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RESEARCH PAPER

Improving aboveground biomass estimates by taking into account density variations between tree components

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Abstract

• ***Key message*** **Strong density differences were observed between stem wood at 1.30 m and other tree components (stem wood, stem bark, knots, branch stumps and branches). The difference, up to 40% depending on the component, should be taken into account when estimating the biomass available for industrial uses, mainly fuelwood and wood for chemistry.**

• ***Context*** Basic density is a major variable in the calculation of tree biomass. However, it is usually measured on stem wood only and at breast height.

• ***Aims*** The objectives of this study were to compare basic density of stem wood at 1.30 m with other tree components and assess the impact of differences on biomass.

• ***Methods*** Three softwood species were studied: *Abies alba* Mill., *Picea abies* (L.) H. Karst., *Pseudotsuga menziesii* (Mirb.) Franco. X-Ray computed tomography was used to measure density.

• ***Results*** Large differences were observed between components. Basic density of components was little influenced by tree size and stand density. Overall, bark, knot and branch biomasses were highly underestimated by using basic density measured at 1.30 m.

• ***Conclusion*** Using available wood density databases mainly based on breast height measurements would lead to important biases (up to more than 40%) on biomass estimates for some tree components. Further work is necessary to complete available databases.

Keywords Wood specific gravity · Bark · Knots · Branches · Softwoods

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Contribution of the co-authors Antoine BILLARD: collected the data, performed the data analysis, wrote the original draft of this paper and was the main writer.
Rodolphe BAUER: helped with the data collection and the validation of the knot volume measurements and contributed to the review and editing.
Frédéric MOTHE: designed the experiment, helped with the data collection and data analysis and contributed to the writing.
Mathieu JONARD: helped with the data analysis and contributed to the discussion, review and editing.
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Fleur LONGUETAUD: participated to the funding acquisition, supervised the work, designed the experiment, helped with data collection and data analysis, and contributed to the writing.

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1 Introduction

This work focuses on the estimation of tree aboveground woody biomass, by detailing the different tree components, on the basis of volume data that are widely available from national forest inventories. Such an approach based on volume and a conversion factor, here the density of the tree component, is referred to as an indirect approach (Somogyi et al. 2007; Longuetaud et al. 2013). As opposed to direct approaches based on equations directly giving the biomass but that are less representative at large-scale areas because they are generally based on local studies (Somogyi et al. 2007), this indirect volume × density approach has the advantage of using the available volume data from national forest inventories that are generally based on sound statistical sampling and to provide at the same time volume and biomass that are both of interest for several industrial uses. Vashum and Jayakumar (2012) provide a review of the existing methods for aboveground biomass estimation, distinguishing direct and indirect approaches. By comparing both approaches, Gómez-García et al. (2015) have shown that the volume × density approach led to less error than a direct method based on biomass equations.

Moreover, with the development of the LiDAR technology for forest inventories, it becomes necessary to provide species-specific density values for each component. It is important that the density values used are reliable and representative of the forest resource (Fearnside 1997; Sagang et al. 2018).

In order to deal simultaneously with the issues of carbon accounting and resource management for the production of products and energy, it is necessary to know the volume and biomass of the different tree components. It is relatively classical to estimate the biomass per tree component based on biomass equations (e.g., Antonio et al. 2007) but not with a volume × density approach with in addition density depending on the component.

More precisely, to convert the volume of standing trees into dry biomass, basic density (BD) has to be used. BD is the ratio of oven-dry weight to green volume.

Accurate and unbiased estimate of biomass is necessary. It is for example usual to estimate carbon sequestration in forests directly from total tree biomass (IPCC 2006; Zhu et al. 2018). The removal of nutrients associated with harvesting is also usually calculated from biomass and average nutrient concentrations (Rothpfeffer and Karltun 2007). In the context of sustainable development, the use of renewable resources has to be optimized. For instance, recent works confirmed that bark and knots contain an important quantity of extractives (Brennan et al. 2020). In particular, knots are a source of lignans (Holmbom et al. 2003) that can be used in cosmetics, medicine and food industries. In order to evaluate the opportunity to develop a wood chemistry industry based on industrial by-products recovery, it is necessary to estimate correctly the amount of biomass available for these novel uses.

However, the biomass of some tree components, especially knots, cannot be assessed correctly until now due to a lack of accurate volume and density data. This particular tree component is also not considered in the direct approaches based on biomass equations because it is not easily measurable. For a given species, the mean density of the different tree components is often poorly known. Indeed, most density measurements reported in the literature were done on knot-free stem wood, generally by sampling a single stem wood core at breast height. Moreover, the measurements were usually carried out on a quite limited number of trees per species and the methods used for density measurements are often questionable (Williamson and Wiemann 2010).

Several recent studies have proved that it is important to consider the variations of wood density within tree to correctly estimate biomass (Repola 2006; Nogueira et al. 2008; Wiemann and Williamson 2013; 2014; Wassenberg et al. 2015; Bastin et al. 2015). Nevertheless, studies focusing on the density of tree components other than the stem wood at breast height are relatively rare.

BD values are provided for stem wood and bark of a lot of North American species by Miles and Smith (2009). Results were highly species-dependent, but, contrary to popular belief, it can be observed that bark was denser than stem wood for most softwood species.

Density of knots was studied by relatively few authors (Wegelius 1940; Boutelje 1966; Hakkila 1971; Lehtonen 1978; Gartner 1995). Knots are generally denser than stem wood for softwood species.

The most studied component are the branches. Several authors found that density of branches was higher than density of stem wood for temperate softwood species (Fegel 1941; Wegelius 1940; McKimmy and Ching 1968; Hakkila 1971; Lehtonen 1978; Gryc et al. 2011; Dibdiakova and Vadla 2012).

In this study, BD of five tree components (stem wood, stem bark, knots, branch stumps and branches) was investigated for three softwood species: *Abies alba* Mill., *Picea abies* (L.) H. Karst., and *Pseudotsuga menziesii* (Mirb.) Franco. Trees were sampled in two contrasted thinning intensity plots. The main objectives were to provide BD values for each tree component for these three species and then to use these values to estimate the biomass of each component and total aboveground biomass. This work with a volume × density approach with BD values measured for five tree components was never done before. A comparison with the use of a single BD value measured at breast height was done. One of the originalities of this work is to consider the knot and branch stump components with the underlying objective of estimating the resource in extractives. Another originality of this work is the accurate method of measurement based on the use of X-rays.

We will verify that, as in the literature, the BD of knots, branches and bark is higher than that of the stem wood.

In this context, two research hypotheses based on our analysis of the literature were investigated:

H1: There is an impact of stand density on the BD of the components. Trees growing in low density stands grow faster and have components with lower BD.

H2: Taking into account the variation of BD between tree components has an impact on the biomass estimates (tree component and total).

2 Materials and methods

2.1 Study sites and sampling design

For each tree species, trees were sampled in a thinning trial managed by the national forest service (ONF): Saint-Prix in the East of France for *A. alba*, Mas-Dorier in the centre of France for *P. abies* and Mélagues in the South of France for *Ps. menziesii*. In these forests, contrasted thinning intensities were tested and trees were monitored from the plantation (for *Ps. menziesii* and *P. abies*) or natural regeneration (for *A. alba*). Site characteristics are presented in Table 1.

Eight trees were sampled for each species: Four trees in the control plot with no thinning (only natural mortality) and four trees in a heavily thinned plot. We looked at all the tree diameters in the plot. We have divided them evenly into four diameter classes. Then, we chose one tree by diameter class directly on the field. Breast height (1.30 m) was marked on each standing tree before measuring the circumference that was converted to over-bark diameter at breast height (DBH).

The trees were cut in February 2018. After felling the trees, the total height and the height to the crown base (i.e., the lowest whorl with at least three-fourths of living branches) were measured. Since *A. alba* trees originated from a natural regeneration, stump discs were sampled to measure tree age.

Main tree characteristics are presented in Table 2.

