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## Wood density proxies of adaptive traits linked with resistance to drought in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco)

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### Abstract

**Key message** Proxies of adaptive traits for resistance to drought were discovered among original annual ring density variables in Douglas fir.

**Abstract** A comparison of dead and surviving Douglas fir trees following the 2003 drought was made to define proxies of adaptive traits for resistance to drought. Increment cores were sampled from trees from three French regions: Centre, Midi-Pyrénées and Burgundy. Original tree-ring variables were calculated, based on a sliding density criterion dividing the microdensity profile into high- and low-density segments. Tree rings were analysed at each site in a number of consecutive annual rings before the 2003 drought event. Comparison between pairs of surviving and dead trees and between pairs of randomly selected trees (whether dead or alive) supports the evidence

of systematic dissimilarities between surviving and dead trees in a number of original density variables. Correlation analysis between original and conventional ring density variables indicates a weak association. We found that the surviving trees were denser than the dead trees in all three sites, but that the denser part of the ring varied from region to region. We identified several original density variables intended to be used as proxies of adaptive traits in future studies of genetic determinism of Douglas fir resistance to drought. **34**

**Keywords** Douglas fir · Drought · Mortality · Survival · Adaptation · Adaptive traits · Wood density · Microdensity **37**

### Introduction **38**

The intensity, frequency and duration of drought conditions and heat waves related to climate change are increasing and have already resulted in serious incidences of drought-related tree mortality (Adams et al. 2009; Van Mantgem et al. 2009; Allen et al. 2010; Williams et al. 2010; Martinez-Vilalta et al. 2012; Wang et al. 2012; Anderegg et al. 2012, 2013). Climate change projections show that many tree species will be more exposed to potential drought (Hanson and Weltzin 2000; Aber et al. 2001; Jump et al. 2006; Pluess and Weber 2012). Whether forest trees are able to adapt successfully to these increasingly severe and more frequent drought events depend on their ability to evolve. Recent studies tend to demonstrate that there is potential for evolutionary responses to climate change in tree populations (Alberto et al. 2013). The evolutionary mechanism that may enable trees to adapt relies on the magnitude of genetic variation and on the heritability of the adaptive traits involved in resistance to drought. **56**

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Precise estimation of genetic variation and heritability requires measurement of a large number of genotypes and individuals (Cregg 2004; Wortemann et al. 2011). However, the usual methodology applied to drought tolerance studies demands intensive and time-consuming measurements (Cregg 2004; Aranda et al. 2012). Hence, it is necessary to find the putative adaptive traits among more easily measurable drought-resistant traits.

An adaptive trait is related to mating ability, fecundity and/or survivorship, i.e. to fitness (also defined as *overall reproductive success*). In most studies involving adaptive traits, the relationship with fitness is inferred from the known or supposed involvement of the traits in functional processes. In this article we look for proxies of adaptive traits by calculating their relationship with fitness. Among the fitness components, it is difficult and time consuming to observe mating ability and fecundity in forest trees, while survivorship is much more easily observed. We therefore concentrate on detecting adaptive traits by calculating their relationship with survivorship.

In comparison with other conifer species, Douglas fir is a relatively drought-tolerant species (Eilmann and Rigling 2012). Despite this, some mortality events were observed in Douglas fir stands following the 2003 drought and heat wave in several regions of France. In three regions, Centre, Burgundy and Midi-Pyrénées, (Martinez-Meier et al. 2008a, b); Sergent (2011) and Sergent et al. (2012) have established that such mortality events were induced by soil moisture deficit. In Douglas fir, there is evidence that the xylem structure and some basic wood properties such as density may be directly or indirectly involved in adaptive functional processes and are related to survival. In a previous study of a Douglas fir provenance trial in the Centre region, systematic differences were found between dead trees and surviving neighbours for latewood density traits after the 2003 drought (Martinez-Meier et al. 2008a, b). Sergent (unpublished data) found a relationship between mortality and earlywood density after recurrent drought. Domec and Gartner (2002) suggested that the proportion of earlywood and latewood could be an adaptive trait linked to hydraulic properties in this species. Douglas fir is more drought tolerant when it originates from dry regions (Kavanagh et al. 1999; Pharis and Ferrell 1966). Sergent (2011) found that interior provenances from dry regions had a higher wood density. These results, together with the relationships found between resistance to cavitation (breaking of the water column within the xylem) and wood density in Douglas fir (Dalla-Salda et al. 2009), show that traits based on wood density components are involved in the response to drought in this species. In this study we selected wood density traits as our candidate proxies of adaptive traits for drought resistance.

Wood density traits used in previous survival studies of Douglas fir were based on ring microdensity profiles. Conventional ring microdensity traits are built from a standard earlywood-latewood boundary criterion established according to Lenz et al. (1976): the density threshold between earlywood and latewood lies exactly at the midpoint between the maximal and the minimal density. This definition of earlywood and latewood is consistent with Mork's index which is based on anatomical differences between these two parts of the ring. The variables based on the earlywood-latewood boundary are called *conventional variables* hereafter. The definition of an earlywood-latewood boundary is relevant from the wood anatomy perspective, but does not directly hint at any physiological process occurring in the xylem. Thus, the authors wonder whether original ring density variables which are not based on the standard earlywood-latewood boundary would optimize the detection of differential vulnerability to drought-induced mortality in Douglas fir. There are some reports about alternative methods aiming at better utilizing the data contained in ring microdensity profiles (Rozenberg et al. 1999; Koubaa et al. 2005; Ivkovic and Rozenberg 2004; Franceschini et al. 2013). Dalla-Salda et al. (2011) showed that original density traits in Douglas fir which were not based on the earlywood-latewood model were more strongly related to resistance to cavitation than conventional density variables based on the earlywood-latewood model.

The objective of this article is to look for proxies of adaptive traits that should be investigated to evaluate the potential of Douglas fir to evolve and adapt to more frequent and severe drought conditions. In the present study, we decided to investigate the relationship between wood traits and survivorship after drought as a means of defining adaptive traits for drought tolerance. We conducted a new comparison of dead and surviving trees spanning a wide geographical area in France with three experimental sites located in three regions: Centre (CE), Burgundy (BO) and Midi-Pyrénées (MP). We re-analysed the microdensity profiles of the Centre region (Martinez-Meier et al. 2008a, b) and used microdensity profiles collected in Burgundy and Midi-Pyrénées regions (Sergent 2011; Sergent et al. 2012) to extend the study to these two regions. We deepened the tree-ring study and investigated more systematically basic wood properties using a wide-ranging definition of density variables (Rozenberg et al. 1999). We built original annual ring variables according to a sliding density criterion, vertically separating the microdensity profiles into high- and low-density segments. We then tested and compared the potential of these new variables to statistically explain the difference between the surviving and dead trees after drought events. The scope of this article is intentionally limited to the definition and the choice of a

163 small set of new wood density traits putatively well suited (Martinez-Meier et al. 2008a, b). Differences due to  
 164 to the analysis of the genetic determinism of drought provenance origin were not considered in this study.  
 165 resistance. The two other stands are a nine-plot trial from the Midi-  
 166 **Materials and methods** Pyrénées region in the south of France and an 18-plot trial  
 167 from the Burgundy region in the centre-north-east of  
 168 France (Sergent 2011; Sergent et al. 2012), respectively.  
 169 Each plot has at least two dead trees per plot. The selected  
 170 stands are pure Douglas fir stands with individuals a min-  
 171 imum of 20 years old at the time of sample collection.  
 172 **Site description**  
 173 The sites and years of study were previously described in  
 174 Martinez-Meier et al. (2008a, b) and Sergent (2011) and  
 175 Sergent et al. (2012). The most important site characteris-  
 176 tics are presented in Table 1. Climatic data were collected  
 177 from the Météo-France weather station nearest to each site  
 178 (Martinez-Meier et al. 2008a, b; Sergent et al. 2012).  
 179 The Centre region (CE) has, according to Joly et al.  
 180 (2010), a modified oceanic climate with mild temperature  
 181 and fairly low precipitation, especially in summer. Bur-  
 182 gundy region (BO) has a semi-continental climate, with a  
 183 higher contrast between summer and winter temperature  
 184 than the CE region and higher precipitation. The site of the  
 185 Midi-Pyrénées region (MP) has a warmer climate than the  
 186 CE and BO region sites, with the greatest contrast between  
 187 winter and summer temperature. Precipitation is the highest  
 188 of the three regions, but with a fairly dry summer (Joly  
 189 et al. 2010).  
 190 **Douglas fir stands**  
 191 Three Douglas fir stands were used in this study. In the  
 192 three experimental trials, mortality was observed and  
 193 proved to be a consequence of drought events by Martinez-  
 Meier et al. (2008a, b) and Sergent (2011) and Sergent  
 et al. (2012).  
 The first stand is a provenance trial established in 1975  
 and located in Vitry-aux-Loges, CE region, Forêt d'Orlé-  
 ans, France, with 60 provenances represented in the sample  
 (Martinez-Meier et al. 2008a, b). Differences due to  
 provenance origin were not considered in this study.  
 The two other stands are a nine-plot trial from the Midi-  
 Pyrénées region in the south of France and an 18-plot trial  
 from the Burgundy region in the centre-north-east of  
 France (Sergent 2011; Sergent et al. 2012), respectively.  
 Each plot has at least two dead trees per plot. The selected  
 stands are pure Douglas fir stands with individuals a min-  
 imum of 20 years old at the time of sample collection.  
**Sampling and microdensity profiles**  
 Details of the randomized approach used for sampling the  
 dead and surviving trees are presented in Martinez-Meier  
 et al. (2008a, b). In each trial, several pairs of dead and  
 immediately adjacent surviving trees were selected. In the  
 CE region, 65 pairs were sampled between April and June  
 2006. In the BO and MP regions, respectively, 45 and 28  
 pairs were sampled between March and October 2009  
 (Sergent 2011; Sergent et al. 2012). One radial increment  
 core was extracted at breast height from each tree using a  
 5.15 mm AND MATTSON mechanical Pressler borer. In  
 total, 276 increment cores were collected and processed.  
 The increment cores were analysed using indirect X-ray  
 wood densitometry (Polge 1978). X-ray films were scanned  
 and digital images were processed using the image analysis  
 software Windendro (Guay et al. 1992). The software  
 “Interdat.exe, version 1.1” developed by Dupouey  
 (unpublished) was subsequently used to cross-date the  
 microdensity profiles, to verify and confirm annual ring  
 identification. The software R was used to control the ring  
 limits and check the quality of the intra-ring density pro-  
 files. The cross-dated microdensity profiles were then used  
 and analysed for a number of consecutive years before the  
 2003 drought, ranging from 1986 to 2002 in CE, and from  
 1993 to 2002 in MI and BO.

