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Variability of European beech wood density as influenced by interactions between tree-ring growth and aspect

Daniela Diaconu*, Marc Wassenberg and Heinrich Spiecker

Abstract

Background: Wood density is considered to be the most important predictor of wood quality but despite its importance, diffuse-porous tree species have been the subject of only a limited number of studies. The importance of European beech forests for Central Europe calls for profound research to examine the potential impact of a warmer climate on the quality of beech timber.

Methods: In this study we analysed the influence of tree-ring width and tree-ring age on the wood density of beech, and whether the wood density response to these two parameters is modified by aspect. A linear mixed-effects model for wood density was constructed for mean density data measured with high frequency densitometry on stem discs from 72 beech trees sampled from two different aspects (northeast -NE and southwest -SW) of a valley in southwestern Germany.

Results: Part of the variability of mean annual wood density was explained by cambial age: an increase in cambial age resulted in an increase in mean wood density. Tree-ring width and aspect had only a small influence on wood density. Wood density on the SW aspect was lower than on the NE with a difference of approximately 0.006 g/cm^3. The between-tree variability was very high.

Conclusions: The significant interaction between cambial age and aspect reflects the importance of site conditions at older tree ages: with increasing cambial age the difference between aspects becomes stronger. Our results give a better understanding of the importance of site conditions on the wood quality of beech.

Keywords: *Fagus sylvatica*, HF densitometry, Wood quality, Wood density, Aspect

Background

The structure and characteristics of tree-rings contain extremely valuable information concerning wood quality. Tree-ring research is essential in developing management guidelines to improve wood quality and productivity (Spiecker 2002). The variation of different tree-ring parameters with changes in climate can be analysed at different scales by the analysis of tree-ring width, cell structure parameters or wood density.

One of the most important parameters of wood quality is wood density, due to its correlation with the calorific value and also with mechanical properties such as hardness, stiffness and strength (Hacke et al. 2001; Niklas and Spatz 2010; Shmulsky and Jones 2011). Analysis of wood density has developed into a valuable dendroecological tool for studying the relationship between environment, tree growth and wood quality. In the context of predictions of a warmer and dryer climate in the future, wood quality becomes a crucial issue. With increased nitrogen deposition and more CO$_2$ in the atmosphere an increase in the radial growth of trees is expected (Becker et al. 1995; Spiecker et al. 1996; Kahle et al. 2008). However, wider tree-rings do not necessarily imply a higher or lower density.

The relationship between tree-ring width and tree-ring density has been intensively studied and it varies according to tree species (Bontemps et al. 2013). For instance for spruce an increase in tree-ring width was found to decrease wood density (Mäkinen et al. 2007; Piispanen

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* Correspondence: Daniela.Diaconu@iww.uni-freiburg.de
Chair of Forest Growth and Dendroecology, Albert-Ludwigs-University, Tennenbacher Str. 4, 79106 Freiburg, Germany

et al. 2014; Franceschini et al. 2010), while for oak Guilley et al. (2004) found that an increase in tree-ring width results in an increase in wood density.

Knowledge of interactions between the effects of radial growth on wood density under different environments becomes very important for the selection process of appropriate silvicultural treatments under projected global warming scenarios. Studies which link wood density to tree-ring width, cambial age, different environmental factors or silvicultural practices were mostly carried out for conifer species (Cregg et al. 1988; Jozsa and Brix 1989; Bouriaud et al. 2005; Filipescu et al. 2014). For broadleaves, due to the vessel distribution within the tree-rings, these studies are limited to ring porous tree species (Bergès et al. 2008; Guilley et al. 1999); wood density variation of diffuse-porous tree species has rarely been analysed (Zhang 1995; Bouriaud et al. 2004; Skomarkova et al. 2006; Bontemps et al. 2013).

European beech (*Fagus sylvatica* L.) is the most abundant broad-leaved forest tree species in Central Europe (Ellenberg 1996), and due to its high ecological and economic importance it is one of the most relevant hardwood tree species for forest management in this region. Therefore, profound research to examine the effects of a warmer and dryer climate on wood quality of beech is needed.

