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Abstract

Studies on wood basic density (BD) vertical variations become essential to predict more accurately the within-stem distributions of biomass and wood quality in the forest resource. The vertical variation of wood BD in the stem has been little studied until now, most BD studies being based on measurements taken at breast height.

The main objective of this work was to observe and to understand the patterns of vertical BD variation within stems in relation to classical dendrometric variables and to propose relevant equation forms for future modelling.

Two softwood species were studied: *Abies alba* and *Pseudotsuga menziesii*. Contrasted thinning intensities were studied including strongly thinned plots *versus* control plots without thinning.

BD was most of the time highest at the base of the tree for both species. Then, after a strong decrease from the base of the tree, an increase in BD was often observed towards the top of the tree especially for *Abies alba*.

The variation in BD with height was stronger for the unthinned plots than for the heavily thinned ones of *Abies alba*. The opposite was observed for *Pseudotsuga menziesii*. The modulation of growth rate and tree size through thinning intensities modifies the observed vertical variations in BD.

Two types of biexponential models were proposed to describe BD variations. The first

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model used the height in the stem and classical easily-measurable tree variables as inputs, the other one additionally used BD at breast height ($BD130$).

The relative RMSE of BD for *Abies alba* and *Pseudotsuga menziesii* were 9.9% and 8.1%, respectively, with the model without $BD130$ and 7.6% and 5.9%, respectively, with the model including $BD130$.

Keywords: Basic specific gravity, axial variations, thinning intensity, *silver fir*, *Douglas fir*

1. Introduction

The modalities of wood formation and the variability of wood properties are being gradually discovered. Wood performs several functions that enable the development of the tree itself and the structuring of forest ecosystems. It provides numerous ecological services such as carbon fixation and economic services through its various uses accompanying human activities (timber, industrial wood, wood for energy, wood for chemical purposes).

Among the characteristics of wood, density is a critical property that is linked on the one hand with the composition and anatomy of its constituent tissues and on the other hand with other wood properties such as strength, stiffness and pulp yield (Barnett and Jeronimidis, 2003). Density is basically a measure of the mass of material in a given volume (Zobel and Van Buijtenen, 1989). Basic density (BD) is defined by the ratio of the oven-dried mass of wood to the corresponding volume of green (or fresh) wood. The volume of green wood is a variable commonly measured and used by foresters and for forest inventories. Many models exist to predict the green aboveground woody volume of trees for most temperate tree species (Henry et al., 2013), whether it is the total aboveground volume or the stem volume, total or up to a given stem diameter. The oven-dried mass of a wood sample can be obtained after drying at 103°C in an oven (Williamson and Wiemann, 2010). The knowledge of the mean BD of tree (or stem) makes it possible to convert the green volume of tree (or stem) to dry mass of matter. Then, the product of dry mass by carbon fraction allows to account for stored carbon (Wiemann and Williamson, 2014; Bouriaud et al., 2015). Similar calculations can be used to estimate the quantities of various extractive compounds available in the resource.

Wood density is highly variable at all levels. It varies between species, between trees of a

given species and within trees. Many studies have already focused on the evaluation of wood BD of most species. They led to the creation of global databases, such as the Global Wood Density Database (Zanne et al., 2009), which provides mean BD for many species around the world. However, such databases derived from literature data should be used with caution and it is advised to check which density was measured, how it was measured and which is the area of validity of each study (Taras and Wahlgren, 1963; Williamson and Wiemann, 2010). For instance, some studies provide air-dried density (i.e., the ratio of air-dried mass to air-dried volume) that needs to be converted to BD. Conversion errors are possible as shown by Vieilledent et al. (2018) who have started to correct the Global Wood Density Database.

Most studies have analysed mean wood density at breast height only. Others have taken the knowledge a step further by looking at the radial variations in BD on cores or discs, taken most often at breast height only (Wahlgren and Fassnacht, 1959; Woodcock and Shier, 2002; Deng et al., 2014).

A general result is that, for most softwoods, the ring density decreases when ring width increases. This is explained by the fact that the wider the rings, the greater the proportion of earlywood made up of thin-walled tracheids and wide lumens dedicated to hydraulic conduction. At the same time the width of the latewood, more dedicated to mechanical resistance, remains relatively constant. Generally speaking, for these softwood species, it is expected that the more heavy the thinning, the wider the growth rings and the lower the density of the wood.

This is generally true for species showing a gradual transition between earlywood and latewood like *Abies* or *Picea* spp.. This is less clear for *Pseudotsuga menziesii*, for example, which shows an abrupt transition between earlywood an latewood (Todaro and Macchioni, 2011). And finally the results about the relationship between ring width and wood density are often conflicting (Jozsa et al., 1994).

Juvenile wood is also often cited as a factor influencing wood density. Larson et al. (2001) gives the definition of juvenile wood as the wood formed in the first three years of a tree. Then, the formed wood near the pith will be corewood, regardless of the height in the tree. Corewood is often confused with juvenile wood. The properties of corewood are highly

variable, especially the wood density. According to Lachenbruch et al. (2011), for softwoods in the Pacific Northwest of North America, BD generally decreases approximately for ring numbers 5 to 20, then increases (sometimes only increases in particular for hard pines). The transition from corewood to outerwood (or mature wood) is usually soft. Thecorewood has a lower BD than mature wood (10–20% of differences). In this article, the term "juvenile wood" will be used for both juvenile wood and corewood.

Vertical (or axial) variations in density have been much less studied than radial variations. There is, however, a real influence of vertical variations on the mean density of the whole stem that can differ significantly from the density at breast height (Nogueira et al., 2008; Wiemann and Williamson, 2014; Wassenberg et al., 2015; Longuetaud et al., 2016, 2017). Studying the vertical variations of wood density allows to refine biomass estimates as well as carbon accounting (Rueda and Williamson, 1992; Liepiņš and Liepiņš, 2017). This knowledge is also required to assess accurately the amount and quality of the wood resource depending on the location along the stem (Tian et al., 1995; Kimberley et al., 2015). And this detailed description should make it possible to optimize the use of the resource for different purposes. Indeed, numerous wood properties are correlated to wood density, like mechanical properties (Niklas and Spatz, 2010), dimensional stability (Hernández, 2007) or durability (Humar et al., 2008) that are of peculiar importance for the structural uses of wood, especially for softwoods. Fuelwood properties can also be related to wood density (Sotelo Montes et al., 2017) as well as paper properties (García-Gonzalo et al., 2016). Moreover, the stem volume represents about 80% of the total aboveground woody volume for softwoods and the precision on such a large volume cannot be neglected (Billard et al., 2020).

Density variations with height can be related to radial variations due to cambial age, ring width or juvenile wood, especially for species showing strong radial variations in density. For instance, the mean wood density at a given height can be related to the proportion of juvenile wood at that height, especially for species showing a strong difference in density between juvenile wood and mature wood (Zobel and Van Buijtenen, 1989).

For softwoods, the density seems to decrease from the bottom of the tree to the top (Gartner et al., 2002; Longuetaud et al., 2017). Sometimes, a U-shaped curve was observed, especially for *Picea abies* which is the most widely studied species (Repola, 2006; Molteberg

and Høibø, 2007; Liepiņš and Liepiņš, 2017). The decrease in density between the bottom and the top of the stem was also observed for *Ps. menziesii* (Kimberley et al., 2017) and *Abies alba* (González-Rodrigo et al., 2013).

Some authors have proposed models for describing the vertical variations in density in the stem. Table 1 presents models which provides wood BD at different heights. Most models are linear models, often of polynomial form (among others, Rueda and Williamson, 1992; Tian et al., 1995; Repola, 2006; Molteberg and Høibø, 2007; González-Rodrigo et al., 2013; Deng et al., 2014). The main tree variables used in these models are tree total height (H) and diameter ($D130$) or circumference at breast height ($C130$). Sometimes the age of the tree was used.

Models using ring number or distance from the pith in addition to the height in the stem as input variable (e.g., Rueda and Williamson, 1992; Tian et al., 1995) are not presented here since this paper focuses on the mean BD of whole discs.

In this study, the vertical variations in BD of two softwood species were studied: *Abies alba* Mill. (*A. alba*) and *Pseudotsuga menziesii* (Mirb.) Franco (*Ps. menziesii*). These species are of major importance in the North-East of France and have the interest of being very different from an ecological point of view with contrasting shading tolerances (Niinemets and Valladares, 2006) and contrasted anatomical characteristics with more or less marked transitions between earlywood and latewood (Saranpää, 2003; Todaro and Macchioni, 2011). To our knowledge, there are almost no studies that address vertical variations in density for these species, except the one from Kimberley et al. (2017) on *Ps. menziesii* and the one from González-Rodrigo et al. (2013) on *A. alba*.

The main objective of this work was therefore to describe these vertical variations of BD in the stems and to propose some explanations for the observed patterns. For this purpose, new forms of models more easily extensible to new data than the previous polynomial approaches, have been proposed and fitted. Considering that BD at breast height can be relatively easily assessed by analysing core samples or by using dedicated models (Kerfriden et al., 2021), we have compared models using and not using this data as input. Such models may serve as a basis for future predictive modelling on a larger data set. To guide this work, and based on the literature, we have formulated four more specific hypotheses to which we will come back

with regard to our results in the discussion:

- **H1**: The proportion of juvenile wood in stem discs contributes to explain the BD variations with height in the stem;
- **H2**: Stem discs showing the larger ring widths, regardless of their height in the tree, have a lower BD (i.e., the ring density-ring width well-known relationship for softwoods may be generalised to the average level of the whole disc, from different trees or different heights in the stem);
- **H3**: On the basis of **H1** and **H2**, the growth rate and/or tree size modulated by thinning intensities modifies the vertical variation of BD in the stems;
- **H4**: BD measured at breast height overestimates significantly the mean BD of the whole stem and as a consequence breast height measurements are not representative of the whole stem.