2.2 Collection of samples

Samples were collected for each tree within each tree component (stem wood, bark, knots and branches) for density measurements. Three sets of samples were collected (Fig. 1):

- Samples (A): For measuring the density of stem wood and bark within the stem, 15 discs were sampled along the stem, avoiding knots. The three first discs were taken at fixed heights: 0.30, 0.80 and 1.30 m. The 12 remaining discs were regularly distributed along the stem.
- Samples (B): Seven short logs with whorl branches and related knots were sampled along the stem. Five logs were sampled above crown base to account for knots connected to living branches and two logs below crown base to account for knots connected to dead branches.
- Samples (C): Branches were selected into three size classes based on the diameter at their insertion (insertion diameter): 0–4 cm, 4–7 cm and more than 7 cm. Branches were sampled in each size class but more intensively in larger branch classes, considering that large branches are more likely to be collected for

Table 1 Site characteristics

Tree species	Site	Location	Altitude (m)	Modality	Stand density (trees per hectare)		Basal area (m^2/ha)	Dominant height (m)
					Initial		Last measurement[1]	
Abies alba	Saint-Prix	46.993 N, 4.055 E	750	Unthinned	13794	7986	39.5	16.5
				Heavily thinned	13649	649	17.2	17.4
Picea abies	Mas-Dorier	45.753 N, 3.654 E	770	Unthinned	1690	1370	54.5	24
				Heavily thinned	2125	221	19.4	24
Pseudotsuga menziesii	Mélagues	43.713 N, 3.058 E	800	Unthinned	1300	835	66.4	-
				Heavily thinned	1300	141	29.7	-

Table 2 Characteristics of sampled trees

Tree species	Age range (years)		DBH range (cm)		Height range (m)	
Thinning modality	Unthinned	Heavily thinned	Unthinned	Heavily thinned	Unthinned	Heavily thinned
Abies alba	44–57	43–48	10.3–28	19.6–41.2	13.6–22.4	17–21.4
Picea abies	53	53	22.3–40.9	33.7–44	22–30.6	25–29.5
Pseudotsuga menziesii	48	48	23.3–47.4	46.5–65.6	27.2–31.8	26.5–34.1

industrial applications. As far as possible, 10 branches per tree were selected for the highest available class and five branches for each other classes, by distributing selected branches as regularly as possible all along the crown. For each selected branch, one sample segment was taken at the insertion of the branch and one in each size class along the branch (Fig.1).

2.3 Wood density measurement

X-Ray-based methods have been developed for a long time to measure wood density (Polge 1966). Among them, X-ray computed tomography (CT) is a non-destructive and fast method (although expensive) able to provide accurate 3D maps of wood density (Longuetaud et al. 2016). CT scanning was applied to measure wood density, i.e., the ratio mass/volume, at different moisture contents (Wei et al. 2011). The oven-dry density D_0 (i.e., the oven-dry mass/oven-dry volume ratio) is obtained by drying the samples at 103 °C until a constant weight is reached. The method developed by Longuetaud et al. (2016) makes it possible to compute also BD (i.e., the ratio oven-dry mass/green volume) from CT scans at both green and oven-dried states. This is especially useful for carbon or biomass accounting since the product of BD by green volume (as it is usually measured by national forest inventories) gives the dry biomass.

In this study, all images were calibrated by using the method described in Freyburger et al. (2009) that was implemented in a specific plug-in called "CalDenQB" for the image analysis software ImageJ (Schneider et al. 2012). We assumed that this calibration works for bark.

The stem discs (A) were scanned twice (green and oven-dried states). The CT images were analysed by using the "sectorization" method described by Longuetaud et al. (2016) to compute both D_0 and BD for each disc. The disc sectors including knots, despite the care taken in the field to avoid knots in these samples (A), were removed

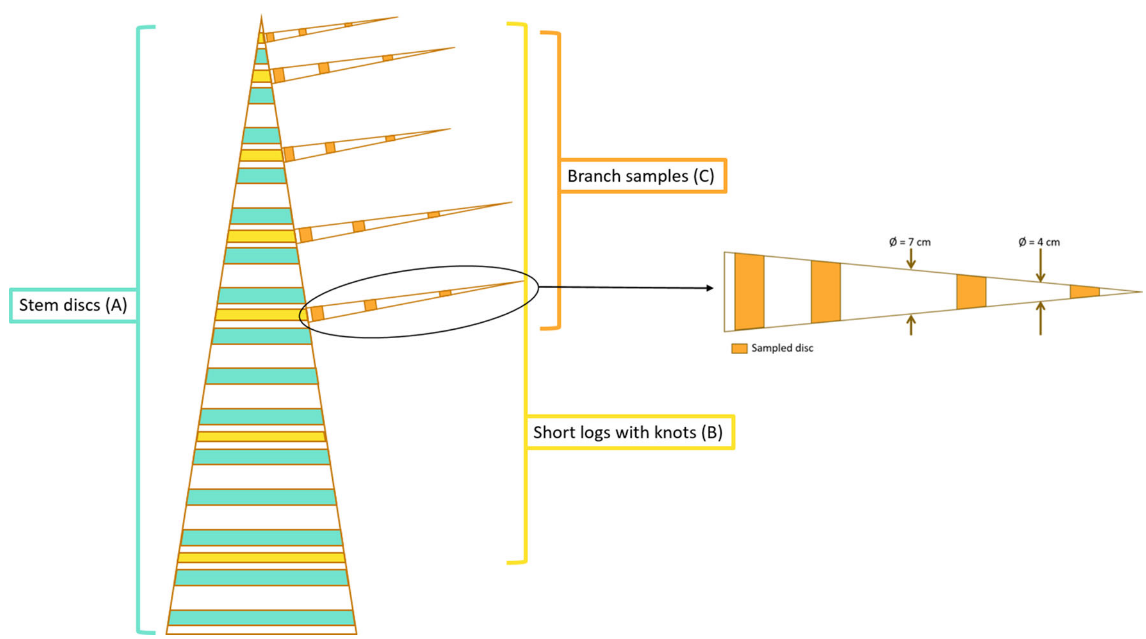

Fig. 1 Description of disc sampling within the tree (on the left). The stem discs (15 stem discs per tree) are in green. The short-logs containing knots (seven per tree: two below the crown base and five above) are in yellow. The branch discs (at least 10 branches per tree) are in orange. On the right: Sampling pattern along a branch belonging to the diameter class > 7 cm. The leftmost disc is taken near the branch insertion. The other samples are taken in the middle of each predefined diameter class: 0–4 cm, 4–7 cm and > 7 cm

virtually in order to compute density in clear of knots areas. The boundary between wood and bark was recorded manually for measuring the density of each component separately. Bark was segmented by thresholding to select pixels beyond the wood/bark boundary with density greater than 200 kg $\cdot$ m^{-3}.

A slight shift in the wood/bark boundary positioning would not greatly affect the measurement of area and density of wood and bark, but for computing accurately BD by this method, a good match between CT images in green and oven-dried states is required. This is specially problematic for bark whose surface area is much smaller than that of wood. For this reason, BD of bark was rather estimated statistically from D_0 (see Section 2.4).

The short logs containing knots (B) and branch discs (C) were scanned only in oven-dried state because it would have been too difficult to get a good match between green and oven-dried images on such large samples (samples (B)) with irregular shape (samples (B) and (C)). D_0 was measured directly on the calibrated CT images, and BD was estimated from D_0 (see Section 2.4).

The knots included in samples (B) were segmented manually using the "Gourmands" plug-in for ImageJ (Colin et al. 2010). The plug-in allows to put markers in the 3D space for delineating the stem pith and both sides of knots. The end of an outgoing knot (i.e., the knot/branch boundary) was fixed as much as possible at the "triple point" where stem wood meets knot wood and bark (left side of Fig. 2). The plug-in computes knot volume as a sum of truncated cones (right side of Fig. 2) and provides corresponding knot wood density. If there are two visible triple points, like in Fig. 2, the plug-in selects the triple point with the shortest distance to the pith (the rightmost point in this example).

