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ORIGINAL PAPER

Influence of tree species, tree diameter and soil types on wood density and its radial variation in a mid-altitude rainforest in Madagascar

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Abstract
· ***Key message*** **In a tropical rainforest of Madagascar, tree species differed in average wood density depending on their light requirements and on the soil type. Tree diameter had no effect. None of these factors influenced the variation of density related to the distance to the pith.**
· ***Context*** Wood density (WD) is an important wood property as it correlates with several functional tree traits and mechanical wood properties. Furthermore, wood density is often used in forest biomass and carbon stock estimates. The variation in wood density depends on a range of intrinsic or environmental factors.
· ***Aims*** This study investigated the effect of species, tree diameter, soil types and the distance from the pith on wood density in native hardwood species from a natural, mid-elevation rainforest in Madagascar.
· ***Methods*** We extracted pith-to-bark core samples from the trunk of 204 trees from 23 species. Each wood core was sectioned into 1 cm-long segments on which measures of volume and weight were performed. Within-tree and between-tree variations of wood density were analysed.
· ***Results*** Average wood density was higher on shade-tolerant than on light-demanding species. It was higher on poor ferralitic than on fertile lowland soils. Tree diameter had no influence on average wood density. Regarding within-tree variation, wood density does not vary from pith to bark.
· ***Conclusion*** These results help fill the gaps in wood properties database for tree forest species in Madagascar.

Keywords Madagascar · Modelling · Species light requirement · Soil types · Wood density

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Contribution of the co-authors
Tahiana Ramananantoandro: designed the study, supervised the work, run the data analysis, discussed the results and wrote the paper
Miora F. Ramanakoto: collected wood cores in the forest, carried out density measurements, run the data analysis, discussed the results and wrote the paper
Gabrielle L. Rajoelison: helped in defining the light requirements of the different species and discussed the results
Jean Chrysostome Randriamboavonjy: helped in soil type definition and discussed the results
Herimanitra P. Rafidimanantsoa: collected wood cores in the forest, carried out density measurements and discussed the results

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1 Introduction

Wood is a complex material with outstanding physical and mechanical properties. Density is one of its most important technological and ecological properties. Wood density is connected to several functional tree traits (Chave et al. 2009; Nock et al. 2009) and is correlated with some wood mechanical properties such as dynamic bending strength, modulus of elasticity and compression strength (Machado et al. 2014). Therefore, wood density provides guidance on the potential uses for a particular wood species. Moreover, wood density reflects the amount of biomass per unit volume of tree trunk and thus is one of the predictor variables usually used in allometric equations to estimate forest aboveground biomass (Chave et al. 2009; Henry et al. 2010).

Several factors can explain the intra- and inter- tree variations of wood density. According to Chave et al. (2009), there is a relation between the wood density and several traits across

Table 1 Number of trees per species, with diameter class and their respective diameters

Scientific name	Family	Number of trees studied			Average DBH (Std) (cm)	
		SD	BD	Total	SD	BD
Albizia gummifera (J.F., Gmel.) C.A. Smith*	Fabaceae	5	4	9	13.62 (1.23)	19.48 (5.07)
Anthocleista madagascariensis Baker*	Gentianaceae	3	3	6	12.3 (0.78)	22.67 (5.8)
Bosqueia danguyana Leandri	Moraceae	5	3	8	9.22 (3.07)	20.63 (3.96)
Calophyllum sp.	Calophyllaceae	5	3	8	11.07 (2.01)	22.3 (3.58)
Chrysophyllum boivinianum (Pierre) Baehni	Sapotaceae	6	5	11	10.68 (1.25)	22.26 (2.6)
Dilobeia thouarsii Roem. & Schult	Proteaceae	5	4	9	11.16 (2.36)	19.53 (3.86)
Dombeya lucida Baill.*	Malvaceae	5	5	10	12.02 (1.4)	21.14 (3.57)
Erythroxyllum corymbosum Boivin ex Baill.	Erythroxylaceae	3	3	6	9.2 (2.78)	18.97 (3.76)
Harungana madagascariensis Lamarck ex. Poiret	Hypericaceae	6	7	13	11.67 (1.46)	18.3 (3.6)
Ilex mitis (L.) Radlkofer*	Aquifoliaceae	6	5	11	10.97 (3.36)	16.26 (0.86)
Macaranga cuspidata Boivin ex Baill.	Euphorbiaceae	6	3	9	11.1 (3.42)	18.03 (1.85)
Micronychia tsiramiramy H. Perrier	Anacardiaceae	5	5	10	11.04 (1.44)	18.38 (1.59)
Mussaenda sp. Linnaeus	Rubiaceae	5	3	8	11.42 (1.61)	19.47 (3.21)
Nuxia capitata Baker	Stilbaceae	5	4	9	10.52 (2.03)	18.58 (3.51)
Ocotea sp.(1)**	Lauraceae	3	3	6	9.73 (0.9)	20.18 (4.05)
Ocotea sp.(2)**	Lauraceae	5	4	9	12.12 (1.72)	19.88 (3.35)
Protorhus ditimena H. Perrier*	Anacardiaceae	5	5	10	9.48 (1.8)	18.94 (1.31)
Ravensara acuminata (Willd ex Meisen) Baillon	Lauraceae	5	5	10	11.56 (2.78)	19.68 (1.06)
Ravensara crassifolia (Baker) Danguy	Lauraceae	6	4	10	10.7 (3.1)	16.46 (1.03)
Schefflera longipedicellata (Lecomte) Bernardi	Araliaceae	5	5	10	12.37 (2.05)	18.02 (2.17)
Schefflera vantsilana (Baker) Bernardi	Araliaceae	4	5	9	9.2 (1.87)	19.46 (4.39)
Syzygium cumini (L.) Skeels*	Myrtaceae	3	3	6	11.2 (1.61)	16.8 (0.53)
Uapaca densifolia Baker*	Phyllanthaceae	3	4	7	9.48 (1.31)	22.28 (1.83)