Table 1: Equations of the literature to model the mean basic density of a disc at a given height in the stem. BD_{disc} is the whole-disc mean density, $BD130$ is the mean density at breast height, hr is the relative height of the disc, age is the age of the tree, $D130$ is the diameter at breast height of the tree, H is the total tree height, b_0,..., b_5 are the fixed-effect parameters, u_0,...,u_3 are the random-effect parameters.

	Article	Species	Number of trees	Equation
Without $BD130$	Repola (2006)	*P. abies*	39	$BD_{disc} = b_0 + b_1 \cdot H + b_2 \cdot \frac{D130}{age} + b_3 \cdot hr + b_4 \cdot hr^2 + u_0 + u_1 \cdot hr + u_2 \cdot hr^2$
	González-Rodrigo et al. (2013)	*Abies alba*	5	$BD_{disc} = b_0 - b_1 \cdot H$
	Deng et al. (2014)	*Pinus massoniana*	108	$BD_{disc} = b_0 + b_1 \cdot age + b_2 \cdot D130 + b_3 \cdot hr + b_4 \cdot hr^2 + b_5 \cdot hr^3 + u_0 + u_1 \cdot hr + u_2 \cdot hr^2 + u_3 \cdot hr^3$
With $BD130$	Kimberley et al. (2015)	*Pinus radiata*	10000	$h_k = \frac{1.4}{H} - 0.4$ $L_k = \frac{BD130 - b_0 - b_1 \cdot h_k - b_2 \cdot h_k^2 - b_3 \cdot h_k^3}{1 + b_4 \cdot h_k}$ $BD_{disc} = (b_0 + L_k) + (b_1 + b_4 \cdot L_k) \cdot (hr - 0.4) + b_2 \cdot (hr - 0.4)^2 + b_3 \cdot (hr - 0.4)^3$
	Kimberley et al. (2017)	*Ps. menziesii*	172	$h_k = \frac{1.4}{H}$ $L_k = BD130 - (b_0 + b_1 \cdot h_k + b_2 \cdot h_k^2 + b_3 \cdot h_k^3)$ $BD_{disc} = L_k + b_0 + b_1 \cdot hr + b_2 \cdot hr^2 + b_3 \cdot hr^3$ $= BD130 + b_1 \cdot (hr - h_k) + b_2 \cdot (hr^2 - h_k^2) + b_3 \cdot (hr^3 - h_k^3)$

Table 2: Table of abbreviations used in the article.

Abbreviation	Meaning
BD	Basic density ($kg \cdot m^{-3}$)
$BD130$	Basic density at breast height ($kg \cdot m^{-3}$)
H	Total height of the tree (m)
h	Height of the measure (m)
$hLLB$	Height of the lowest living branch (m)
hLC	Height to the base of the living crown (m)
hr	Relative height of the measure (%)
$hrLC$	Relative height of the living crown (%)
$D130$	Diameter at breast height (cm)
$C130$	Circumference at breast height (cm)
$RW130$	Mean ring width at breast height (mm)

2. Materials and Methods

All the abbreviations used in this paper are listed in Table 2.

2.1. Study sites and sampling design

The trees were sampled within the framework of two projects named "ExtraFor_Est" and "ModelFor". In both datasets, contrasted thinning intensities were tried out. For each species, trees from "ExtraFor_Est" were selected from two plots: a plot without thinning (only natural mortality) and another one with heavy thinning. For each species, trees from "ModelFor" were selected from three plots: without thinning, moderate thinning and heavy thinning. Table 3 provides information about the stands. More information is available in Table A.1 of Appendix A. The trees came from the Office National des Fôrets (ONF) experimental monitoring forest for which the history of the trees has been kept since the plantation. Moreover, *Ps. menziesii* from "ModelFor" came from the experimental network of Douglas stands managed by the *GIS Coop* (`https://www6.inrae.fr/giscoop`, Seynave et al. (2018))

Our forest identifiers have been constructed as follows: the first two letters correspond to the species "Aa" means *Abies alba* and "Pm" means *Pseudotsuga menziesii*, the number following these two letters 1, 2 or 3 represents the number of the forest (see Table 3 for more details). These two letters and this number are sometimes followed by an hyphen and a letter which represent the thinning modality. "-u" means unthinned modality, "-m" means moderate thinning and "-h" means heavy thinning.

Table 3: Site characteristics.

Tree species	Forest	ID	Location	Altitude (m)	Number of trees	Age of trees	Project
A. alba	Saint-Prix	Aa1	46.97 N, 4.07 E	750	8	43-57	ExtraFor_Est
	Saint-Prix	Aa2	46.97 N, 4.07 E	750	14	36-80	ModelFor
	Mont-Sainte-Marie	Aa3	46.79 N, 6.31 E	1000	15	36-41	ModelFor
Ps. menziesii	Mélagues	Pm1	43.71 N, 3.06 E	800	8	48	ExtraFor_Est
	Grison	Pm2	46.66 N, 4.74 E	210	15	43	ModelFor
	Quartier	Pm3	46.15 N, 2.77 E	630	15	20	ModelFor

The trees from "ExtraFor_Est" were cut in February 2018. The trees in each thinning modality were classified into four diameter classes (defined by the 25^{th}, 50^{th} and 75^{th} percentiles) and one tree was felled in each diameter class. The circumference at breast height (1.30 m) was measured. After felling the trees, the total height and the height to the base of the living crown (the lowest whorl with at least 3/4 of living branches) were measured. A total of 15 discs were sampled along the stem, avoiding knots. The first three discs were taken systematically at heights 0.3 m, 0.8 m and 1.30 m. The 12 other discs were regularly distributed along the stem.

The same protocol was applied to the trees from "ModelFor" dataset except that the number of discs depended on the tree length. Above breast height, the discs were sampled every 2 m at the maximum. For *Ps. menziesii* of Grison and Quartier forests, five trees per thinning modality were chosen in order to represent the different diameters present in the plot (i.e., one tree in each of the five diameter classes based on the 20^{th}, 40^{th}, 60^{th} and 80^{th} percentiles), resulting in 15 trees per forest. For *A. alba*, 14 trees per forest were felled (and one more at Mont-Sainte-Marie). There were four trees sampled in heavy thinning and moderate thinning modalities (five in moderate thinning modality at Mont-Sainte-Marie) and six trees in the plot without thinning. The number of trees per thinning modality is given

in table A.1 of Appendix A. The trees were also chosen within the different diameter classes based on the corresponding percentile values as this was described above. The *A. alba* trees were cut in February 2014 and the *Ps. menziesii* trees were cut in March 2015.

All the *Ps. menziesii* plots were issued from even aged plantations. The *A. alba* plots being issued from naturally generated forests, the age of the trees was estimated using an additional disc taken at the stump.

Table A.2 of Appendix A provides dendrometric variables about the trees.

2.2. Wood density measurement

The discs were X-ray scanned in a green state with a medical computed tomograph (CT) scanner. The discs were then dried in an oven at 103 °C to a constant weight. They were scanned again in the oven-dried state. More information about the wood density measurements by CT scanning is available in Freyburger et al. (2009).

Basic density (BD) of wood was computed for each disc from the two scans (in green and oven-dried states) as described in Longuetaud et al. (2016).

2.3. Calculation of variables

The relative height hr_{ij} of disc j from tree i is calculated as follows:

$$hr_{ij} = \frac{h_{ij}}{H_i}$$

with h_{ij} the height of disc j from tree i and H_i the total height of tree i.

The mean ring width at breast height $RW130_i$ from tree i is estimated as follows, considering the units of measurements given in table 2:

$$RW130_i = \frac{D130_i \cdot 10}{2 \cdot age_i}$$

with $D130_i$ the diameter at breast height of tree i and age_i its age (actual or estimated).

The mean BD of stem wood for tree i is calculated from the mean BD of each disc j from the tree i weighted by the volumes of wood of the stem short logs represented by each disc, i.e. a portion of the stem on either side of the disc calculated so that each part of the stem is associated with the closest disc.

2.4. Statistical modelling

The R software was used for statistical analyses (R Core Team, 2020). The main functions used were: the `lm`, `nls`, `anova`, `AIC` and `TukeyHSD` functions from the `stats` package and the `nlsList`, `nlme`, `gnls` and `ACF` functions from the `nlme` package.

In each case, for our vertical profiles of BD, mixed-effect models were fitted to obtain for each tree the best set of parameters and then to assess step by step the predictive power of thinning modality and tree variables on those model parameters. When required, an autoregressive correlation structure of order 1 (`corAR1`) was used to take into account the correlation of within-group errors related to the multiple BD observations done along the stem of a given tree (Pinheiro and Bates, 2000).

