rabev., *Diospyros chitoniophora* Capuron ex A.G. Linan, G.E. Schatz & Lowry and *Diospyros platycalyx* Hiern (Fig. 6 and Fig. 7). Furthermore, table 3 indicate that these species exhibit a strong negative correlation (r or rho > 0.5) between wood density and the radial distance from the pith. The wood density for *Dalbergia bathiei* R. Vig., *Diospyros crassifolia* A.G. Linan, G.E. Schatz & Lowry and *Diospyros occlusa* H. Perrier decreases as one moves from pith towards the bark. However, the difference in density along the radial direction is not statistically significant ($p < 0.5$). This decrease is likely associated with the accumulation of extractives in the inner wood during the heartwood formation (Lehnebach et al. 2019). The accumulation of extractives can effectively raise the wood density, resulting in the heartwood being denser than the sapwood. Some researchers have suggested that the shade tolerance and physiological strategy of species during ontogeny also influence the radial density pattern of wood (Woodcock 2015). However, very little data is available in existing literature regarding the shade tolerance of *Dalbergia* and *Diospyros* species from Madagascar. The available information, nevertheless, suggests that there may be both shade-tolerant and light-demanding species within the same genus of *Dalbergia* or *Diospyros* (Blaser et al. 1993; Cooke et al. 2008; Razafimamonjy 2011; CITES 2016). The decreasing trend of radial wood density from the pith to the bark might be a characteristic feature of shade-tolerant species, as they generally produce dense wood during the juvenile stage (Hietz et al. 2013; Plourde et al. 2014) to limit growth and enhance survival in the understory of forests, providing protection against the risks of mechanical injury and pathogen attacks (Alvarez-Clare and Kitajima, 2007). They subsequently produce lighter wood in the adult stage to promote further growth when they reach higher levels in the canopy (Woodcock 2015). The prevalence of the decreasing trend in the radial density profile, observed in 10 out of the 17 analyzed species, is consistent with the literature which confirms that species from the *Dalbergia* and *Diospyros* genera are generally semi-shade tolerant (CITES 2016). Conversely, the increasing trend of radial wood density variation can be observed in light-demanding species that produce low-density wood during the juvenile stage to promote growth, and then denser wood in the outer part of the trunk during the adult stage (Woodcock 2015).

Six of the studied species show a U-shaped or inverted U-shaped radial density trend. The factors underlying this trend are not well-known in the literature, but according to some authors, such a trend is particularly found in trees in humid tropical forests (Williamson et al. 2012). This is consistent with four species analyzed species in our study (*Dalbergia glaucocarpa , Dalbergia suaresensis, Diospyros ultima,* and *Diospyros ferrea*), which display a similar trend and are found in forests located in humid or subhumid bioclimatic zones. However, the findings of this study also show that this trend can be observed in species inhabiting dry tropical forests (*Dalbergia lemurica* and *Dalbergia emirnensis*).

Table 3 Effect of radial distance from the pith to the bark on HWD and its trend along the radial direction of the wood

Genus	Botanical name	n	p-value	r	rho
Dalbergia	*Dalbergia abrahamii* Bosser & R. Rabev.	3	**0.033**	**-0.64**	
	Dalbergia bathiei R. Vig.	2	0.310		**-0.59**
	Dalbergia bemarivensis Phillipson & N. Wilding	2	1		0.02
	Dalbergia emirnensis var. *decaryi* Bosser & R. Rabev.	6	**< 0.010**		0.23
	Dalbergia glaucocarpa Bosser & R. Rabev.	3	0.820		-0.06
	Dalbergia lemurica Bosser & R. Rabev.	2	0.560		-0.25
	Dalbergia obtusa Lecomte	5	0.210	-0.43	
	Dalbergia suaresensis Baill.	3	0.410	-0.31	
Diospyros	*Diospyros analamerensis* H. Perrier	3	**< 0.010**	-0.07	
	Diospyros bardotiae H.N. Rakouth. G.E. Schatz & Lowry	4	0.850	0.20	
	Diospyros chitoniophora Capuron ex A.G. Linan. G.E. Schatz & Lowry	4	**< 0.001**		**-0.86**
	Diospyros clusiifolia (Hiern) G.E. Schatz & Lowry	2	0.0819	-0.34	
	Diospyros crassifolia A.G. Linan. G.E. Schatz & Lowry	2	0.055	**-0.92**	
	Diospyros ferrea (Willd.) Bakh.	3	0.103	0.36	
	Diospyros occlusa H. Perrier	2	0.182		**-0.71**
	Diospyros platycalyx Hiern	3	**< 0.0001**	**-0.82**	
	Diospyros ultima G.E. Schatz & Lowry	3	0.570	-0.33	

n: number of cores, P-value: significance of Anova or Kruskall Wallis test, r and rho: Pearson and Spearman correlation coefficients, (r/ rho > 0.5 means strong correlation). Values in bold indicate a significant variation in radial density value and a strong correlation between density and radial distance from pith to bark.