SD small diameter (5 cm ≤ DBH < 15 cm), *BD* big diameter (DBH ≥ 15 cm), *DBH* diameter at breast height, *Std* standard deviation

*Indicates the seven most abundant species according to Rajaonera (2008)

**The two species belonging to Ocotea genus could not be defined. Their botanical characteristics are different

the whole-plant, including leaf size, minimum leaf water potential and perhaps rooting depth. The radial variation in wood density represents tree strategies throughout its development by investing in height growth or investing in wood tissue for structural support. Wood density is related to the light requirement of the species. Previous studies have shown that pioneer species have low density while emerging species have intermediate density and sub-canopy slow-growing species have high density (King et al. 2006; Muller-Landau 2004; Van Gelder et al. 2006). When studying 1653 trees across the Amazon Basin, Patino et al. (2009) found that altitude is negatively correlated with the density whereas temperature is positively correlated with the density. Because of the terrain slope and competition for soil reserves, soil types affect the dynamics of tree growth, thus the variations in wood properties. A steep terrain is particularly sensitive to erosion, so soil resources are easily eroded. To adapt itself to this environment, tree develops wood with higher physical and mechanical properties (Coutand et al. 2004; Wimmer et al. 2002).

Density varies also within a given tree. The radial variation of wood density can be explained first by the gradual transition from juvenile to mature wood (Fukazawa 1984). The ageing of the cambial meristem causes the intra-tree density variation, as well as a pith-to-bark increase in fibre length and in vessel diameter (Thibaut et al. 1997). The evolution of wood extractives from pith to bark also accounts for density variation within tree (Guilley 2000).

Several studies on the variations of wood density with distance from the pith have been carried out on temperate species (McLean et al. 2011; Machado et al. 2014) and tropical wood from South America (Montes et al. 2007), Africa (Henry et al. 2010) and Asia (Nock et al. 2009). According to these authors, wood density of fast-growing pioneer species increases from pith to bark, whereas slower-growing trees exhibit the reverse pattern. The stiffness of the juvenile wood decreases from pith to bark for primary forest trees, whereas it

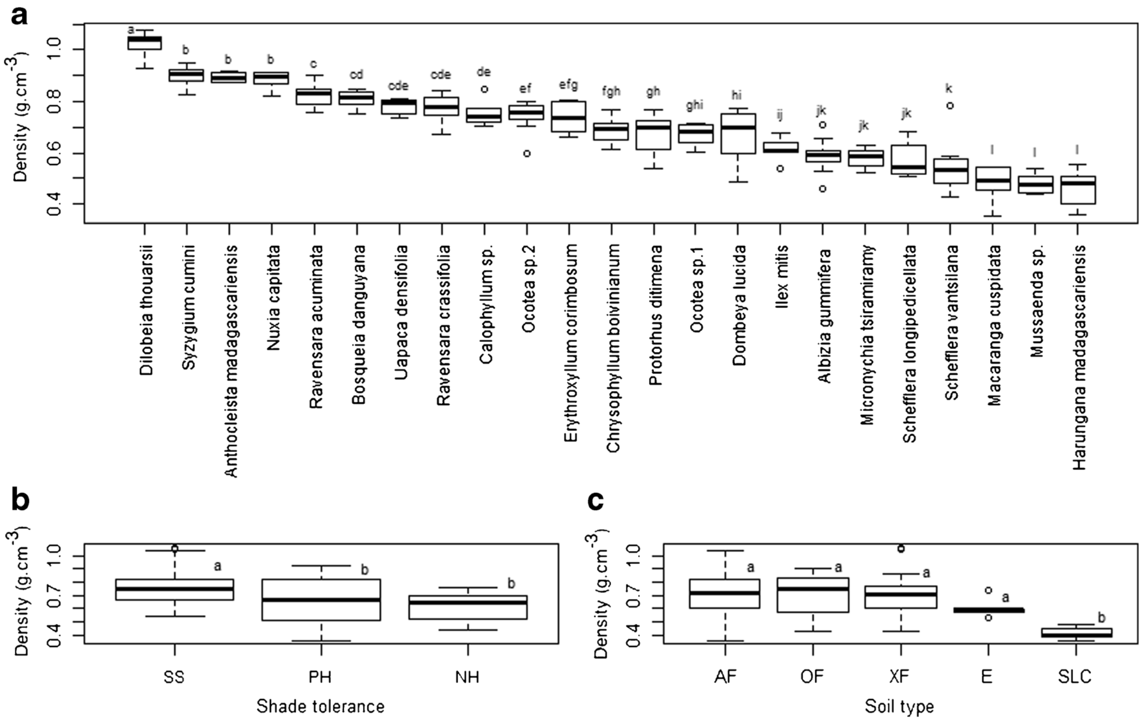


Fig. 1 Average wood density according to **a** tree species, **b** light requirement–*SS* semi-shade-tolerant, *PLD* pioneer light demander, *NLD* nomad light demander, **c** soil types–*AF* acric ferralsol, *OF* orthic ferralsol, *XF* xanthic ferralsol, *E* entisols, *SLC* soils of lowland complex. Box plot shows the median, quartiles, lowest and highest data. *Identical letters* indicate no statistical difference in wood density value (ANOVA and Fisher's LSD test, $p < 0.05$)