Multiple linear regressions were also fitted at the disc level in order to predict BD from mean ring width and mean cambial age whatever the height in the tree. These regressions were fitted for comparison purpose with the previous models for vertical BD profiles, especially with the models that take as input only external variables that are easily measurable in the forest. As density models as a function of ring width and cambial age are usually developed at the annual ring level, we also tried to calculate mean ring width and mean cambial age by weighting by the area of each ring to be more representative of the disc.

For comparison with other models from the literature, RMSE, relative RMSE and AIC were used. The models from the literature have been fitted on our data set. The models were then compared on the basis of their fixed-effects only (b_0,..., b_5 in Table 1).

Since most of the vertical density profiles had a U-shape pattern, we chose a biexponential model as described by Crawley (2012) rather than a polynomial model. Most of the approaches found in the literature are based on polynomial models. We made the hypothesis that the biexponential model is more robust and that the parameters are easier to interpret because they are less correlated than in a polynomial model.

The general form of the model is given in Equation 1:

$$BD_j = f(hr_j) = a \cdot \exp(b \cdot hr_j) + c \cdot \exp(d \cdot hr_j) \quad (1)$$

with BD_j the basic density of disc j (in kg $\cdot$ m^{-3}) at the relative height h_j and a, b, c and d the model parameters.

At the ground level, the BD predicted by model (1) is:

$$f(0) = a + c = k \tag{2}$$

It is thus expected to have a relationship between k and the BD at breast height ($BD130$).

By replacing a by $k - c$ and factoring by c in Equation 1, we obtained:

$$BD_j = c \cdot (\exp(d \cdot hr_j) - \exp(b \cdot hr_j)) + k \cdot \exp(b \cdot hr_j) \tag{3}$$

For each species, two models derived from Equation 3 were tested: A first model not using $BD130$ as input variable (model called NBD) and a second one with $BD130$ as input variable (model called WBD). The reason for distinguishing both cases is that, as it will be shown, $BD130$ considerably helps to predict the BD profile, but is rarely measured in the field. The interest of WBD model is that it could take as input the output of a $BD130$ model that would be developed on a larger number of trees and that would take into account tree variables and ecological characteristics at the resource scale. This is one objective of the XyloDensMap project for instance (Jacquin et al., 2019).

Apart from $BD130$, the other candidate explanatory variables tested in our models were: the relative height of the disc (hr), the circumference at breast height ($C130$), the total tree height (H), the height to the base of the living crown (hLC), the relative height to the base of the living crown ($hrLC$), the ratio height/diameter ($\frac{H}{D130}$), the tree age (age) and the mean annual ring width at breast height ($RW130$).

Other vertical profile models in which a minimum of basic density was imposed at the height of the base of the living crown were tested. But these models were too constrained and less efficient.

Mixed models were fitted on all trees at once by testing random effects on each parameters for each species, resulting in a set of parameters k, b, c and d for each tree. By analysing the relations of k, b, c, d with the tree descriptors (avoiding to use in the same equations correlated variables), several relations were obtained for several parameters (see section 3.5). We therefore introduced these relations in the general models to verify, for each species, if random tree effect parameters were still necessary.

240 *2.4.1. Model without basic density at breast height (NBD)*

241 For this model, Equation 3 was used as is for calibration and search for explanatory
242 variables.

243 *2.4.2. Model including basic density at breast height (WBD)*

244 By forcing the model to pass through $BD130$ at 1.30 it was possible to remove one
245 parameter from the model. Indeed, for $hr_j = 1.30/H$ in Equation 3, it is possible to express
246 c as:

$$c = \frac{BD130 - k \cdot \exp\left(b \cdot \frac{1.30}{H}\right)}{\exp\left(d \cdot \frac{1.30}{H}\right) - \exp\left(b \cdot \frac{1.30}{H}\right)} \tag{4}$$

247 Then, replacing c in Equation 3, we obtain:

$$BD_j = \frac{BD130 - k \cdot \exp\left(b \cdot \frac{1.30}{H}\right)}{\exp\left(d \cdot \frac{1.30}{H}\right) - \exp\left(b \cdot \frac{1.30}{H}\right)} \cdot \left(\exp\left(d \cdot hr_j\right) - \exp\left(b \cdot hr_j\right)\right) + k \cdot \exp\left(b \cdot hr_j\right) \tag{5}$$

248 where b, d and k are the model parameters

249 For comparison with the WBD models, the Kimberley models were tested by replacing
250 in the equations the breast height 1.4 m by 1.3 m in our study.

251 **3. Results**

252 *3.1. Relationship between thinning intensity and the measured variables*

253 *3.1.1. Dendrometric variables*

254 By plotting boxplots of tree related variables for each plot (Appendix B), it can be verified
255 that the measured dendrometric variables were well adapted to characterize the effect of
256 thinning intensities.

257 *3.1.2. Basic density*

258 $BD130$ did not seem to highly depend on the thinning intensity, except maybe for the
259 mature stands of *Ps. menziesii* (variation significant only for forest Pm2). While for *A.*
260 *alba* $BD130$ seemed to be higher in the unthinned stand of forest Aa3 (even if the difference
261 was not significant), for *Ps. menziesii* $BD130$ tended to be lower in the unthinned mature
262 stands.

For the mean BD of the stem, the difference between thinning intensities was statistically significant for stands Aa1 and Pm2. For these two forests, it was clear that BD was higher in heavy thinning modalities. Even if the results were not significant, we observed the same tendencies for the other forests with less important differences and with the exception of Aa3 and Pm3.

3.2. Basic density at breast height versus mean basic density of the stem wood

Breast height is the reference height for many measurements (diameter, ring width, density...). In a first analysis, the mean BD of the whole stem was compared with the mean BD of the disc taken at breast height (Figure 1). A paired t-test was applied (Table 4). This part of the work is a continuation of the work done previously in Longuetaud et al. (2017).

Table 4 shows that the mean BD of the stem is significantly different from that at breast height for *A. alba* and *Ps. menziesii*. The BD at breast height is generally higher than the mean BD of the stem. Results were the same regardless of the data source.

Table 4: Mean basic density of the whole stem wood and mean basic density of the disc at breast height. The symbols indicate the significance of the difference based on a paired t-test: NS: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Tree species	Number of trees	Mean BD at breast height ($kg \cdot m^{-3}$)	Mean BD of the stem wood ($kg \cdot m^{-3}$)	Difference between BD at breast height and mean BD of the stem wood ($kg \cdot m^{-3}$)	Signifiance of the difference
A. alba	37	378.80	358.24	20.56	***
Ps. menziessii	36	445.74	423.03	21.45	***

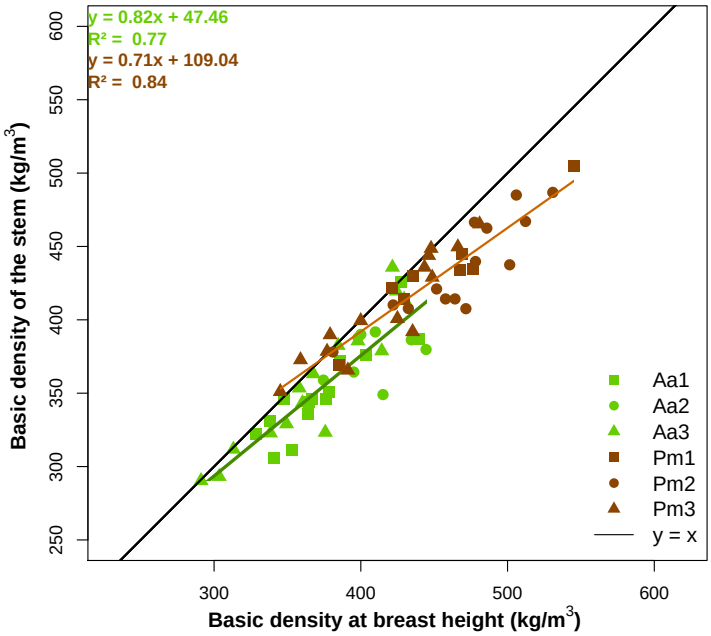

Figure 1: Mean basic density of the whole stem wood as a function of the mean basic density of the breast height disc for each species and each stand (refer to Table 3 for the meaning of the abbreviations in the legend). The black line is the y=x line. The green line is the linear regression for *A. alba* and the brown one the linear regression for *Ps. menziesii*. The regression equations and the coefficients of determination for each species are given in the same colors as the points.

3.3. Basic density of a disc versus ring width and cambial age

When considering the whole sample for each species, there was no clear relationship between BD and ring width at the disc level, with R^2 ranging from 0.01 to 0.14 depending on the species (Figure 2). Considering that each ring should contribute to the disc BD in proportion to its area we have also tried to relate BD of discs to the mean ring width weighted by ring areas: The results were not much better (Figure C.1 in Appendix C).

BD was slightly more correlated with the mean cambial age (*i.e.* half the number of rings in the disc), especially for *Ps. menziesii* with R^2 from 0.12 to 0.17 (Figure 2). The mean cambial age weighted by ring areas was not more correlated to the disc BD (Figure C.1 in Appendix C).

Multiple linear regressions were fitted with mean ring width, mean cambial age and interaction between the two variables as explanatory variables. For comparison purpose, AIC, RMSE and relative RMSE are given in Table 7.

3.4. Variation of basic density along the stem

The variation of BD with height (Appendix D) shows that for *A. alba*, the variation seemed to be strong for unthinned plots with a high BD at the bottom of the tree. Variation was lower for heavy thinning plots and the BD at the bottom of the tree was lower than that of trees from unthinned plots.