3.3. Influence of growth site climatic conditions and tree diameter on average wood density

The results of correlation tests between wood density and climatic parameters are given in table 4. For both *Dalbergia* and *Diospyros* species, wood density increases with increasing temperature at the tree's growing site. This positive correlation is weak for SWD and moderate for HWD. On the other hand, an increase in precipitation corresponds to a decrease in wood density, although this correlation is weak, except for HWD in *Diospyros* species.

As shown in table 5, the forest stands location sites has therefore a significant influence on the CWD, SWD, and HWD, for both *Dalbergia* (p = 0.002; p = 0.011; p = 0.020) and *Diospyros* (p = 0.001; p = 0.03; p = 0.004). For the two genera, trees in subarid and dry bioclimates have higher values of CWD, SWD, and HWD compared to trees growing in subhumid and humid bioclimates. However, average CWD for the *Diospyros* genus is higher in humid bioclimates, where there is more precipitation, than in subhumid bioclimates. These results are in line with previous research by Vaughan et al. (2019) who observed an increase in wood density during drought conditions. Similarly, Ibanez et al. (2016) found that aridity conditions characterized by low precipitation and high temperatures promote the formation of high-density wood. In hardwood species, these results can be attributed to the reduction in average vessel width to limit maximum xylem hydraulic conductivity in response to water scarcity and high temperature (Hacke et al. 2016; Fajardo and Piper 2022). The variation in vessel diameter serves as a crucial characteristic for assessing the tree's adaptation to water availability (Hacke et al. 2016) and the decrease in average vessel width is an ecophysiological response of the tree to resist embolism (Mendez-Alonzo et al. 2012; Hacke et al. 2016). Additionally, Thomas et al (2007) affirmed that higher temperatures promote increased wood density by reducing vessel and fiber lumen area while increasing fiber wall thickness.

Regarding the influence of tree diameter on wood density, the Dbh of sampled trees varied widely between species and collection sites, ranging from 1.5 to 80 cm. The correlation between average core density and the diameter of the trees is very weak, whether for CWD (rho = - 0.08), SWD (rho = -0.06), or HWD (rho = -0.11). This can be attributed to the influence of multiple factors on tree diameter, including tree age, tree growth rate, environmental growth conditions, etc. (Ramananantoandro et al. 2016; Dey et al. 2017; Nabais et al. 2018; Mevanarivo et al. 2020). Furthermore, wood density can be influenced by other factors such as wood chemical composition (Vermaas 1975; Singleton et al. 2003) and anatomical structure (Pritzkow et al. 2014). All these factors can interact in complex ways, resulting in varying effects on wood density. The results of this study are consistent with those of Ramananantoandro et al. (2016) who worked on trees from the humid forests of Madagascar, as well as Flore et al. (2021) who studied trees from the lower stratum of the semi-deciduous forest in Cameroon. Both studies observed no significant correlation between wood diameter and its average density. However, Tenouewa et al. (2022) reported contradictory results for *Acacia auriculiformis* wood, where density increased with increasing tree diameter. This suggests that the influence of tree diameter on wood density may vary among different species. Limited data regarding the relationship between tree diameter and wood density can be found in the existing literature. Therefore, a comparative approach with other wood genera or species could provide additional information to more accurately assess this relationship.

Table 4 Values of rho correlations between climatic parameters (Temperature and precipitation) and average wood density (CWD, SWD, and HWD).

	Dalbergia			*Diospyros*		
	CWD	**SWD**	**HWD**	**CWD**	**SWD**	**HWD**
Temperature	0.46	0.33	0.48	0.35	0.25	0.49
Precipitation	-0.32	-0.36	-0.22	-0.30	-0.17	-0.49

Table 5 Mean value ± standard deviation of CWD, SWD and CWD for species belonging to the genus *Dalbergia* and *Diospyros* according to bioclimatic zones.