Our work complements the study done by Bouriaud (2004) and brings new arguments to the discussion on wood density variation of beech due to changing environmental conditions. We measured the mean annual density of European beech sampled from two opposing slopes with high frequency (HF) densitometry, a method which utilises the dielectric properties of wood (Torgovnikov 1993). This technique is based on the high frequency (HF) propagation of electromagnetic waves by a microelectrode system through the wood sample (Schinker et al. 2003; Boden et al. 2012). The signal received by the dielectric measuring device is directly influenced by the dielectric properties of the wood sample along the radius, and the variation of the dielectric permittivity is correlated with the density variations (Schinker et al. 2003). HF densitometry has been shown to perform reliable measurements of wood density (Wassenberg et al. 2014; Wassenberg et al. 2015b) and results compare well to X-ray densitometry (Schinker et al. 2003). When compared to X-ray measurements this method provides the advantage that it is extremely fast, non-destructive and relatively inexpensive; this method was used in several dendroclimatological studies in recent years (Fan et al. 2009; Bender et al. 2012; Montwé et al. 2014; Shchupakivskyy et al. 2014; Wassenberg et al. 2015a; Hackenberg et al. 2015).

The objectives of our study were 1) to analyse the effect of tree-ring width and tree-ring age on mean annual density of European beech and 2) to test whether the wood density response to ring width and cambial ring age is modified by aspect.

Methods

Study site and experimental design

The study area is located in southwestern Germany in a beech-dominated forest in the Swabian Alb, about 100 km south-southwest from Stuttgart. Experimental sites are situated on two opposite-exposed slopes: northeast (NE) and south-west (SW) aspects of a narrow valley close to the city of Tuttlingen. Elevation is ~800 m and ~760 m a.s.l. for the NE and SW aspect respectively, both with an inclination of 23–30°. The climate in the area is semi-continental, with a mean annual air temperature of ca 7.0 °C, and annual precipitation of 900 mm. Rainfall does not vary significantly across the valley (Geßler 2001). The stands have an average age of 80–100 years (Hauser 2003).

The first difference between the aspects is regarding the soil profiles. On the SW aspect the soil profile is particularly rocky, with soils containing 20–45 vol% rocks and stones in the upper 20 cm and up to 80 % below 0.50 m compared with the NE aspect where the soils contain only 15 vol% rocks in the upper soil layer and 30 vol% rocks below 0.50 m (Hildebrand et al. 1998; Geßler et al. 2005). The second important difference between aspects is that due to the higher radiation interception at the canopy layer on the SW site, the temperature is higher, the evapotranspiration is increased, and therefore, the water availability is permanently lower than on the NE aspect (Mayer et al. 2002). Differences between aspects are noticeable also regarding the site index, the mean height of the dominant trees (h_{100}) at base age 100 years being 29.2 m on the NE and 23.4 m on the SW aspect (Spiecker et al. 2001).

The rocky soil profile merged with the lower water availability on the SW aspect makes the study area resemble a model ecosystem where the climate projections for the next 50 to 100 years are represented by the relatively warm and dry SW aspect, and the current climate typical for the majority of beech forests in central Europe is represented by the relatively cold and wet NE facing slope (Rennenberg 1998).

In winter of 1998–1999, within the framework of a larger interdisciplinary study (*SFB 433: Beech dominated deciduous forests under the influence of climate and management: ecological, silvicultural and social analyses"*), a thinning experiment was established in the study area. The objective of the study was to develop operational stand management concepts for enhancing the resilience and adaptive capacity of beech forests to changing climatic conditions, especially to summer drought, taking into account ecological and economic aspects.

The experimental design included different thinning treatments in a randomised block design established on each aspect and replicated three times on the NE and two times on the SW aspect.

Sampling and measurements

All trees inside experimental plots were numbered and marked at 1.3 m stem height for repeated diameter measurements. The diameter measurements were assessed for all trees with a calliper, in 1999 before thinning.

The material of this study study is represented by the trees which were removed during the thinning operation. On each aspect a total of 36 random trees from different blocks (treatment replication) were selected ($N_{NE} = 36$, $N_{SW} = 36$, $N_{total} = 72$). The selected trees are equally distributed in different social classes, according to the Kraft class. From each tree a stem disc at a height of 1.3 m from the ground was removed and analysed in the laboratory. The surface of all cross sections was prepared with a diamond fly cutter (Spiecker et al. 2000) and four radii per sample were measured for tree-ring width and wood density.

