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Estimation of tree ring density by coupling CT scanning and ring width measurements: Application to the analysis of the ring width – ring density relationship in *Picea abies* trees

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Abstract

Tree growth in volume and wood density are the two factors that determine tree biomass. They are important for assessing wood quality and resource availability. Analysing and modelling the relationships between these two factors are important for improving silvicultural practices of softwoods like Norway spruce, for which a negative relationship is generally observed between ring width and ring density.

We describe an original method for obtaining ring density data (*RD*) by coupling conventional ring width measurements (*RW*) and air-dry density measurements obtained with X-ray computer tomography at high-speed but with lower resolution than the *RW* data. The method was applied to 200 discs of Norway spruce trees sampled in a plantation to assess its relevance.

The *RW–RD* relationship was analysed as a function of cambial age and

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disc height in the stem. Descriptive statistical models were developed and compared to models in the literature. These models made it possible to analyse the variations of RD as a function of height in the tree at a given cambial age or for a given calendar year and also to observe a shift in the juvenile wood – mature wood boundary between the bottom of the tree and the rest of the stem. The $RD - RW$ relationship was observed in the juvenile wood at the base of the stem but not in the juvenile wood higher up. Furthermore, the juvenile wood formed at the base of the tree was denser than the juvenile wood formed higher up and the mature wood formed at the same height.

In conclusion, the proposed method was found to be relevant, especially when wood discs are readily available, and the results obtained highlighted the importance of distinguishing juvenile wood formed at the base of the tree from that formed higher up.

Keywords: Wood density, Ring width, Cambial age, Height in the stem, Juvenile wood, Norway Spruce

Title Page

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We describe an original method for obtaining ring density data (RD) by coupling conventional ring width measurements (RW) and air-dry density measurements obtained with X-ray computer tomography at high-speed but with lower resolution than the RW data. The method was applied to 200 discs of Norway spruce trees sampled in a plantation to assess its relevance.

The RW – RD relationship was analysed as a function of cambial age and disc height in the stem. Descriptive statistical models were developed and compared to models in the literature. These models made it possible to analyse the variations of RD as a function of height in the tree at a given cambial age or for a given calendar year and also

to observe a shift in the juvenile wood – mature wood boundary between the bottom of the tree and the rest of the stem. The $RD - RW$ relationship was observed in the juvenile wood at the base of the stem but not in the juvenile wood higher up. Furthermore, the juvenile wood formed at the base of the tree was denser than the juvenile wood formed higher up and the mature wood formed at the same height.

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4. **Keywords:**

Wood density; Ring width; Cambial age; Height in the stem; Juvenile wood; Norway Spruce

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- **Availability of data and material:** Two datapapers have been written to describe the database generated in the framework of the ANR Treetrace project. All the data used in this article come from the **TreeTrace_spruce** database and will be made available to the research community before the end of 2022 on the Data INRAE repository at: <https://doi.org/10.57745/WKLTJI>
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- **Authors' contributions:**
 - Tojo RAVOAJANAHARY participated to the data collection, performed the data analysis and contributed to the writing.
 - Frédéric MOTHE participated to the funding acquisition, designed the experiment, participated to the data collection, supervised the work, performed the data analysis and contributed to the writing.
 - Fleur LONGUETAUD participated to the funding acquisition and is the coordinator of the ANR Treetrace project, designed the experiment, participated to the data collection, supervised the work, performed the data analysis and contributed to the writing.
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Not applicable.
- **Consent to participate (include appropriate statements)**
All authors agreed with the content.
- **Consent for publication (include appropriate statements)**
All authors gave explicit consent for publication.

7. Key Message

The original method proposed provides useful data for the analysis of ring density variations in stems, highlighting the particular behaviour observed at the base of the tree.

1. Introduction

The relationship between ring width (RW) and ring density (RD) has been studied quite extensively for several reasons. RW is included in wood grading standards because it is related to wood density, the latter being an indicator of the mechanical properties and performance of the wood material (Saranpää, 2003; Lin et al., 2007; Kiaei et al., 2012). The properties of fuelwood (Sotelo Montes et al., 2017) and paper (García-Gonzalo et al., 2016) are also related to wood density. The RW – RD relationship has been observed and modelled in many dendrochronological studies that attempt to relate within-ring characteristics to climate variables (e.g., Wimmer and Grabner, 2000; Franceschini et al., 2013) in order to reconstruct past climate or predict tree growth in future climate.

For softwoods, a negative relationship between RW and RD is generally accepted. More specifically, this relationship is mostly observed for species with a gradual transition between early wood and late wood (Todaro and Macchioni, 2011), such as Norway spruce (*Picea abies*). When this negative relationship is observed, it is largely due to the fact that for wide rings, the amount of early wood (of lower density) becomes more important while the amount of late wood (of higher density) remains roughly constant. This negative relationship probably reflects a trade-off between volume growth and density of wood formed, and can be illustrated by a few examples among others. In the context of forest productivity or carbon fluxes, Bouriaud et al. (2015) has worked on this relationship for Norway spruce to improve estimates of annual biomass increments. Indeed, inter-annual density variations must be taken into account to avoid underestimating biomass increments

26 in years when volume growth is reduced. Over the last century, increased
27 growth associated with decreased wood density has been observed for several
28 species including Norway spruce (Badeau et al., 1996; Franceschini et al.,
29 2010; Bontemps et al., 2013; Pretzsch et al., 2018).

30 The $RW-RD$ relationship has been extensively studied for Norway spruce
31 (e.g., Olesen, 1977; Lindström, 1996b; Wimmer and Downes, 2003; Jyske
32 et al., 2008). The classical profile of radial density variation is described by
33 Olesen (1977) as follows: a decrease from the pith to ring 8-10, followed by an
34 increase and stabilization between the 15th and 20th annual ring, which would
35 correspond to the boundary between juvenile wood (area of high variation in
36 properties) and mature wood. In addition, a density peak near the pith was
37 reported to occur in the second or third ring (Olesen, 1977; Saranpää, 1994).
38 For softwoods, it is accepted that juvenile wood is on average less dense than
39 mature wood (Olesen, 1977; Lachenbruch et al., 2011).

40 Most of the time for practical reasons the $RW-RD$ relationship is studied
41 at 1.30 m, but some studies have focused on its variation with height in the
42 tree, for a given cambial age or for a given calendar year (Olesen, 1977;
43 Saranpää, 1994; Jyske et al., 2008).

44 The data used to study RD profiles and the $RW-RD$ relationship are
45 usually obtained by microdensitometry (Jacquin et al., 2017) on wood sam-
46 ples dried at 12%, with equipment such as the SilviScan (e.g., Piispanen
47 et al., 2014) or other X-ray equipments (Jyske et al., 2008; Bouriaud et al.,
48 2015). Conventional microdensitometry provides RW and RD with high ac-
49 curacy but requires a significant amount of time to prepare samples of strictly
50 constant thickness (usually 1-2 mm thick) which limits its use. Several meth-

51 ods have been developed recently to analyse unprepared wood core samples
52 for ring width and density at high resolution (De Mil et al., 2016; Van den
53 Bulcke et al., 2019); but the acquisition of such images is still slow. Faster
54 methods of measuring density from unprepared cores have been developed
55 (Steffenrem et al., 2014; Jacquin et al., 2019; Kerfriden et al., 2021) but the
56 accuracy is lower than conventional microdensitometry and these methods
57 are still limited for the analysis of individual growth rings. On the other
58 hand, the acquisition of wood cores is fast and non-destructive but cores
59 have the disadvantage that they do not always include the first rings close to
60 the pith and represent only a single radius which may not be representative
61 of the entire section (e.g., in the presence of compression wood).