For *Ps. menziesii*, it was the opposite (Appendix E). The variation was higher for heavy thinning plots and lower for unthinned plots. This time, the BD at the bottom of the tree was higher for heavy thinning plots than for unthinned plots. This observation is not applicable to stand Pm3 in which the trees were the youngest (20 years) and the variations in BD were quite low.

For both species, BD decreased as the height in the stem increased.

Figures 3, 4 and 5 show that the models manage to express well the variability at the bottom of the trees.

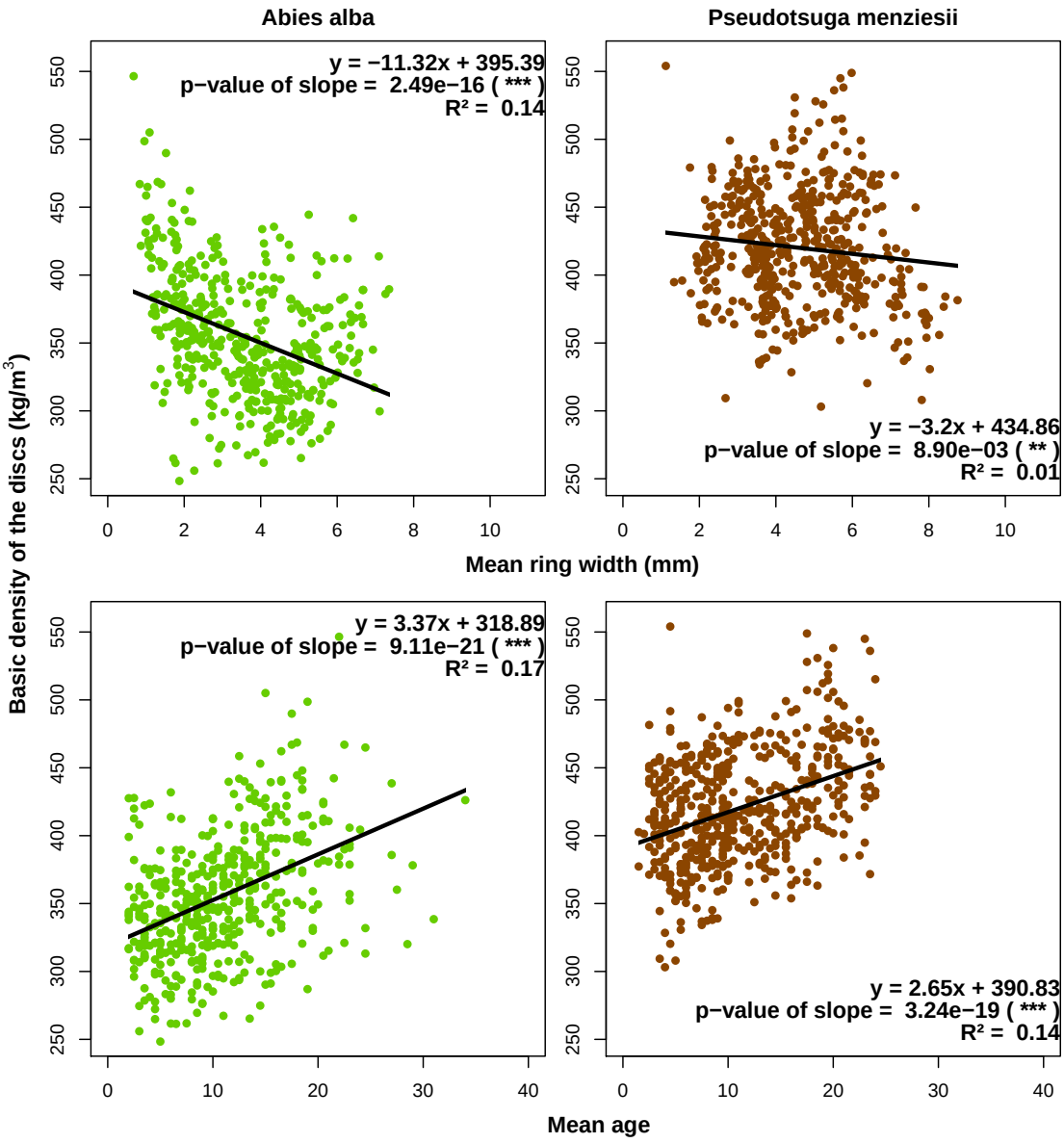

Figure 2: Mean basic density as a function of ring width and cambial age at the disc level. The black lines correspond to the regression lines. The regression equations and the significance of the slope parameters (p-values) are given on each plot: NS: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

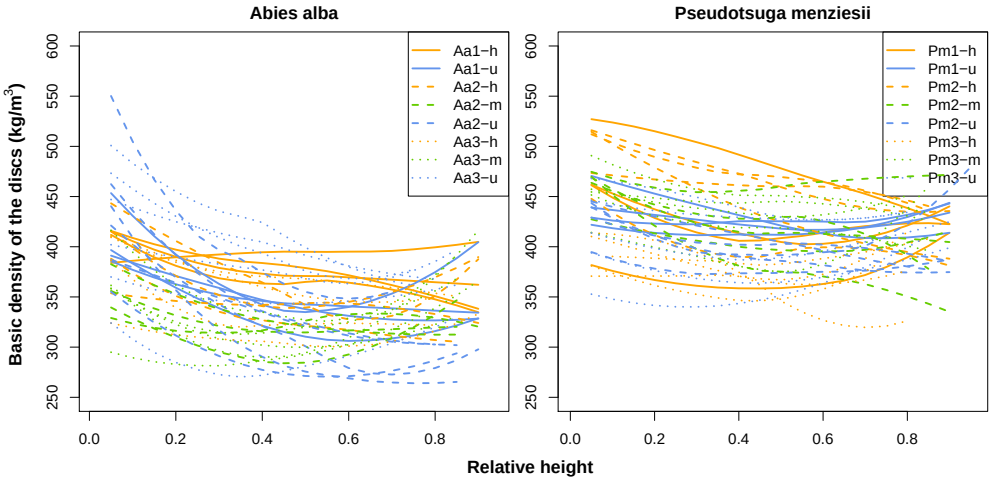

Figure 3: Smoothed curves of basic density variation with relative height for all the trees for each species. The colors represent the thinning intensities: Orange is for trees from the heavy thinning plots, green for trees from moderate thinning plots and blue for trees from plots without thinning. The line type identifies the stand.

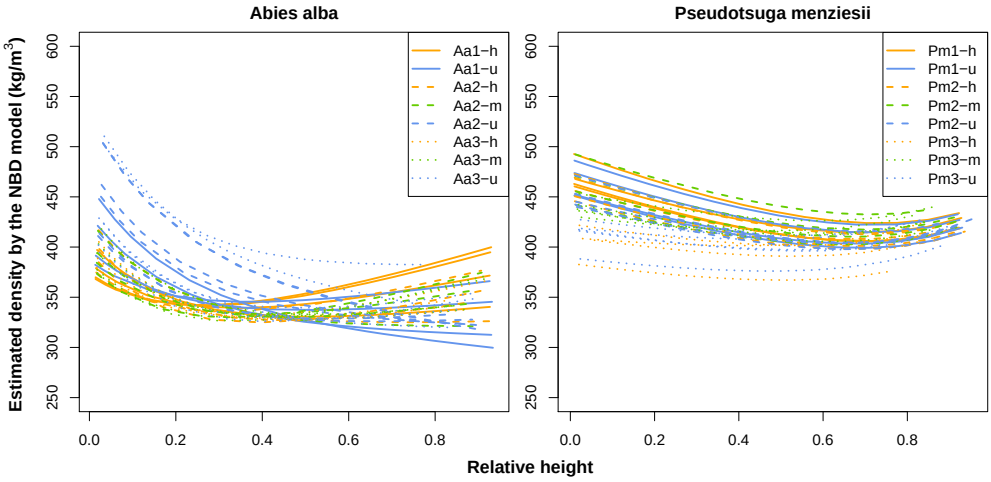

Figure 4: Profiles of basic density estimated by the NBD models for each tree (*A. alba* and *Ps. menziesii*). The colors represent thinning: Orange is for the trees from the heavy thinning plots, green is for the trees from the moderate thinning plots and blue is for the trees from without thinning plots. The line type identifies the stand.

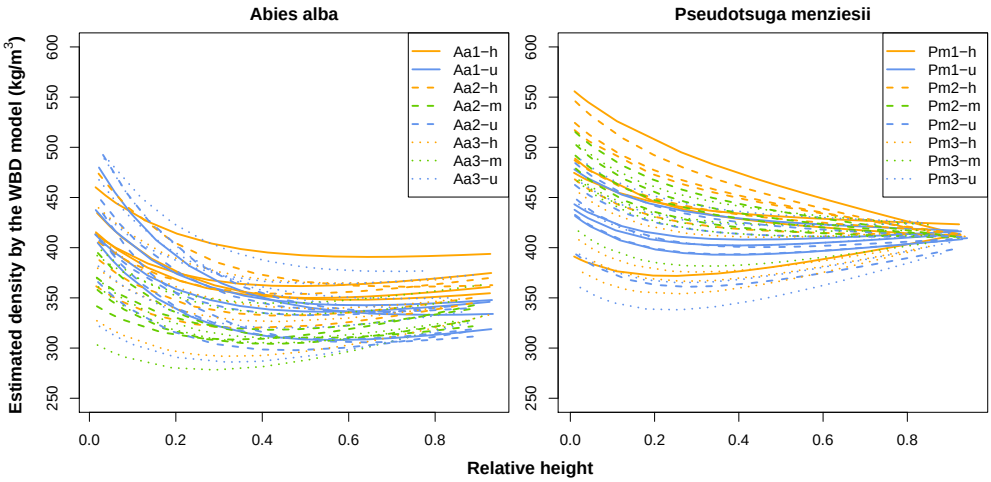

Figure 5: Profiles of basic density estimated by the WBD models for each tree (*A. alba* and *Ps. menziesii*). The colors represent thinning: Orange is for the trees from the heavy thinning plots, green is for the trees from the moderate thinning plots and blue is for the trees from without thinning plots. The line type identifies the stand.