increases for plantation trees. Increments are greater in wet tropical forests than in drier tropical forests. However, to our knowledge, there was no study yet about the variation of wood in natural forests of Madagascar. Given that 96 % of Malagasy tree and shrub species are endemic (Schatz 2000), we address the following question: Do internal (species, tree diameter) and external factors (soil types) affect wood density and its radial variation for native rainforest tree species? Three hypotheses are tested: (i) Species have different average density and different radial variation patterns. This difference is explained by the species light requirement. We expect pioneer species to have less dense wood and increasing density from pith to bark and a reverse pattern in shade-tolerant species; (ii) Average wood density is different for large and small trees; (iii) Soil types influence wood density between trees and its radial variation. We expect less dense wood and increasing density from pith to bark in very fertile stands.

2 Material and methods

The experimental approach consisted of three steps: (i) determination of the factors underlying the variation of wood density – species, tree diameter, distance from the pith, soil types; (ii) measurement of the wood density in laboratory; (iii) development of the models of radial variation of density by incorporating the four factors of variation.

2.1 Study area

The study was carried out in Mandraka natural forest, District of Manjakandriana, Region Analamanga, Madagascar (47°54′–47°56′ E and 18°53′–18°55′ S). It is located 67 km East of Antananarivo. Mandraka is managed by the Forestry Department, School of Agronomy, University of Antananarivo. Annual precipitation averages 2300 mm. The wettest months are from December to March with maximum rainfall in January (342 mm). There is no ecologically dry month. Temperatures range from 13.7 to 20.2 °C with an annual average of 17.5 °C. The relatively high elevation (800–1300 m) confers a permanent relative humidity with an average of 82 %. The climate is tropical fresh and humid. The terrain is rugged, characterized by overall slopes of 50 % but reaching 90 % in some places (Rajaonera 2008). The natural vegetation is an evergreen montane forest, characterized by high tree density, reduced height and pluristrata structures. A recent forest survey identified 73 tree species distributed within

Table 2 Linear model of intra-tree wood density variation according to the three factors studied

Factors	Parameter	Estimate	Std. error	*t* value	Pr(>|t|)	
Tree diameter	(Intercept)	0.670397	0.013347	50.23	<2e-16	***
	Distance to pith Dp	0.007174	0.003025	2.371	0.0179	*
	Diameter					
	Small diameter	0.021917	0.023336	0.939	0.3479	–
	Interaction Diameter × Dp					
	Small diameter × Dp	−0.004962	0.008087	−0.614	0.5397	–
	Residual standard error: 0.1556 Multiple R-squared: 0.006677, Adjusted R-squared: 0.03171 F-statistic: 1.904, *p* value: 0.1273 *P values for Diameter and Diameter × Dp test are for significant differences relative to "Big Diameter"* *R^2 (model) = 1.27 %, R^2 (Diameter) = 0.0003 %, R^2 (Dp) = 0.96 %, R^2 (Diameter x Dp) = 0.31 %*					
Light requirement	(Intercept)	0.61	0.03	17.80	<2e−16	***
	Distance to pith Dp	0.004	0.01	0.47	0.64	–
	Light requirement					
	Pioneer light demander	0.03	0.04	0.90	0.37	–
	Semi-shade-tolerant	0.14	0.04	3.64	0.00	***
	Interaction: Light requirement × Dp					
	Pioneer light demander × Dp	0.002	0.01	0.20	0.84	–
	Semi-shade-tolerant × Dp	−0.001	0.01	−0.10	0.92	–
	Residual standard error: 0.1509 Multiple R-squared: 0.1064, Adjusted R-squared: 0.1007 F-statistic: 18.69, *p* value: <2.2e−16 *P values for Light requirement and Light requirement × Dp test are for significant differences relative to "Nomad light demander"* R^2 (model) = 11.4 %, R^2 (*Light requirement*) = 10.2 %, R^2 (*Light requirement*) = 0.8 %, R^2 (*Light requirement* × Dp) = 0.4 %					
Soil type	(Intercept)	0.41	0.06	6.49	<0.001	***
	Distance to pith Dp	0.004	0.02	0.25	0.80	–
	Soil type					
	Xanthic ferralsol	0.28	0.06	4.35	<0.001	***
	Orthic ferralsol	0.28	0.07	4.26	<0.001	***
	Acric and xanthic ferralsol	0.28	0.07	3.93	<0.001	***
	Entisols	0.16	0.10	1.63	0.10	–
	Interaction: Soil type × Dp					
	Xanthic ferralsol × Dp	0.002	0.02	0.12	0.91	–
	Orthic ferralsol × Dp	−0.01	0.02	−0.41	0.68	–
	Acric and xanthic ferralsol × Dp	0.01	0.02	0.39	0.70	–
	Entisols × Dp	0.01	0.03	0.38	0.71	–
	Residual standard error: 0.1475 Multiple R-squared: 0.1141, Adjusted R-squared: 0.1046 F-statistic: 12.07, *p* value: <2.2e−16 *P values for Soil type and Soil type × Dp test are for significant differences relative to "Soils of lowland complex"* R^2 (model) = 12.5 %, R^2 (*Soil type*) = 10.62 %, R^2 (Dp) = 0.78 %, R^2 (*Soil type* × Dp) = 1.08 %					

Wood density is in g.cm-3

*** significant at the 0.1 % level, ** significant at the 1 %, * significant at the 5 %, – non significant

52 genera and 42 families, most of which are endemic. Secondary formations locally called *savoka* represent about 30 % of the natural area and are composed mainly of pioneer, light-demanding species. This study sampled trees from both the primary and secondary forest formations that cover a total of 14.51 ha.