		Bioclimatic zone			
Genus	**Density (g•cm^{-3})**	**Subarid**	**Dry**	**Subhumid**	**Humid**
Dalbergia	CWD	1013.6 ± 59.2 (a)	995.6 ± 57.6 (a)	911.3 ±117.8 (b)	829.7 ± 58.5 (c)
	SWD	1011.9 ± 63.4 (a)	963.4 ± 79.5 (a)	898.1 ± 103.3 (b)	835.6 ± 89.9 (c)
	HWD	1022.3 ± 94.0 (a)	1012.6 ± 116.8 (a)	911.6 ± 141.1 (b)	827.7 ± 125.1 (b)
Diospyros	CWD	1123.1 ± 129.0 (a)	984.9 ± 86.3 (a)	869.5 ± 44.6 (b)	888.6 ± 52.3 (a)
	SWD	1131.4 ± 123.0 (a)	994.7 ± 84.4 (a)	886.0 ± 47.8 (b)	873.0 ± 42.4 (b)
	HWD	1121.0 ± 68.6 (a)	1016.0 ± 4 6.5 (a)	924.1 ± 25.0 (b)	869.7 ± 18.1 (b)

Different letters indicate groups with significantly different average density values

3.4. Operational application of the results

The updated density database of Malagasy *Dalbergia* and *Diospyros* wood can be harvested to manage sustainably forest ressources and enhance the valorization of wood properties. It can be firstly used to estimate the aboveground biomass (AGB) and carbon content for malagasy *Dalbergia* and *Diospyros* trees throughout allometrics models (Chave et al. 2005). Several authors have used wood density in the development of allometric equations for estimating AGB in dense rainforests (Vieilledent et al. 2012; Ramananantoandro et al. 2015) and secondary forests of Madagascar (Randrianasolo et al. 2019). Njana et al. (2016) worked on three species from Tanzanian mangrove forests (*Avicennia marina* (Forssk.) Vierh, *Sonneratia alba* J. Smith, and *Rhizophora mucronata* Lam.) and found that, in addition to dendrometric parameters, the accuracy of multispecies allometric models improves when wood density is considered. An accurate knowledge of AGB can significantly contribute to the sustainable utilization of forest resources as a decision tool regarding timber harvesting, conservation, restoration, and forest regeneration. Furthermore, the quantification of AGB provides a better understanding of a forest's capacity to sequester carbon from the atmosphere (Chave et al. 2005; Ramananantoandro et al. 2015). This holds paramount importance in the context of climate change, as forests play a crucial role in reducing atmospheric carbon dioxide (CO2) levels.

In the context of wood utilization, understanding interspecific density variation allows to better valorize wood properties by choosing the most suitable species for the intended use. In the furniture industry, for example, *Dalbergia* and *Diospyros* are highly sought after, even though wood density value is unknown for the majority of species in these two genera. The availability of such knowledge contributes however to improve the aesthetics, durability, and quality of furnitures, as density is correlated with various mechanical properties (Larjavaara and Muller-Landau 2011) and wood durability (Chave et al. 2009; Larjaavara and Muller-Landau 2010). Denser woods are inherently harder, more resistant to impacts and wear, less susceptible to deformation, and better equipped to withstand changes in humidity and temperature (Cabral et al. 2022). These makes wood density as an important criterion for selecting wood species for the production of furniture subject to heavy use.

4. Conclusion

The average wood density of *Dalbergia* and *Diospyros* species varies depending on the type of wood analyzed (CWD, SWD, HWD), with the interspecific variation being more pronounced for HWD. The studied species can be divided into eleven classes for *Dalbergia* and seven classes for *Diospyros,* based on the range of their average HWD values. Species within the same group have similar average HWD values, while significant differences in average HWD can be observed between different groups. The radial density trend of the wood differs among species, although a common pattern is observed in most species with notable radial density variation, showing a decrease from the pith to the bark. Regarding the effect of climatic conditions on wood density, findings show that species growing in regions with low rainfall and high temperature tend to have denser wood. On the other hand, tree diameter does not influence density values.

The results of this research have significant implications for expanding the database on the density of precious woods from Madagascar. Currently, the available data on wood density is limited to only a few species of *Dalbergia* and *Diospyros*. The new data obtained in this research will contribute to a better valorization of these species. Additionally, these results will help in species differentiation withing the *Dalbergia* and *Diospyros* genera. Measuring wood density using standard methods can be a labor-intensive process, especially when analyzing a large number of samples. To overcome this challenge, an interesting alternative is to use the obtained density values as references for calibrating prediction models of wood density based on alternative methods such as Near Infrared Spectroscopy. This non-destructive technique would enable for rapid and efficient characterization of wood density.