**Table 1** Site characterization

Site	Mean annual precipitation (mm) for the period indicated	Annual mean of minimum temperature (°C)	Annual mean of maximum temperature (°C)	Geological background
Centre region (CE) Vitry-aux-Loges, Orléans forest 47° 57' N, 2° 16'E <sup>a</sup>	748 1986–2003	6°	15.9°	Mainly sand and clay of geological type “Sologne”
Burgundy region (BO), in NE of the Massif-Central <sup>b</sup>	973 1971–2000	−1.5 °C	24.6°	Plot spreads over a range of bedrock types, mainly granite, and others such as clay, basalt and shale
Midi-Pyrénées (MP) region, in SW of France <sup>b</sup>	1,123 1971–2000	−1.1	24.9 °C	Plot spreads over a range of bedrock types, mainly schist and others such as gneiss, shale and granite

<sup>a</sup> From Martinez-Meier et al. (2008a, b)

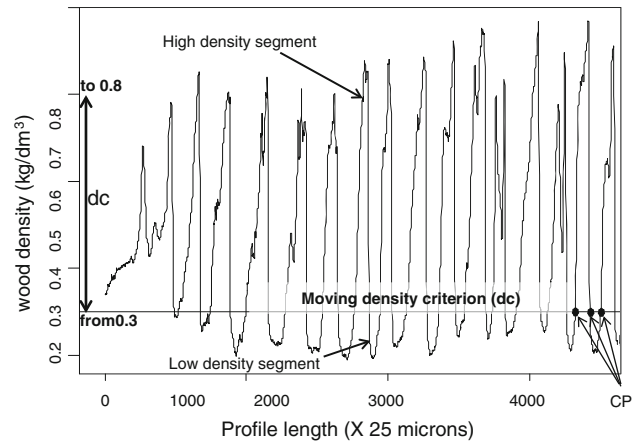
<sup>b</sup> From Sergent (2011)

## 228 Definition of the density variables

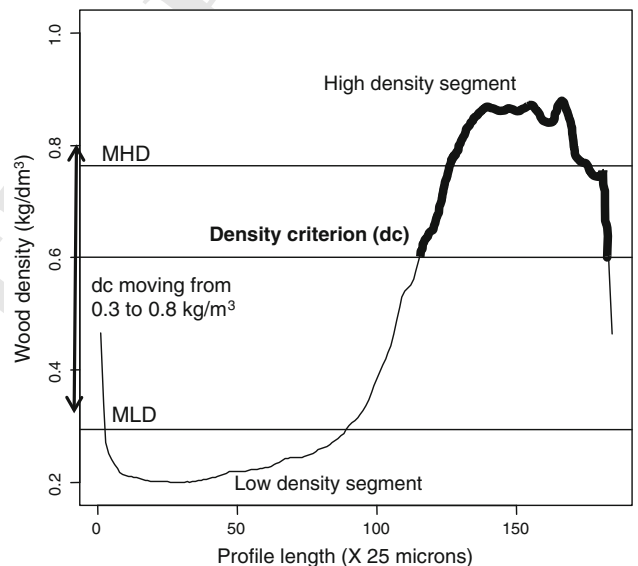
229 In the “**Introduction**” we explained that the annual ring  
 230 density variables are usually defined according to the  
 231 position of a boundary between earlywood and latewood  
 232 which is similar to Mork’s definition used in wood anat-  
 233 omy. The annual ring variables based on this earlywood-  
 234 latewood model are hereafter referred to as *conventional*  
 235 *ring variables*. In this study we defined a set of uncon-  
 236 ventional density variables not based on the earlywood-  
 237 latewood model. We used an original procedure based on a  
 238 sliding density criterion (the *dc* horizontal threshold)  
 239 defined and used by Rozenberg et al. (1999). The same  
 240 variables were calculated at two levels: first at the total  
 241 microdensity profile level and second at the annual ring  
 242 level. In each case, the microdensity profiles and the annual  
 243 rings were *vertically* divided into two parts: high- and low-  
 244 density segments based on the local segment density  
 245 compared to the *dc* values (Fig. 1 shows the total micro-  
 246 density level and Fig. 2 shows the annual ring level). The  
 247 values of the *dc* parameter ranged from 0.3 to 0.8 kg dm<sup>-3</sup>  
 248 with a 0.1 kg dm<sup>-3</sup> increment. For each *dc* value, the  
 249 following wood density variables were then calculated: the  
 250 mean of the high-density segment (the part of the profile  
 251 which is over the threshold, MHD), the mean of the low-  
 252 density segment (the part of the profile which is under the  
 253 threshold, MLD), the coefficient of variation of the high-  
 254 density segment (CVHD), the coefficient of variation of the  
 255 low-density segment (CVLD) and the proportion of high-  
 256 density segment (the length of the high-density segment  
 257 divided by the total profile length at the total profile level  
 258 or by ring width at ring level, PHD). For each variable and  
 259 each *dc* value, there is only one value per tree at the total  
 260 profile level, while there are as many values as there are  
 261 annual rings in the total profile for the variables calculated  
 262 at the annual ring level. At the total profile level, an  
 263 additional variable was calculated: the number of inter-  
 264 sections between the microdensity profile and the *dc*  
 265 threshold, referred to as the number of crossing points  
 266 (CP). The total number of original variables calculated is  
 267 36 at the profile level and 30 at the annual ring level (i.e.  
 268 six *dc* values times the number of original variables,  
 269 Figs. 1 and 2). All calculations used computer routines  
 270 written in R language (R Core Team 2013).

## 271 Statistical analysis

272 To investigate the possible differences between surviving and  
 273 dead trees for all original variables, we used the following  
 274 statistical analysis: for each variable, an ad hoc Monte Carlo  
 275 procedure was applied to construct a reference population of  
 276 differences between trees of randomly associated pairs, without  
 277 replacement and without consideration of health status



**Fig. 1** Applying a sliding density criterion (*dc*) vertically and dividing the microdensity profile into two density segments: one high density and one low density. Here, the value of *dc* is 0.3 kg dm<sup>-3</sup>. Some crossing points between *dc* and the microdensity profile are shown (CP)



**Fig. 2** Applying a sliding density criterion (*dc*) vertically and dividing the annual ring into two density segments: a high-density segment and a low-density segment. Here the value of *dc* is 0.6 kg dm<sup>-3</sup>. The mean of the high-density segment (MHD) and of the low-density segment (MLD) are shown

(Martinez-Meier et al. 2008a, b). By bootstrapping these ran-  
 278 dom differences 10,000 times, the reference population con-  
 279 structed follows a normal distribution with a mean of zero. This  
 280 reference population was then used for hypothesis testing on  
 281 observed mean differences between dead and surviving trees.  
 282 This enabled the optimum value for the moving density cri-  
 283 terion (*dc*) that enhances the discrimination between the sur-  
 284 viving and dead trees to be recorded. Randomization was  
 285 carried out using a Monte Carlo routine written in R language  
 286

**Table 2** Absolute value of  $\log_{10}$  of associated probabilities of observed mean differences between surviving and dead trees under  $H_0 = \text{no difference}$  for original variables calculated at the total microdensity profile level