Radial growth was measured using a semi-automatic image analysis software developed at the Chair of Forest Growth and Dendroecology. The individual tree growth series were cross-dated with a reference chronology with the software PAST4 (Personal Analysis System for Tree-Ring Research, SCIEM, version 4.3.1014).

Wood density was determined using HF densitometry (Schinker et al. 2003). We used the same HF probe for all samples (type D, approximately 80 μm integration width, see Fig. 1 – Wassenberg et al. 2015b). The mean density was calculated per year, tree and aspect as an arithmetic mean between the four radii that were measured. In order to convert the voltage units to real density values we used the calibration method developed by Wassenberg et al. (2014).

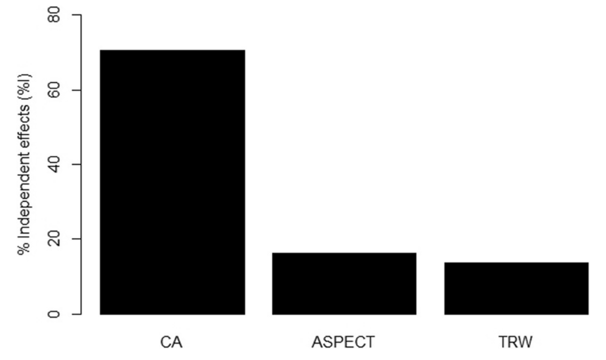

Fig. 1 Hierarchical distribution of independent variables included in the model: cambial age (CA), aspect and tree-ring width (TRW) and their influence on mean wood density

Data analysis

All data exploration, analysis and graphics were carried out using the R programming environment 3.1.3 (R Core Team 2014). The R packages used for the analysis were: *reshape2* (Wickham 2007), *ggplot2* (Wickham 2009) and *plyr* (Wickham 2011). For computing the mixed-effects models we used the package *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al., 2014). The hierarchical partitioning of the independent variables was computed with the package *hier.part* (Walsh and Mac Nally 2013).

We analysed the effect of tree-ring width, tree-ring age, site and their interactions on wood density. For this purpose, we computed a mixed-effects model for mean annual wood density with tree-ring width, aspect, cambial age and their interactions as fixed effects and tree and year as random effects (Eq. 1).

$$\begin{aligned} y_i = \alpha_1 + \alpha_2 \overset{\ddot{A}}{n}\mathrm{Aspect}_i + \alpha_3 \overset{\ddot{A}}{n}\mathrm{TRW} + \alpha_4 \overset{\ddot{A}}{n}\mathrm{CA} \\ + \alpha_5 \overset{\ddot{A}}{n}\mathrm{Aspect}_i \\ : \mathrm{TRW} + \alpha_6 \overset{\ddot{A}}{n}\mathrm{Aspect}_i : \mathrm{CA} + \mathrm{Tree} + \mathrm{Year} \end{aligned} \tag{1}$$

with y_i being mean annual density of individual trees on the ith aspect, TRW - tree- ring width and CA - cambial age (tree-ring age counted from the pith). α_n are coefficients to be estimated.

The mixed effects modelling approach provides a flexible tool for the analysis of grouped data, giving the possibility to incorporate fixed as well as random effects within one model. Fixed effects parameters are common to all subjects, whereas random effects parameters are specific to each subject (Pinheiro and Bates 2000). Fixed effects have an influence on the mean of the dependent variable, while random effects influence the variance of the dependent variable (Crawley 2007). The effect of tree (from different blocks of treatment replication) and year were treated as random effects to properly account for their random variability.

A significant interaction between two main effects means that the effect of a variable depends on the level of the other (Dormann 2013). The interaction term *TRW:Aspect* allows the magnitude of the tree-ring width on mean annual wood density to vary across the valley. The second interaction term *CA:Aspect* permits the effect of tree-ring age on mean annual wood density to vary with aspect.

Results

The hierarchical contributions of each independent variable included in the model on mean annual wood density are illustrated in Fig. 1. From the three independent variables, most of wood density variability was explained by cambial age, followed by site effects and tree-ring width.

The difference between the two aspects was larger for ring width than for wood density (Fig. 2). Results of *t*-test comparisons showed that both parameters were significantly different between expositions, but the trees on the NE aspect display significantly wider tree-rings and only slightly higher wood density than the ones on the opposite slope. Specifically, the mean tree-ring width of the trees on the NE aspect was 4.2351 mm/y (±1.9423) and 3.0794 mm/y (±1.3147) on the SW aspect. Mean annual wood density on the NE exposed slope was on average 0.5968 (±0.0312) g/cm^3 and slightly lower on the SW with 0.5908 (±0.0299) g/cm^3.