The branch samples (C) were placed in holding boxes to be scanned in batches of about 10 samples (Appendix A). An ImageJ macro was developed for processing semi-automatically the images. The mean D_0 of each sample (including bark) was recorded.

2.4 Relationship between basic density and oven-dry density

Conversion formulas are available for converting wood density measured at a given moisture content to BD (Williamson and Wiemann 2010). The theoretical relationship linking BD to D_0 and wood shrinkage, by assuming linear shrinkage from fibre saturation point to oven-dry state, is:

$$BD = D_0 \cdot (1 - S) \quad (1)$$

where S is the total volumetric shrinkage (unitless).

In previous works performed in our laboratory, BD and D_0 were obtained on stem discs for several species, including *A. alba* and *Ps. menziesii* (Longuetaud et al. 2016), and linear regressions of the following form were fitted for verifying the theoretical relationship:

$$BD = \alpha + \beta \cdot D_0 \quad (2)$$

where α and β are the intercept and the slope of the regression, respectively.

Considering Eqs. 1 and 2, β should estimate $1 - S$ and α should be null. Actually, in most cases, α was found to be statistically not null because the shrinkage S was itself varying with D_0.

Regressions were fitted with the X-ray measurements of BD and measured D_0 performed on the 15 stem discs for each eight trees per species. The obtained parameters are given in Table 3. The same relationship was applied to all components (i.e., knots, branches and bark) of a given tree species.

2.5 Basic density of the components

For each tree, the BD of the stem wood component (knot-free) was computed as the mean BD of the 15 stem discs

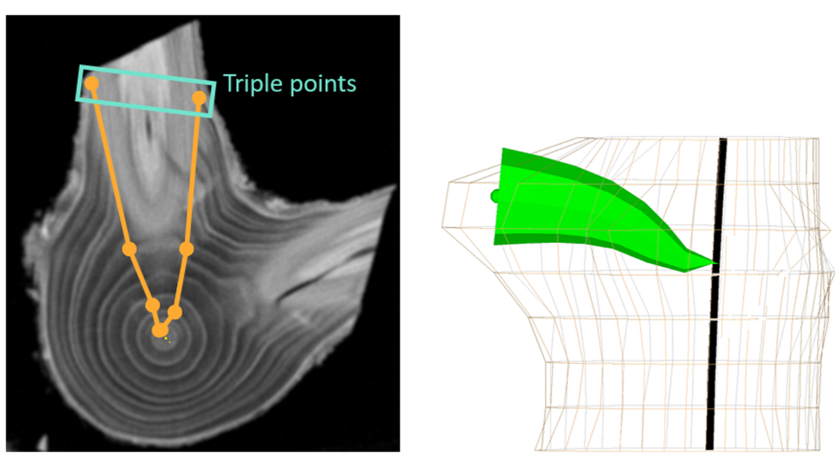

Fig. 2 Manual segmentation of a knot in oven-dried state with ImageJ and "Gourmands" plug-in (on the left). The plug-in allows putting markers in the 3D space for delineating the stem pith and both sides of knots. The end of an outgoing knot (i.e., the knot/branch boundary) was fixed as much as possible at the "triple point" where stem wood meets knot wood and bark. 3D representation of the knot (on the right)

Table 3 Parameters of the statistical relationships used to convert D_0 into BD

Tree species	α (kg/m^3)	β (unitless)
Abies alba	38	0.790
	**	***
Picea abies	67	0.710
	***	***
Pseudotsuga menziesii	-	0.879
	NS	***

The stars indicate the significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

(wood part only) 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 in such a way that each height fraction of the stem is associated with the disc closest to it.

In the same way, the BD of the bark of each tree was converted from the mean D_0 of the bark of the 15 stem discs weighted by the volumes of bark contained in the stem short logs represented by each disc.

BD of knots was estimated as the mean BD of all the measured knots of each tree.

Due to technical constraints, the BD of the knot component of *Ps. menziesii* was obtained only for five of the eight sampled trees.

The branch samples were separated into two groups: the branch insertion samples (closest to the stem) and the remaining samples of the branches.

For each tree, the BD of the "branch insertion" component was computed as the mean BD of the branch insertion samples. The average of the remaining branch samples (one to three samples per branch, depending on the branch size class) was computed to be the BD of the "branch without insertion" component. The reason for this distinction is a significantly much higher wood density at the branch insertion (first 50 cm from the stem) than in the remaining part of the branch where the density is relatively constant as shown by Hakkila (1971) and in an unpublished work that we have done recently on our three species.

At this stage, a mean BD value was available for each component of each tree. For each species, the mean BD of each tree component was computed by averaging the corresponding values for the eight trees. Last, the BD of each individual tree was computed by averaging the BD of its components weighted by their volume as computed in Section 2.6. Then, the mean BD of the eight trees per species was computed and given in Appendix B as the lines "Aboveground total".

2.6 Volume of the components

For each tree, over-bark stem volume (V^{ob}_{stem}) was obtained by summing truncated cones defined by the distance between the stem discs (A) and their over-bark areas. Under-bark stem volume (V^{ub}_{stem}) was measured in the same way using the under-bark disc areas. The over-bark and under bark disc areas were measured on the CT images obtained from X-ray scans in green state.

The volume of stem bark was obtained by difference between over-bark and under-bark stem volumes.

The volume of knots was assessed by assuming a constant ratio $k = 1\%$ of knot volume to V^{ob}_{stem} for *Albies alba* and *P. abies* and $k = 1.3\%$ for *Ps. menziesii*. These ratios were measured on a subsample of 11 trees of *Albies alba* and 9 trees of *Ps. menziesii* from Longuetaud et al. (2016) that were entirely X-ray scanned, and for which total knot volume was assessed manually on CT images. The knot ratio per tree varied from 0.5 to 1.4% for *Albies alba* and from 0.9 to 1.7 for *Ps. menziesii*.

For assessing the volume of branches, the total aboveground volume was first estimated by using an expansion factor (Pretzsch 2009). The volume expansion factors (VEF) proposed by Longuetaud et al. (2013) allow computing total aboveground over-bark volume (V^{ob}_{tot}) from the over-bark volume of the stem part with a diameter higher than 7 cm ($V^{ob}_{stem>7}$):

$$V^{ob}_{tot} = V^{ob}_{stem>7} \cdot VEF \tag{3}$$

$V^{ob}_{stem>7}$ was computed with the same method as V^{ob}_{stem}, based on truncated cones. VEF was computed for each tree from diameter at breast height and total tree height by using the species-specific models of Longuetaud et al. (2013). The total volume of branches was obtained by difference between V^{ob}_{tot} and V^{ob}_{stem}, and then divided into "branch insertion" and "branch without insertion" by assuming that insertions accounted for $i = 5\%$ of the total volume of branches. The value of 5% was assessed by detailed X-ray scans of six entire branches, two for each species (unpublished work).

We finally obtained the volume of five tree components: volume of stem under bark without knots ($V_{stem\ w/o\ knots}$), volume of bark (V_{bark}), volume of knots (V_{knots}), over-bark volume of branch insertions ($V_{br\ ins}$) and over-bark volume of the remaining part of the branches ($V_{br\ w/o\ ins}$):

$$\begin{aligned} V_{stem\ w/o\ knots} &= V^{ub}_{stem} - V_{knots} \\ V_{bark} &= V^{ob}_{stem} - V^{ub}_{stem} \\ V_{knots} &= k \cdot V^{ob}_{stem} \\ V_{br\ ins} &= i \cdot (V^{ob}_{tot} - V^{ob}_{stem}) \\ V_{br\ w/o\ ins} &= (1 - i) \cdot (V^{ob}_{tot} - V^{ob}_{stem}) \end{aligned} \tag{4}$$

where V_{stem}^{ub} is the under-bark volume of stem, V_{stem}^{ob} the over-bark volume of stem and V_{tot}^{ob} the total aboveground over-bark volume.