3.5. Vertical profile models without basic density at breast height (NBD)

Table 7 gives the values of absolute and relative RMSE (by using the fixed-effects only) and AIC obtained with our model and models from literature that do not include $BD130$. All the models were calibrated on our data set for comparison purpose. For the Deng et al. (2014) model, we used a diagonal variance-covariance matrix for the random-effect parameters otherwise it was not possible to obtain the convergence of the model.

3.5.1. A. alba

For the model without $BD130$ as input variable, we obtained for *A. alba* the following modeling of the initial parameters as a function of tree variables:

$$\begin{cases} k_i = k_1 \cdot \frac{1}{C130_i} + k_2 + \alpha_i \\ b_i = b_1 \cdot \frac{H_i}{D130_i} + b_2 + \beta_i \\ c_i = c_1 \cdot H_i + c_2 + \gamma_i \end{cases} \quad (6)$$

Random-effect parameters α_i, β_i and γ_i were needed for k_2, b_2 and c_2, respectively, and were kept in the final model.

Since no relation was obtained for parameter d, it was let as is in the general model. Table 5 gives the values of the fixed-effect parameters for the final mixed-effect model. The standard deviations of random-effect parameters α_i, β_i and γ_i were 3.29e+01, 2.22e-01 and 5.06e+01, respectively.

Table 5: Fixed-effect parameters and their standard deviations (in brackets) for the NBD model not using basic density at breast height for *A. alba*.

Species	k_1	k_2	b_1	b_2	c_1	c_2	d
A. alba	3.890985e+03	3.421220e+02	-5.849102e-03	6.240366e-01	-5.648390e+00	1.966764e+02	-5.160087e+00
	(5.056307e+02)	(1.188139e+01)	(9.198257e-04)	(9.707743e-02)	(1.500177e+00)	(2.595777e+01)	(7.320403e-01)

3.5.2. Ps. menziesii

We obtained for *Ps. menziesii* the following model of the initial parameters as a function of tree variables:

$$\begin{cases} k_i = k_1 \cdot \frac{1}{H_i} + k_2 \cdot RW130 + k_3 \cdot hrLC_i + k_4 + \alpha_i \\ b_i = k \cdot (b_1 \cdot \frac{1}{H_i} + b_2 + \beta_i) \end{cases} \tag{7}$$

The analysis showed that random-effect parameters α_i and β_i were needed for k_4 and b_2 respectively in the final model. Since no relation were obtained for parameters d and c, there were let as is in the general model. Table 6 gives the values of the fixed-effect parameters of the final mixed-effect model. The standard deviations of random-effect parameters α_i and β_i were 3.65e+01 and 1.93e-04, respectively.

The plots of BD predicted by the different models as a function of the relative height in the tree are presented in Appendices D and E.

Table 6: Fixed-effect parameters and their standard deviations (in brackets) for the NBD model not using basic density at breast height for *Ps. menziesii*.

Species	k_1	k_2	k_3	k_4	b_1	b_2	c	d
Ps. menziesii	-1.842987e+03	-1.828230e+01	-1.494966e+02	6.978071e+02	5.841137e-03	-8.275563e-04	2.996460e+00	3.411697e+00
	(4.272549e+02)	(6.591333e+00)	(5.491386e+01)	(7.067386e+01)	(1.875783e-03)	(1.398871e-04)	(4.052021e+00)	(1.205966e+00)

Table 7: AIC, RMSE and relative RMSE for the NBD models and various models from the literature not using basic density at breast height.

Tree species	Model	Number of parameters	AIC	RMSE (kg · m^{-3})	Relative RMSE (%)
Abies alba	NBD	7	4230.29	35.29	9.92
	Multiple regression at disc level	4	4717.58	40.82	11.47
	Repola (2006)	5	4256.82	40.90	11.50
	González-Rodrigo et al. (2013)	2	4785.11	44.13	12.40
	Deng et al. (2014)	6	4305.45	46.76	13.14
Pseudotsuga menziesii	NBD	8	4571.37	34.19	8.11
	Multiple regression at disc level	4	5097.03	38.01	9.01
	Repola (2006)	5	4544.92	37.64	8.93
	González-Rodrigo et al. (2013)	2	5155.69	40.45	9.59
	Deng et al. (2014)	6	4568.35	37.98	9.01

3.6. Vertical profile models with basic density at breast height (WBD)

Table 10 gives the values of AIC, RMSE and relative RMSE (by using the fixed-effects only) obtained with our model and Kimberley et al. (2015) model which was calibrated on our data set for comparison purpose.

3.6.1. A. alba

For the WBD model, we obtained for *A. alba* the following models of the initial parameters as a function of tree variables:

$$\begin{cases} k_i = (k_1 \cdot \frac{1}{C130_i} + k_2 + \alpha_i) \cdot BD130_i \\ d_i = d_1 \cdot \frac{1}{BD130_i} + d_2 + \beta_i \end{cases} \quad (8)$$

Random-effect parameters α_i and β_i were needed for k_2 and d_2 respectively and a diagonal variance-covariance matrix was used. An autoregressive correlation structure of order 1 was used. The single correlation parameter was 2.39e-01.

Since no relation was obtained for parameter b, it was let as is in the general model. Table 8 gives the values of the fixed-effect parameters for the final mixed-effect model. The standard deviations of random-effect parameters α_i and β_i were 2.57e-02 and 1.26e-01, respectively.

3.6.2. Ps. menziesii

We obtained for *Ps. menziesii* the following modeling of the initial parameters as a function of tree variables:

$$\begin{cases} k_i = (k_1 \cdot H_i + k_2) \cdot BD130_i \\ d_i = (d_1 + \alpha_i) \cdot BD130_i + d_2 \end{cases} \quad (9)$$

Since no relation was obtained for parameter b, it was let as is in the general model. Random-effect parameter α_i was needed for $d1$. An autoregressive correlation structure of order 1 was used. The single correlation parameter was 2.10e-01.

Table 9 gives the values of the fixed-effect parameters for the final mixed-effect model. The standard deviation of random-effect parameter α_i was 2.22e-04.

Table 8: Fixed-effect parameters and their standard deviations (in brackets) for the WBD model with basic density at breast height for *A. alba*.

Species	k_1	k_2	b	d_1	d_2
A. alba	4.2497463e+00	1.0127349e+00	-4.3583799e+00	2.962377782e+02	-6.015024e-01
	(6.484259e-01)	(1.178484e-02)	(5.784795e-01)	(1.025718e+02)	(2.801850e-01)

Table 9: Fixed-effect parameters and their standard deviations (in brackets) for the WBD model with basic density at breast height for *Ps. menziesii*.

Species	k_1	k_2	b	d_1	d_2
Ps. menziesii	-2.097975e-03	1.090797856e+00	-6.142812835e+00	-2.819938e-03	1.285744246e+00
	(5.025279e-04)	(1.708982e-02)	(1.332227e+00)	(4.137676e-04)	(1.928312e-01)

Table 10: AIC, RMSE and relative RMSE for the WBD models and various models from the literature with basic density at breast height.

Tree species	Model	Number of parameters	AIC	RMSE (kg · m^{-3})	Relative RMSE (%)
A. alba	WBD	6	4250.76	27.09	7.62
	Kimberley et al. (2015)	5	4402.06	28.88	8.12
	Kimberley et al. (2017)	3	4532.56	33.44	9.40
Ps. menziesii	WBD	6	4529.57	24.83	5.89
	Kimberley et al. (2015)	5	4679.22	25.04	5.94
	Kimberley et al. (2017)	3	4938.27	32.52	7.71

The graphs representing the BD predicted by the different models as a function of the relative height in the tree are given in Appendices D and E.

3.7. Relevance of the models

In the models based on Equation 3, the parameter k represents the BD at the ground level. For *A. alba* this parameter was controlled by tree size since k increased when $C130$ decreased in the NBD model. For the WBD model, the same trend was observed. Thus, smaller trees would have higher BD at the bottom of the stem.

For *Ps. menziesii* the parameter k of the NBD model was found to be related to H, $RW130$ and $hrLC$. Considering the values of the corresponding parameters it appears that, here also k increased when ring width decreased. In addition, more the tree was small in height, lower dense it was at the ground level (e.g., a 20 m high tree is 18 kg.m^{-3} less dense than a tree of 25 m high tree). For the WBD model, a large part of the variation between trees was already taken into account through the variable $BD130$, which could explain that the effect of H on k was weaker than above and not in the same direction (e.g., $k = 1.05 \cdot BD130$ for a 20 m height tree versus $1.04 \cdot BD130$ for a 25 m height tree).