The results of the developed mixed-effects model showed that as main effect, aspect was not statistically significant ($p > 0.05$), but the interaction between aspect and tree-ring width as well as between cambial age and aspect were significant. All coefficients with statistically significant influence on wood density indicated plausible relationships with respect to biological interpretation. The parameter estimates, standard errors, and *p*-values of the parameters for the model presented in Equation 1 are listed in Table 1. The plot of the obtained residuals against the predicted values did not indicate any systematic deviation.

Wood density was slightly positively influenced by an increase in tree-ring width and cambial age (Figs. 3 and 4). For both parameters the annual density variability among trees was rather high. The significant interactions between tree-ring width and aspect, and cambial age and aspect are illustrated in Figs. 5 and 6. With an increase in tree-ring width, wood density increases much faster for the trees on the SW aspect compared with trees on the opposite slope (Fig. 5). Nevertheless, with increasing cambial age, wood density is significantly higher for the trees on the NE aspect than on the SW (Fig. 6).

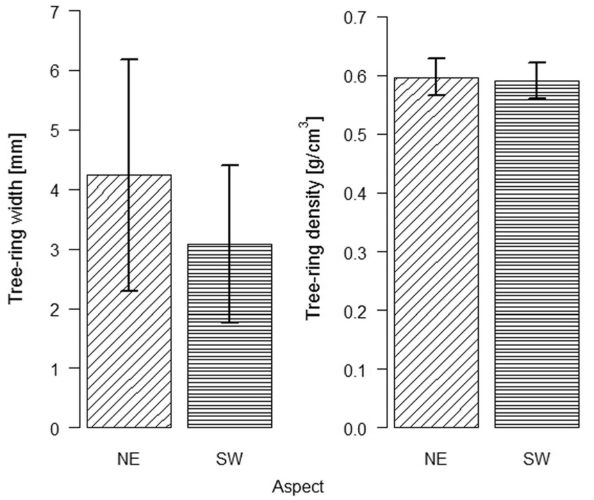

Fig. 2 Mean tree-ring width and tree-ring wood density according to aspect

Table 1 Parameter estimates and error statistics for the mean annual wood density model

	Estimate	SE	t-Value	p > |t|
Fixed parameters				
(Intercept)	5.547e-01	4.794e-03	115.720	<2e-16
TRW	2.963e-03	3.115e-04	9.513	<2e-16
Aspect SW	4.082e-03	6.179e-03	0.661	0.5105
CA	7.453e-04	5.676e-05	13.131	<2e-16
TRW:Aspect SW	1.900e-03	4.978e-04	3.817	0.0001
CA: Aspect SW	−3.877e-04	3.394e-05	−11.425	<2e-16
Random parameters				
Groups	Names	Variance	St.Dev.	
Year	(Intercept)	8.024e-05	0.008958	
Tree	(Intercept)	5.937e-04	0.024366	
Residual error		3.008e-04	0.017344	

Discussion

In this case study we evaluated differences in mean annual wood density of European beech as influenced by tree-ring width and tree-ring age under differing climatic site conditions. We showed that wood density of European beech in southwestern Germany is influenced by tree-ring age, and slightly by tree-ring width and environment, but there is a very high variability between individual trees.

Cambial age effect

Cambial age or the age of the tree-rings starting from the pith was found to have a significant role in wood density variation for different tree species. In our study the mean annual wood density was correlated with the tree-ring age from the pith - an increase in tree-ring age resulting in an increase in tree-ring wood density. Our results are in contradiction with the results of Bouriaud (2004) who found a negative relationship between ring density and ring age. This might be explained by the different age of the samples (45–70 years in Bouriaud vs 80–90 years in our case), by the different sample size (30 vs. 72 trees) or by environmental influence. A similar tree-ring age effect has been shown by De Bell et al. (2002) who studied wood density variation in young poplars and found an increase in wood density in the first three years, a decrease in the 4th and 5th year followed again by an increase until the 9th year. However, the weak influence of cambial age on mean annual wood density, reflects also that part of the total variation of annual wood density might be explained by other factors such as weather and climate.