2.7 Biomass of the components

For each tree, the biomass of each component was computed as the product of the component BD and volume. A first estimate, $Biomass_{1,tree,component}$ was obtained by using the actual value of the BD for the component and a second one by using the BD of the knot-free stem wood measured at breast height as it is often done ($Biomass_{2,tree,component}$). The relative difference between the two methods was computed as:

$$\Delta B_{tree,component}^{rel} = \frac{Biomass_{2,tree,component} - Biomass_{1,tree,component}}{Biomass_{1,tree,component}} \times 100$$

For each species and component, a mean relative difference was computed based on the eight trees. A confidence interval of each mean relative difference was computed providing information on the significance. Note that the relative difference can be interpreted in the same way in terms of BD by simplifying by the volume of the component.

The same approach was applied for the whole tree. The sum of the five components (knot-free stem wood, stem bark, knots, branch insertions and branches without insertions) gave an estimate of the total aboveground biomass of each tree:

$$Biomass_{1,tree} = \sum_{component=1}^{5} BD_{tree,component} \times V_{tree,component}$$

This value was compared to the biomass that would be obtained by assuming a constant BD equal to the value measured at breast height and applied for the whole tree:

$$Biomass_{2,tree} = BD_{1.30m,tree} \times V_{tot,tree}^{ob}$$

$BD_{1.30m,tree}$ was the average BD of wood for the stem disc taken at breast height for the considered tree. In the same way as for each component, a relative biomass difference was computed for each tree as:

$$\Delta B_{tree}^{rel} = \frac{Biomass_{2,tree} - Biomass_{1,tree}}{Biomass_{1,tree}} \times 100$$

The mean value ΔB^{rel} and its confidence interval were computed for each species from these eight ΔB_{tree}^{rel} values.

The R software was used for the analysis (R Core Team 2018).

3 Results

3.1 Mean basic density of the tree components

On average for all three species, the density values are in the following decreasing order: knots, branch insertions, branches without insertion, bark and knot-free stem wood (Fig. 3 and Appendix B to compare with the values reported in public databases in Appendix D). Except for *Ps. menziesii*, the mean BD of knots, branch insertions, branches without insertion and bark were all larger than the breast height BD that was of 407, 356 and 453 kg · m^{-3} for *A. alba*, *P. abies* and *Ps. menziesii*, respectively.

3.2 Effect of tree species, stand density and tree component on basic density

For each tree component, the BD averaged by tree is represented as a function of DBH (Fig. 4). For each species and each component, a Pearson's correlation coefficient r

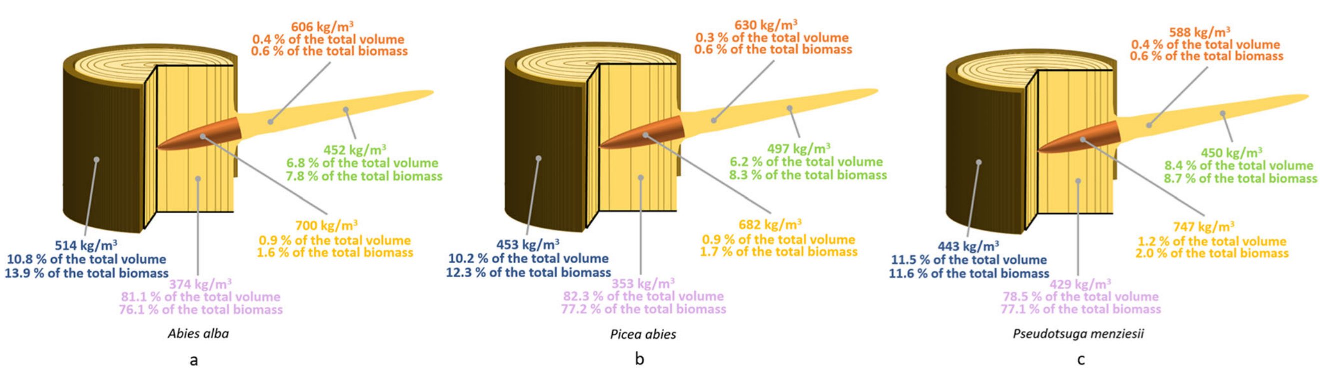

Fig. 3 Mean measured basic density, volume fraction and biomass fraction of each tree component for *A. alba* (**a**), *P. abies* (**b**) and *Ps. menziesii* (**c**)

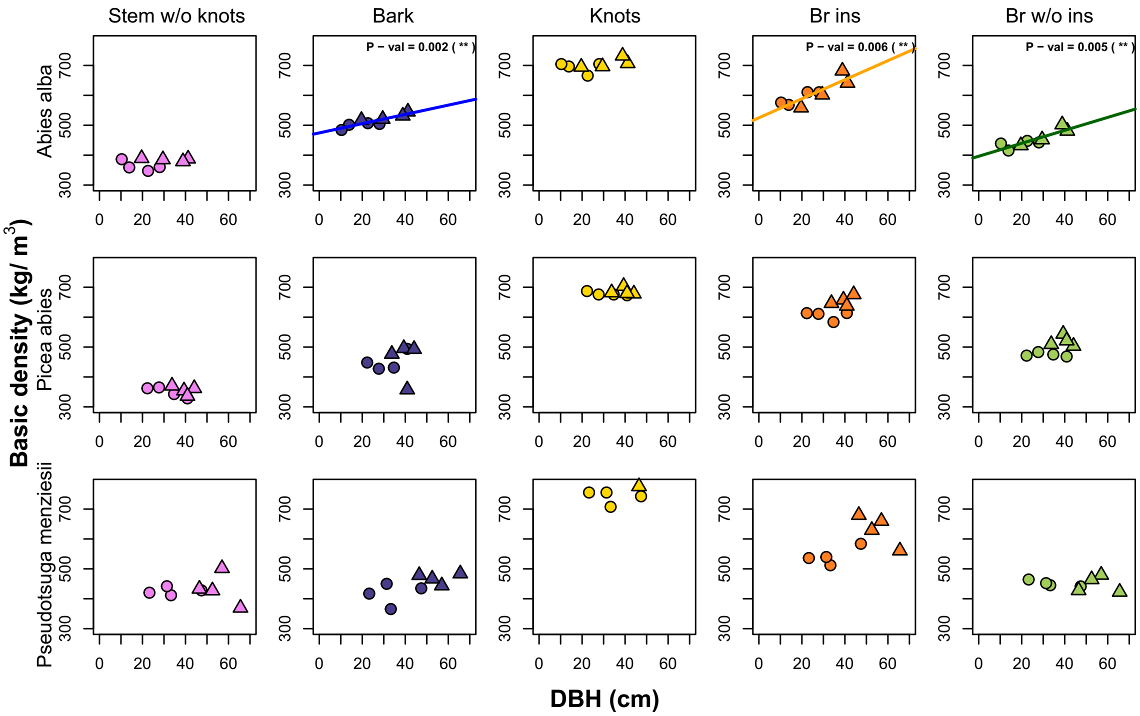

Fig. 4 Relationship between the mean BD of tree components and the DBH of the tree for every tree species in unthinned (circles) and heavily thinned (triangles) plots. $Stem\ w/o\ knots$ is the stem under bark without knots, $Br\ ins$ are the branch insertions and $Br\ w/o\ ins$ are the branches without their insertion. The regression line and the p value of the slope are indicated in the plot when it was significant. The stars indicate the p value significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

was calculated and its significance was assessed (Pearson test with function *cor.test* of R statistical software).

The r coefficients obtained were not significant (Table 4), except for *A. alba* for which BD of bark and branches increased with DBH. BD of bark and branch insertions for *Ps. menziesii* ($r = 0.64$ and 0.55, respectively) and to a lesser extent BD of branch insertions for *P. abies* ($r = 0.53$) seemed to increase with DBH as well (Fig. 4) but it was not statistically significant probably due to the small sample size.

Student t tests performed for comparing BD of trees from unthinned and heavily thinned plots (Table 5) did not show significant differences, except for the bark of *A. alba* and the branches of *P. abies* that were both denser in the heavily thinned plots.