62 The first objective of this work was to propose a new and complementary
63 method for assigning an average density value to each ring of a disc. The first
64 originality lies in the analysis of the density of a ring on a whole disc rather
65 than a limited number of radii (only one generally in the case of a core), which
66 can lead to biased density measurements in the presence of compression wood
67 for example (Alméras et al., 2005; Gryc and Horáček, 2007). The second
68 was the challenge of matching two types of measurements: RW from high-
69 resolution RGB images (regardless of the method of measuring RW , manual
70 in our case) and wood density from a fast but lower resolution X-ray scan of
71 the whole disc. The second objective was to test the relevance of this new
72 method by analysing the data collected. For this purpose, a model describing
73 RD as a function of RW , cambial age and height in the tree was proposed
74 and compared to other models in the literature. In order to demonstrate the
75 relevance of our method, we formulated the following hypotheses, based on

76 the literature review:

- 77 • **H1:** Juvenile and mature wood can be delimited by analysis of radial
78 density variations; with mature wood corresponding to the zone where
79 density variations become less important;
- 80 • **H2:** There is a negative correlation between RW and RD in Norway
81 spruce, at least in the mature wood;
- 82 • **H3:** The $RW-RD$ relationship is valid whatever the height in the tree.
83 This relationship has been relatively little studied at heights in the tree
84 other than breast height.

85 2. Materials and Methods

86 2.1. Sampling

87 Logs were sampled from a Norway spruce plantation near Corcieux (48.1968
88 N; 6.8869 E, Grand-Est region, France). The trees were about 55 years old.
89 Unfortunately, the history of silvicultural interventions in this stand was not
90 available. A clear cut was carried out on the site in March 2019. The logs
91 were already cut at the time of sampling. One hundred logs with a length
92 of 4.5m were selected for our study. In our sampling, it was therefore possi-
93 ble that several logs belonged to the same tree but the information was not
94 available. One 5cm thick disc was sampled at each end of the log ($n = 200$
95 discs in total). The discs were labelled with the log number (from #1 to
96 #100) and the position of the disc in the log (bottom or top). The positions
97 were recorded as “gb” for discs sampled at the bottom of the logs and “fb”

98 for discs sampled at the top of the logs. For example, “E001.fb” was the disc
99 sampled at the top of log number #1.

100 *2.2. Preliminary data processing*

101 The position of each log in a given tree was unknown. However, as all
102 trees were of the same age, the number of growth rings in the discs gave
103 information on the height of the disc, even though each tree has not had
104 exactly the same growth in height. A histogram of the distribution of the
105 number of rings on the 200 discs (Fig. 1) was made to assign each disc and
106 log a level of height in the stem. Looking at the distribution of the number
107 of rings on the discs taken from the bottom of the logs (blue bars in Fig.
108 1), three modes are clearly visible, suggesting that there were three height
109 levels for the logs. Three positions $p = 1, 2$ or 3 were assigned to the logs
110 according to the number n of rings at their lower end, such that $n > 47$,
111 $47 \geq n > 39$ and $n \leq 39$, respectively. Disc height levels were deduced from
112 the log positions: The bottom disc of a log at position p was set at p while
113 the top disc was set at $p + 1$. The heights in the stem at approximately
114 0m, 4.5m, 9m and 13.5m were then assigned for each position 1, 2, 3 and 4,
115 respectively.

116 The numbers of bottom discs obtained at positions 1, 2 and 3 were 46,
117 43 and 11, respectively. Consequently, the numbers of top discs obtained
118 at positions 2, 3 and 4 were also 46, 43 and 11, respectively. All the discs
119 collected were measured as described in Sections 2.3 and 2.4 but, in order
120 not to oversample height levels 2 and 3, only the 100 bottom discs plus the
121 11 top discs at position 4 were used in the analyses presented below.

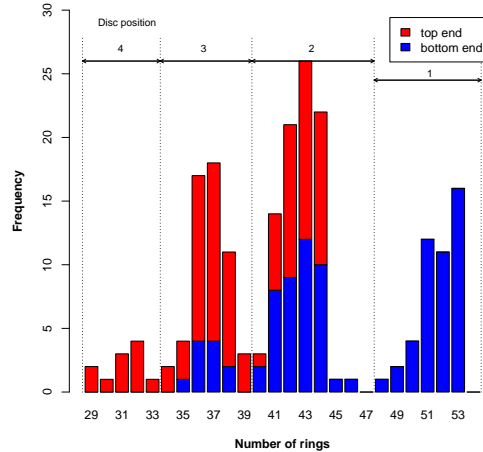


Figure 1: Histogram of the number of rings for the 200 discs (bottom discs in blue and top discs in red). Three height positions $p = 1, 2$ or 3 were assigned to the logs according to the number n of rings in their bottom disc such that $n > 47$, $47 \geq n > 39$ and $n \leq 39$, respectively. The bottom disc of a log at position p was set at p while the top disc was set at $p + 1$.

122 *2.3. Wood density measurements*

123 After air-drying for several months in a ventilated room, the discs were
 124 scanned with a General Electric Brightspeed Excel medical X-ray scanner.
 125 X-ray computer tomography (CT) allows a 3D reconstruction of an object
 126 according to the absorption of X-rays by the object. The scanner settings
 127 were: 80 kVp, 50 mA, "DETAIL" convolution filter and a slice thickness of
 128 1.25mm. Cross-sectional images of the discs were obtained with a resolution
 129 of 0.5 to 1 pixels/mm depending on the diameter of the discs.

130 The grey levels of the raw images are expressed in a standardised unit
 131 called the Hounsfield Unit (HU), which allows comparison between images
 132 from different scanners. Calibration is done so as to obtain a value of 0

133 HU in water and -1000 HU in air. In addition, the wood-specific calibration
134 protocol described by Freyburger et al. (2009), based on the analysis of HU
135 measured on various wood species, was applied. After calibration, each pixel
136 in the CT-image is assigned a value corresponding to the density of the wood
137 at that point.

138 In practice, about ten discs were positioned vertically and scanned in
139 a single pass, resulting in a stack of CT-images. Then, a single CT-image
140 corresponding to each disc was isolated from the image stack.

141 The 200 CT-images were then processed with ImageJ software (Schneider
142 et al., 2012). The under-bark boundary of the disc and the position of the
143 pith were first recorded using a plug-in called “Gourmand” (Colin et al.,
144 2010).

145 The manually annotated images were then processed by a second plug-
146 in called “Sectoriseur” (Longuetaud et al., 2016). The “Sectoriseur” plug-in
147 creates, for each disc image, artificial rings of configurable average width
148 (Fig. 2) centred on the pith. This width was set to 1 mm, considering the
149 resolution of the CT images (0.5 to 1 mm per pixel). The plug-in takes as
150 input the average radius of the disc and the desired average width of the
151 artificial rings to calculate how many artificial rings are needed, and then
152 divides each radius ($n = 360$ radii) by this value. Each artificial ring is then
153 assigned an air-dried density value equal to the average density of the pixels
154 within it (background pixels with a density of less than 100 kg.m^{-3} are not
155 considered). These artificial rings are derived from the outer boundary of
156 the wood disc and do not necessarily follow the actual annual growth rings.
157 Artificial rings may intersect actual rings or encompass several rings at the

158 same time. The expected accuracy for wood density is therefore not at the
159 ring level but rather at the ring group level. The artificial rings may not
160 follow the actual rings at all in the case of irregularly shaped wood discs or
161 where knots are present within the discs (e.g., Fig. 2 on the right). In the
162 case of very regular shaped discs (circular or oval) the accuracy is better.

163 All density measurements (one row per artificial ring) were saved in the
164 `density` dataset.

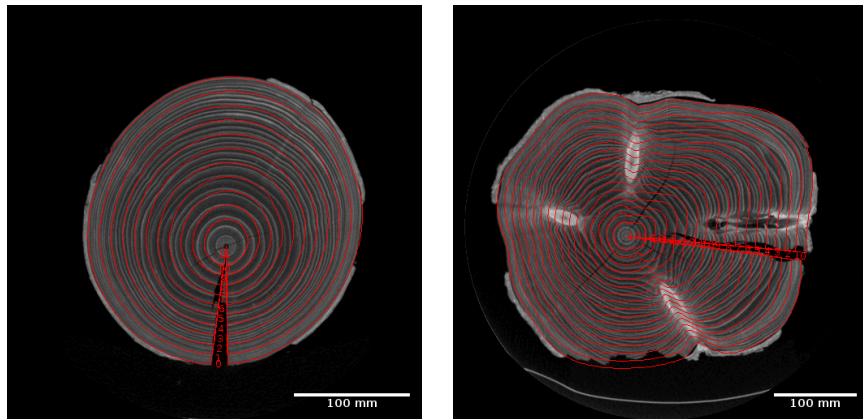


Figure 2: Artificial rings obtained with the “Sectoriseur” plugin (Longuetaud et al., 2016). To facilitate visualisation, the average width of each ring was set at 10mm instead of 1mm.