$dc$ ( $\text{kg dm}^{-3}$ )	MHD	MLD	CVHD	CVLD	PHD	CP
Centre region (CE)						
0.3	2.13**	0.32 ns	1.77*	0.20 ns	0.86 ns	0.52 ns
0.4	2.55**	0.46 ns	0.31 ns	0.32 ns	0.91 ns	1.65*
0.5	2.14**	0.26 ns	0.37 ns	0.12 ns	1.68*	3.17***
0.6	1.45*	0.17 ns	1.10 ns	0.14 ns	2.58**	4.42***
0.7	1.36*	0.25 ns	1.82*	0.32 ns	2.40**	3.28***
0.8	1.55*	0.52 ns	1.62*	0.42 ns	2.06**	1.83*
Midi-pyrenees region (MP)						
0.3	5.24***	12.92***	3.44***	9.64e-17 ns	3.57***	1.16 ns
0.4	7.94***	10.46***	0.63 ns	1.45e-16 ns	2.84**	0.038 ns
0.5	8.00***	7.46***	0.48 ns	3.85e-16 ns	3.57***	0.08 ns
0.6	6.60***	3.17***	2.26**	2.56e-14 ns	5.35***	0.54 ns
0.7	6.25***	2.27**	3.47***	1.55e-10 ns	6.08***	4.40***
0.8	4.56***	2.18*	1.40*	2.92e-07 ns	7.52***	7.72***
Burgundy region (BO)						
0.3	0.75 ns	2.08**	0.63 ns	0.0007 ns	1.07 ns	0.19 ns
0.4	0.81 ns	1.73*	0.44 ns	0.001 ns	1.06 ns	0.73 ns
0.5	0.77 ns	1.51*	0.53 ns	0.004 ns	1.11 ns	1.57*
0.6	0.82 ns	1.24 ns	0.42 ns	0.004 ns	0.93 ns	0.99 ns
0.7	0.60 ns	0.60 ns	0.52 ns	0.005 ns	1.13 ns	1.15 ns
0.8	0.42 ns	1.41*	0.43 ns	0.027 ns	0.56 ns	0.51 ns

$dc$  density criterion,  $\log_{10}$  of associated probabilities, *ns* not significant (\*\*\*) for  $p < 0.001$ , (\*\*) for  $p < 0.01$  and (\*) for  $p < 0.05$

(R Core Team 2013). The results are presented as the  $\log_{10}$  of the probabilities associated with the observed differences between the surviving and dead trees. Descriptive statistics summarizing mean, standard deviation, coefficient of variation and box plot analysis were calculated for each variable per site.

To study the relationship between the conventional ring variables and our original ring variables, we performed a Pearson product-moment correlation analysis taking into account a data matrix combining the information on all the individual trees and the annual rings studied from the three sites. The selected conventional variables are ring width (RW), mean ring density (MRD) and other conventional variables chosen among those found to be significantly related to induced cavitation resistance by Dalla-Salda et al. (2011) Thus, we expect them to be involved in survival of drought by trees. The variables are minimum ring density (MID), maximum ring density (MAD), earlywood density (EWD), latewood density (LWD) and earlywood proportion (EWP). A non-conventional variable defined by Dalla-Salda et al. (2011) and strongly related to resistance to cavitation, the mean of the first 100 density values along earlywood (SEQ), was also added.

## Results

We found significant differences between dead and surviving trees for several of our original variables, at least for

some values of  $dc$  and in some regions (Table 2). The variables for which the differences were most significant varied from region to region.

Table 2 shows the statistics ( $\log_{10}$  of the probability) of the test used to investigate the differences between surviving and dead trees at the total microdensity profile level in the three regions.

In the CE region, significant differences between surviving and dead trees were found for all the high-density segment variables. The surviving trees are significantly different from their dead counterparts in MHD (mean of the high-density segment) across all the  $dc$  values, PHD (proportion of the high-density segment) for the  $dc$  values from 0.5 to 0.8  $\text{kg dm}^{-3}$  and CVHD (coefficient of variation of the high-density segment) for the  $dc$  values of 0.3  $\text{kg dm}^{-3}$  and between 0.7 and 0.8  $\text{kg dm}^{-3}$ . The surviving trees appear to be significantly different from the dead trees in CP (number of cross points) in the range of the  $dc$  values between 0.4 and 0.8  $\text{kg dm}^{-3}$ .

In all cases, the surviving trees have a significantly higher density (higher MHD), a higher number of cross points (CP) and a higher proportion of high-density segments (PHD) than the dead trees (Table 2).

No significant differences were observed for the variables of the low-density segments in this site.

In the MP region, the surviving and dead trees are significantly different for all the variables of both the high- and low-density segments, except CVLD. The surviving

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trees are significantly different from their dead counterparts in MHD, MLD (mean of the low-density segment) and PHD in the whole range of the  $dc$  values. Highly significant differences are observed for CVHD for the  $dc$  values of 0.3 and 0.7  $\text{kg dm}^{-3}$ . For all the variables in this site except CVLD, the surviving trees have higher values than the dead trees (Table 2).

In the BO region, the surviving trees are significantly different from the dead trees in MLD for  $dc$  values in the range 0.3–0.5 and for  $dc$  equalling 0.8  $\text{kg dm}^{-3}$ . Significant differences are observed in CP for the  $dc$  value 0.5  $\text{kg dm}^{-3}$  (Table 3). The surviving trees have a significantly higher density in the low-density segment (higher MLD) than the dead trees for almost all the  $dc$  values and a higher number of cross points (CP) only for  $dc$  value 0.5  $\text{kg dm}^{-3}$  (Table 2). No significant differences were observed in the variables of the high-density segment in this site.

The denser microdensity profiles of the surviving trees of the three regions are illustrated in Fig. 3.

Figure 3 illustrates the main trends of the results in the three regions.

At the annual ring level, the difference between the dead and surviving trees is observed year by year in each annual ring before 2003 (Tables 4, 5 and 6). In the CE region, the differences between dead and surviving trees began to be significant for the high-density segment variables generally in the 1990 annual ring (Table 4 annex Tables). For MHD the effect was significant across all the  $dc$  values, while for PHD it was significant for the  $dc$  values between 0.5 and 0.8  $\text{kg dm}^{-3}$ . In subsequent annual rings, the surviving trees appeared to be significantly different from the dead trees from the annual ring 1994 up to the annual ring 2002 for both variables, for a range of  $dc$  values and with different levels of significance ( $p < 0.05$  to  $p < 0.001$ ). The strongest differences were observed immediately before 2003. The range of the  $dc$  critical values was located between 0.4 and 0.7  $\text{kg dm}^{-3}$ , for MHD and between 0.5 and 0.8  $\text{kg dm}^{-3}$  for PHD (Table 4). The surviving and dead trees also appeared to be significantly different for CVHD for several  $dc$  values, in particular the annual rings 1994, 1995 and 2002. For MLD, in the low-density segment, some differences were observed for some  $dc$  values for a few years (i.e. 1994, 1997 and 2001). No significant differences were observed for CVLD (Table 4).

In the MP region, significant differences between the surviving and dead trees were observed for almost all the annual rings from 1993 to 2002 for MHD and MLD, in both the high- and low-density segments, for several  $dc$  values and levels of significance (Table 5). The critical range for MHD was located between 0.4 and 0.6  $\text{kg dm}^{-3}$  while for MLD it was between 0.3 and 0.5  $\text{kg dm}^{-3}$ . In this site, significant differences between the surviving and dead trees were observed for PHD and CVHD in several annual

rings before 2003. The critical range of the  $dc$  values was located between 0.7 and 0.8  $\text{kg dm}^{-3}$  for PHD, while it was between 0.3 and 0.5  $\text{kg dm}^{-3}$  and from 0.6 to 0.8  $\text{kg dm}^{-3}$  for CVHD. No significant differences were observed for CVLD.

In the BO region, the annual rings of the surviving trees appeared to be significantly different from those of the dead trees, from 1996 up to 2001 for MLD, in the low-density segment, with different levels of significance (Table 6). The critical  $dc$  values were variable and dependent on the year and were distributed between 0.3 and 0.5 or 0.6  $\text{kg dm}^{-3}$  (Table 4.). For the variables linked to the high-density segment, the surviving trees appeared to be significantly different from the dead trees in few  $dc$  values in only one annual ring (1998) for MHD, CVHD and PHD.

In all three regions, for all the variables with significant differences between the surviving and dead trees, the surviving trees had a higher density (higher MHD and MLD), a higher proportion of high-density segment (PHD) and a higher within-segment variation (higher CVHD and CVLD). The denser microdensity profiles of the surviving trees in the three regions are illustrated in Fig. 3.

The results of the correlation study between the original and the conventional variables are presented in Table 7 (Annex Tables). In general, weak or relatively weak values of the correlation coefficient (lower than 0.70) or not significant association was observed between the original and the conventional ring variables. The only exception was a high degree of positive association between LWD and MHD for almost all  $dc$  values.

## Discussion

According to our results, the original microdensity variables used in this study reveal systematic differences between surviving and dead trees in Douglas fir. These results support those obtained in the CE region with the conventional microdensity variables only (Martinez-Meier et al. 2008a, b), increasing the statistical significance of the tests and extending this result to the two new regions BO and MP.