Declarations

Aknowledgements

We are very grateful to the Society for Wood Science and Technology (SWST) which funded the mobility to INRAe Nancy-Champenoux through its 2020's Short Term Scientific Mission (STSM). We would like to thank Dr. Jean Michel Leban, Mr. Maxime Lecarin, Ms. Caroline Jaozandry from the "Biogéochimie des Ecosystèmes Forestiers (BEF)" team, Mr. Phillipe Jacquin, and Mr. Etienne Farre from the "Silva" team at "Institut National de Recherche pour xl'Agriculture, l'Alimentation et l'Environnement (INRAe)" for their warm welcome and the supervision of all works during the period of stay. We are also thankful to "Centre de cooperation Internationale en Recherche Agronomique pour le Développement (CIRAD)" for covering the cost of the Madagascar-France flight ticket. We would like to thank the Missouri Botanical Garden of Madagascar (MBG) for their support in the fieldwork and the taxonomic identification of wood samples conducted by the MBG-Madagascar and the National Museum of Natural History-Paris (MNHN). Furthermore, we express our gratitude to the "Gestion Durable des bois précieux *Dalbergia* et *Diospyros* de Madagascar (G3D)" project, funded by the European Union, the precious wood consortium (DBEV, MBG, ESSA-Forêts) for funding field missions and allowing us to use the wood cores for this study.