165 2.4. Ring width measurements

166 The measurements of RW were made using WinDENDRO software (WinDen-
167 dro, 2021) on four orthogonal radii for each wood disc. The resolution used
168 was set at 400dpi. A binocular magnifying glass was used to check the first
169 rings near the pith when the ring boundaries were difficult to see with the
170 naked eye.

171 Then, for each growth ring, an average width was obtained by subtracting
172 the root mean square of successive external and internal radii (each calculated
173 from the values measured on the four radii). This average *RW* was used in
174 this study.

175 A calendar year of growth (*GY*) and a cambial age (*CA*), *i.e.*, the ring
176 number counted from the pith, were associated with each annual ring.

177 All *RW* measurements (one row per annual ring) were recorded in the
178 `ringwidth` dataset.

179 *2.5. Coupling of ring width and density measurements*

180 The objective was to obtain a density value for each individual ring of
181 a disc (*RD*). For this purpose, the `ringwidth` dataset containing the *RW*
182 measurements of each annual ring and the `density` dataset containing the
183 density values of each artificial ring of 1mm width (on average) were used.

184 A scale normalisation, using relative radial positions from 0 to 1, was
185 used to link the two datasets. The coupling algorithm (Fig. 4) first consisted
186 of establishing, from the dataset `density`, an approximation function f of
187 wood density at any relative radial position by linear interpolation from
188 the artificial ring density data. The function `approxfun` of R generates a
189 function that performs such interpolation. Thus, from a given set of x_i
190 values (the relative radial positions of the artificial rings) and corresponding
191 y_i values (the air-dried density of the artificial rings), the generated function f
192 returns for any relative radial position x_j a linearly interpolated density value
193 $y_j = f(x_j)$. Then, for each actual ring of a disc, 100 relative radial positions
194 x_j were considered to generate 100 density values y_j . The average density of
195 a given annual ring was obtained as the average of the corresponding 100 y_j

196 values. An example of the output of the algorithm is given in Fig. 3.

197 The two types of measurements did not always match perfectly, as shown
198 by the offset, for the widest rings, between the density maxima (which should
199 be at the outer end of the rings) and the actual ring boundaries (Fig. 3).
200 However, at the scale of a whole ring or a few rings, the overall variations in
201 RD and RW seemed quite consistent.

202 At the end of this step, each annual ring of a disc could be described by
203 its CA , GY , RW and RD values.

204 *2.6. Annual ring density models from the literature*

205 Several RD prediction models that had been developed for spruce (Table
206 1) were tested and fitted to our dataset. We mainly present models that take
207 as input explanatory variables available in our dataset (i.e., cambial age, RW
208 and estimated height in the stem). Bouriaud et al. (2015) proposed several
209 models with RW and either cambial age or diameter of the stem at 1.30 m
210 as explanatory variables. As the diameter at 1.30 m was not available in
211 our dataset, only the models with cambial age could be tested. Piispanen
212 et al. (2014) compared the ring density of Norway spruce for even-aged and
213 uneven-aged stands and fitted a model accordingly. In their study, Molteberg
214 and Høibø (2007) proposed more efficient but more complex models taking
215 as input the site fertility index, diameter at 1.30 m and tree height but we
216 do not present them in Table 1 as we have none of these variables on our
217 trees. Even earlier, Olesen (1977) proposed a model depending only on RW
218 for comparison between several cambial ages demonstrating the importance
219 of the two variables, RW and cambial age.

Table 1: Equations found in the literature for predicting tree ring density (RD) for spruce. Only equations taking as inputs RW , cambial age and/or height in the tree were retained.

References	Number of trees	Equations
Bouriaud et al. (2015)	12	(1) $RD_{ij} = a_0 + a_1RW_{ij} + a_2RW_{ij}^2 + \frac{a_3}{X_{ij}^{a_4}}$
		(2) $RD_{ij} = a_0 + \frac{a_1}{1+RW_{ij}} + \frac{a_2}{X_{ij}^{a_3}}$
		(3) $RD_{ij} = a_0 + a_1RW_{ij}^{a_2} + \frac{a_3}{X_{ij}^{a_4}}$
		with i the tree, j the year, RD the ring density (air dry), RW ring width and X either the cambial age or the diameter at 1.30 m
Piispanen et al. (2014)	123	$RD_{ij} = a_0 + a_1CA_{ij} + a_2CA_{ij}^2 + a_3 \ln(CA_{ij}) + a_4 \ln(RW_{ij})$ $+ a_5 \ln(RW_{ij})CA_{ij} + a_6 DBH_i / Ddom$ with i the tree, j the year, RD the ring density (air dry), RW the ring width, CA the cambial age, DBH the diameter at 1.30m and $Ddom$ the mean diameter of the 100 thickest trees per hectare
Molteberg and Høibø (2007)	46	(1) $RD_{ij} = a_0 + a_1CA_{ij}$
		(2) $RD_{ijk} = a_0 + a_1H_{ik} + a_2 \ln(H_{ik} + 1) + a_3CA_{ijk}$
		with i the tree, j the year, k the disc, RD the basic density of the sample, H the height of the measurement, CA mean of the cambial age of the sample
Grammel (1990) in Lindström (1996b)	unknown	$RD_{ij} = a \exp(bRW_{ij})$ with i the tree, j the year, RD the ring basic density and RW the ring width
Olesen (1977)	≈ 150	$RD_{ij} = a_0 + \frac{a_1}{RW_{ij} + a_2}$ with i the tree, j the year, RD the ring basic density and RW the ring width
Hakkila (1968) in Lindström (1996b)	unknown	$RD_{ij} = a + b \log(RW_{ij})$ with i the tree, j the year, RD the ring basic density and RW the ring width

2.7. Statistical analysis

Data processing was carried out with the R software (R Core Team, 2021). Regressions were fitted to describe the variations of RD as a function of explanatory variables available in our study: RW , CA and the height level in the stem (H). The main functions used were: `t.test`, `lm`, `nls`, `anova`, `AIC` from `stats` package, `nlsLM` from `minpack.lm` package, and `nlsList`, `nlme` from `nlme` package.

For modelling purposes, we chose to retain most of the annual rings belonging *a priori* to juvenile wood but to remove the very first ring (ring number #1) from each disc, which was clearly much lower in density than subsequent rings. This strong increase would have been difficult to model as

231 it only occurs between rings one and two, and was of limited interest given
232 the small area represented by these rings as also highlighted by Molteberg
233 and Høibø (2007).

234 **3. Results**

235 *3.1. Descriptive analysis*

236 Depending on the height in the stem, the averaged air-dry densities RD
237 plotted against RW followed more or less the same trend: a decrease of RD
238 when RW increases (Appendix A). The rings at the bottom of the stems were
239 denser than those at other height levels for RW greater than approximately
240 3mm.

241 As proposed by Saranpää (1994), the juvenile wood limit was set at 10
242 rings in order to analyse the potential effect of juvenile wood on the $RW-RD$
243 relationship (Fig. 5 and Table 2). In rings considered mature by this defini-
244 tion, a significant negative $RW-RD$ correlation was observed at each height
245 level. In juvenile wood, the relationship between RW and RD was only ob-
246 served at stem bottom (0m) and shifted upward compared to mature wood.
247 Juvenile wood was significantly less dense, on average, than mature wood,
248 except at the base of the tree where it was significantly denser (confirmed by
249 a Student t-test for each height level given in Appendix B).

250 Plots of RD and RW as a function of cambial age (Fig. 6) and growth
251 year (Appendix C) help refine these observations. Regardless of height level,
252 a density peak is observed at ring #2, followed by a decrease in density until
253 approximately ring #10, and finally an increase for the higher cambial ages
254 toward the bark. The density minimum, around ring #10, seems to occur

Table 2: Slope parameters and significances for the eight regressions between air-dry density (RD) and ring width (RW) presented in Fig. 5. Rings less than 10 years old were assumed to belong to juvenile wood. The statistical significance is indicated by: ns: $p \geq 0.05$; *: $0.05 > p \geq 0.01$; **: $0.01 > p \geq 0.001$; ***: $p < 0.001$.