2.2 Species selection and diameter threshold

We selected the 23 most abundant native species both in the primary and secondary forests. The species identified by Rajaonera (2008) as most abundant were all included (indicated by the symbol * in Table 1).

Table 3 Linear model of the intra-tree wood density variation for the 23 species

Parameter	Estimate	Std. error	*t* value	Pr(>|t|)	
(Intercept)	0.780	0.020	38.784	<2e−16	***
Distance to pith Dp	0.001	0.005	0.169	0.8662	–
Species sp					
Syzygium cumini	0.113	0.032	3.513	0.0005	***
Dilobeia thouarsii	0.220	0.030	7.420	<0.001	***
Schefflera longipedicellata	−0.214	0.029	−7.294	<0.001	***
Anthocleista madagascariensis	0.139	0.027	5.048	<0.001	***
Ilex mitis	−0.158	0.028	−5.657	<0.001	***
Micronychia tsiramiramy	−0.215	0.029	−7.429	<0.001	***
Ocotea sp.(2)	−0.072	0.028	−2.552	0.0109	*
Ocotea sp.(1)	−0.121	0.031	−3.944	0.0001	***
Chrysophullum boivinianum	−0.102	0.027	−3.838	0.0001	***
Protorhus ditimena	−0.124	0.029	−4.273	<0.001	***
Dombeya lucida	−0.161	0.028	−5.806	<0.001	***
Ravensara crassifolia	0.014	0.029	0.474	0.6355	–
Harungana madagascariensis	−0.350	0.027	−13.015	<2e−16	***
Macaranga cuspidata	−0.336	0.034	−9.779	<2e−16	***
Bosqueia danguyana	0.011	0.029	0.390	0.6968	–
Schefflera vantsilana	−0.234	0.027	−8.577	<2e−16	***
Calophyllum sp.	−0.069	0.028	−2.438	0.0150	*
Nuxia capitata	0.099	0.029	3.387	0.0007	***
Mussaenda sp.	−0.292	0.033	−8.707	<2e−16	***
Erythroxyllum corymbosum	−0.068	0.033	−2.088	0.0372	*
Ravensara acuminata	0.047	0.028	1.711	0.0874	–
Albizia gummifera	−0.194	0.027	−7.169	<0.001	***
Interaction sp. × Dp					
Syzygium cumini × Dp	−0.002	0.008	−0.237	0.8127	–
Dilobeia thouarsii × Dp	0.002	0.008	0.315	0.7529	–
Schefflera longipedicellata × Dp	−0.001	0.008	−0.085	0.9326	–
Anthocleista madagascariensis × Dp	−0.006	0.006	−1.152	0.2495	–
Ilex mitis × Dp	−0.002	0.007	−0.257	0.7976	–
Micronychia tsiramiramy × Dp	0.006	0.008	0.797	0.4256	–
Ocotea sp.(2) × Dp	0.011	0.007	1.524	0.1279	–
Ocotea sp.(1) × Dp	0.0001	0.007	0.027	0.9783	–
Chrysophullum boivinianum × Dp	−0.002	0.006	−0.240	0.8103	–
Protorhus ditimena × Dp	0.0001	0.007	−0.018	0.9860	–
Dombeya lucida × Dp	0.008	0.007	1.111	0.2669	–
Ravensara crassifolia × Dp	−0.010	0.008	−1.267	0.2054	–
Harungana madagascariensis × Dp	0.005	0.006	0.825	0.4093	–
Macaranga cuspidata × Dp	0.017	0.011	1.558	0.1197	–
Bosqueia danguyana × Dp	0.008	0.007	1.144	0.2530	–
Schefflera vantsilana × Dp	−0.003	0.006	−0.443	0.6577	–
Calophyllum sp. × Dp	0.006	0.007	0.870	0.3847	–
Nuxia capitata × Dp	0.003	0.007	0.342	0.7328	–
Mussaenda sp. × Dp	0.001	0.009	0.135	0.8925	–
Erythroxyllum corymbosum × Dp	0.011	0.009	1.244	0.2140	–
Ravensara acuminata × Dp	−0.002	0.007	−0.338	0.7358	–
Albizia gummifera × Dp	0.001	0.006	0.115	0.9085	–

Residual standard error: 0.06387

Table 3 (continued)

Parameter	Estimate	Std. error	*t* value	Pr(>|t|)
Multiple R-squared: 0.841, Adjusted R-squared: 0.8321				
F-statistic: 94.95, *p* value: <2.2e−16				

p values for sp. and sp. × Dp test are for significant differences relative to *Uapaca densifolia*

R^2 (Species) = 83.6 %, R^2 (Distance to pith) = 0.05 %, R^2 (species × Distance to pith) = 0.05 %