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Figures

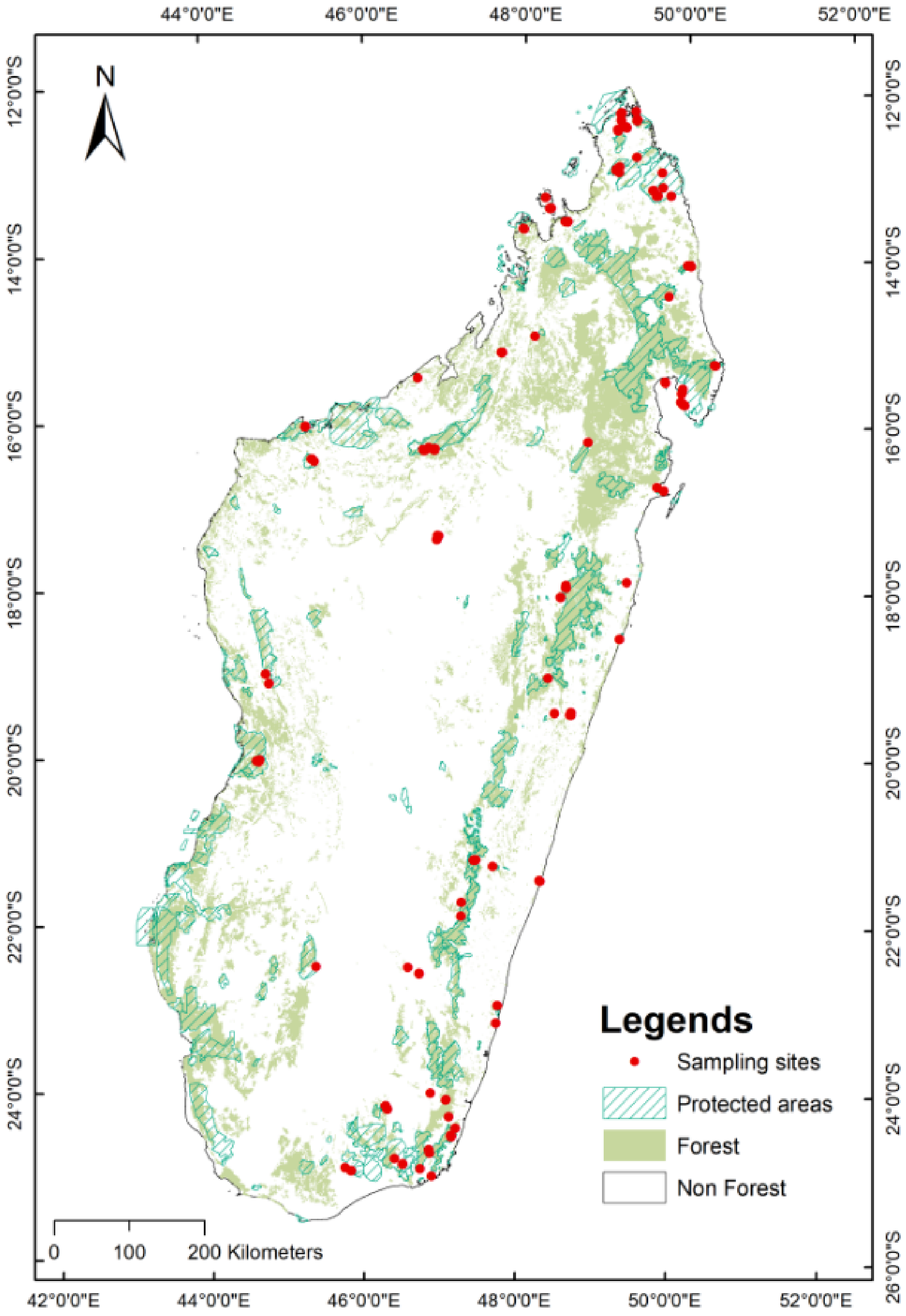

Figure 1

Wood core sampling sites for density analysis

Source : Institut Géographique et Hydrologique de

Madagascar (FTM) BD500; Google earth, 2021

Geographic coordinate system: GCS International 1924

Realization: Andry Clarel Raobelina

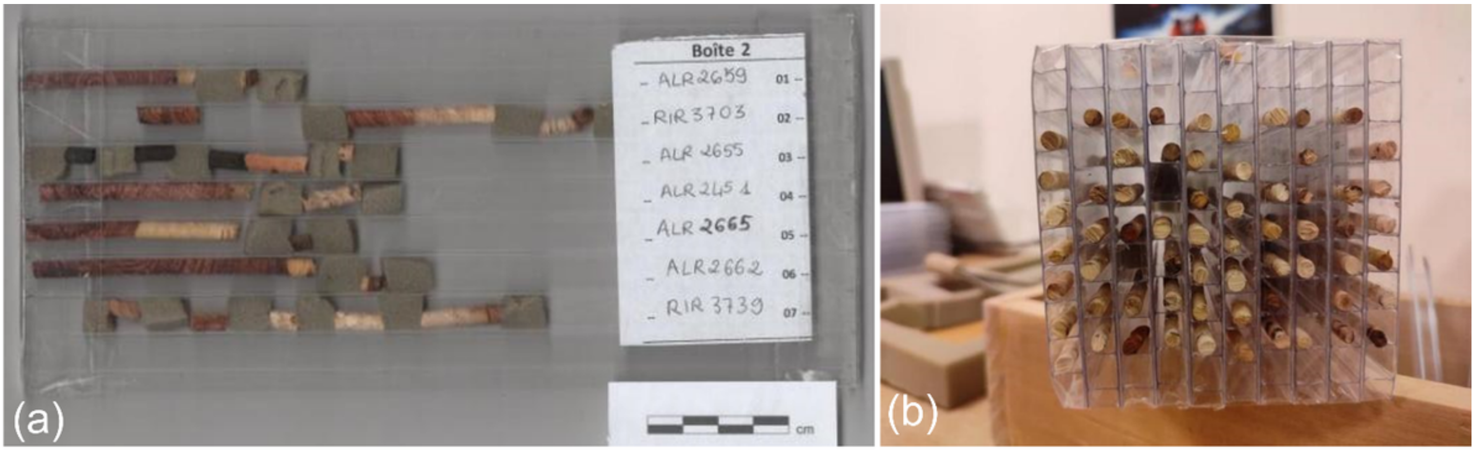

Figure 2

(a) A box filled with 7 wood cores with their respective core numbers. (b) A packet formed by 10 boxes. ALR2659, ALR2662, ALR2665 : *Dalbergia emirnensis*Bosser & R. Rabev.; RIR3703, RIR3739: *Dalbergia abrahamii* Bosser & R. Rabev. ; ALR2655 : *Diospyros humbertiana* H. Perrier; ALR2451 : *Dalbergia purpurascens* Baill