Figure 5 and Table 6 show BD variations for each tree component as a function of the sample diameters (i.e., stem, knot or branch diameters). The BD of all components of *A. alba* tended to increase with their size. The correlation was particularly strong for bark, branch insertions and branches without insertion ($r = 0.68, 0.72, 0.73$, respectively). The same increase in BD with the sample diameter was observed for branches (insertions and without insertion) and to a lesser extent for knots of *P. abies*. A significant negative correlation ($r = -0.49$) was observed for the stem wood of *P. abies*. For *Ps. menziesii*, a low but significant positive

Table 4 Pearson's correlation coefficient r between BD and DBH for each tree component and each species where $stem\ w/o\ knots$ means stem under bark without knots, $Br\ ins$ means branch insertions and $Br\ w/o\ ins$ means branches without insertions

Tree species	Stem w/o knots	Bark	Knots	Br ins	Br w/o ins
Abies alba	0.21	0.90	0.45	0.86	0.87
	NS	**	NS	**	**
Picea abies	−0.48	0.18	−0.05	0.53	0.47
	NS	NS	NS	NS	NS
Pseudotsuga menziesii	−0.04	0.64	0.20	0.55	-0.22
	NS	NS	NS	NS	NS

The stars indicate the r significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Table 5 t tests of BD between the two thinning modalities: average values for heavy thinning on the left and for no thinning on the right where $stem\ w/o\ knots$ means stem under bark without knots, $Br\ ins$ means branch insertions and $Br\ w/o\ ins$ means branches without insertions

Tree species	Stem at breast height	Stem w/o knots	Bark	Knots	Br ins	Br w/o ins
Abies alba	410.99 ; 402.23	385.43 ; 363.19	528.52 ; 499.21	707.6 ; 692.87	620.87 ; 591.21	466.88 ; 436.16
	NS	NS	*	NS	NS	NS
Picea abies	355.04 ; 356.77	355.75 ; 349.59	455.77 ; 450.22	685.97 ; 677.97	654.49 ; 605.4	519.45 ; 474.5
	NS	NS	NS	NS	**	*
Pseudotsuga menziesii	467.54 ; 438.75	432.9 ; 425.47	468.36 ; 416.87	775.66 ; 740.13	632.34 ; 542.9	448.73 ; 450.74
	NS	NS	NS	-	*	NS

The stars indicate the t test significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

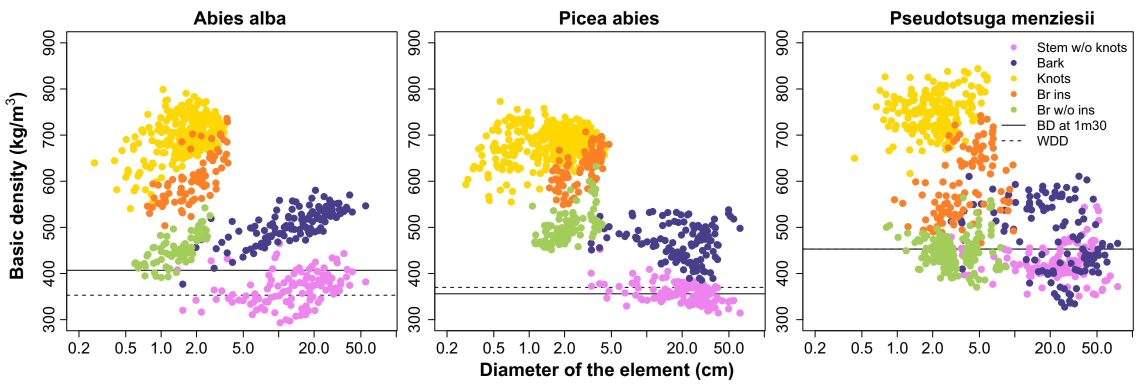

Fig. 5 BD of tree components as a function of their corresponding diameter (i.e., diameter of each sample) for each tree species (for bark component the stem diameter was used): knot-free stem wood ($stem\ w/o\ knots$; purple), bark (blue), knots (yellow), branch insertions ($Br\ ins$; orange), branches without insertion ($Br\ w/o\ ins$; green). The horizontal line is the mean BD measured at breast height while the dotted line represents the Global Wood Density Database value

Table 6 Pearson's correlation coefficient r between component BD and diameter of all tree components for each tree species (stem diameter for bark) where $stem\ w/o\ knots$ means stem under bark without knots, $Br\ ins$ means branch insertions and $Br\ w/o\ ins$ means branches without insertions

Tree species	Stem w/o knots	Bark	Knots	Br ins	Br w/o ins
Abies alba	0.35	0.68	0.41	0.72	0.73
	***	***	***	***	***
Picea abies	−0.49	−0.03	0.21	0.67	0.59
	***	NS	***	***	***
Pseudotsuga menziesii	0.07	−0.33	0.26	0.32	0.03
	NS	***	***	***	NS

The stars indicate the r significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

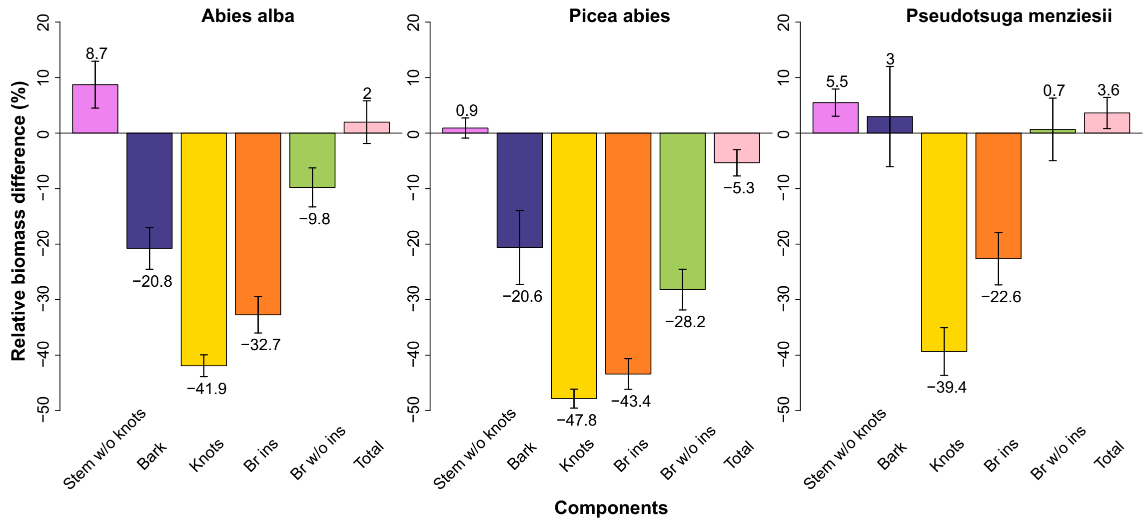

Fig. 6 Mean relative biomass differences ΔB^{rel} between biomasses calculated with the breast height basic density value and with the actual basic density of the component relatively to the actual basic density of the component. $Stem\ w/o\ knots$ is the stem under bark without knots, $Br\ ins$ are the branch insertions and $Br\ w/o\ ins$ are the branches without their insertion

correlation was observed for branch insertions ($r = 0.32$) and low negative correlations for bark ($r = -0.33$) and knots ($r = -0.24$). This decrease of bark density with stem diameter seemed to reflect actually a stronger effect of height ($r = 0.74$ between BD of bark and height from the ground).

The variations of the component BD with height in the tree (Appendices 4 and 5) are consistent with the previous observations, considering that the size of each element decreases with the height in the tree.

3.3 Biomass estimates

Figure 6 shows the relative error on biomass estimates when using the BD measured at breast height instead of average component-specific BD. A value of 0% means that taking into account component-specific BD does not change the quantity of biomass compared to an estimation made on the basis of the density at breast height.