The parameters b and d controlled the slopes of the BD variation in the stem and were more difficult to interpret since both effects can add up or offset each other to a certain extent. For the models including $BD130$, b was negative for both species with a relatively constant value for all trees of a given species (no random effect). The decrease seemed strong for both species (Appendices D and E).

On the other hand, the parameter d was dependent on $BD130$. When $BD130$ increased, the value of d decreased and even became negative for *Ps. menziesii* (e.g., for *A. alba*, $d = 0.39$ for $BD130 = 300$ kg.m^{-3} and $d = 0.14$ for $BD130 = 400$ k.m^{-3}, and for *Ps. menziesii*, $d = 0.16$ for $BD130 = 400$ kg.m^{-3} and $d = -0.12$ for $BD130 = 500$ kg.m^{-3}).

4. Discussion

4.1. Two very different softwood species

Firstly, these species are ecologically very different with contrasted strategies. *A. alba* is a shade-tolerant and late-successional species with a shade-tolerance score of 4.60 (0.06)[1]

[1]Shade-tolerance score and standard deviation in brackets. Tolerance scores range from 0 (no tolerance) to 5 (maximal tolerance).

(Niinemets and Valladares, 2006) and is known to have a very slow radial growth in the early years. At the opposite, *Ps. menziesii* is rather shade-intolerant with a score of 2.78 (0.18).

From an anatomical point of view these species are also different. *A. alba* shows a progressive transition between earlywood and latewood while *Ps. menziesii* shows an abrupt transition. Todaro and Macchioni (2011) suggest that there is a link between these anatomical characteristics and the presence of a negative correlation between ring wood density and ring width. This negative correlation is often reported for *P. abies* but the results are sometimes controversial, especially for *Ps. menziesii* (Jozsa et al., 1994).

4.2. Factors that influence wood density and its vertical variation in the stem

The observed patterns of vertical variation in BD were the following. For *A. alba*, BD tended to decrease from the butt to the height of the living crown then sometimes to increase towards the top (U-shape). For *Ps. menziesii*, BD decreased from the butt to the top of the stem for most of the trees. A few trees followed the opposite trend. *Ps. menziesii* and *A. alba* were few studied for their vertical variation in density. On *Ps. menziesii*, Kimberley et al. (2017) found a sigmoidal pattern with an increase in density towards the bottom of the stem and a decrease towards the top which is in overall consistent with our observations, except maybe towards the top of the stem. On *A. alba*, González-Rodrigo et al. (2013) used a linear model to describe the decrease in wood density with height in the stems.

To try to explain these vertical variations we can return to the more widely studied radial variations. Indeed, radial variations in density can have an impact on vertical variations in the stem, as the proportions (of the wood disc area) of different types of wood (e.g., juvenile *versus* mature wood), or the proportion of narrow rings, for instance, can change with the height in the tree.

4.2.1. The juvenile wood

For Lachenbruch et al. (2011), the typical radial pattern for the wood density of most softwood species is to have a corewood with a lower density than the outerwood. Woodcock and Shier (2002) highlighted the relationship between such radial patterns and species strategies. In Longuetaud et al. (2017), less dense wood was observed in about the first five cm around the pith for *Ps. menziesii* followed by an increase in BD with a sigmoid pattern.

While for *A. alba* a progressive decrease in BD from the centre of the stem was observed in this previous study. This was consistent with the successional status of these two species. As reported by Lachenbruch et al. (2011), the amount of corewood varies with the height in the stem. As a consequence, for species showing a strong difference in density between juvenile and mature wood, it is automatic that a variation of density with height is observed due to the variation with height of the proportion of juvenile wood which increases from the base to the top of the tree (Zobel and Van Buijtenen, 1989). From these considerations we could expect a higher BD, at least for *Ps. menziesii*, at the bottom of the stem than at the top, which was generally the case on our trees.

From the literature (Zobel and Van Buijtenen, 1989; Henin et al., 2018; Fabris, 2000), the effect of the proportion of juvenile wood on the wood density at a given height level is clear, as well as the effect on the variations in density with height. For a given tree, in our data, the proportion of juvenile wood increased from the bottom to the top of the stem and it contributes to explain at least partially the vertical variations in BD. Thus hypothesis **H1** seems to be verified.

4.2.2. The growth rate

The well-known negative correlation between ring density and ring width has been observed and extensively studied especially on *Picea* spp. (e.g., Bouriaud et al., 2015). The few studies related to this relationship on *A. alba* (Hamada et al., 2018; Sopushynskyy et al., 2020) lead to believe that this species behaves in the same way that *P. abies*. On the contrary, according to Jozsa and Brix (1989) and Fabris (2000), the growth rate has little impact on the whole-ring density for *Ps. menziesii*.

These results were confirmed by our study which shows a decrease of the whole disc BD with the increase of the average ring width for *A. alba* and a weaker but significant relationship for *Ps. menziesii*. If we refer to the Pressler's law, the rings are wider at the top of the stem (Pressler, 1864; Cortini et al., 2013) and this should lead to have a higher BD at the bottom of the stem than at the top, at least for *A. alba*. It was generally the case for our trees.

With respect to the hypothesis **H2**, the regression of the disc BD as a function of the

corresponding mean ring width was significant for both species although very weak for *Ps. menziesii* but this relationship was not sufficient to explain the observed BD variations in the stem. For *Ps. menziesii*, it was quite clear that a dynamic growth rate had not the expected negative effect on the wood density at the disc or stem levels.

4.2.3. The cambial age

For *Ps. menziesii*, Fabris (2000) has reported that radial variations in density are mainly due to variations in cambial age. Filipescu et al. (2014) on the same species have described a radial increase in density as a function of cambial age. These results were confirmed by our study which shows an increase in disc BD with increasing cambial age for *Ps. menziesii*. For *A. alba*, we observed the same behaviour while the results of Hamada et al. (2018), concerning only four trees, do not show a clear trend of ring density with cambial age at breast height. For both species the relationship between whole disc BD and cambial age was stronger than the aforementioned potential relationship between density and average ring width. Indeed, it is difficult to separate the two effects and, as pointed out by Jozsa et al. (1994), the true effect of growth rate on annual ring wood density should be studied for comparable cambial ages. Finally, as the number of rings decreases from the base to the top of the tree, we could expect a higher BD at the bottom of the stem than at the top, which was generally the case on our trees.

Despite the observed relationships of BD with ring width and age, the multiple linear regressions that were tested at the disc level to explain the vertical variations of BD from these variables only were clearly less efficient than our NBD models. It probably means that the vertical variations in BD were also due to other variables such as the proportion of juvenile wood (Section 4.2.1).

4.2.4. The compression wood

The reaction wood, called compression wood (CW) for softwood species, has an impact on density. It has already been shown that CW is denser than normal wood (Pillow and Luxford, 1937; Harris, 1977; Gryc and Horáček, 2007; Tarmian et al., 2012) because it is characterized by cells with large walls (Li et al., 2014) and wide rings with a high proportion of latewood (Lee and Eom, 1988). CW can be found all along the stem, even in small quantities, because

the tree must be able to face the wind, to restore vertical growth (gravitropy), to incline stems (e.g., heliotropy) (Barnett et al., 2014). It is more generally located along limited portions of the stem except for a relatively straight and vertical tree becoming inclined for its entire length, for which CW can be found all along the stem (Pillow and Luxford, 1937).

The amount of CW is often more important in the lower part of the stem (Pillow and Luxford, 1937; Westing, 1965; Donaldson et al., 2004).

The greater presence of CW at the bottom of the stem may also explain the higher BD in this part, especially since some of our plots were located on slopes.

4.2.5. The thinning intensity

The thinning intensity makes it possible to modulate the growth rate which we have already discussed above. However, we could not say whether the observed BD variations, especially regarding vertical patterns, were related to a difference in growth rate or tree size.

In overall, for *A. alba*, a steeper decreasing slope of BD from the base of the stem was observed in the unthinned plots. Conversely, for *Ps. menziesii*, steeper decreasing slope from the base of the stem was rather observed in thinned stands while trees from unthinned stands showed more constant patterns. It could be expected that the most cylindrical trees, i.e. those of the unthinned stands, show more variability between the bottom and the top of the stem because it is known that in case of unfavourable conditions for growth the annual increase is more strongly reduced at the bottom than at the top (Courbet, 1999). This would be consistent with what was observed for *A. alba*. Sometimes the difference observed between trees could also be explained by a steeper local slope in the field leading to the formation of CW.

An original and unexpected result was the observation of a higher BD of discs in average (i.e., at disc and stem levels) for the heavier thinning intensities in one mature stand of *Ps. menziesii* and one of *A. alba*, while there was no effect of the thinning intensity for the other stands. Intuitively, one would tend to think that trees from dense stands will have denser wood. In general, a higher BD is expected for slow-growing softwood trees with narrow ring widths, i.e., in the unthinned modalities, due to the well-known relationship between ring width, proportion of latewood and wood density (see also Section 4.2.2). Moreover,

according to Pillow and Luxford (1937), young trees having their crown free from competition have smaller CW rate than young trees grown in dense stands, which should contribute to increase density in the unthinned modalities. Nevertheless, the opposite was observed.