Figure 3

CT scanning of wood cores

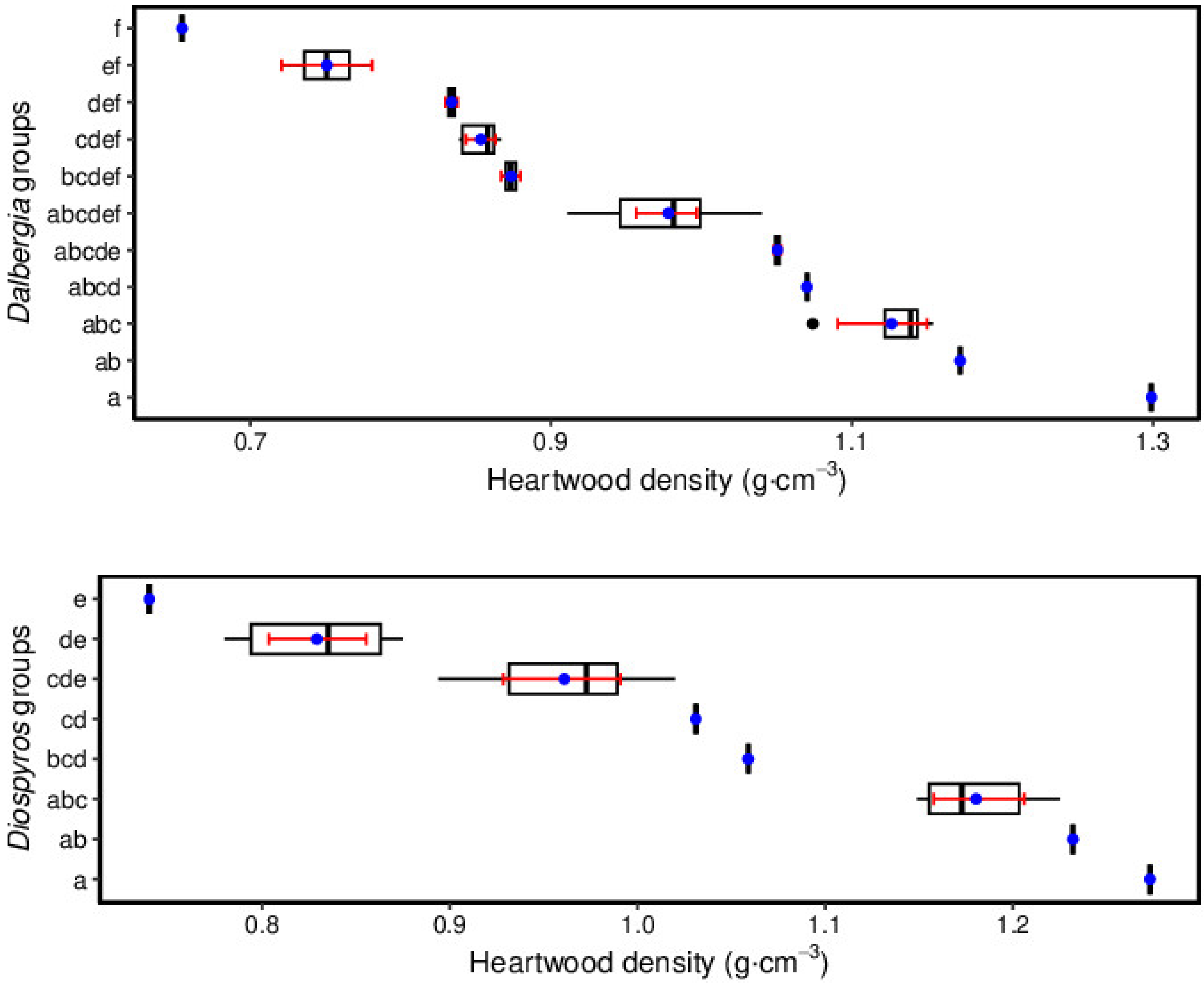

Figure 4

Boxplots of heartwood density values for the different groups within the two genera.

For each group, the blue dots and the red dash indicates respectively the mean HWD density and the confidence interval.