The biomass of bark (except for *Ps. menziesii*), knots and branches (except branch part without insertion for *Ps. menziesii*) was strongly underestimated when using BD measured at breast height: by about 40 to 50% for the knots whatever the species and 20% for the bark of *A. alba* and *P. abies*.

For the knot-free stem wood, on the contrary, the biomass was overestimated by 8.7% for *A. alba* and by 5.5% for *Ps. menziesii*.

The use of the average BD at breast height results in an overestimation by 3.6% for *Ps. menziesii* and an underestimation by 5.3% for *P. abies* of the total aboveground biomass (Fig. 6), whereas the difference was not significant for *A. alba*.

In complement, a non-parametric test giving the significance of the difference between the two biomass estimates for each component and each species was made (Wilcoxon-Mann-Whitney test). The test confirmed the results and significance of the differences of Fig. 6 except for knots of *Ps. menziesii*. This can be explain by the fact that only five *Ps. menziesii* trees were sampled for knots while eight trees were sampled for the other species.

4 Discussion

4.1 Difference of *BD* between tree components

Our values of BD at breast height were slightly higher than values found in available databases for *A. alba*, lower for *P. abies* and similar for *Ps. menziesii*.

The mean knot-free stem BD was lower than the BD at breast height for all the species and the difference was significant for *A. alba* and *Ps. menziesii*. This is a commonly found result as in Cown (1967) for *Ps. menziesii* or Wassenberg et al. (2015) for various species. And it perfectly confirms the results obtained by Longuetaud et al. (2017) on other trees from the same species.

Bark, knot and branch components were all found denser than the knot-free stem wood, although it was less pronounced for Douglas fir. This confirms what we have seen in the literature.

Miles and Smith (2009) also found bark density higher than stem wood density for several North American *Abies* species[1] (360 kg · m^{-3} for stem wood and 490 kg · m^{-3} for

[1]Not including *A. alba*.

bark in average) and *P. abies* (360 kg · m^{-3} for stem wood and 440 kg · m^{-3} for bark). For *Ps. menziesii*, they found the opposite with stem slightly denser than bark (450 kg · m^{-3} vs. 440 kg · m^{-3}). Overall, our results are very close and in total agreement with Miles and Smith (2009) for the comparison between bark density and BD at breast height (more widely used than knot-free stem density). Our values for BD at breast height and bark density were respectively 407 and 514 kg · m^{-3} for *A. alba*, 356 and 453 kg · m^{-3} for *P. abies* and 453 and 443 kg · m^{-3} for *Ps. menziesii*. Dibdiakova and Vadla (2012), who studied the density of *P. abies* bark, also found it denser than density of the stem wood regardless of the height in the tree. The same result was reported by Petráš et al. (2019) for *P. abies* and other species.

Anatomical features could explain the high density of bark. For Douglas fir for instance, Patel (1975) observed that phloem contained fibres with very thick walls and narrow lumen. The high density of bark could also be related to a higher concentration of inorganic elements. Indeed, Rothpfeffer and Karltun (2007) found on *P. abies* that the concentration of inorganic elements is more than 2 to 15 times higher in bark than in the stem wood. For *Pinus sylvestris*, when wood is burned, the quantity of ashes is five times more important for bark than for stem wood (Filbakk et al. 2011). Moreover, bark has a high concentration of tannins (Norin and Winell 1972) that could increase the density by filling the pores.

For the density of knots, few studies are available due to the difficulty of carrying out the measurements. For *P. abies*, Hakkila (1971) found the highest density in the knots. Lehtonen (1978) obtained similar results with knots 351 kg · m^{-3} denser than stem wood for *Pinus sylvestris* and 490 kg · m^{-3} denser for *P. abies*. The mean BD of knots calculated from Gartner (1995) for *P. abies* is of 673 kg · m^{-3}, very close to 682 kg · m^{-3} in our study. In our study, the differences between knot density and BD measured at breast height were approximately 293 kg · m^{-3} for *A. alba*, 326 kg · m^{-3} for *P. abies* and 294 kg · m^{-3} for *Ps. menziesii*. Several hypotheses can be made concerning the higher density of knots: their high content in extractives (Kebbi-Benkeder et al. 2015; Kebbi-Benkeder et al. 2016), the presence of compression wood (Wegelius 1940) and the narrow ring widths within the knots. Indeed, it is known that for most softwood species the stem wood density increases when the ring width decreases due to a higher latewood proportion (e.g., Koga and Zhang (2004) for *Abies balsamea*, Franceschini et al. (2013) for *P. abies*, Cown (1967) for *Ps. menziesii*).

Branches were generally denser than stem wood for softwoods (e.g., McKimmy and Ching 1968, Hakkila 1971, Lehtonen 1978, Gryc et al. 2011, Dibdiakova and Vadla 2012). This is in accordance with our results. Hakkila (1971) found branches denser than stem wood for *Pinus sylvestris* and *P. abies*, and McKimmy and Ching (1968) obtained similar result for *Ps. menziesii*. This is also the case of Dibdiakova and Vadla (2012) and Gryc et al. (2011) on *P. abies*. Lehtonen (1978) found that the difference between branch density and stem wood density was of 221 kg · m^{-3} for *Pinus sylvestris* and 407 kg · m^{-3} for *P. abies*. Branches contain more extractives like resin than stem wood, especially near the insertion (Wegelius 1940; Hakkila 1971). However, McKimmy and Ching (1968) found no significant difference in specific gravity due to extractives. The high content of compression wood at the proximal part of softwood branches (Wegelius 1940; Hakkila 1971; Spicer and Gartner 1998) could also contribute to increase their high density. Moreover, the high density of branches could be related to their slow radial growth associated to narrow annual rings (Franceschini et al. 2013) as for the knots of which they are the extension. Finally, there are more inorganic elements in branches than in stem wood and bark (Rothpfeffer and Karltun 2007).

4.2 Effects of growth rate and tree size on basic density

Small differences in BD of the tree components were found between unthinned and heavily thinned plots. Hypothesis H1 is therefore somewhat supported but these results should be considered with caution since there were only four trees in each modality. Moreover, the difference was in favour of the heavily thinned stands regardless of tree component that is the opposite of what was expected.

The effect of tree DBH on BD was also rather small, except for bark and branches of *A. alba* whose BD tended to increase with DBH. This is in line with the previous observation since DBH was on average higher in heavily thinned stands.

All the trees from the same species having the same age (or the same age range for *A. alba*), the biggest trees had in average wider growth rings at breast height than the smaller ones. One could have therefore expected that the BD (of knot-free stem wood at least) would be higher for the slowest growing trees, due to the already mentioned relationship usually observed between wood density and ring width. Actually, looking at the average ring width and BD at breast height, the relationship was only observed for *P. abies* (Appendix 6). It is important to note that the density-ring width relationship is generally obtained for the individual rings of a given tree measured at breast height and not for average values of density and ring width that are compared between trees. When they were young, out of competition, the trees from both modalities probably grew at the same speed. And when competition appeared, the trees of the heavily thinned modality started to grow faster. As a result, the proportion of juvenile wood is probably lower in these trees. And in general, the stem wood density is lower in juvenile wood than in mature wood for softwoods (Lachenbruch et al. 2011). This could maybe explain the lower BD in unthinned stands due to a higher proportion of juvenile wood of lower density.

The higher density observed for bark and branches of some species for the bigger trees or for trees from the heavily thinned stands could be due to a higher content of inorganic elements in these components since these trees had an easier access to resources.

4.3 Effects of component diameter and height in the tree on basic density

The observed variations of the knot-free BD with the stem diameter are coherent with the vertical variations reported by Longuetaud et al. (2017): a decrease with the height in the tree for *A. alba* and *Ps. menziesii*, contrary to *P. abies* for which BD increased with height.

As above, bark density of *Ps. menziesii* was found to decrease with stem diameter. This result could be related to the changes in bark structure from the stem base (flaky patches of cork) to the top levels (rather smooth and only slightly fissured) that were reported for this species (Cardoso et al. 2019). It was the opposite for *A. alba* with a strong increase of bark BD with the stem diameter that could be due to differences in strategy between species. Depending on the environment (cold, fire, biotic attacks), would it be better to invest in a thicker and less dense bark or on the contrary in a thinner and denser one?