Height in the stem (m)		0	4.5	9	13.5
Juvenile wood	Slope	-22.15	0.39	0.24	-7.89
	P-value	***	ns	ns	*
Mature wood	Slope	-18.14	-35.12	-30.01	-16.35
	P-value	***	***	***	***

255 closer to the pith as the height level increases in the tree (i.e., for cambial
 256 age >10 at the base of the tree and <10 higher up).

257 By observing the annual variations of the correlation coefficient with CA
 258 (Fig. 7), it appears that the level of correlation is stable except around the
 259 density minimum near ring #10 where the correlation coefficient becomes
 260 close to zero.

261 The analysis of RW variations according to calendar year (Appendix
 262 C) allows us to make some assumptions about the history of the stand: It
 263 suggests for instance a thinning around 1992 (followed by an increase in RW),
 264 a drought event in 2003 (decrease in RW), as mentioned by Martinez-Meier
 265 et al. (2008), and probably another thinning around 2006.

266 Logically, the density curve appears smoother because the density mea-
 267 surements were averaged over the artificial rings which do not exactly follow
 268 the actual rings. However, it was interesting to observe a general decrease in
 269 density and ring width in subsequent years.

270 Fig. D.1 in Appendix D, which can be compared to the similar plot of
271 Wimmer and Downes (2003), does not show a clear effect of growth year on
272 the $RW-RD$ relationship except for the last years (starting around 2017)
273 where the correlation coefficient begins to increase toward zero.

274 3.2. Statistical analysis

275 On the basis of the previous observations, statistical models were fitted
276 to describe the variations of RD as a function of RW , CA and H .

277 A piecewise linear regression of RD with a first breakpoint at cambial
278 age $CA = x_0$ (in juvenile wood) and a second breakpoint at growth year
279 $GY = y_1$ (for the limit before the last decline of both RD and RW toward
280 bark) was first fitted on the whole dataset (except ring at $CA = 1$; see
281 Section 2.7). Full details of this preliminary modelling, including equations
282 and parameter estimates, are given in Appendix F. Most parameters were
283 found to vary as an exponential function of disc height, but the parameter
284 y_1 was found to be constant and equal to 2009.5 regardless of disc height,
285 showing that the decline in RD and RW began in 2009. The latter decline
286 was therefore probably related to an external event (presumably an attack
287 by the European spruce bark beetle *Ips typographus*) and not to a classical
288 evolution related to tree ontogeny.

289 For this reason, we decided to focus on modelling the first two parts as a
290 function of CA , RW and H (i.e., primarily ontogeny-related variation). After
291 removing the first ring ($CA = 1$) and the last growth years ($GY > 2009$),
292 the final dataset included 3846 rings. The following model (Eq. 1) was first
293 used:

$$RD = \begin{cases} a \cdot CA + b, & \text{if } CA \leq x_0 \\ c \cdot \exp(d \cdot CA) + e, & \text{if } CA > x_0 \end{cases} \quad (1)$$

294 where $e = a \cdot x_0 + b - c \cdot \exp(d \cdot x_0)$.

295 Then, mixed models including a random effect corresponding to the height
 296 level on the different parameters (tested one after the other) showed that the
 297 parameters x_0 , b and c varied with the height in the tree, especially at the
 298 bottom of the tree (see details in Appendix G). The following equations (Eq.
 299 2) were therefore used to account for this:

$$\begin{aligned} x_0 &= x_{01} \cdot \exp(H)^{-1} + x_{02} \\ b &= b_1 \cdot \exp(H)^{-1} + b_2 \\ c &= c_1 \cdot \exp(H)^{-0.5} + c_2 \end{aligned} \quad (2)$$

300 The parameters of the final model #1 were thus: a , b_1 , b_2 , c_1 , c_2 , d , x_{01}
 301 and x_{02} and their estimates and standard errors are given in Table 3. The
 302 RMSE, relative RMSE and AIC are given in Table 4. In Fig. 8 the model
 303 was used to simulate air-dry density for several height levels and to plot the
 304 results as a function of cambial age and calendar year. It appeared that the
 305 relationship between RD and CA was very different at the base of the tree
 306 compared to the other height levels (on the left). For a given CA , RD tended
 307 to be higher at 0m than at other height levels in juvenile wood and lower
 308 in mature wood. More generally, for a given CA and in mature wood, RD
 309 tended to increase with increasing height in the stem. For a given calendar
 310 year and in mature wood, the RD tended to decrease with increasing height

311 in the tree (ignoring the 0m height). The model predictions and observations
 312 are shown in Fig. 9.

313 The analysis of the residuals as a function of RW showing a clear trend
 314 (Fig. G.2 in Appendix G), the effect of RW was introduced in the following
 315 way:

$$\begin{aligned}
 X_{RW} &= f \cdot \exp(RW)^{-1} + g \cdot RW \\
 RD &= \begin{cases} a \cdot CA + b + X_{RW}, & \text{if } CA \leq x_0 \\ c \cdot CA + e + X_{RW}, & \text{if } CA > x_0 \end{cases} \quad (3)
 \end{aligned}$$

316 where $e = (a - c) \cdot x_0 + b$.

317 The parameters x_0 , b and c depended on the height in the stem following
 318 the same equations as for model #1 (Eq. 2).

319 The parameters of the final model #2 were thus: a , b_1 , b_2 , c_1 , c_2 , x_{01} , x_{02} ,
 320 f and g and their estimates and standard errors are given in Table 3. The
 321 RMSE, relative RMSE and AIC are given in Table 4. This model including
 322 RW was only slightly better than the one including only CA and H . The
 323 model predictions and observations are shown in Fig. 9.

Table 3: Parameters obtained when fitting the models (estimates and standard errors in brackets): Model #1 taking as input cambial age (CA) and height in the tree (H) (Eq. 1 and 2) and model #2 taking as input CA , H and RW (Eq. 2 and 3).

	a	b_1	b_2	c_1	c_2	d	x_{01}	x_{02}	f	g
Model #1	-2.22e+01 (7.71e-01)	1.21e+02 (3.70e+00)	4.93e+02 (3.97e+00)	1.62e+02 (2.74e+01)	-4.08e+02 (3.82e+01)	-2.81e-02 (5.17e-03)	4.23e+00 (1.84e-01)	6.12e+00 (1.43e-01)		
Model #2	-1.49e+01 (6.43e-01)	8.88e+01 (3.36e+00)	5.16e+02 (4.84e+00)	-3.16e+00 (2.10e-01)	5.30e+00 (1.73e-01)		4.27e+00 (2.51e-01)	7.33e+00 (2.02e-01)	6.79e+01 (8.24e+00)	-7.83e+00 (6.37e-01)

Table 4: Comparison of our models (#1 and #2) with other models from the literature for Norway spruce. The models have been here fitted on annual rings from years ≤ 2009 and excluding the ring number one of each disc.