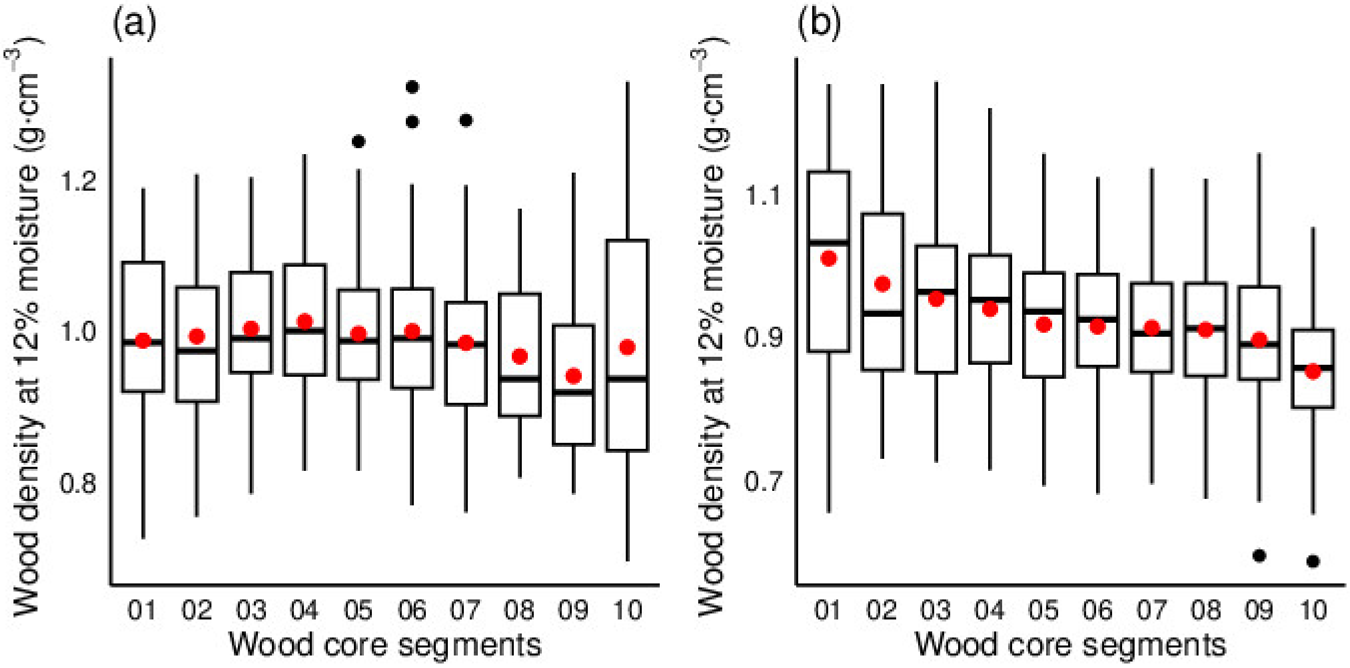

Figure 5

Radial density profile of *Dalbergia*and *Diospyros* wood cores

Each wood core segment is equal to one tenth of the core length; segments 1 to 10 are ordered in the direction from pith to bark. The density of a segment is the average of the density values along the segment. The red dot represent the average density value of the corresponding segment