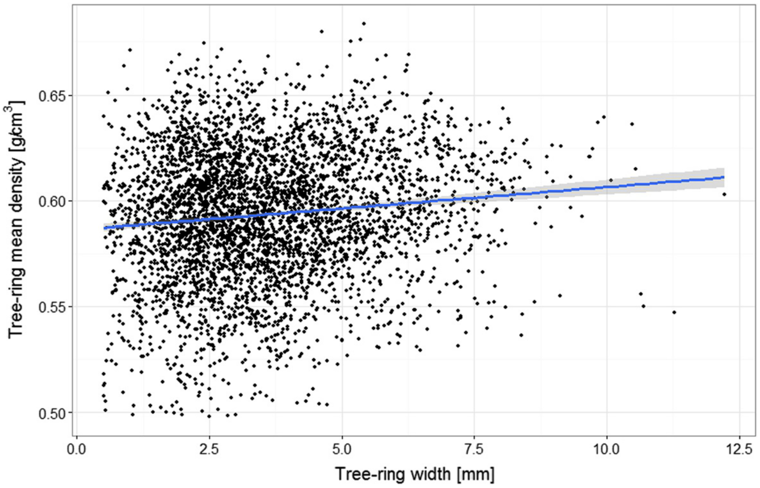

Fig. 3 Wood density variation with tree-ring width and the respective linear regression line

Site effect

Environmental influence in our study was represented by the aspect effect, the water stress for trees on the SW exposed slope being higher, and the soil profile being particularly rocky. Bouriaud (2004) did not find any influence of soil water deficit on ring density. In our study the difference in mean annual wood density between expositions was very small: 0.006 g/cm^3 less for trees on the SW aspect. Our results highlight higher sensitivity of tree-ring width to dry conditions compared with wood density - the difference in radial growth between expositions was more significant than for wood density. Particularly, the mean tree-ring width of trees on the NE aspect was approximately 40 % higher than on the SW, while the mean annual density was only 1 % higher than on the SW exposed slope (Fig. 2). The significant interaction between aspect and tree-ring age showed that with an increasing tree age the annual wood density of trees on the SW aspect is significantly lower than on the NE. This provides evidence that in older trees such a difference in wood density between moist and dry conditions might become larger.

Z'Graggen (1992) showed that maximum wood density in beech towards the end of the growing season is mostly explained by climate. Likewise, work by Sass and Eckstein (1995) also found that vessel formation at the end of the vegetation period is strongly influenced by the amount of rainfall in July. Moreover, van der Maaten (2012) found that water stress has a main impact on wood formation in beech. Hence, the local environmental factors play a significant role on the variation of wood density.

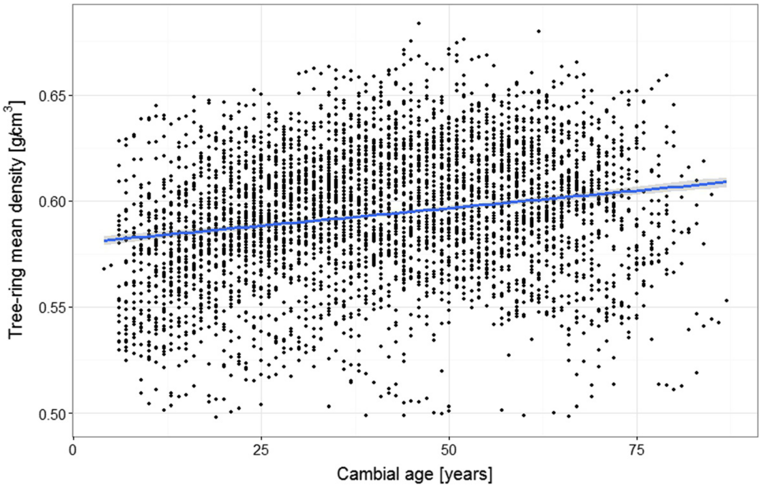

Fig. 4 Wood density variation with cambial age and the respective linear regression line