References	Equation number	Df	RMSE (kg.m ⁻³)	Relative RMSE (%)	AIC
	(1) in Table 1	3842	51.73	11.50	41277
Bouriaud et al. (2015)	(2) in Table 1	3843	52.48	11.66	41386
	(3) in Table 1	3841	51.28	11.40	41212
Piispanen et al. (2014)	-	3840	48.58	10.80	40799
Molteberg and Høibø (2007)	(2) in Table 1	3842	59.84	13.30	42398
Grammel (1990) in Lindström (1996b)	-	3844	54.37	12.08	41657
Olesen (1977)	-	3843	52.65	11.70	41412
Hakkila (1968) in Lindström (1996b)	-	3844	52.79	11.73	41429
Model #1 taking as input CA and H	(1) and (2) in Section 3.2	3838	44.98	9.99	40209
Model #2 taking as input CA , H and RW	(2) and (3) in Section 3.2	3837	42.40	9.42	39758

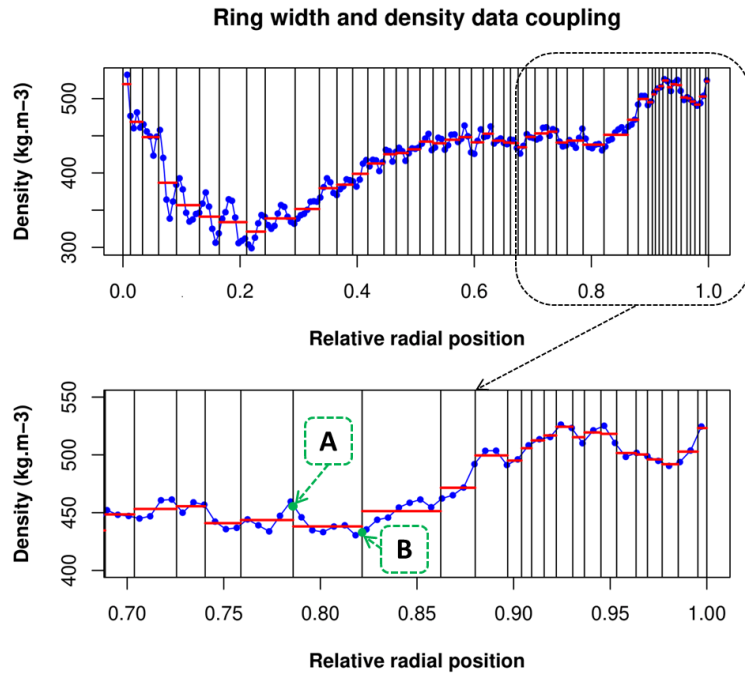


Figure 3: Coupling of ring width and density data over the whole radius of the disc (top) and zooming in on a part of the radius (bottom). The blue points represent the air-dry densities of the artificial rings obtained every millimetre. The black vertical lines are the boundaries of the actual annual rings. For a given actual ring, a sequence of 100 radial positions was considered. A and B are the points of intersection of the density curve of the artificial rings (in blue) with the boundaries of the actual ring considered. For each of the 100 radial positions (i.e., between points A and B), a density value was generated by means of an interpolation function. Finally, for a given actual ring, the horizontal red segment represents the average density obtained from the 100 interpolated density values. The case of the disc “E001.gb” is presented.

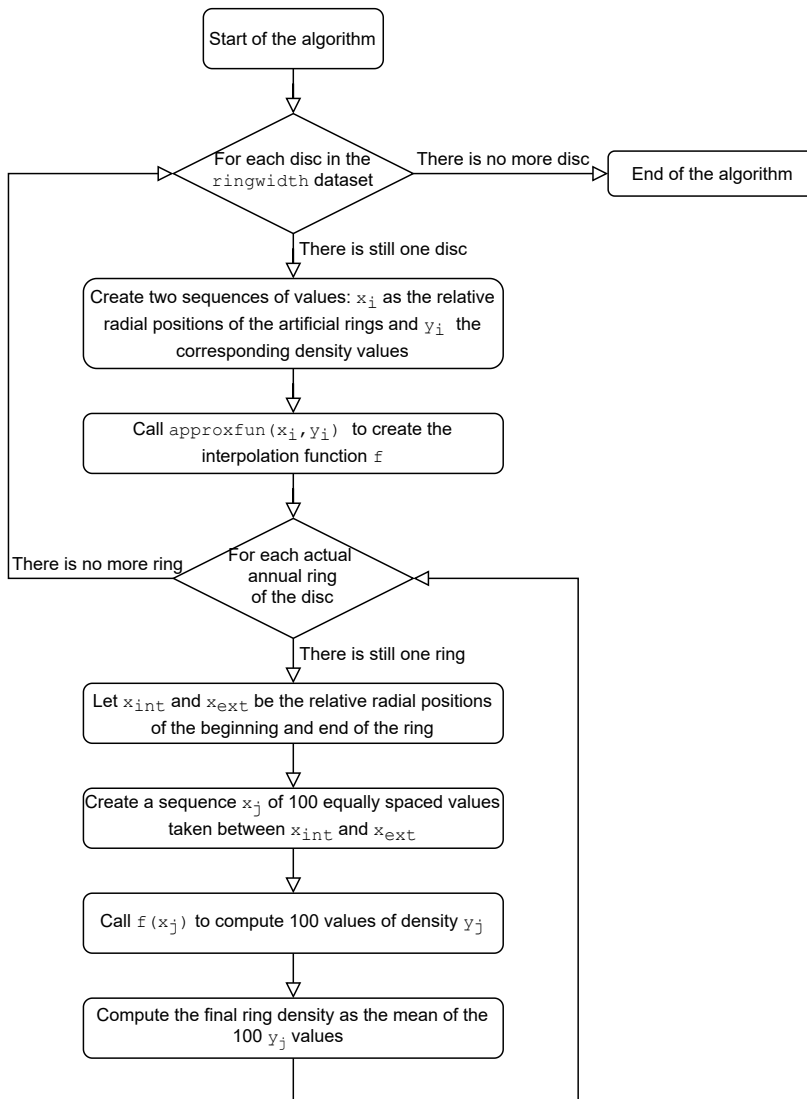


Figure 4: Diagram of the coupling algorithm.

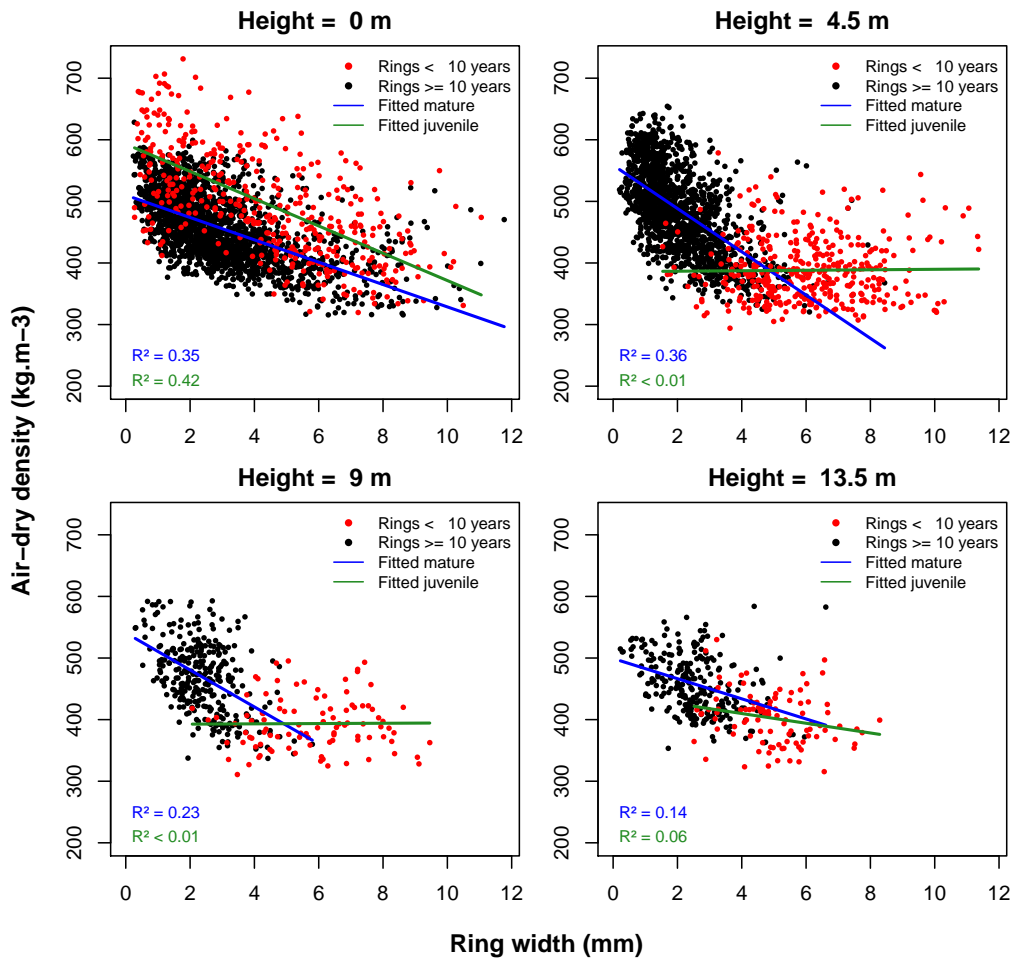


Figure 5: Air-dry density versus ring width (RW) for the different heights in the stem (0m, 4.5m, 9m and 13.5m) distinguishing juvenile wood (red points) from mature wood (black points). Regression lines were fitted for juvenile wood (in green) and for mature wood (in blue).