Lehtonen (1978) pointed out for *P. abies* that the bigger the knot was, the less dense it was. Our results do not confirm this observation: The bigger knots (all trees together) were denser for all species. For *A. alba*, the clear decreasing trend of BD with height in the tree could be explained by variations in the extractive content of knots. Indeed, Kebbi-Benkeder et al. (2017) observed that concentrations in hexane and acetone extracts decreased from the crown base toward the tree tip. They attributed the smaller extractive concentrations in the highest knots to their young age and their higher content of sapwood.

For branches of the three species, BD increased with the branch diameter and generally decreased with insertion height. These results are in agreement with those of Hakkila (1971) for spruce: branches near the bole were denser than branches far from the bole, and when branches were classified in diameter classes, the density was higher for the thickest branches. Lehtonen (1978) showed that wood density of branch stumps decreases with increasing branch diameter for *P. abies*. The author mentions that his result is in agreement with Boutelje (1966) but in contrast with Enčev (1962) (in Lehtonen (1978)) for the same species. These contradictory results could be attributed to geographical variations or genetical factors.

4.4 Total aboveground biomass estimates

The biomass of bark, knots and branches was in most cases largely underestimated when using BD measured at breast height. This result is very interesting for these tree components that are particularly rich in extractives and that are specifically targeted for the development of a green chemistry industry. This means for example that the amount of extractives in the knots was also underestimated by 40 to 50%. On the other hand, the knots represented only 1.6 to 2% of the total biomass, which is very low and relatively negligible. Bark had a higher weight with 11.6 to 13.9% of the total biomass depending on the species. On the contrary, the biomass of the knot-free stem wood was significantly overestimated with BD measured at breast height for *A. alba* and *Ps. menziesii* since BD is higher at the lower part of the stem for these species. Comparable results were observed by Longuetaud et al. (2017) for *A. alba* (overestimation by 5%), by Cown (1967) and Longuetaud et al. (2017) for *Ps. menziesii* (overestimation by 5%) and by Repola (2006) for *P. abies* (overestimation by less than 1%). Finally, since the stem volume is bigger than the volume of all other tree components, the total aboveground biomass was significantly underestimated by 5.3% for *P. abies* and overestimated by 3.6% for *Ps. menziesii* when BD at breast height was used. There is a compensatory effect between the reference breast height density, which is generally too high in relation to BD of the whole stem, and BD of the other components (bark, knots and branches) which is largely underestimated but whose volumes are smaller. The impact of accounting BD of each component (Hypothesis H2) is clear for each component but thanks to this compensatory effect, the biases on the total aboveground biomass remain relatively small, even if it is statistically significant. For Sagang et al. (2018), using BD at the base of the tree rather than the weighted average density (stem wood, branches, leaves and reproductive parts) leads to overestimating the total aboveground biomass of tree by 10% based on fifteen tropical species. In practice, applying this volume × density approach for evaluating biomass of each component as well as total aboveground biomass would require models accounting for the BD variations of each component (at intra- and inter-tree levels) and models for better assessing the volume of each component (Corral-Rivas et al. 2017). We are now working on such models. Furthermore, the method has to be compared with direct approaches predicting biomass of some tree components through allometric equations (Gómez-García et al. 2015) and validated with biomass field measurements. But the advantages of volume × density approaches are numerous:

volume data are widely available through forest inventories, both volume and biomass of tree components are provided, and with the development of the LiDAR technology for measuring the volume of tree components (e.g., Stovall et al. 2017), it is necessary to have the corresponding BD values.

4.5 Methodological aspects

In this exploratory study, trees were measured very intensively. This was never done before. The field operations followed by drying and density measurements were both complex and time consuming, justifying that only eight trees per species could be processed. For a Student t test with four trees in each group, a significance level of 0.05, BD standard deviation of about 25 $\mathrm{kg \cdot m^{-3}}$ for each group and mean difference between the two groups of about 50 $\mathrm{kg \cdot m^{-3}}$, the power of the test was about 0.7 (function *pwr.t.test* of R), which is acceptable. Nevertheless, our results have to be verified and validated on more trees. This study should help reducing the sampling intensity within trees so that more trees can be sampled for the same costs.

The relations used to convert the oven-dry density into BD can be criticised. They were calibrated on stem wood values and used for the other components. In an unpublished work on *P. abies*, we adjusted the statistical equation both for stem wood and branch samples (for which BD was measured by water displacement method), all issued from one single tree. An important result of this work was that the relationships between oven-dry density and BD were similar for stem wood and branch components. By using the statistical relationships, we assumed that they were applicable to all components of each species. From our point of view, this approach is better than applying the mechanistic equations involving shrinkage because it is clear that the shrinkage value varies depending on component and component density. Further research will be necessary to better assess BD of components like bark whose properties are probably far from those of stem wood.

The volume of the branch insertion component used is an approximation. Some observations on six entire X-rayed branches (not published) confirmed that the wood density is much higher in the first 50 cm of branches in agreement with Hakkila (1971). This helped us estimate the volume of this tree component and then the weight of 5% to apply in our biomass computations by also taking into account the fact that the discs sampled at the branch insertions represent rather the first 10 cm of branches. This point should be studied in more detail in a further study.

We measured the actual volume of the bark component thanks to the CT scanner by analysing images. But volume of bark is often determined from tape measures first over and then under bark, or in the field with a Swedish bark gauge. The problem is that for the part of tree stems (most of the time only the bottom part) with a rough and cracked bark (depending on the species and tree age), the tape measure overestimates the actual bark volume. For our biomass estimates, we used the actual bark volumes of our trees: on average 11.5, 10.9 and 12.6% of the total over-bark stem volume, for *A. alba*, *P. abies* and *Ps. menziesii*, respectively, against 11% for *A. alba* and *P. abies*, and 14.5% for *Ps. menziesii* as obtained in the EMERGE project (Bouvet and Deleuze 2013) and then published in the online FCBA Memento 2019. Logically, the difference is more important for *Ps. menziesii* than for species with a smooth bark.

The knot manual segmentation method has already been discussed in Billard et al. (2019)

5 Conclusion

Very large differences in BD were observed between the studied tree components (stem wood, bark, knots and branches). These differences should be taken into account to estimate correctly the biomass of each tree component but also the total aboveground biomass of tree in avoiding biases. In particular, the biomass of knots and bark was strongly underestimated when using a BD measured at breast height or provided by available databases. These two tree components are targeted to be used as sources of extractives in the development of an industry based on wood chemistry and the assessment of their availability in terms of biomass at the resource scale must be accurate.

A lighter sampling protocol has to be proposed in order to increase the number of trees and environmental contexts.

The next step will be to study the variation of basic density within each component and to develop predictive models or (1) the vertical variation of density along the stem and the bark, and (2) the variation along the branch, including the knot. Correction factors starting from the BD measured or estimated at breast height should be developed with the objective to provide accurate biomass estimates for each component of each species at the resource level. In further work, the results of such volume $\times$ density method have to be compared with allometric approaches for assessing aboveground biomass and with biomass field measurements.

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Appendix 1: CT image of branch samples

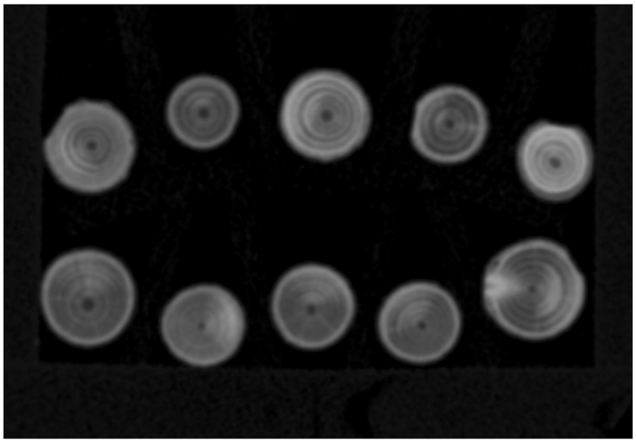

Fig. 7 CT image of 10 branch samples (C) in oven-dried state. The holding box made of a very light material is not visible by X-rays

Appendix 2: Basic density, volume and biomass for each component and species

The table below shows, for each species and each compartment, the number of samples used to calculate the mean basic density of the component and the standard deviation of the basic density. The last two columns give the percentage of volume and biomass of the component in relation to the total volume/biomass of the tree. The average density of the tree is calculated from the averages of each component, weighted by their relative percentage of volume.