Wood density is in g.cm-3

***significant at the 0.1 % level, **significant at the 1 %, *significant at the 5 %, – non significant

According to Rajaonera (2008), more than a half of the trees in Mandraka have a diameter at breast height (DBH) between 5 and 15 cm. Trees with DBH above 40 cm are almost nonexistent. Thus, in order to understand whether tree diameter affects the variability of wood density, we considered two classes: (1) small trees, 5 cm ≤ diameter < 15 cm and (2) large trees, diameter ≥ 15 cm. We randomly selected a minimum of three trees per diameter class that is a minimum of six trees per species. Given the previous threshold, the number of trees studied per species was different because of the random sampling used. In total, 204 trees were sampled (Table 1). The DBH ranged from 9.2 to 13.6 cm and from 16.3 to 22.7 cm for small trees and larger ones, respectively.

We sampled pith-to-bark wood cores using an electric drill powered by a generator. The cores had a diameter of 15 mm and were extracted at DBH level. Because of the possible existence of tension wood from the sloping ground, the pith-to-bark wood cores were taken from the downslope side of the trees.

2.3 Determination of species light requirement

Plants are classified on the basis of their relative light requirements for overall vegetative development as heliophytes and sciophytes (Sharma 2005). To date, there have been few data in the literature regarding the light requirement of native tree species in Madagascar. Several methods have been used in the literature to determine the light requirements of species. These include the study of the natural regeneration, the survival and the growth of seedlings in different light conditions (Ducrey and Labbé 1985), and the use of hemispherical photographs taken directly above the crown of each sapling (Baltzer and Thomas 2007). But none of these practical methods were available to us, thus forcing us to opt for an empirical one. According to Rollet (1984), tree diameter distribution reflects the current position of each species in the stand and is the result of a 'development strategy' (growth and mortality) in the whole ecosystem. Therefore, there are striking differences between size-class distribution of light-demanding and shade-tolerant species in mature tropical rainforest. Several authors (e.g., Dupuy et al. 1998; Hall and Swaine 1981; Whitmore 1990) used the distribution curves of the species abundance per diameter class in 1 ha of forest to determine species light requirement. Therefore, we assessed the light requirement using the same method.

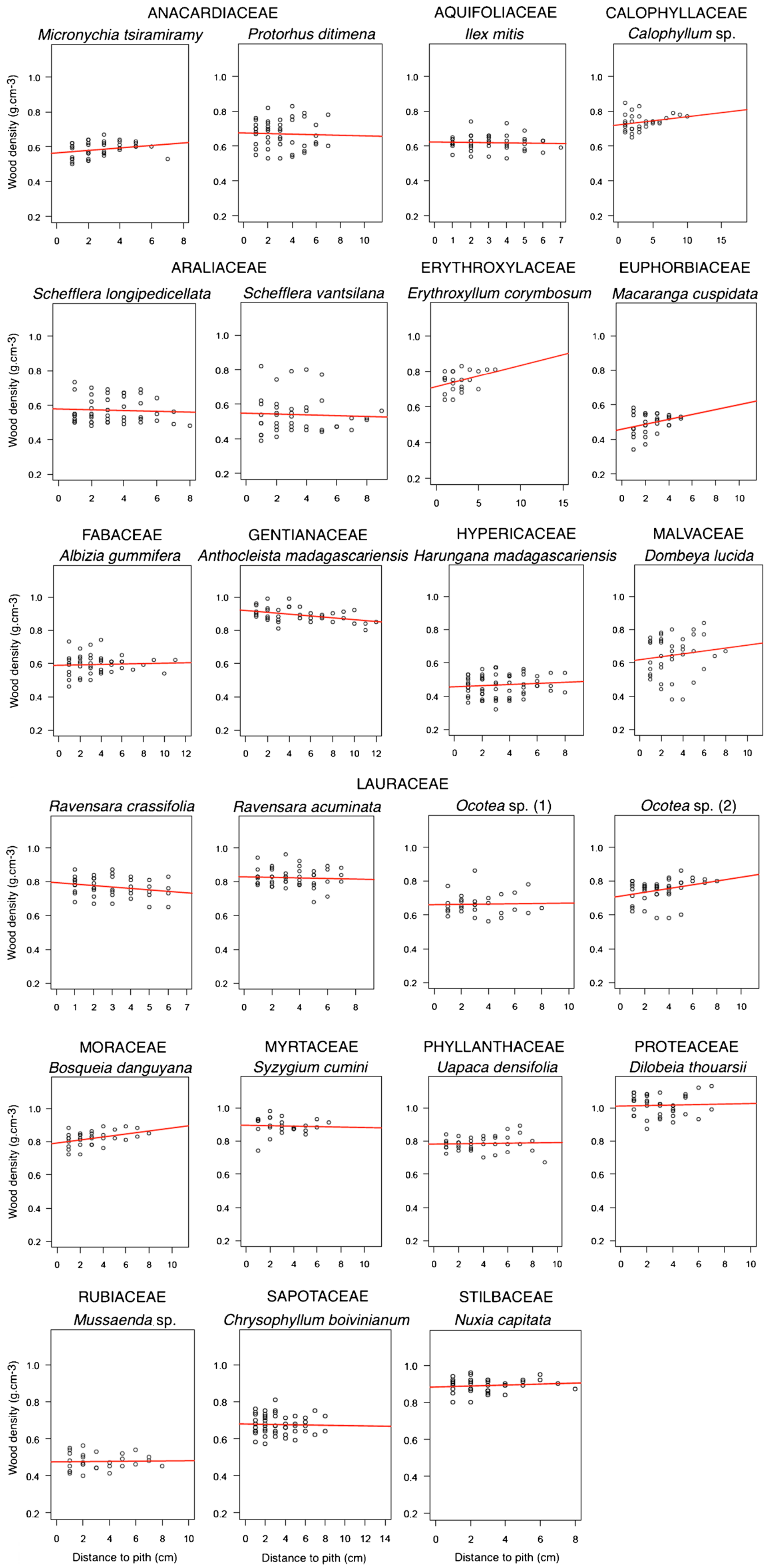
Mandraka forest has been modified from its original state by various natural and anthropogenic pressures. Thus, to validate the approach, we simultaneously used three forest survey results on mid-elevation rainforests: (1) the national forestry and ecological inventory IEFN (MEF 1996) which covered all types of forests including mid-elevation rainforests, (2) the inventory done in the Anjozorobe-Angavo forest corridor (Goodman et al. 2007) as 74 % of Mandraka species are listed in this corridor, and (3) the forest inventory carried in Mandraka forest by Rajaonera (2008).