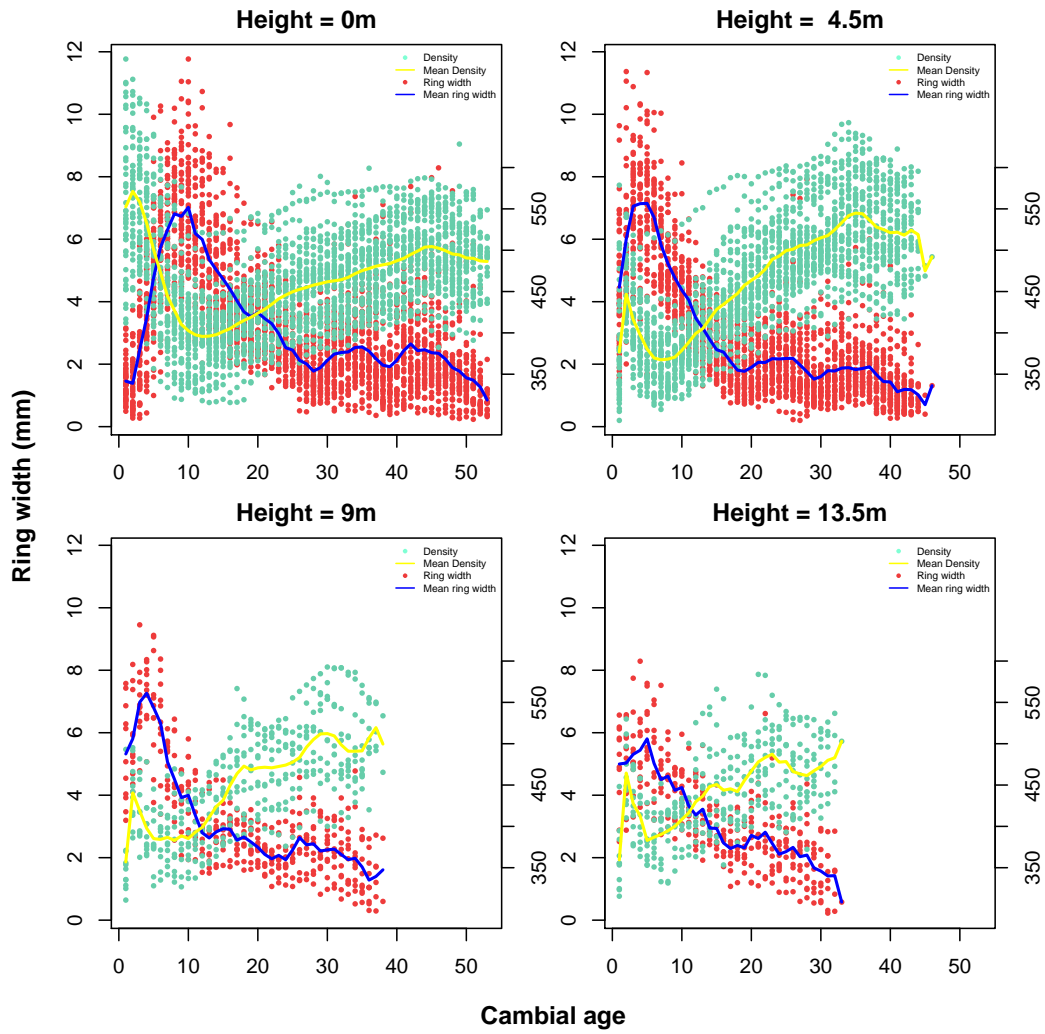


Figure 6: Ring width (red points) and air-dry density (green points) as a function of cambial age for the different heights in the stem (0m, 4.5m, 9m and 13.5m). Trend curves for ring width (in blue) and density (in yellow) are plotted.

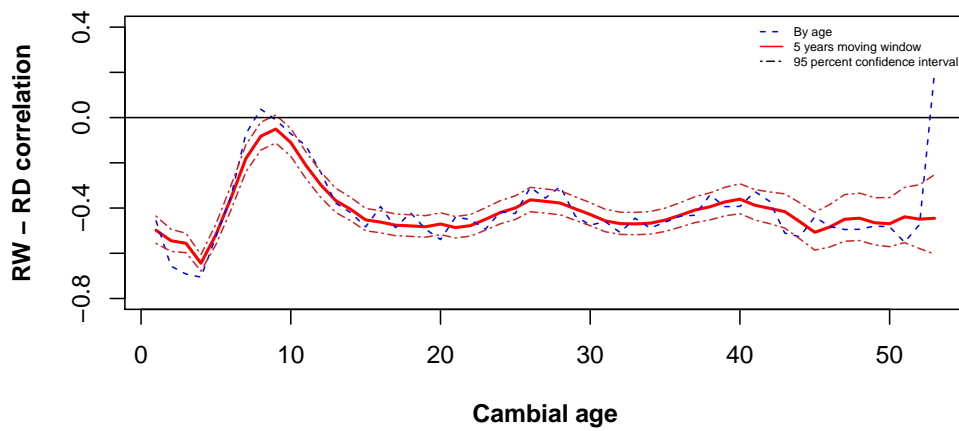


Figure 7: Pearson correlation coefficient between air-dry ring density (RD) and ring width (RW) as a function of cambial age, including all height levels. The coefficients are computed for each cambial age (dashed blue line) and then using a five years moving window for the computation to obtain a smoothed curve (red line). A 95% confidence band is plotted for the smoothed curve (dashed red line).

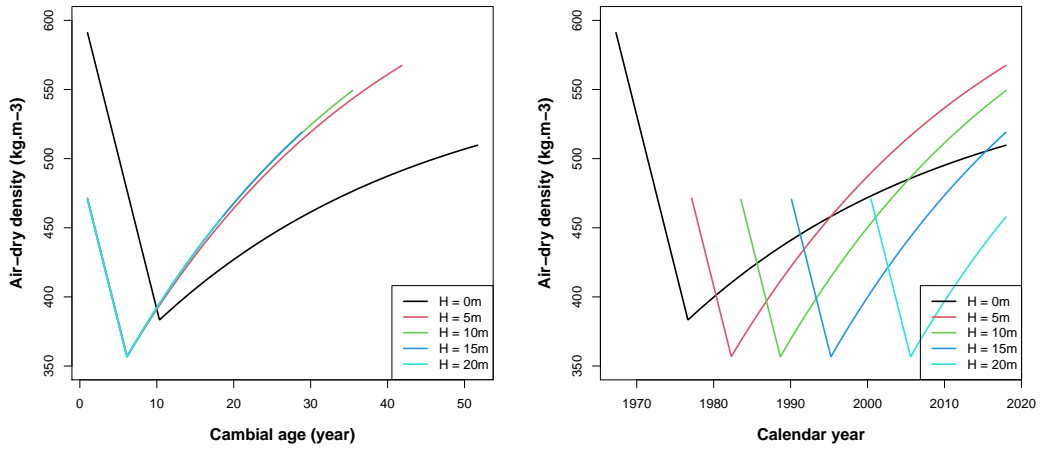


Figure 8: Simulations of air-dry density obtained by using model #1 for several height levels (0m, 5m, 10m, 15m and 20m). The model was used in extrapolation for heights 15m and 20m. The average total number of rings at each height level was extrapolated with the `splinefun` function of R (Appendix E).