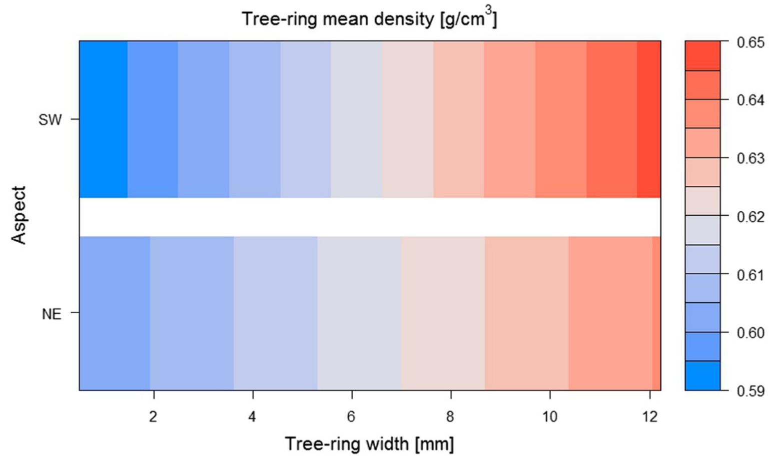

Fig. 5 Contour plot visualising the wood density variation with tree-ring width per aspect

In a more extreme climate, with more frequent summer droughts, site conditions similar to the ones presented in this study (SW aspect) might have a stronger impact on beech wood anatomy, and therefore, on wood density. Wood density depends on the number of vessels per unit area and also their size (Preston et al. 2006). The variation of these two parameters as well as the way vessels are grouped within the xylem, directly influences wood density. For instance, von Arx et al. (2013) found that on dry sites vessels are grouped in more and larger clusters than on moist sites. These findings imply that wood density on dry sites might be lower than on moist sites due to the higher vessel area within any single tree-ring. However, our results showed that the difference in mean annual wood density between aspects is very small. Moreover, only with two aspects, and due to the very high variability between individual trees it is hard to draw decisive conclusions regarding the environmental influence on wood density. This is why we encourage future studies also to investigate the intra-annual density profile linked to the architecture of the water conducting system of European beech or other diffuse-porous tree species under contrasting site conditions.

Tree-ring width effect

Due to the arrangement of vessels along the tree-ring (Sass and Eckstein 1995), wood density of diffuse-porous tree species might be only slightly influenced by a change in tree-ring width. In our study, the relationship between these two parameters was positive, significant but relatively weak - an increase in tree-ring width results in slightly higher tree-ring wood density. Our results are confirmed by Zhang (1995) who observed only a little influence of growth rate on specific gravity and mechanical proprieties of other diffuse-porous tree species (birch and poplar). Likewise, Bontemps et al. (2013)

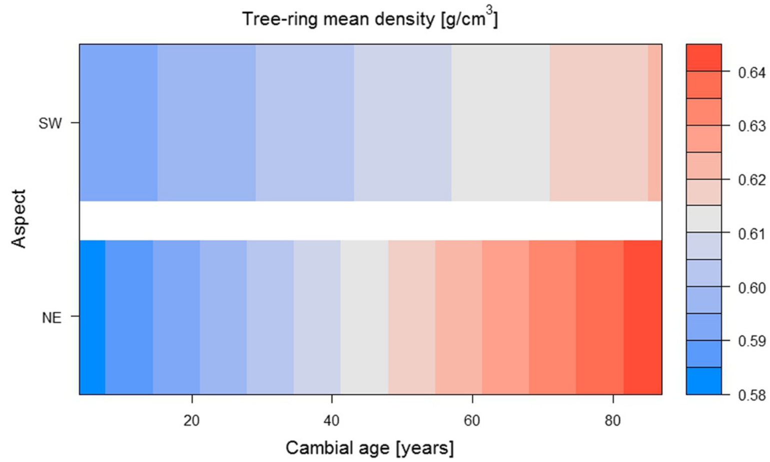

Fig. 6 Contour plot visualising the wood density variation with cambial age per aspect

found a positive but weak relationship between these two parameters for common beech in Northeastern France. Bouriaud (2004) reported no significant influence of tree-ring width on wood density. Both studies stated very large between-tree variability, which was considered to weaken the correlation.