Using data from these three sources, species light requirements were determined based on population structure by establishing the distribution curves of the species abundance per diameter class. The resulting curves were compared with those of Rollet (1984) in order to identify the light requirement of each species.

2.4 Soil types in Mandraka

We recorded the geographical coordinates and altitude of each studied tree. Combining these data with results from a soil survey done by Rajoelison et al. (2007) in Mandraka, we were able to determine the type of soil on which the trees were growing. Five types of soils were identified: acric ferralsol (AF), xanthic ferralsol (XF), orthic ferralsol (OF), entisols (E) and soils of lowland complex (SLC). All types of soils are ferralitic with lumpy and polyhedric textures. They differ in the degree of rejuvenation by the occurrence of primary minerals at a certain depth. The more we go downslope, the more we

Fig. 2 Pith-to-bark variation of wood density of the 23 species studied. ▶ *Red lines* represent best-fit linear regression models. Species are ordered by alphabetical order of family


ANACARDIACEAE
Micronychia tsiramiramy
Protorhus ditimena
AQUIFOLIACEAE
Ilex mitis
CALOPHYLLACEAE
Calophyllum sp.
ARALIACEAE
Schefflera longipedicellata
Schefflera vantsilana
ERYTHROXYLACEAE
Erythroxyllum corymbosum
EUPHORBIACEAE
Macaranga cuspidata
FABACEAE
Albizia gummifera
GENTIANACEAE
Anthocleista madagascariensis
HYPERICACEAE
Harungana madagascariensis
MALVACEAE
Dombeya lucida
LAURACEAE
Ravensara crassifolia
Ravensara acuminata
Ocotea sp. (1)
Ocotea sp. (2)
MORACEAE
Bosqueia danguyana
MYRTACEAE
Syzygium cumini
PHYLLANTHACEAE
Uapaca densifolia
PROTEACEAE
Dilobeia thouarsii
RUBIACEAE
Mussaenda sp.
SAPOTACEAE
Chrysophyllum boivinianum
STILBACEAE
Nuxia capitata
Wood density (g.cm-3)
Distance to pith (cm)

find primary minerals. Soils of lowland complex can be entisols rich in humus layers or hydromorphic soils.

2.5 Recording wood density

In order to study the radial variation of density, each core was cut into 1 cm-long segments, starting at 0.5 cm from the pith. Segments containing bark and pith were excluded. In total, 204 core samples were collected. The number of cores obtained per species ranged from 6 to 13. In total, 2342 segments were obtained from these cores. The density of a segment was calculated as its weight divided by its volume, both measured at 12 % humidity (stabilised in a climatic chamber at 20 °C and 65 % relative humidity). The weight was measured with a precision scale with 0.01 g resolution. We used the Archimedes water displacement method to measure the volume (Chave et al. 2006). Wood density of a tree was the average density of the pith-to-bark segments. Similarly, the density for a species was the average of the densities of all the sampled trees belonging to that species.

2.6 Modelling the variation in wood density among trees and within a tree

Statistical analysis was performed with the R software (R Development Core Team 2012). For all species, we first calculated the mean, the range and the standard deviation of the density. We then run an analysis of variance to assess the effect of the following factors: species, tree diameter, soil types and distance from pith on the wood density variation. Fisher's LSD test was used to identify significant differences between each level of factors that explained the variability of wood density.

Models of the radial variability of the density were developed based on a linear mixed-effects model (Nock et al. 2009). In this linear model, the factor *species* was considered as a random effect while *diameter*, *soil type* and *distance from pith* were taken to have fixed effects. Moreover, the interaction between factors was taken into account, given that the effects of these factors are non-additive. Therefore, the final linear mixed-effects model was:

$D_{ijk} = \beta_0 + \beta_1 Dp_{ij} + \beta_2 F_k + \beta_3 F_k Dp_{ij} + \varepsilon_{ijk}$ where D_{ijk} is the wood density for the i-th segment of the j-th tree of the k-th species, Dp_{ij} is the distance to the pith, F_k is the factor considered and $\beta_0, \beta_1, \beta_2, \beta_3$ are the fixed effects, ε_{ijk} are the errors. The goodness of fit of the model was assessed with the coefficient of determination R^2.