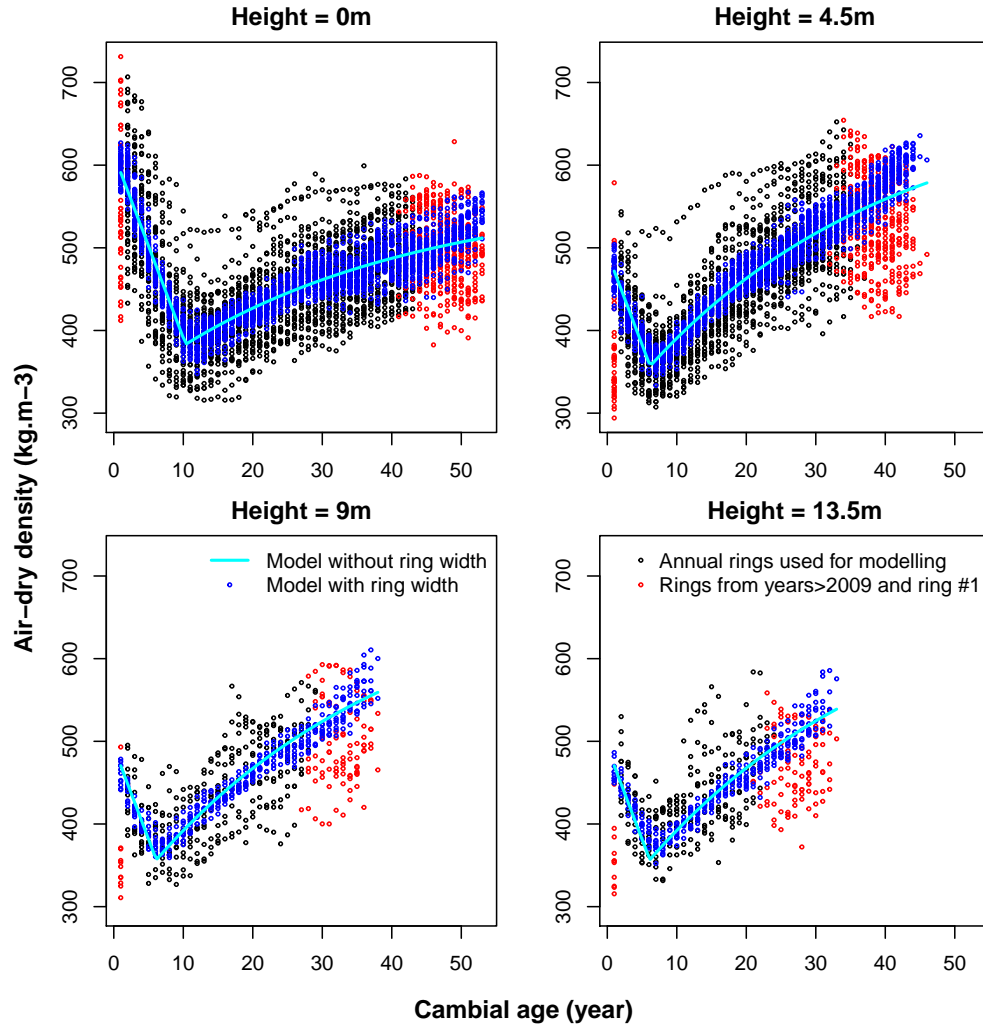


Figure 9: Observations and model predictions for each height level. Black dots correspond to data that were used for fitting the models. Red dots correspond to data that were not used for fitting the models (i.e., rings number one and rings from years > 2009). Predictions from the model that does not include ring width (RW) are in cyan (model #1; Eq. 1 and 2) and predictions from the model that includes RW (model #2; Eq. 2 and 3) are the blue dots.

324 4. Discussion

325 4.1. Factors involved in ring density variations

326 4.1.1. Cambial age

327 The radial patterns of *RD* that were observed in our study are consistent
328 with the most common results found in the literature (e.g., Olesen, 1977;
329 Petty et al., 1990; Molteberg and Høibø, 2006). Olesen (1977) reported a
330 density higher than that of mature wood for the innermost rings (density
331 is maximum at ring #3), then a decrease in density until rings #8-10 and
332 then an increase until reaching the average density of mature wood around
333 rings #15-20. Saranpää (1994) also chose to focus on the first 10 rings to
334 study the juvenile wood. In these 10 rings, the author observed a maximum
335 of density at ring #2 or #3 and then a decrease. In young Norway spruce
336 trees, Molteberg and Høibø (2006) found the minimum of density around
337 rings #5-8 followed by an increase in density towards the bark in mature
338 wood. This is the most commonly reported pattern for radial variations
339 in density, although differences are sometimes observed depending on stand
340 type (e.g., Petty et al., 1990; Piispanen et al., 2014), social status of the trees
341 or site fertility (e.g., Molteberg and Høibø, 2007), or fertilization (Lindström,
342 1996b). Piispanen et al. (2014) observed that trees in uneven-aged stands
343 had a very high density in the juvenile wood near the pith, then density
344 decreased until about ring #20 before rising again and decreasing slightly
345 at the end near the bark, which is a fairly typical pattern except for the
346 final decrease towards the bark. The density peak near the pith as well as
347 the decrease in density for the outermost rings were not observed for even-
348 aged stands. In our case, in an even-aged stand, the maximum density was

349 observed at ring #2, then a decrease in density was observed until ring #10
350 and finally the *RD* increased continuously from ring #10 to around ring
351 #45. At the bottom of the stem, the average density of the 10 first rings was
352 higher than the average density of mature wood. For the other height levels,
353 the overall patterns were about the same, but with a lower density in the
354 innermost rings and in juvenile wood in general. Such results suggest that
355 the limit between juvenile and mature wood was around ring #10. However,
356 this limit appeared to depend on the height in the stem for our sample. On
357 the basis of our model #1, the limit was estimated at ring #10 at 0m, #7
358 at 1.30m and #6 at 15m. These results, which support Hypothesis **H1**, but
359 with a variation according to the height in the tree, are original and have not
360 been found in the literature.

361 According to Olesen (1977), the strong decrease in density in juvenile
362 wood is related to a rapid increase in tracheid width in these first rings
363 (as an example, there are five times as many tracheids per unit area in the
364 innermost rings as in mature wood) although the cell walls are relatively thin,
365 particularly in the late wood. For Jyske et al. (2008), the decrease in density
366 in juvenile wood is due to a decrease in early wood density, which is not
367 inconsistent with the observation made by Olesen (1977). At the same time,
368 the proportion of late wood as well as its density increases with cambial age
369 (Olesen, 1977; Jyske et al., 2008) and this explains the increase in density
370 from juvenile wood outward.

371 This is broadly consistent with the observation that wood formed around
372 the pith in softwoods is of lower density than wood formed outside (Lachen-
373 bruch et al., 2011).

374 The presence of compression wood of higher density than normal wood
375 in the first rings near the pith may also help explain the trend of decreasing
376 wood density observed in juvenile wood (Gryc and Horáček, 2007).

377 4.1.2. Ring width

378 In our study, the negative $RW-RD$ relationship was observed regardless
379 of height in the stem in mature wood, thus supporting the Hypothesis **H2**.
380 A negative correlation between RW and RD has often been reported for
381 Norway spruce (e.g., Lindström, 1996a; Bouriaud et al., 2015).

382 At stem bottom, as reported by Olesen (1977), the slope of the negative
383 $RW-RD$ relationship was almost the same for juvenile and mature wood
384 but, for the same RW , the density was often higher in the juvenile wood. In
385 our study, a quite constant negative correlation was found in mature wood,
386 much more constant than what was observed in the study of Wimmer and
387 Downes (2003). In juvenile wood at other height levels, there was little or
388 no relationship between RD and RW , invalidating hypothesis **H3**. The ob-
389 served increase of RW from about 1 to 7mm on average during the first 10
390 years at stem bottom could allow the young tree to delay material allocation
391 until leaves and roots are sufficiently developed, while the decrease in density
392 would correspond to an increased need for hydraulic conductivity. Later in
393 the tree life, the decrease in RW (and especially of early wood width, leading
394 to an increase in late wood proportion and thus in RD) could make the con-
395 ductive area of the rings to remain broadly constant. From a biomechanical
396 point of view, there is also an interest for the young tree to be flexible so as
397 not to break under the effect of the wind, whereas a larger tree must gain in
398 rigidity by building denser wood so as not to fall. The tree must invest in its

399 structural stability as it grows. According to Lindström (1996a), crown de-
400 velopment acts as a primary regulator of wood structure and density through
401 four independent theories of wood formation (mechanical theory, nutritional
402 theory, water conduction theory and hormonal theory). The author points
403 out that the size of the crown influences the transpiration requirements and
404 therefore the proportions of conduction tissue and strength tissue (early- and
405 latewood).