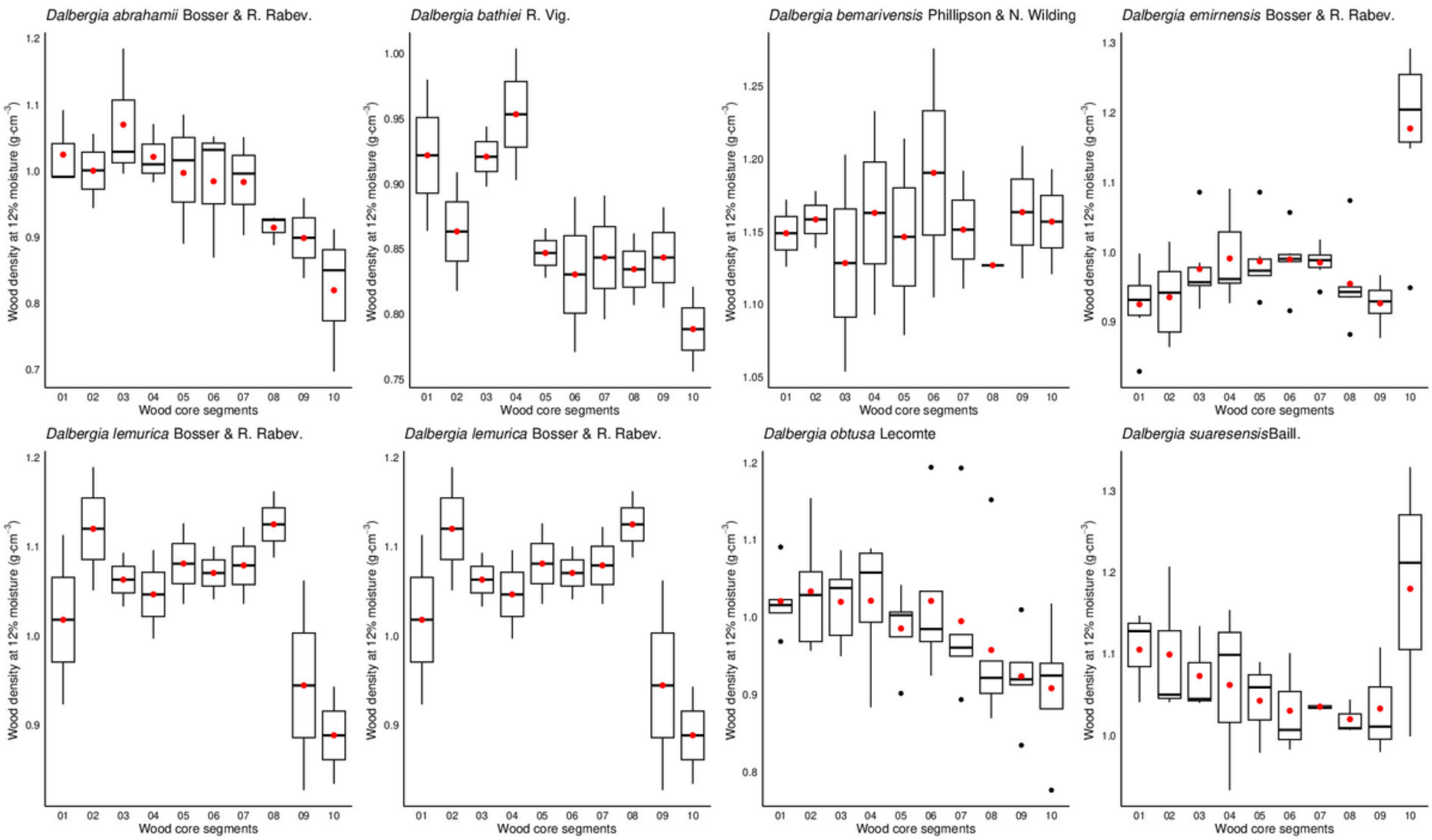

Figure 6

Pith to bark wood density profiles for eight *Dalbergia* species

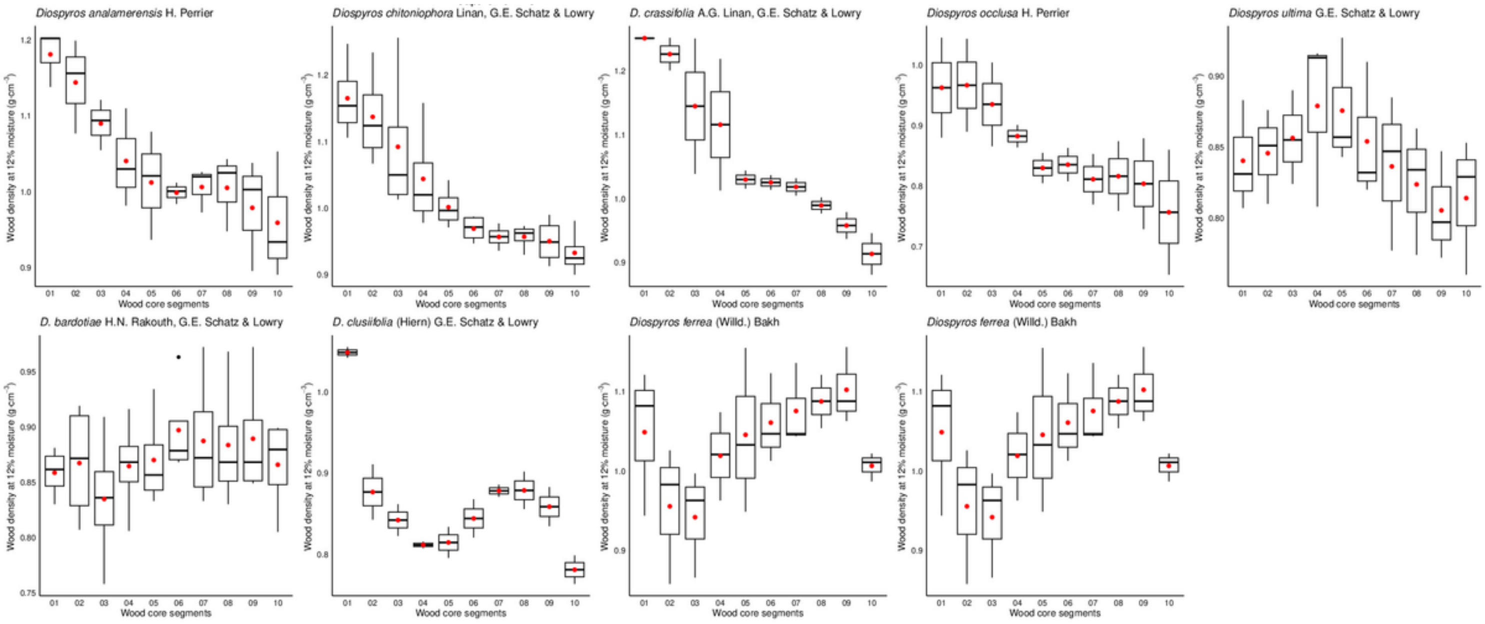

Figure 7

Pith to bark wood density profiles for nine *Diospyros* species