3 Results

3.1 Effect of tree species and diameter on the average wood density

Different species displayed significantly different wood densities ($p < 0.001$, $\alpha = 0.05$, df = 22). Average wood density of the 23 species ranged from 0.47 to 1.01 (Fig. 1a). *Harungana madagascariensis* and *Dilobeia thouarsii* displayed respectively the lowest and highest average densities. Furthermore, the distribution of the minimum and maximum density values for each species showed the existence of within-species variability. The factor *tree diameter* had no influence on the average wood density (Table 2).

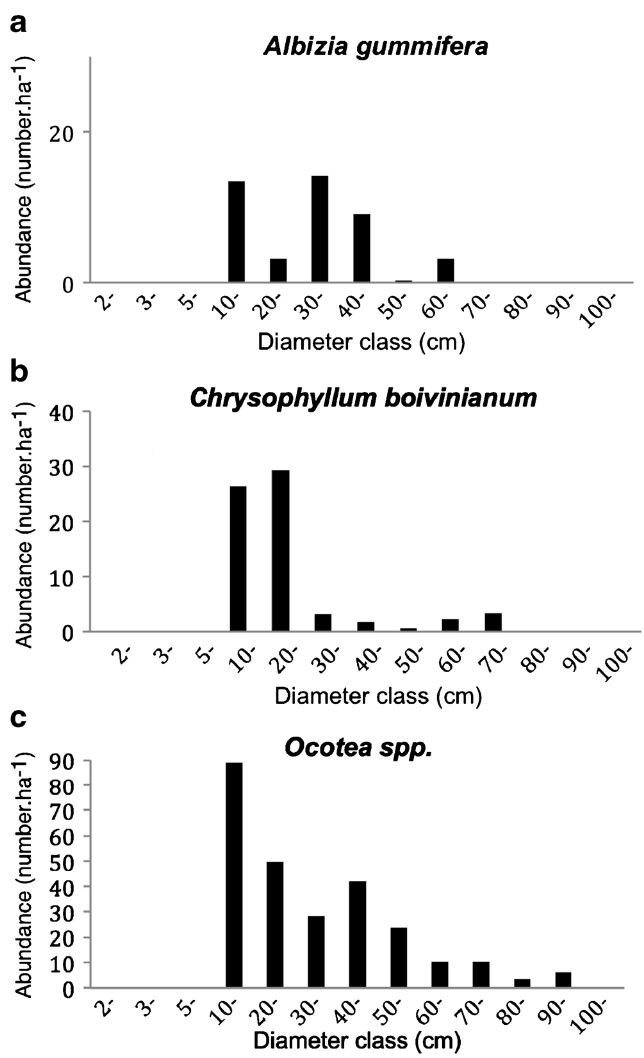


Fig. 3 Light requirement of some species in the study site. Typical distribution of light demander pioneer species e.g., *Albizia gummifera* (**a**), light demander nomad species e.g., *Chrysophyllum boivinianum* (**b**), edifice shade-tolerant species e.g., *Ocotea* spp. (**c**). Curves derived from combined data of the three inventories (Goodman et al. 2007, MEF 1996, Rajaonera 2008)

Table 4 Light requirements of the 23 species studied

Species behaviours	Group	Taxa
Light demanders (Sun species)	Pioneer	*Albizia gummifera*
		Nuxia capitata
		Schefflera longipedicellata
		Schefflera vantsilana
		Harungana madagascariensis
		Ravensara crassifolia
		Ravensara acuminata
		Anthocleista madagascariensis
		Dombeya lucida
		Macaranga cuspidata
	Nomad	*Chrysophyllum boivinianum*
		Mussaenda sp.
Shade-tolerant (Shade species)	Semi-shade-tolerant	*Protorhus ditimena*
		Calophyllum sp.
		Ocotea sp.(1)
		Ocotea sp.(2)
		Bosqueia danguyana
		Syzygium cumini
		Uapaca densifolia
		Dilobeia thouarsii
		Ilex mitis

Tree distribution of the two species *Erythroxyllum corymbosum* and *Micronychia tsiramiramy* could not be identified because none of the inventories used have complete information on their abundance

3.2 Effect of soil types on the average wood density

Soil type had a significant effect on the average wood density at the 5 % level (Table 2). The wood density of trees on soils of the lowland complex (0.41 g.cm^{-3}) was significantly lower than on the three ferralsol and entisol (0.69 g.cm^{-3}) (Fig. 1c). Average wood densities did not differ between the three ferralsols (Table 2).

3.3 Effect of light requirement on the average wood density

Light requirement had an effect on the average wood density (Table 2). The average wood density of shade-tolerant species (0.75 g.cm^{-3}) was significantly greater than that of light-demanding species (nomad = 0.61 g.cm^{-3}, pioneer = 0.64 g.cm^{-3}) at the 5 % level (Fig. 1b).

3.4 3.3. Radial variation of wood density

Table 3 shows that the distance from pith had no effect on the intra-tree density variability since the part of the variability due to this factor was low (R^2 = 0.05 %). Density increased slightly from pith to bark for 13 species, decreased for 8 species and did not vary for 2 species (Fig. 2). None of the factors (species, tree diameter, soil type) had an influence on the radial variation of wood density (Table 2).