As pointed out by Fabris (2000) for *Ps. menziesii*, for sufficiently long rotation periods, trees with high growth rate will have lower proportion of juvenile wood than slow-growing trees. In his work, the growth rate was mainly modulated by initial spacing while in our study the thinning intensity was the main studied factor. A lower proportion of juvenile wood in the thinned stands could explain at least partially the observed differences in BD.

In our case, the surface of the first inner rings was in average clearly lower in the trees from the unthinned stands (Figure F.3 in Appendix F) may be due to uncontrolled factors (genetic, juvenile wood definition). Despite this, it appeared that for most stands, except Aa1 and Pm1, the proportion of juvenile wood was finally higher in the trees from the unthinned modality (Figure F.2 in Appendix F), tending to confirm the above explanation of Fabris (2000).

If the BD radial variation is mainly due to cambial age and to the juvenile or mature nature of wood (hypothesis **H1**) there would be an interest in making the trees grow faster in order to decrease the proportion of juvenile wood. This is not inconsistent with the advice of Henin et al. (2018), for minimising the proportion of juvenile wood, to maintain high stand density in the initial phase of growth.

As a result, the average BD of the fast-growing trees from heavily thinned stands would be higher since juvenile wood or more generally corewood is known to be of lower density for most softwood (Lachenbruch et al., 2011). Moreover, the annual rings corresponding to the highest cambial ages and therefore the densest ones will represent a larger surface in fast-growing trees. On the other hand, Todaro and Macchioni (2011) found a higher BD in unthinned stands of young 31-year-old *Ps. menziesii* trees. For our 20-year-old trees of stand Pm3, the results were more or less similar with lower BD in the heavily thinned plot than in the unthinned one.

Finally, hypothesis **H3** seems verified. Indeed, the effects of thinning intensity on growth rate, tree size and therefore on the variations of juvenile wood proportions are reflected, but in a complex way, on the vertical variations in BD.

4.3. Representativeness of breast height measurements

In analogy to the radial patterns of density variation and their relationship with species strategies proposed in the literature (Plourde et al., 2015; Woodcock and Shier, 2002), we can propose a similar rule for vertical variations, that would rather be associated with the strategy of the tree according to its growing conditions. In Figure 3, 4 and 5, and in a very schematic way, it can be observed that trees with the lowest BD at 1.30 m tend to show an increase with height while those with the highest BD at 1.30 m tend to show a decrease with height.

The results obtained in Longuetaud et al. (2017) were confirmed with the additional trees that were sampled in this extended study. The BD was significantly higher at 1.30 m than in average for the whole stem for *A. alba* and *Ps. menziesii*, which confirms hypothesis **H4**. Mitchell and Denne (1997) found the same results for *Picea sitchensis* and hypothesized that this difference can be explained by tracheids with wider walls at breast height. Wassenberg et al. (2015) have observed a higher density at the bottom of the stem for six species and raise the question of the best sampling strategy for density and biomass estimations. As explained in Section 4.2, several factors vary along the stem and could explain the higher BD observed at the base of the stem and thus the difference in BD between 1.30 m and the whole stem: the proportion of juvenile wood, the mean ring width, the number of rings and the amount of CW.

5. Conclusion

Vertical variations of wood density in the stem have been little studied so far. Moreover, few species have been treated in the literature. Only one study providing a model at the disc level was found for *Ps. menziesii* and another one for *A. alba*. This study was exploratory and based on a limited number of trees due to the destructive sampling and time consuming measurements. The results have to be confirmed by further studies carried out on a larger number of trees, probably with a simplified measurement protocol based on the results obtained in this type of study.

It has been shown that the variation in wood density along the stem did not follow the same pattern for *A. alba* and *Ps. menziesii*. While the density of *Ps. menziesii* was

decreasing continuously from the bottom to the top of the stem, with for some trees an increase towards the top of the stem, that of *A. alba* presented generally a U-shape pattern with first a decrease followed by an increase in the upper part of the stem.

The thinning intensity had an impact on the slope of the decrease in BD at the bottom of the stem. BD decreased faster, as the height in the stem increased, in unthinned plots than in thinned ones for *A. alba* while it decreased faster for thinned plots than in unthinned ones for *Ps. menziesii*.

For these two species, the BD measured at breast height was not representative of the whole stem BD due to these vertical variations.

Two types of models, including or not including BD at breast height as an input, have been proposed for *A. alba* and *Ps. menziesii* in order to best represent the variation of BD with height as a function of tree growth related variables. A comparison with more traditional approaches, which are based on the well-known relationship for softwood species between annual ring density and both ring width and cambial age, have shown that our biexponential models using easily measurable external variables were relevant and gave better results to describe BD variations in the stem.

The continuation of this work will be to study the vertical variations in BD for the bark component and the variation in BD along the knot-branch continuum.

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Data availability:

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declaration on conflicts of interest:

The authors declare that they have no conflict of interest.

References

Barnett, J., Gril, J., Saranpää, P., 2014. The biology of reaction wood introduction.

Barnett, J.R., Jeronimidis, G., 2003. Wood quality and its biological basis. CRC Press.

Billard, A., Bauer, R., Mothe, F., Jonard, M., Colin, F., Longuetaud, F., 2020. Improved aboveground biomass estimates by taking into account density variations between tree components. Annals of Forest Science 77. doi:https://doi.org/10.1007/s13595-020-00999-1.

Bouriaud, O., Teodosiu, M., Kirdyanov, A., Wirth, C., 2015. Influence of wood density in tree-ring based annual productivity assessments and its errors in Norway spruce. Biogeosciences 12.

Cortini, F., Groot, A., Filipescu, C.N., 2013. Models of the longitudinal distribution of ring area as a function of tree and stand attributes for four major canadian conifers. Annals of forest science 70, 637–648.

Courbet, F., 1999. A three-segmented model for the vertical distribution of annual ring area: application to Cedrus atlantica Manetti. Forest ecology and management 119, 177–194.

Crawley, M.J., 2012. The R book. John Wiley & Sons.

Deng, X., Zhang, L., Lei, P., Xiang, W., Yan, W., 2014. Variations of wood basic density with tree age and social classes in the axial direction within Pinus massoniana stems in Southern China. Annals of Forest Science 71, 505–516. doi:https://doi.org/10.1007/s13595-013-0356-y.

Donaldson, L.A., Grace, J., Downes, G.M., 2004. Within-tree variation in anatomical properties of compression wood in radiata pine. IAWA journal 25, 253–271.

Fabris, S., 2000. Influence of cambial ageing, initial spacing, stem taper and growth rate on the wood quality of three coastal conifers. Ph.D. thesis. University of British Columbia.

Filipescu, C.N., Lowell, E.C., Koppenaal, R., Mitchell, A.K., 2014. Modeling regional and climatic variation of wood density and ring width in intensively managed Douglas-fir. Canadian journal of forest research 44, 220–229.

Freyburger, Cand Longuetaud, F., Mothe, F., Constant, T., Leban, J.M., 2009. Measuring wood density by means of X-ray computer tomography. Annals of Forest Science 66, 804.

García-Gonzalo, E., Santos, A.J., Martínez-Torres, J., Pereira, H., Simões, R., García-Nieto, P.J., Anjos, O., 2016. Prediction of five softwood paper properties from its density using support vector machine regression techniques. BioResources 11, 1892–1904.

Gartner, B.L., North, E.M., Johnson, G.R., Singleton, R., 2002. Effects of live crown on vertical patterns of wood density and growth in Douglas-fir. Canadian Journal of Forest Research 32, 439–447. doi:https://doi.org/10.1139/X01-218.

628 González-Rodrigo, B., Esteban, L.G., de Palacios, P., García-Fernández, F., Guindeo, A.,
629 2013. Variation throughout the tree stem in the physical-mechanical properties of the
630 wood of abies alba mill. from the spanish pyrenees. Madera y Bosques 19, 87–107.

631 Gryc, V., Horáček, P., 2007. Variability in density of spruce (picea abies [l.] karst.) wood
632 with the presence of reaction wood. Journal of forest science 53, 129–137.

633 Hamada, J., Pétrissans, A., Ruelle, J., Mothe, F., Colin, F., Pétrissans, M., Gérardin, P.,
634 2018. Thermal stability of abies alba wood according to its radial position and forest
635 management. European Journal of Wood and Wood Products 76, 1669–1676.

636 Harris, J.M., 1977. Shrinkage and density of radiata pine compression wood in relation to
637 its anatomy and mode of formation. New Zealand Journal of Forestry Science 7, 91–106.

638 Henin, J.M., Pollet, C., Jourez, B., Hébert, J., 2018. Impact of tree growth rate on the
639 mechanical properties of Douglas fir lumber in Belgium. Forests 9, 342.

640 Henry, M., Bombelli, A., Trotta, C., Alessandrini, A., Birigazzi, L., Sola, G., Vieilledent, G.,
641 Santenoise, P., Longuetaud, F., Valentini, R., Picard, N., Saint-André, L., 2013. GlobAl-
642 lomeTree: international platform for tree allometric equations to support volume, biomass
643 and carbon assessment. Iforest-biogeosciences and forestry 6, 326–330.

644 Hernández, R.E., 2007. Swelling properties of hardwoods as affected by their extraneous
645 substances, wood density, and interlocked grain. Wood and Fiber Science 39, 146–158.