At the total profile level, the only variable which highly discriminates the dead from the surviving trees in all three regions is CP (Table 3). It is the sole trait calculated only at the total profile level. For a given  $dc$  value, the higher the CP value, the higher are the number and height of the density peaks in the profile. The surviving trees have a higher CP than the dead trees, hence they react more strongly and/or more frequently to environmental variation: in other words, they are more plastic. MLD is the main discriminating trait in the MP and BO regions, followed by PHD, CVHD and more marginally by MHD.

**Table 3** Descriptive statistics of the original variables measured in the surviving and dead trees for each *dc* value at the total microdensity profile level

<i>dc</i> (kg dm <sup>-3</sup> )	MLD kg dm <sup>-3</sup>				CVHD				CVLD				PHD				CP							
	D		S		D		S		D		S		D		S		D		S		D			
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd		
<b>Centre region</b>																								
0.3	0.60	0.03	0.58	0.03	0.24	0.01	0.24	0.01	0.32	0.03	0.32	0.02	0.11	0.03	0.11	0.02	0.63	0.08	0.61	0.07	41.72	8.03	41.15	5.40
0.4	0.67	0.03	0.65	0.03	0.27	0.02	0.27	0.01	0.23	0.02	0.23	0.02	0.19	0.03	0.19	0.03	0.50	0.06	0.47	0.06	49.84	5.70	48.0	4.0
0.5	0.72	0.03	0.71	0.03	0.30	0.02	0.30	0.01	0.16	0.02	0.16	0.01	0.26	0.04	0.26	0.03	0.40	0.05	0.37	0.05	51.08	4.28	48.52	3.66
0.6	0.77	0.03	0.75	0.03	0.33	0.02	0.33	0.02	0.12	0.01	0.11	0.01	0.33	0.04	0.33	0.03	0.31	0.05	0.28	0.05	47.83	4.92	43.85	5.26
0.7	0.81	0.03	0.80	0.02	0.36	0.03	0.36	0.02	0.08	0.01	0.08	0.01	0.39	0.05	0.39	0.03	0.22	0.06	0.19	0.05	37.12	8.65	31.75	8.26
0.8	0.87	0.02	0.86	0.02	0.41	0.03	0.40	0.03	0.05	0.01	0.05	0.01	0.45	0.04	0.45	0.03	0.12	0.05	0.09	0.05	18.72	11.06	14.32	9.43
<b>Midi-pyrenees region</b>																								
0.3	0.60	0.03	0.58	0.04	0.22	0.01	0.20	0.01	0.30	0.02	0.28	0.02	0.15	0.02	0.15	0.06	0.52	0.06	0.50	0.08	56.82	8.6	56.60	11.9
0.4	0.66	0.03	0.64	0.03	0.24	0.01	0.23	0.02	0.21	0.01	0.20	0.01	0.24	0.03	0.24	0.05	0.42	0.05	0.40	0.07	63.78	9.8	56.21	10.88
0.5	0.71	0.03	0.68	0.03	0.26	0.01	0.25	0.02	0.16	0.01	0.15	0.01	0.32	0.04	0.31	0.05	0.35	0.05	0.32	0.06	59.5	11.01	52.53	9.76
0.6	0.75	0.02	0.73	0.02	0.30	0.02	0.29	0.03	0.11	0.01	0.11	0.01	0.41	0.04	0.4	0.04	0.27	0.04	0.24	0.06	45.4	10.4	39.93	10.48
0.7	0.80	0.02	0.78	0.02	0.33	0.02	0.32	0.03	0.07	0.01	0.07	0.01	0.47	0.04	0.47	0.04	0.18	0.04	0.15	0.06	25.71	12.31	20.64	10.42
0.8	0.85	0.02	0.84	0.01	0.37	0.02	0.36	0.03	0.04	0.01	0.03	0.01	0.52	0.04	0.52	0.03	0.09	0.03	0.06	0.04	8.32	8.42	4.14	6.03
<b>Burgundy region</b>																								
0.3	0.58	0.04	0.57	0.05	0.22	0.01	0.22	0.01	0.30	0.03	0.28	0.02	0.15	0.03	0.16	0.03	0.56	0.06	0.54	0.06	53.75	7.93	53	8.67
0.4	0.64	0.05	0.63	0.05	0.25	0.01	0.24	0.02	0.21	0.02	0.20	0.02	0.24	0.03	0.26	0.04	0.44	0.05	0.42	0.05	60.22	7.51	55.95	8.84
0.5	0.70	0.04	0.68	0.05	0.27	0.01	0.27	0.02	0.16	0.01	0.15	0.01	0.32	0.04	0.33	0.05	0.35	0.05	0.33	0.06	58.04	9.37	53.5	8.10
0.6	0.74	0.04	0.73	0.04	0.31	0.02	0.30	0.02	0.11	0.01	0.10	0.01	0.40	0.04	0.41	0.05	0.26	0.06	0.24	0.07	45.68	13.31	41.62	12.37
0.7	0.79	0.03	0.78	0.03	0.35	0.02	0.34	0.02	0.07	0.01	0.07	0.01	0.45	0.04	0.47	0.05	0.17	0.07	0.14	0.08	25.08	17.29	22.08	15.60
0.8	0.85	0.02	0.84	0.02	0.39	0.02	0.37	0.03	0.04	0.01	0.03	0.01	0.50	0.03	0.50	0.05	0.08	0.06	0.06	0.06	9.44	12.09	7.33	11.89

*sd* standard deviation, *S* surviving trees, *D* dead trees, *dc* density criterion



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443 MHD, PHD and CVHD are the most discriminating traits  
 444 in the CE and MP regions (Table 3). As a consequence, in  
 445 the CE and MP regions, the surviving trees have a higher  
 446 proportion of higher-density wood than the dead trees. In  
 447 the MP and BO regions, the surviving trees have a higher  
 448 density of low-density segment.

449 The results obtained at ring level corroborate and  
 450 specify the trends observed at the total profile level  
 451 (Tables 4, 5 and 6 in Annex Tables). PHD, MHD, MLD  
 452 and CVHD are discriminating traits in the three regions,  
 453 with a variable ranking of their discrimination power  
 454 between regions. As for the total profile traits, we find that  
 455 the surviving trees have a higher density, proportion and  
 456 variation of the high-density segments in many annual  
 457 rings than the dead trees in the CE and MP regions and, to a  
 458 lesser extent, in the BO region. In the BO and MP regions,  
 459 the surviving trees also have a higher density of low-den-  
 460 sity segments in many annual rings (Fig. 3).

461 In our study, there are converging significant results for  
 462 CP and CVHD for the  $dc$  values between 0.5 and 0.8 kg  
 463  $dm^{-3}$  in the CE region and between 0.7 and 0.8 kg  $dm^{-3}$  in  
 464 the MP region. These results indicate that the microdensity  
 465 profiles of the surviving trees are more heterogeneous than  
 466 those of the dead trees. We suggest that the surviving trees  
 467 may react more strongly and/or more frequently to varia-  
 468 tion in water availability: the surviving trees may be more  
 469 plastic than the dead trees.

470 In all cases, the mean density of the surviving trees is  
 471 higher than that of the dead trees (Fig. 3). However, the  
 472 denser part of the ring is different from region to region.  
 473 This may reflect variation among the three regions in terms  
 474 of the attributes of the drought episodes leading to the  
 475 observed diebacks. Some results suggest that, depending on  
 476 the characteristics of a drought, the critical part of the ring  
 477 may be different: Domec and Gartner (2002) have shown  
 478 that latewood was more vulnerable to embolism than ear-  
 479 lywood in high trunk water potential, but as trunk water  
 480 potential decreased, the latewood showed very little further  
 481 embolism. They also suggested that latewood is a water  
 482 storage organ that can release water at very small water  
 483 potential differences. Dalla-Salda et al. (2011) found that  
 484 during the cavitation process, the low water potential  
 485 controlling early embolism was related to latewood den-  
 486 sity, while the high water potential controlling late embo-  
 487 lism was related to earlywood density. Furthermore, during  
 488 a spring drought only earlywood is present in the current  
 489 annual ring, while during a late summer drought both  
 490 earlywood and latewood exist. This indicates that,  
 491 according to the residual conductance of the successive  
 492 sapwood rings, the dynamics, the seasonal progression and  
 493 the intensity of the drought, earlywood and latewood may  
 494 play different roles in cavitation resistance.