4 Discussion

4.1 Effect of species on wood density

The results of this study show that species had an effect on the average wood density (Table 2). Several authors suggested tree light requirement as one of the main reasons for the difference in wood density between species (e.g., Van Gelder et al. 2006; Muller-Landau 2004). Light-demanding species are fast-growing, which favours a lower wood density than shade-tolerant, slow-growing species.

The analysis of the diameter class using the data from the three forest surveys showed three groups of species light requirements. Three examples of distributions are shown for each group of light requirement (Fig. 3). For example, based on the models established by Rollet (1984), *Albizia gummifera* (Fig. 3a) is a light-demanding pioneer species because of its erratic distribution. This species requires full light from the beginning to the end of its life cycle. The large number of individuals with small diameters in the Mandraka forest indicated the presence of a previous canopy gap that has been restored. *Chrysophyllum boivinianum* (Fig. 3b) is a light-demanding nomad species that can germinate in the shadows of the other trees, but requires light to grow higher. The "balanced L" distribution for species like *Ocotea* sp. is close to the negative exponential distribution model (Fig. 3c). This model is characteristic of edifice shade-tolerant species that regenerate in the shade of the stand and may be able to survive in the shade throughout its entire life. The light requirements of the other species are shown in Table 4. The analysis of the distribution of trees by diameter class showed that ten species are light-demanding pioneers, two are nomadic and nine are semi-shade-tolerant. Sun species (57 %) were more common than shade species (43 %).

A number of studies have suggested that light-demanding species have greater growth potential than shade-tolerant species, regardless of the light environment (Baltzer and Thomas 2007; Nock et al. 2009). The results of this study are in accordance with the literature. Thus, for light-demanding species, low wood density facilitates rapid canopy ascension whereas for shade-tolerant species, higher wood density contributes to higher survival beneath the canopy.

4.2 Effect of tree diameter on wood density

Tree diameter had no influence on the within- and between-tree variability of wood density. This finding is inconsistent with the results from similar studies. For example, Woodcock and Shier (2003) and Chowdhury et al. (2013) found that small-diameter trees in temperate forests and plantations have lower density than larger trees. In these studies, the trees reached 60 cm in diameter. The structure of a temperate forest is different from that of a tropical mountain forest; this latter being largely dominated by small-diameter trees (Rajaonera 2008). The maximum tree diameter recorded in this study was indeed below 30 cm. It would have been interesting to study the effect of tree age (De Castro et al. 1993) but the fact that the studied species do not produce annual growth rings hindered that investigation.

4.3 Effect of soil types on wood density

Soil types influence the average wood density between trees. The average wood density is higher on poor ferralitic soils than on lowland ones. Uphill and along the slope, the soil is chemically poor, dominated by young loamy soils that feature low structural stability and are easily eroded. In contrast, soils in the lowlands are more fertile because of the accumulation of nutrients from the higher ground due to erosion (Rajoelison et al. 2007). For the same reason, entisol contains more nutrients, especially potassium. This study suggests that tree growth is moderate on poor soil, subsequently enabling the wood to become more densely structured (Baker et al. 2004; Muller-Landau 2004).

4.4 Wood density radial variation

Several authors have shown that wood density varies significantly from pith to bark, with a difference that can reach 200 to 300 % in some species (De Castro et al. 1993). This is particularly the case for temperate forests (*Corylus colurna* L. by Zeidler (2012)) and plantations (*Eucalyptus grandis* × *urophylla* by Baillères et al. (2005)). Radial variation in wood density is associated with competition for light (Wiemann and Williamson 1989). Early in their growth, light-demanding trees use their resources for height growth in order to reach the light at the top of the canopy quickly so that the leaves perform the photosynthesis. Once the necessary height is reached, the trees correct their structural imbalance by producing denser xylem. Our results are not in accordance with those studies, as the distance to pith did not influence wood density. One possible reason may be that temperate forests and plantations are often monospecies, and the favourable environment allows tree to grow fast. Thus, densities change significantly for each growth phase. In contrast, because of the environmental stresses conditions in the medium-altitude natural forest of Mandraka, with high overall slopes of 50 % (reaching 90 % in some places) and exposure to wind, the growth of trees in Mandraka is slowed. Thus, no significant trend occurs on densities for each growth phase.

5 Conclusion

This study is the first to investigate the factors responsible for the variability of wood properties in Madagascar. It also provides light requirements of 23 species that have never been published before. In the case of the natural forest of Mandraka, tree species and soil types have an effect on average wood density, whereas tree diameter does not. The average wood density is higher on poor ferralitic soils than on fertile lowland soils. Shade-tolerant species exhibited higher average wood density than light-demanding species. However, wood density did not show significant variation from pith to bark. Consequently, none of the factors considered have significant effects on radial variation of density.

Information on the variation in wood density is important to guide forest management activities. In addition, these results help fill the gaps in wood properties database for tree forest species in Madagascar. Knowledge of wood density can help address current issues of finding substitutes for precious Malagasy woods, such as rosewood, which are highly valued by consumers. Malagasy consumers prefer heavy wood (i.e., density > 0.7 g.cm^{-3}) for their furniture (Ramananantoandro et al. 2013). This study highlights four heavy woods: *Dilobeia thouarsii, Anthocleista madagascariensis, Syzygium cumini* and *Nuxia capitata*, which could be selected as alternatives to the rare precious woods. However, studies on the aesthetic, mechanical and woodworking properties of these species are needed before a complete conclusion can be drawn.

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Compliance with ethical standards

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