406 4.1.3. Height in the stem

407 As shown by the relationships between the model parameters and H
408 (Appendix G.1), the changes in density with height in the stem were more
409 pronounced at the stem base. From our model, it thus appeared that the
410 $RW-RD$ relationship varied with height in the stem, contradicting Hypoth-
411 esis **H3** of stability of the relationship. In the absence of measurements
412 between 0 and 4m height in our study, precise variations in density could not
413 be assessed, but it is likely that the effect of height is not negligible at breast
414 height, at which density data are most often measured. Although according
415 to several studies cited by Saranpää (1994), species in the genus *Picea* show
416 only slight changes in wood properties with height.

417 As can be seen from our results, juvenile wood tended to be denser on
418 average at the base of the tree. While for the other height levels, the density
419 was on average lower in juvenile wood than in mature wood.

420 In juvenile wood, RD at stem base was found to be higher than RD at the
421 same cambial ages at 4.5 m or higher in the stem (see model simulations).
422 Conversely, the density of mature wood for given cambial ages tended to
423 increase with height in the tree, but the important difference in RD was

424 primarily observed in our study between the base of the tree and the rest of
425 the stem. The increase in density with height in the stem for given cambial
426 age classes was also observed by Molteberg and Høibø (2006) and Jyske et al.
427 (2008), and would be related to apical meristem maturity (Jyske et al., 2008).

428 Inversely, model simulations showed that for a given GY , RD tended to
429 decrease with increasing height in the tree, in agreement with the results of
430 Olesen (1977) and Jyske et al. (2008). This decrease in density can logically
431 be explained by the increase in RW with height in the tree for a given calen-
432 dar year, associated with the decrease in latewood proportion, and also with
433 the increase in the proportion of juvenile wood (Jyske et al., 2008). Ole-
434 sen (1977) explained this decrease in density by a greater width of tracheids
435 toward the top of the tree in a given ring.

436 On a more global scale, Gryc and Horáček (2007) observed on one *Picea*
437 *abies* tree a decrease in density with increasing height in the stem in a region
438 of the stem including compression wood, while density was slightly increasing
439 in the region of opposite wood. Molteberg and Høibø (2007), at the disc level,
440 observed a decrease in density from butt end to 7-8 m.

441 4.2. Statistical modelling

442 Several models from the literature, as shown in Table 4, were fitted to our
443 data, and new models were developed, that were more suitable for describing
444 both the radial and vertical variations of RD . It should be noted that the
445 purpose of developing new models was primarily to be able to explain our
446 data. They are therefore explanatory models rather than predictive models.
447 The results obtained are relevant compared to others found in the literature
448 and prove that our new method is relevant to obtain fully exploitable data

449 of high scientific value. In particular, an important difference, not often
450 mentioned in the literature, was highlighted between juvenile wood at the
451 base of the tree (of higher density) and juvenile wood at other height levels.

452 4.3. *Juvenile wood definition*

453 Analysis of the $RW-RD$ relationship and the observed variations in ju-
454 venile wood raise questions about the definition of juvenile wood area and
455 its variation with height in the stem. For Saranpää (1994), the properties
456 of juvenile wood change with height in the stem. Lachenbruch et al. (2011),
457 quoting Larson (1969), pointed out that the term juvenile wood is more ap-
458 propriate for wood formed by young trees, *i.e.*, at the base of the tree, while
459 corewood (or also sometimes crown-formed wood) is more appropriate for
460 wood formed near the pith but higher up. Finally, Burdon et al. (2004) pro-
461 posed a new terminology where juvenility *versus* maturity is appropriate for
462 vertical variations while corewood *versus* outerwood is rather for radial vari-
463 ations. Through our study we have indeed highlighted important differences
464 between juvenile wood formed at the base of the tree and that formed higher
465 up, and it appeared important to distinguish these two types of wood. It
466 would also be interesting to make other measurements to study the corre-
467 spondence between the patterns of radial density variation and those of fibre
468 length or microfibril angle, for example.

469 4.4. *Methodological aspects*

470 We found in our data the classical pattern of radial density variation
471 for Norway spruce: First a decrease in density from a ring near the pith to
472 a minimum around ring #10 and then an increase towards the bark (Jyske

473 et al., 2008). The original coupling method developed for this study therefore
474 seems appropriate to obtain relevant data in agreement with the main results
475 of the literature.

476 A likely source of uncertainty was that density was measured on the whole
477 discs while ring width was measured on four orthogonal radii whose location
478 on the discs was not precisely known. For a better match, it might be more
479 efficient in the future to cut four radial strips to ensure that the same regions
480 of the discs are measured for density and ring width.

481 This method allowed us to go even further with original results on the
482 vertical variations of the radial density variation pattern and the $RW-RD$
483 relationship, relatively unstudied in the literature, and also on particular
484 phenomena such as the drop in density from the year 2009. We do not know
485 what is responsible for this sudden decrease but one hypothesis would be an
486 attack by the European spruce bark beetle *Ips typographus*. The phenomenon
487 of fungal infestation associated with an attack of the bark was proved to re-
488 duce drastically the wood quality with also weight losses (Hýsek et al., 2021).
489 The degree of degradation depends on the duration of the fungi activity. Be-
490 fore three years, there is no strong loss of quality. In our study, the decrease
491 in wood density was observed for the last 10 years of growth.

492 **5. Conclusion**

493 The proposed method is suitable to process wood discs and does not re-
494 quire extensive sample preparation or long X-ray image acquisition time. It
495 has the advantage of measuring the density over the entire surface of the
496 discs. The method is original because it makes it possible to couple precise

497 RW measurements made on high-resolution colour images with high-speed
498 density measurements made on lower resolution X-ray images, without any
499 sample preparation. The initial idea of this work was to propose an inter-
500 mediate method, a little less accurate but faster than the classical methods
501 used in dendrochronology, which require fine and time-consuming sample
502 preparation.

503 The primary objective of this work was to provide data for research on
504 density variation in the tree (radially and vertically) in relation to volume
505 growth for the purpose of, for example, fitting models. As an example of
506 application, we are currently developing technologies to automatically mea-
507 sure ring widths in industry from RGB images of log cross-sections and these
508 models would be needed to provide information on the quality of these woods.

509 This coupling method proved to be relevant. The coupling between the
510 two types of measurements was conclusive insofar as it made it possible
511 to reproduce the classic trends known through the literature regarding the
512 existing relationships between RW and RD in the case of spruce: Mostly
513 negative relationships. The data obtained allowed us to go further with
514 original and little studied results, notably on the evolution of the radial
515 variation pattern of density and on the RW – RD relationship with height,
516 and to question the definition of the juvenile wood zone.

517 The models fitted on the basis of our data were able to describe the
518 variations of RD with CA , RW and height in the stem.

519 The definition of juvenile wood area and its variations with height in the
520 stem could also be better explored with these data. In our study, density
521 variations in juvenile wood were different at the base of the tree compared

522 to higher height levels. Juvenile wood at the base of the tree tended to have
523 relatively narrow RW associated with high RD , compared to juvenile wood
524 formed at higher height levels and even to mature wood formed at the base
525 of the tree. A negative RW – RD relationship was observed in juvenile wood
526 at the base of the tree but not at other height levels. This study therefore
527 validates the relevance of distinguishing between juvenile wood formed at
528 the base of the tree and that formed higher up as several authors have also
529 suggested.

530 The simulations of air-dried RD using the developed models allowed to
531 conclude that for these spruce trees the variations in RD were more influenced
532 by CA than by the height in the tree except at the base of the tree where the
533 trends were really different. The two models developed from our data (one
534 taking into account RW and the other not) showed very comparable results
535 although the model using RW , in addition to CA and height in the stem, was
536 logically better. Compared to other models from the literature, our models
537 were also more accurate, which is only to be expected given that our models
538 were designed for our dataset, but it further validates the relevance of the
539 proposed method. Our models allowed to explore and better understand the
540 variations in wood density of spruce.

541 The next step would be to apply this method on a larger scale on a better
542 described sample (e.g., through a better knowledge of the stand history, with
543 more measurements at the bottom of the stems) and extended to other species
544 to confirm its interest.

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