## Selection of adaptive variables

495

496 At ring level, we used the number of annual rings with sig-  
 497 nificant differences between surviving and dead trees to  
 498 select the proxies for adaptive traits for resistance to drought:  
 499 the most discriminant traits in the largest number of annual  
 500 rings were assumed to be the best candidates. For most traits  
 501 the  $dc$  value had little effect on the discriminating power:  
 502 MHD, PHD and CVHD have more or less the same dis-  
 503 criminating power for any value of  $dc$ . Conversely, MLD is  
 504 always more discriminant when it is calculated for the lowest  
 505  $dc$  values, i.e. 0.3, 0.4 and 0.5 kg  $dm^{-3}$ . We selected MHD  
 506 (mean of the high-density segment), PHD (proportion of the  
 507 high-density segment) and CVHD (coefficient of variation of  
 508 the high-density segment) calculated at any  $dc$  level and  
 509 MLD calculated at the  $dc$  values 0.3, 0.4 and 0.5 kg  $dm^{-3}$  as  
 510 the best adaptive traits for resistance to drought. These traits  
 511 will be used in another study for estimating the genetic  
 512 determinism of resistance to drought in Douglas fir. If these  
 513 traits are found to be adequately genetically variable and  
 514 heritable, then it will be possible to select more drought-  
 515 resistant trees in breeding populations and in forest stands  
 516 intended to be naturally regenerated.

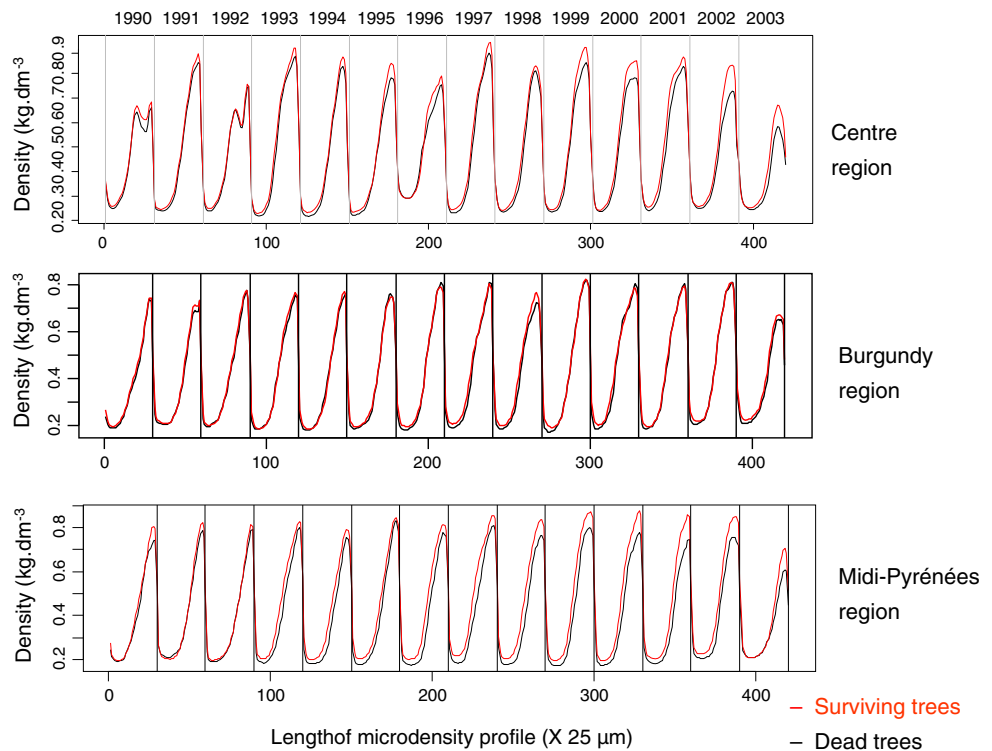
## Original and conventional variables

517

518 Of the three sites, the original variables better explain the  
 519 difference between the surviving and dead trees than the  
 520 conventional variables in the CE region (Martinez-Meier  
 521 et al. 2008a, b). The original variables based on the sliding  
 522 density criterion have the advantage of providing a rela-  
 523 tively finer localization of the wood segment that is critical  
 524 for survival. The original variables are based on a sliding  
 525 density criterion separating the total profile or the ring  
 526 density profile into high- and low-density segments. This  
 527 definition can be understood as an extension of the early-  
 528 wood-latewood model. Thus, we expected strong or very  
 529 strong correlations between several original and conven-  
 530 tional variables. However, we found high correlation val-  
 531 ues only between latewood density and MHD (mean of the  
 532 high-density segment, Table 7 in Annex Tables). In gener-  
 533 al, weak or not significant correlation coefficient values  
 534 indicate that the original variables can be considered a new  
 535 set of variables with no phenotypic correlation with con-  
 536 ventional ring variables.

537 As expected, the conventional variables have a lower  
 538 discriminating power than the original variables (results  
 539 not shown). Only LD (latewood density) has a similar  
 540 discriminating power to MHD (mean of the high-density  
 541 segment) for  $dc$  values over 0.5 kg  $dm^{-3}$ . This is consistent  
 542 with the high correlation coefficient found between these  
 543 two variables.

**Fig. 3** Average microdensity profiles of the dead (black line) and surviving (red line) trees of the three regions. **a** the Centre region, **b** Burgundy region and **c** the Midi-Pyrénées region. In each region the annual ring density profiles were standardized to the same number of density values (30), then averaged at the level of the dead and surviving trees and put together to reconstruct a total microdensity profile



### High-density wood, survival and drought

Negative relationships across species between wood density and survival have often been found in tropical forests (Kraft et al. 2010). Martinez-Vilalta (2010) observed the same pattern across temperate and Mediterranean species. Fewer results are available at the intraspecific level: Kukowski et al. (2013) found that mortality rates correlated with wood density in oak and elm. Across or intra-species, the mortality factors are not often clearly identified. When they are, they include mechanical breakdown, attack by pathogens and fungi (Poorter et al. 2010; Larjavaara and Muller-Landau 2010) and, in few cases, drought-induced embolism (Hiromi et al. 2012; Kukowski et al. 2013). This is the case in our study, where Martinez-Meier et al. (2008a, b) and Sargent (2011) and Sargent et al. (2012) demonstrated that the main factor in Douglas fir mortality in all three regions was water deficit.

In Douglas fir, wood density is strongly related to wood anatomy: wood density is mainly related to cell wall thickness and cell diameter (Rathgeber et al. 2006). The wider tracheids associated with low-density wood increase the risk of cavitation, causing water conduction to decline if cells become embolized (air filled) and leading to tree death in extreme cases (Hacke et al. 2001; Hacke and Sperry 2001; Cruziat et al. 2002; Breda et al. 2006). We therefore conclude that, in Douglas fir, the lower mortality rate of the high-density individuals correlates with an increased resistance to drought-induced embolism. Such a conclusion is consistent with the

negative relationship found in Douglas fir between density and resistance to cavitation (Dalla-Salda et al. 2011). This result may not relate to other species, since in some trees such as Norway spruce (Rosner et al. 2007) and maritime pine (Lamy et al. 2011, 2012) no relationship was found between wood density and resistance to cavitation. In beech, Barigah et al. (2013) proposed that cavitation resistance was related to tree mortality during extreme drought events. Wortemann et al. (2011) found no variation between populations and concluded that cavitation resistance was probably not an adaptive trait submitted to selection. These results may suggest that in these species, adaptation to drought may depend more on traits such as stomatal closure, leaf abscission and carbon storage rather than on xylem resistance to embolism (Jones 1992; McDowell et al. 2008) and that wood density may not play the same critical role as in Douglas fir.

### Directional selection

In their study based on conventional ring data from the Centre region Martinez-Meier et al. (2008) wrote that “(...) some degree of selection against trees with low-density wood may happen after heat wave events like the one in 2003”. Our results suggest that directional selection is occurring in the Douglas fir stands of the Centre, Midi-Pyrénées and Burgundy regions following the dieback triggered by the 2003 drought event. This directional selection does not orient Douglas fir to a unique drought-resistant phenotype. The magnitude of the density increase and the part of the ring

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which is modified are different from region to region. In the Centre region the density increase is significant only in the high-density wood (similar to latewood) and reaches 0.015 kg dm<sup>-3</sup> on average. In Burgundy region the density increase is significant only in the low-density wood (similar to earlywood) and reaches 0.008 kg dm<sup>-3</sup>. In the Midi-Pyrénées region the density increase is significant in both types of wood and reaches 0.020 and 0.012 kg dm<sup>-3</sup> in the high and low-density wood, respectively (results not shown). Whether these phenotypic changes are functionally significant and whether they will be transferred to the next generations will be the subject of future studies.

## Conclusion and perspectives

According to Domec and Gartner (2002), hydraulic safety is a primary force of natural selection acting on wood structure in Douglas fir. In the present study, we dealt with the problem of defining proxies of wood-based adaptive traits in Douglas fir, specifically traits that maximize the survival of individuals in water-constrained environments. We found that it is possible to define a new set of proxies of adaptive traits with a high discriminating power between surviving and dead individuals. These proxies can be used to estimate the potential of evolutionary adaptation of Douglas fir to drought. The

evolutionary mechanism that enables plants to adapt relies on the magnitude of genetic variation and of heritability. Hence, the next step is to precisely estimate the genetic variation and the heritability of the original proxies of adaptive traits based on the density profiles that we discovered in this study.

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**Conflict of interest** The authors declare that they have no conflict of interest.