646 Humar, M., Fabčič, B., Zupančič, M., Pohleven, F., Oven, P., 2008. Influence of xylem growth
647 ring width and wood density on durability of oak heartwood. International Biodeterioration
648 & Biodegradation 62, 368–371. doi:https://doi.org/10.1016/j.ibiod.2008.03.010.

649 Jacquin, P., Mothe, F., Longuetaud, F., Billard, A., Kerfriden, B., Leban, J.M., 2019. Car-
650 Den: A software for fast measurement of wood density on increment cores by CT scanning.
651 Computers and Electronics in Agriculture 156, 606–617.

652 Jozsa, L., Brix, H., 1989. The effects of fertilization and thinning on wood quality of a
653 24-year-old Douglas-fir stand. Canadian Journal of Forest Research 19, 1137–1145.

Jozsa, L., Middleton, G., et al., 1994. A discussion of wood quality attributes and their practical implications. Forintek Canada Special Publication No.SP-34. .

Kerfriden, B., Bontemps, J.D., Leban, J.M., 2021. Variations in temperate forest stem biomass ratio along three environmental gradients are dominated by interspecific differences in wood density. Plant Ecology 222, 289–303.

Kimberley, M.O., Cown, D.J., McKinley, R.B., Moore, J.R., Dowling, L.J., 2015. Modelling variation in wood density within and among trees in stands of New Zealand-grown radiata pine. New Zealand Journal of Forestry Science 45, 1–13. doi:https://doi.org/10.1186/s40490-015-0053-8.

Kimberley, M.O., McKinley, R.B., Cown, D.J., Moore, J.R., 2017. Modelling the variation in wood density of New Zealand-grown Douglas-fir. New Zealand Journal of Forestry Science 47, 15.

Lachenbruch, B., Moore, J.R., Evans, R., 2011. Radial variation in wood structure and function in woody plants, and hypotheses for its occurrence, in: Size-and age-related changes in tree structure and function. Springer, pp. 121–164.

Larson, P.R., Kretschmann, D.E., Clark, A.I., Isebrands, J., 2001. Formation and properties of juvenile wood in southern pines: a synopsis. Gen. Tech. Rep. FPL-GTR-129. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory. 42 p. 129.

Lee, P.W., Eom, Y.G., 1988. Anatomical comparison between compression wood and opposite wood in a branch of korean pine (pinus koraiensis). IAWA journal 9, 275–284.

Li, X., Evans, R., Gapare, W., Yang, X., Wu, H.X., 2014. Characterizing compression wood formed in radiata pine branches. IAWA journal 35, 385–394.

Liepiņš, J., Liepiņš, K., 2017. Mean basic density and its axial variation in Scots pine, Norway spruce and birch stems. Research for Rural Development 1. doi:https://doi.org/10.22616/rrd.23.2017.003.

679 Longuetaud, F., Mothe, F., Fournier, M., Dlouha, J., Santenoise, P., Deleuze, C., 2016.
680 Within-stem maps of wood density and water content for characterization of species: a
681 case study on three hardwood and two softwood species. Annals of Forest Science 73,
682 601–614. doi:https://doi.org/10.1007/s13595-016-0555-4.

683 Longuetaud, F., Mothe, F., Santenoise, P., Diop, N., Dlouha, J., Fournier, M., Deleuze, C.,
684 2017. Patterns of within-stem variations in wood specific gravity and water content for
685 five temperate tree species. Annals of Forest Science 74. doi:https://doi.org/10.1007/
686 s13595-017-0657-7.

687 Mitchell, M.D., Denne, M.P., 1997. Variation in density of Picea sitchensis in relation to
688 within-tree trends in tracheid diameter and wall thickness. Forestry: An International
689 Journal of Forest Research 70, 47–60.

690 Molteberg, D., Høibø, O., 2007. Modelling of wood density and fibre dimensions in mature
691 Norway spruce. Canadian Journal of Forest Research 37, 1373–1389. doi:https://doi.
692 org/10.1139/X06-296.

693 Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of tem-
694 perate Northern Hemisphere trees and shrubs. Ecological monographs 76, 521–547.

695 Niklas, K.J., Spatz, H.C., 2010. Worldwide correlations of mechanical properties and green
696 wood density. American Journal of Botany 97, 1587–1594. doi:https://doi.org/10.
697 3732/ajb.1000150.

698 Nogueira, E.M., Fearnside, P.M., Nelson, B.W., 2008. Normalization of wood density in
699 biomass estimates of Amazon forests. Forest Ecology and Management 256, 990–996.
700 doi:https://doi.org/10.1016/j.foreco.2008.06.001.

701 Pillow, M.Y., Luxford, R.F., 1937. Structure, occurrence, and properties of compression
702 wood. Technical Report.

703 Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects models in S and S-PLUS. Springer. ISBN0-
704 387-98957-0 , 1–537.

Plourde, B.T., Boukili, V.K., Chazdon, R.L., 2015. Radial changes in wood specific gravity of tropical trees: inter-and intraspecific variation during secondary succession. Functional Ecology 29, 111–120.

Pressler, M., 1864. Das gesetz der stamanpildung. Amoldiscne Buchnanalung, Liepzig .

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL: https://www.R-project.org/.

Repola, J., 2006. Models for vertical wood density of Scots pine, Norway spruce and birch stems, and their application to determine average wood density. Silva Fennica 40, 673–685. doi:https://doi.org/10.14214/sf.322.

Rueda, R., Williamson, G.B., 1992. Radial and vertical wood specific gravity in Ochroma pyramidale (Cav. ex Lam.) Urb.(Bombacaceae). Biotropica 24, 512–518. doi:https://doi.org/10.2307/2389013.

Saranpää, P., 2003. Wood density and growth. in Barnett and Jeronimidis (2003) , 87–117.

Seynave, I., Bailly, A., Balandier, P., Bontemps, J.D., Cailly, P., Cordonnier, T., Deleuze, C., Dhôte, J.F., Ginisty, C., Lebourgeois, F., Merzeau, D., Paillassa, E., Perret, S., Richter, C., Meredieu, C., 2018. GIS Coop: networks of silvicultural trials for supporting forest management under changing environment. Annals of Forest Science 75, 48. doi:https://doi.org/10.1007/s13595-018-0692-z.

Sopushynskyy, I., Maksymchuk, R., Kopolovets, Y., Ayan, S., 2020. Intraspecific structural signs of curly silver fir (abies alba mill.) growing in the ukrainian carpathians. Journal of Forest Science 66, 299–308.

Sotelo Montes, C., Weber, J.C., Abasse, T., Silva, D.A., Mayer, S., Sanquetta, C.R., Muñiz, G.I., Garcia, R.A., 2017. Variation in fuelwood properties and correlations of fuelwood properties with wood density and growth in five tree and shrub species in niger. Canadian Journal of Forest Research 47, 817–827.

730 Taras, M.A., Wahlgren, H.E., 1963. A comparison of increment core sampling methods for
731 estimating tree specific gravity. volume 7. US Department of Agriculture, Forest Service,
732 Southeastern Forest Experiment.

733 Tarmian, A., Remond, R., Dashti, H., Perré, P., 2012. Moisture diffusion coefficient of
734 reaction woods: compression wood of picea abies l. and tension wood of fagus sylvatica l.
735 Wood science and technology 46, 405–417.

736 Tian, X., Cown, D.J., McConchie, D.L., 1995. Modelling of Pinus radiata wood properties.
737 Part 2: Basic density. New Zealand Journal of Forestry Science 25, 214–230.

738 Todaro, L., Macchioni, N., 2011. Wood properties of young Douglas-fir in Southern Italy:
739 results over a 12-year post-thinning period. European Journal of Forest Research 130,
740 251–261.

741 Vieilledent, G., Fischer, F.J., Chave, J., Guibal, D., Langbour, P., Gérard, J., 2018. New
742 formula and conversion factor to compute basic wood density of tree species using a global
743 wood technology database. American Journal of Botany 105, 1653–1661.

744 Wahlgren, H.E., Fassnacht, D.L., 1959. Estimating tree specific gravity from a single incre-
745 ment core. USDA Forest Service, Forest ProductsLaboratory report No. 2146 , 24 p.

746 Wassenberg, M., Chiu, H.S., Guo, W., Spiecker, H., 2015. Analysis of wood density profiles
747 of tree stems: Incorporating vertical variations to optimize wood sampling strategies for
748 density and biomass estimations. Trees 29, 551–561. doi:https://doi.org/10.1007/
749 s00468-014-1134-7.

750 Westing, A.H., 1965. Formation and function of compression wood in gymnosperms. The
751 Botanical Review 31, 381–480.

752 Wiemann, M.C., Williamson, G.B., 2014. Wood specific gravity variation with height and its
753 implications for biomass estimation. USDA Forest Service, Forest Products Laboratory,
754 Research Paper, FPL-RP-677, 2014; 12 p. 677, 1–12. doi:https://doi.org/10.2737/
755 FPL-RP-677.

Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity... correctly. American Journal of Botany 97, 519–524. doi:https://doi.org/10.3732/ajb.0900243.

Woodcock, D.W., Shier, A.D., 2002. Wood specific gravity and its radial variations: The many ways to make a tree. Trees 16, 437–443. doi:https://doi.org/10.1007/s00468-002-0173-7.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Global wood density database doi:https://doi.org/10.5061/dryad.234.

Zobel, B.J., Van Buijtenen, J.P., 1989. Wood variation: Its causes and control. Springer Science & Business Media.