Tree species	Component	No. of samples	$Mean BD$ (kg.m^{-3})	Standard deviation	Volume (%)	Biomass (%)
Abies alba	Stem at 1m30	8	407	23	-	-
	Stem w/o knots	8	374	16	81.1	76.1
	Bark	8	514	19	10.8	13.9
	Knots	8	700	18	0.9	1.6
	Br ins	8	606	41	0.4	0.6
	Br w/o ins	8	452	28	6.8	7.8
	Aboveground total		398	-	100.0	100.0
Picea abies	Stem at 1m30	8	356	18	-	-
	Stem w/o knots	8	353	15	82.3	77.2
	Bark	8	453	48	10.2	12.3
	Knots	8	682	10	0.9	1.7
	Br ins	8	630	30	0.3	0.6
	Br w/o ins	8	497	27	6.2	8.3
	Aboveground total		376	-	100.0	100.0
Pseudotsuga menziesii	Stem at 1m30	8	453	47	-	-
	Stem w/o knots	8	429	37	78.5	77.1
	Bark	8	443	38	11.5	11.6
	Knots	5	734	25	1.2	2
	Br ins	8	588	62	0.4	0.6
	Br w/o ins	8	450	19	8.4	8.7
	Aboveground total		437	-	100.0	100.0

Appendix 3: Basic density values reported in three public databases for three softwood species

Tree species	CARBOFOR (kg/m^3)	GWDD (kg/m^3)	TROPIX (kg/m^3)
Abies alba	380	353	404
Picea abies	370	370	372
Pseudotsuga menziesii	430	453	448

Basic density values for three softwood species as reported by three public databases: CARBOFOR (Loustau 2004) was a project about carbon sequestration in France

Appendix 4: Variation of the basic density with the height of the sample in the tree

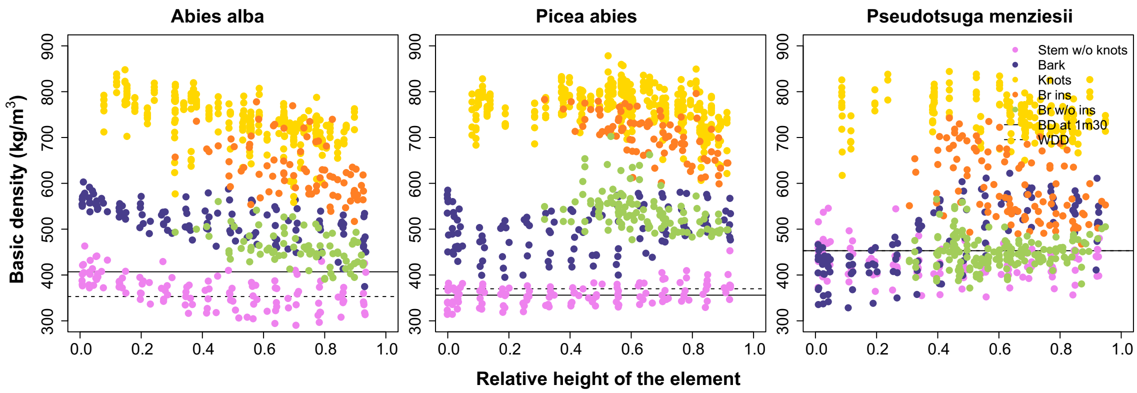

Fig. 8 Basic density versus relative height of each sample for the three species: knot-free stem wood (purple), bark (blue), knots (yellow), branch insertions (orange), branches without insertion (green). The straight line is the mean basic density measured at breast height while the dotted line represents the Global Wood Density Database value

Appendix 5: Pearson's correlation coefficient *r* between basic density and height of the sample in the tree

Table 7 Pearson's correlation coefficient r between BD and relative height of each sample for each tree component and each species

Tree species	Stem w/o knots	Bark	Knots	Br ins	Br w/o ins
Abies alba	−0.52 ***	−0.64 ***	−0.55 ***	−0.45 ***	−0.48 ***
Picea abies	0.36 ***	0.24 **	−0.28 ***	−0.62 ***	−0.42 ***
Pseudotsuga menziesii	−0.26 **	0.74 ***	−0.24 **	−0.48 ***	0.03 NS

The stars indicate the r significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

that delivered a database for the main French species, TROPIX (Paradis et al. 2015) is a large database constituted by the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD) including many tropical species and that is often used in industry, and the Global Wood Density Database (GWDD) (Zanne et al. 2009a) is an international database compiling a huge number of literature references. The values from TROPIX, that were given for a moisture content of 12%, were converted to basic density (using the usual conversion equation given by Vieilledent et al. (2018)). Note that the GWDD is being corrected due to an error in the conversion formula used in the original publication (Zanne et al. 2009b; Vieilledent et al. 2018) and the corrected database is not available yet.

Appendix 6: Relationship between mean ring width and basic density at breast height for each species

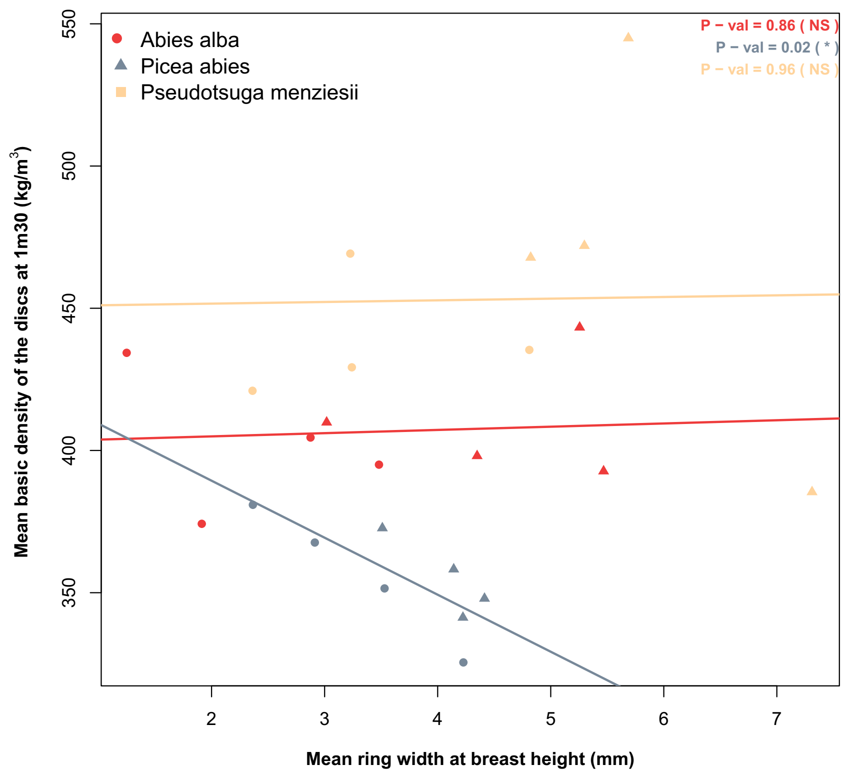

Fig. 9 Mean basic density at breast height as a function of mean ring width at breast height for each species (red = *Abies alba*, blue = *Picea abies*, beige = *Pseudotsuga menziesii*) from unthinned plots (circles) and heavily thinned plots (triangles). The p values of the slope are indicated on the graph. The stars indicate the r significance: NS, $p \geq 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

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