## Annex

See Annex Tables 4, 5, 6, 7

**Table 4** log10 of associated probabilities of observed mean differences between surviving and dead trees under H<sub>0</sub> = no difference for original variables calculated at the annual ring level in Centre region

Annual ring	Centre region						Centre region					
	MHD			MLD			MHD			MLD		
	<i>dc</i>						<i>dc</i>					
	0.3	0.4	0.5	0.6	0.7	0.8	0.3	0.4	0.5	0.6	0.7	0.8
1986	0.21 ns	0.60 ns	0.60 ns	0.46 ns	0.44 ns	0.38 ns	0.74 ns	0.88 ns	0.70 ns	0.60 ns	0.5 ns	0.54 ns
1987	0.23 ns	0.15 ns	0.12 ns	0.08 ns	0.50 ns	0.43 ns	0.20 ns	0.26 ns	0.46 ns	0.52 ns	1.47*	0.65 ns
1988	0.30 ns	0.34 ns	0.30 ns	0.25 ns	0.32 ns	0.18 ns	0.40 ns	0.56 ns	0.56 ns	0.54 ns	0.52 ns	0.55 ns
1989	0.37 ns	0.46 ns	0.62 ns	0.73 ns	0.52 ns	0.44 ns	0.1 ns	0.33 ns	0.43 ns	0.36 ns	0.09 ns	0.07 ns
1990	2.17**	2.58**	2.87**	1.90*	2.66**	0.70 ns	0.22 ns	0.47 ns	0.32 ns	0.03 ns	0.15 ns	1.35*
1991	0.56 ns	1.16 ns	1.50*	1.40*	1.20 ns	0.80 ns	0.31 ns	0.52 ns	0.70 ns	0.5 ns	0.22 ns	0.28 ns
1992	0.60 ns	0.65 ns	0.38 ns	0.42 ns	0.82 ns	0.83 ns	0.19 ns	0.34 ns	0.32 ns	0.34 ns	0.36 ns	0.44 ns
1993	0.57 ns	0.73 ns	1.00 ns	0.94 ns	1.46*	1.53*	0.65 ns	0.75 ns	0.89 ns	0.36 ns	0.47 ns	0.16 ns
1994	0.64 ns	0.93 ns	1.40*	2.23**	1.70*	1.76*	1.56*	1.46*	1.80*	1.68*	0.61 ns	0.33 ns
1995	1.08 ns	1.94*	2.80**	2.86**	3.42***	1.50*	0.70 ns	1.24 ns	1.12 ns	0.76 ns	0.13 ns	0.10 ns
1996	2.50**	4.14***	3.38***	2.74**	1.65*	0.75	0.16 ns	0.20 ns	0.22 ns	0.05 ns	0.04 ns	0.50 ns
1997	0.72 ns	1.50*	1.58*	1.32*	1.15 ns	1.31*	1.37*	1.98*	1.63*	0.80 ns	0.42 ns	0.50 ns
1998	1.17 ns	1.42*	1.50*	1.23 ns	1.10 ns	1.1 ns	0.2 ns	0.46 ns	0.41 ns	0.33 ns	0.25 ns	0.72 ns
1999	1.73*	2.17**	2.08**	1.88*	1.37*	0.77 ns	0.67 ns	0.60 ns	0.46 ns	0.22 ns	0.06 ns	0.12 ns
2000	2.32**	2.75**	2.84**	2.38**	2.21**	2.10**	0.82 ns	1.13 ns	0.55 ns	0.43 ns	0.45 ns	0.86 ns
2001	2.24**	2.30**	2.12**	2.02**	1.56*	1.88*	1.62*	1.90*	0.82 ns	0.78 ns	0.65 ns	1.17 ns
2002	4.61***	5.86***	6.65***	6.46***	4.3***	2.62**	0.73 ns	0.74 ns	0.68 ns	0.11 ns	0.03 ns	0.3 ns

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Centre region

CVHD

*dc*

0.3 0.4 0.5 0.6 0.7 0.8

CVLD

*dc*

0.3 0.4 0.5 0.6 0.7 0.8

Annual ring

1986	1.0 ns	0.23 ns	0.14 ns	0.27 ns	0.36 ns	0.43 ns	0.14 ns	0.20 ns	0.07 ns	0.1 ns	0.12 ns	0.13 ns
1987	0.17 ns	0.18 ns	0.60 ns	0.50 ns	0.87 ns	0.18 ns	0.47 ns	0.40 ns	0.28 ns	0.29 ns	0.64 ns	0.14 ns
1988	0.35 ns	0.26 ns	0.16 ns	0.40 ns	0.30 ns	0.30 ns	0.61 ns	0.32 ns	0.30 ns	0.15 ns	0.18 ns	0.25 ns
1989	0.48 ns	0.66 ns	0.23 ns	0.05 ns	0.25 ns	0.56 ns	0.68 ns	0.41 ns	0.62 ns	0.23 ns	0.06 ns	0.25 ns
1990	1.60*	0.60 ns	0.16 ns	0.71 ns	3.41***	0.60 ns	0.52 ns	0.24 ns	0.22 ns	0.04 ns	0.53 ns	0.98 ns
1991	1.47*	0.60 ns	0.42 ns	0.56 ns	0.38 ns	0.88 ns	0.32 ns	0.54 ns	0.56 ns	0.11 ns	0.08 ns	0.13 ns
1992	0.31 ns	0.08 ns	0.23 ns	0.62 ns	0.90 ns	1.04 ns	0.90 ns	0.27 ns	0.30 ns	0.22 ns	0.35 ns	0.26 ns
1993	1.26 ns	1.09 ns	0.73 ns	1.08 ns	1.51*	0.90 ns	0.33 ns	0.30 ns	0.28 ns	0.15 ns	0.10 ns	0.08 ns
1994	1.87*	1.77*	1.56*	1.0 ns	0.91 ns	2.18**	0.03 ns	0.02 ns	0.04 ns	0.02 ns	0.001 ns	0.006 ns
1995	2.70**	2.45**	1.32*	2.06**	3.43***	1.44*	0.11 ns	0.05 ns	0.04 ns	0.008 ns	0.01 ns	0.11 ns
1996	1.0 ns	0.37 ns	0.27 ns	0.68 ns	0.92 ns	0.64 ns	0.47 ns	0.66 ns	0.06 ns	0.073 ns	0.36 ns	1.10 ns
1997	1.72*	0.42 ns	0.35 ns	0.83 ns	1.70*	1.64*	0.05 ns	0.03 ns	0.03 ns	0.006 ns	0.005 ns	0.02 ns
1998	0.74 ns	0.74 ns	0.77 ns	0.60 ns	0.85 ns	0.80 ns	0.43 ns	0.16 ns	0.23 ns	0.20 ns	0.21 ns	0.40 ns
1999	0.74 ns	0.28 ns	0.15 ns	0.10 ns	0.40 ns	1.20 ns	0.08 ns	0.12 ns	0.16 ns	0.11 ns	0.06 ns	0.18 ns
2000	1.25 ns	1.16 ns	1.14 ns	1.44*	2.12**	1.63*	0.06 ns	0.23 ns	0.15 ns	0.09 ns	0.11 ns	0.09 ns
2001	0.71 ns	0.46 ns	0.50 ns	0.67 ns	1.45*	1.78*	0.02 ns	0.008 ns	0.04 ns	0.13 ns	0.06 ns	0.04 ns
2002	4.00***	4.63***	3.70***	3.05***	3.06***	1.42*	0.08 ns	0.09 ns	0.03 ns	0.03 ns	0.06 ns	0.57 ns

Centre region

PHD

*dc*

0.3 0.4 0.5 0.6 0.7 0.8

Annual ring

1986	0.90 ns	0.54 ns	0.58 ns	0.66 ns	0.77 ns	0.63 ns
1987	0.70 ns	1.02 ns	0.90 ns	0.81 ns	0.15 ns	0.28 ns
1988	0.63 ns	0.60 ns	0.55 ns	0.46 ns	0.36 ns	0.37 ns
1989	0.40 ns	0.23 ns	0.1 ns	0.08 ns	0.34 ns	0.54 ns
1990	0.78 ns	0.83 ns	1.09 ns	2.61**	3.04***	1.89*
1991	1.43*	1.05 ns	0.75 ns	0.92 ns	1.35*	1.22 ns
1992	0.58 ns	0.63 ns	0.80 ns	0.54 ns	0.63 ns	0.80 ns
1993	1.05 ns	0.80 ns	0.54 ns	1.0 ns	0.60 ns	1.08 ns
1994	1.50*	1.18 ns	0.78 ns	0.56 ns	1.26 ns	1.92
1995	1.58*	0.98 ns	0.68 ns	0.77 ns	2.27**	3.40***
1996	0.46 ns	0.54 ns	1.32*	2.81**	3.76***	2.61**
1997	1.93*	1.23 ns	1.34*	1.80*	1.93*	1.70*
1998	1.45*	1.50*	1.97*	2.24**	2.51**	1.47*
1999	1.15 ns	1.12 ns	1.56*	2.06**	2.92**	3.31***
2000	1.67*	1.52*	2.92**	3.75***	3.72***	2.16**
2001	2.06**	2.20**	3.9***	4.20***	3.96***	2.38**
2002	1.05 ns	1.40*	1.96*	3.97***	7.0***	6.50***

*dc* density criterion, *log*10 of associated probabilities, *ns* not significant

(\*\*\*) for  $p < 0.001$ , (\*\*) for  $p < 0.01$  and (\*) for  $p < 0.05$

**Table 5**  $\log_{10}$  of associated probabilities of observed mean differences between surviving and dead trees under  $H_0 =$  no difference for original variables calculated at the annual ring level in the Midi-Pyrénées region

Midi-pyrenees region												
MHD						MLD						
<i>dc</i>						<i>dc</i>						
0.3	0.4	0.5	0.6	0.7	0.8	0.3	0.4	0.5	0.6	0.7	0.8	
Annual ring												
1993	2.17**	1.81*	1.34*	0.99 ns	1.0 ns	0.71 ns	2.35**	1.50*	0.92 ns	0.51 ns	1.23 ns	1.94*
1994	1.09 ns	1.33*	1.09 ns	0.95 ns	0.56 ns	1.09 ns	2.40**	2.07**	1.24 ns	1.0 ns	1.52*	1.16 ns
1995	0.64 ns	0.85 ns	0.90 ns	0.64 ns	0.27 ns	0.28 ns	3.47***	2.80**	2.58**	1.45*	1.32*	1.70*
1996	1.24 ns	1.60*	1.86*	1.33*	1.14 ns	0.82 ns	3.94***	3.60***	2.97**	1.54*	1.12 ns	0.14 ns
1997	0.85 ns	1.42*	1.43*	1.00 ns	0.81 ns	1.08 ns	4.47***	4.22***	2.62**	0.92 ns	0.86 ns	0.25 ns
1998	1.45*	2.12**	2.33**	2.07**	1.74*	1.00 ns	4.08***	4.00***	2.57**	1.44*	0.55 ns	0.87 ns
1999	1.46*	2.13**	2.54**	2.95**	2.67**	1.90*	3.80***	3.47***	2.75**	1.53*	0.72 ns	0.19 ns
2000	2.63**	3.23***	3.36***	3.03***	2.90**	1.26 ns	2.20**	2.03**	1.05 ns	0.4 ns	0.17 ns	0.11 ns
2001	3.20***	4.17***	4 ***	3.62***	2.26**	1.76*	3.05***	2.45**	1.53*	1.0 ns	0.64 ns	1.11 ns
2002	0.60 ns	1.25 ns	1.18 ns	1.68*	1.74*	2.54**	3.75***	3.60***	4.11***	1.76*	2.04*	0.17 ns
Midi-pyrenees region												
CVHD						CVLD						
<i>dc</i>						<i>dc</i>						
0.3	0.4	0.5	0.6	0.7	0.8	0.3	0.4	0.5	0.6	0.7	0.8	
Annual ring												
1993	0.22 ns	0.12 ns	0.19 ns	0.61 ns	1.31 ns	0.70 ns	0.0008 ns	0.0001 ns	0.0005 ns	0.005 ns	0.04 ns	0.001 ns
1994	0.82 ns	0.31 ns	0.60 ns	0.70 ns	1.20 ns	1.11 ns	0.005 ns	0.002 ns	0.002 ns	0.13 ns	0.0004 ns	0.002 ns
1995	0.80 ns	0.42 ns	0.20 ns	0.45 ns	0.40 ns	0.24 ns	7.7e-05 ns	7.8e-05 ns	0.002 ns	0.0002 ns	0.001 ns	0.008 ns
1996	0.69 ns	0.42 ns	0.14 ns	0.22 ns	0.34 ns	0.50 ns	2.5e-05 ns	4.3e-05 ns	0.0002 ns	0.0002 ns	0.0004 ns	0.008 ns
1997	1.81*	0.66 ns	0.50 ns	0.21 ns	0.62 ns	1.34*	4.4e-05 ns	9.4e-05 ns	2.4e-05 ns	0.0001 ns	0.0008 ns	0.001 ns
1998	1.72*	0.94 ns	1.06 ns	1.28 ns	1.30*	0.83 ns	5.9e-05 ns	0.0004 ns	0.0001 ns	0.0002 ns	5.6e-05 ns	0.014 ns
1999	2.94**	2.40**	1.87*	1.79*	1.57*	2.06**	0.0004 ns	0.001 ns	0.0008 ns	0.0002 ns	0.0005 ns	0.002 ns
2000	2.58**	2.26**	2.31**	1.93*	2.14**	1.62*	0.007 ns	0.006 ns	0.002 ns	0.001 ns	0.01 ns	0.093 ns
2001	3.24***	1.50*	2.22**	1.60*	1.80*	2.36**	0.0002 ns	0.0005 ns	0.0007 ns	0.002 ns	0.002 ns	0.004 ns
2002	3.05***	3.32***	3.80***	2.86**	2.20**	2.90**	0.0005 ns	0.0001 ns	0.001 ns	0.03 ns	0.0008 ns	0.002 ns
Midi-pyrenees region												
PHD												
<i>dc</i>												
0.3	0.4	0.5	0.6	0.7	0.8	0.3	0.4	0.5	0.6	0.7	0.8	
Annual ring												
1993	1.37*	1.78*	2.07**	2.7**	1.91*	0.90 ns						
1994	0.97 ns	0.85 ns	1.25 ns	1.25 ns	0.67 ns	0.68 ns						
1995	1.11 ns	0.93 ns	0.87 ns	1.09 ns	1.02 ns	0.54 ns						
1996	0.85 ns	0.72 ns	0.71 ns	1.09 ns	1.05 ns	1.33*						
1997	0.80 ns	0.45 ns	0.60 ns	1.03 ns	0.95 ns	1.76*						
1998	1.02 ns	0.75 ns	0.96 ns	1.23 ns	1.90*	0.74 ns						
1999	1.18 ns	0.84 ns	0.84 ns	1.0 ns	1.36*	2.36**						
2000	0.87 ns	0.81 ns	1.36*	1.72*	2.70**	1.82*						
2001	1.91*	2.07**	2.80**	2.74**	3.32***	2.94**						
2002	2.72**	1.7*	1.07 ns	0.48 ns	0.75 ns	1.93*						

*dc* density criterion,  $\log_{10}$  of associated probabilities, *ns* not significant

(\*\*\*) for  $p < 0.001$ , (\*\*) for  $p < 0.01$  and (\*) for  $p < 0.05$

**Table 6** *log*10 of associated probabilities of observed mean differences between surviving and dead trees under  $H_0 =$  no difference for original variables calculated at annual ring level in the Burgundy region

Burgundy Region												
MHD						MLD						
<i>dc</i>												
	0.3	0.4	0.5	0.6	0.7	0.8	0.3	0.4	0.5	0.6	0.7	0.8
Annual ring												
1993	0.85 ns	0.88 ns	0.90 ns	1.07 ns	0.7 ns	0.66 ns	0.60 ns	0.47 ns	0.22 ns	0.30 ns	0.03 ns	0.20 ns
1994	0.38 ns	0.24 ns	0.30 ns	0.40 ns	0.35 ns	0.56 ns	0.70 ns	0.40 ns	0.73 ns	0.81 ns	1.13 ns	0.66 ns
1995	0.24 ns	0.39 ns	0.60 ns	0.42 ns	0.30 ns	0.32 ns	1.76*	1.54*	1.34*	0.97 ns	1.17 ns	1.14 ns
1996	0.34 ns	0.55 ns	0.53 ns	0.31 ns	0.33 ns	0.40 ns	2.70**	2.60**	2.07**	0.98 ns	0.75 ns	1.09 ns
1997	0.24 ns	0.36 ns	0.36 ns	0.46 ns	0.45 ns	0.34 ns	2.85**	2.09**	2.40**	1.87*	1.15 ns	1.23 ns
1998	1.57*	1.34*	1.30*	1.54*	0.83 ns	0.88 ns	2.26**	1.75*	1.40*	1.70*	1.27 ns	0.61 ns
1999	0.51 ns	0.74 ns	0.78 ns	0.85 ns	0.30 ns	0.33 ns	4.08***	4.17***	2.96*	2.48**	0.32 ns	0.35 ns
2000	0.75 ns	0.88 ns	0.81 ns	0.83 ns	0.44 ns	0.76 ns	2.48**	2.27**	1.79*	1.50*	0.64 ns	0.74 ns
2001	1.08 ns	1.04 ns	0.84 ns	0.75 ns	0.64 ns	0.78 ns	1.75*	1.48*	0.92 ns	0.85 ns	0.60 ns	0.50 ns
2002	0.85 ns	1.0 ns	1.09 ns	1.04 ns	0.66 ns	1.63*	1.80*	1.33*	0.97 ns	0.82 ns	0.30 ns	0.22 ns
Burgundy region												
CVHD						CVLD						
<i>dc</i>												
	0.3	0.4	0.5	0.6	0.7	0.8	0.3	0.4	0.5	0.6	0.7	0.8
Annual ring												
1993	0.71 ns	0.84 ns	1.08 ns	0.73 ns	0.60 ns	0.76 ns	0.04 ns	0.04 ns	0.05 ns	0.10 ns	0.05 ns	0.03 ns
1994	0.31 ns	0.85 ns	0.77 ns	0.56 ns	0.47 ns	0.87 ns	0.04 ns	0.04 ns	0.32 ns	0.30 ns	0.14 ns	0.01 ns
1995	1.18 ns	1.00 ns	0.62 ns	0.75 ns	0.40 ns	0.44 ns	0.005 ns	0.005 ns	0.024 ns	0.008 ns	0.005 ns	0.02 ns
1996	0.80 ns	0.34 ns	0.33 ns	0.78 ns	0.84 ns	0.43 ns	0.002 ns	0.003 ns	0.001 ns	0.0009 ns	0.006 ns	0.12 ns
1997	0.81 ns	0.50 ns	0.58 ns	0.31 ns	0.53 ns	0.32 ns	0.0002 ns	0.0001 ns	0.003 ns	0.001 ns	0.001 ns	0.0004 ns
1998	0.86 ns	1.48*	1.80*	1.63*	1.16 ns	0.96 ns	0.003 ns	0.0009 ns	0.01 ns	0.006 ns	0.001 ns	6.5e-05 ns
1999	1.02 ns	0.30 ns	0.40 ns	0.25 ns	0.55 ns	0.77 ns	5.0e-05 ns	0.0004 ns	6.9e-05 ns	0.0002 ns	3.4e-05 ns	0.05 ns
2000	0.66 ns	0.28 ns	0.45 ns	0.45 ns	0.23 ns	0.55 ns	2.2e-05 ns	0.0002 ns	0.0008 ns	0.0004 ns	0.0006 ns	0.06 ns
2001	0.27 ns	0.23 ns	0.77 ns	0.55 ns	0.40 ns	0.97 ns	0.005 ns	0.003 ns	0.001 ns	0.024 ns	0.02 ns	0.11 ns
2002	0.83 ns	1.0 ns	1.22 ns	0.83 ns	0.36 ns	1.38*	0.001 ns	0.0005 ns	0.002 ns	0.005 ns	0.02 ns	0.02 ns
Burgundy region												
PHD												
<i>dc</i>												
	0.3	0.4	0.5	0.6	0.7	0.8						
Annual ring												
1993		0.27 ns		0.30 ns		0.56 ns		0.35 ns		1.08 ns		0.84 ns
1994		0.53 ns		0.90 ns		0.61 ns		0.43 ns		0.32 ns		0.44 ns
1995		0.98 ns		0.73 ns		0.61 ns		0.72 ns		0.60 ns		0.24 ns
1996		0.70 ns		0.48 ns		0.52 ns		0.63 ns		0.50 ns		0.09 ns
1997		1.07 ns		0.90 ns		0.67 ns		0.39 ns		0.50 ns		0.28 ns
1998		1.74*		2.70**		2.80**		1.97*		0.93 ns		1.37*
1999		1.27 ns		0.81 ns		0.76 ns		0.62 ns		1.10 ns		0.77 ns
2000		1.56*		1.18 ns		1.18 ns		0.84 ns		1.0 ns		0.97 ns
2001		1.28 ns		1.27 ns		1.58*		0.97 ns		0.90 ns		0.97 ns
2002		0.51 ns		0.40 ns		0.46 ns		0.50 ns		0.48 ns		1.13 ns

*dc* density criterion, *log*10 of associated probabilities, *ns* not significant

(\*\*\*) for  $p < 0.001$ , (\*\*) for  $p < 0.01$  and (\*) for  $p < 0.05$

**Table 7** Pearson's coefficient of correlation between original ring variables and conventional ring variables

Variables	RW	MRD	EWD	LWD	MID	MAD	SEQ	EWP
MHD 0.3 <i>df</i> = 2916	-0.041*	0.42***	-0.15***	0.62***	-0.11***	0.23***	-0.062***	-0.36***
MHD 0.4 <i>df</i> = 2912	-0.093***	0.57***	0.067***	0.84***	0.15***	0.30***	0.15***	-0.30***
MHD 0.5 <i>df</i> = 2920	-0.078***	0.56***	0.15***	0.89***	0.23***	0.33***	0.19***	-0.20***
MHD 0.6 <i>df</i> = 2906	-0.057**	0.51***	0.22***	0.88***	0.27***	0.34***	0.22***	-0.086***
MHD 0.7 <i>df</i> = 2865	-0.04*	0.44***	0.28***	0.73***	0.31***	0.31***	0.25***	-0.024 ns
MHD 0.8 <i>df</i> = 2728	-0.012 ns	0.40***	0.30***	0.62***	0.31***	0.27***	0.24***	-0.026 ns
MLD 0.3 <i>df</i> = 2937	-0.11***	0.38***	0.50***	0.11***	0.53***	0.036 ns	0.48***	-0.19***
MLD 0.4 <i>df</i> = 2937	-0.11***	0.43***	0.60***	0.12***	0.60***	0.043*	0.56***	-0.21***
MLD 0.5 <i>df</i> = 2937	-0.078***	0.43***	0.68***	0.069***	0.66***	0.036 ns	0.61***	-0.18***
MLD 0.6 <i>df</i> = 2938	-0.024 ns	0.40***	0.69***	-0.049**	0.63***	0.011 ns	0.58***	-0.18***
MLD 0.7 <i>df</i> = 2938	-0.038*	0.37***	0.61***	-0.17***	0.57***	-0.02 ns	0.54***	-0.28***
MLD 0.8 <i>df</i> = 2937	-0.069***	0.46***	0.52***	-0.070***	0.52***	-2.5e-05 ns	0.50***	-0.42***
CVHD 0.3 <i>df</i> = 2916	-0.011 ns	0.33***	0.54***	0.34***	0.57***	0.15***	0.44***	0.046*
CVHD 0.4 <i>df</i> = 2912	0.023 ns	0.30***	0.51***	0.32***	0.52***	0.15***	0.40**	0.065***
CVHD 0.5 <i>df</i> = 2920	0.038*	0.30***	0.51***	0.31***	0.50***	0.16***	0.38***	0.062***
CVHD 0.6 <i>df</i> = 2906	0.066***	0.30***	0.49***	0.31***	0.48***	0.17***	0.35***	0.044*
CVHD 0.7 <i>df</i> = 2865	0.07***	0.33***	0.46***	0.36***	0.47***	0.18***	0.34***	0.02 ns
CVHD 0.8 <i>df</i> = 2728	0.047*	0.36***	0.37***	0.50***	0.37***	0.21***	0.26***	0.0012 ns
CVLD 0.3 <i>df</i> = 2937	0.12***	0.067***	0.11***	0.20***	0.071***	0.11***	0.021 ns	0.090***
CVLD 0.4 <i>df</i> = 2937	0.083***	0.19***	0.30***	0.23***	0.28***	0.13***	0.20***	0.044*
CVLD 0.5 <i>df</i> = 2937	0.075***	0.21***	0.35***	0.22***	0.33***	0.13***	0.24***	0.034 ns
CVLD 0.6 <i>df</i> = 2938	0.07***	0.23***	0.37***	0.22***	0.36***	0.13***	0.26***	0.022 ns
CVLD 0.7 <i>df</i> = 2938	0.060***	0.25***	0.36***	0.24***	0.38***	0.13***	0.27***	0.004 ns
CVLD 0.8 <i>df</i> = 2937	0.044*	0.26***	0.36***	0.30***	0.40***	0.14***	0.28***	0.012 ns
PHD 0.3 <i>df</i> = 2938	-0.037*	0.47***	0.62***	0.28***	0.64***	0.14***	0.55***	-0.13***
PHD 0.4 <i>df</i> = 2938	-0.02 ns	0.47***	0.58***	0.30***	0.58***	0.14***	0.51***	-0.17***
PHD 0.5 <i>df</i> = 2938	-0.027 ns	0.50***	0.55***	0.31***	0.57***	0.15***	0.50***	-0.20***
PHD 0.6 <i>df</i> = 2938	-0.045*	0.53***	0.51***	0.37***	0.56***	0.16***	0.49***	-0.25***
PHD 0.7 <i>df</i> = 2938	-0.082***	0.57***	0.48***	0.48***	0.54***	0.18***	0.48***	-0.27***
PHD 0.8 <i>df</i> = 2938	-0.12***	0.57***	0.42***	0.61***	0.47***	0.21***	0.42***	-0.20***

Pearson's product-moment correlation under  $H_0$  true correlation is equal to 0. The density criterion  $dc$  ranges from 0.3 to 0.8 kg dm<sup>-3</sup>  
 ns Not significant, RW ring width, MRD mean ring density, MID minimum ring density, MAD maximum ring density, EWD earlywood density, LWD latewood density, EWP earlywood proportion, SEQ *i* MHD mean of high-density segment, MLD mean of low-density segment, *df* degree of freedom for each variable

Associated probabilities (\*\*\*)  $p < 0.001$ , (\*\*)  $p < 0.01$ , (\*)  $p < 0.05$

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