When considering also the aspect, an increase in tree-ring width on the SW aspect increased wood density more than on the NE. This implies, that the wider tree-rings of trees on the SW aspect have less total vessel area within xylem than on the NE. It is well known that different silvicultural treatments such as thinning increase radial growth. This has been shown also for European beech (Boncina et al. 2007; Le Goff and Ottorini 1993, 1999; van der Maaten 2012; Diaconu et al. 2015). In this context our results reveal that thinning might not only give higher radial growth rates but also higher wood density. Eilmann et al. (2014) found a significant positive relationship between tree-ring width and total vessel area of beech, showing that if trees have higher growth rates, this is due to the formation of large vessels. At the same time, they found a strong negative relationship between vessel density and tree-ring width meaning that with wider tree-rings vessel density is decreasing. With low conduit density, wood density might also increase. This is confirmed by another analysis within the study area concerning the xylem plasticity in the hydraulic architecture of European beech in response to thinning, here, where the mean vessel area, the vessel density and the number of vessel groups within xylem significantly decreased in thinned trees compared to the unthinned trees (unpublished observation). These correlations show as well the investment in different types of tissues with increasing tree-ring width, and prove that with higher growth rates trees invest more in carbon sequestration than in their hydraulic system. In our study, considering the significant interaction effect between tree-ring width and aspect on wood density, thinning might represent a potential adaptation measure to a warmer climate by making the water conducting system more robust against hydraulic failure especially of the trees growing under more drought-prone climate.

Conclusion

In this study we have described the wood density variation of European beech trees as influenced by interactions between tree-ring growth and aspect. We showed that wood density of beech is influenced by tree-ring age, followed by site effects and tree-ring width. The influence of site effects on wood density was less sensitive than for tree-ring width. The significant interaction between aspect and tree-ring age showed that the present difference of 6 kg/m^3 between NE and SW aspect might increase at older ages. At the same time, the interaction between aspect and tree-ring width reflects that silvicultural treatments such as thinning applied to increase radial growth could have different effects on wood density according to the local climate.

The high sample size coupled with the long time series, offers an indication of the effect of tree-ring age, tree-ring width and local climate on wood density of European beech, and highlights as well the high variability between individual trees. Our findings bring new arguments into the present discussion of wood quality in a warmer climate and represent an important aspect for the forest management sector. Nevertheless, as our study is not replicated at other sites, the presented results are valid only for the climatic conditions in our study region and in order to generalise our findings a broader analysis needs to be carried out. Likewise, further analysis on the same or similar material but focused on wood anatomy (fibre, conduit and ray characteristics), together with climate or dendrometer data might offer a more precise indication of the influencing factors on wood density and might explain more of the inter-annual wood density variability of European beech trees.

Competing interests

The authors declare that they have no competing interest.

Authors' contributions

HS conceived the study and contributed to its design and coordination. All TRW and HF-density measurements were carried out by MW. Data analysis was performed by DD. The manuscript was written by DD with advice from MW and HS. All authors contributed to the interpretation and discussion of the results. All authors read and approved the final manuscript.

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References

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. doi:10.18637/jss.v067.i01

Becker M, Bert GD, Bouchon J, Dupouey JL, Picard JF, Ulrich E (1995) Long term changes in forest productivity: the dendrochronological approach. In: Landmann G, Bonneau M (eds) Forest decline and atmospheric deposition effects in the French mountains. Springer, Berlin, Heidelberg

Bender BJ, Mann M, Backofen R, Spiecker H (2012) Microstructure alignment of wood density profiles: an approach to equalize radial differences in growth rate. Trees 26(4):1267–1274. doi:10.1007/s00468-012-0702-y

Bergès L, Nepveu G, Franc A (2008) Effects of ecological factors on radial growth and wood density components of sessile oak (Quercus petraea Liebl.) in Northern France. For Ecol Manage 255(3–4):567–579. doi:10.1016/j.foreco.2007.09.027

Boden S, Schinker MG, Duncker P, Spiecker H (2012) Resolution abilities and measuring depth of high-frequency densitometry on wood samples. Measurement 45(7):1913–1921. doi:10.1016/j.measurement.2012.03.013

Boncina A, Kadunc A, Robic D (2007) Effects of selective thinning on growth and development of beech (Fagus sylvatica L.) forest stands in south-eastern Slovenia. Ann For Sci 64(1):47–57. doi:10.1051/forest:2006087

Bontemps J, Gelhaye P, Nepveu G, Hervé J (2013) When tree rings behave like foam: moderate historical decrease in the mean ring density of common beech paralleling a strong historical growth increase. Ann For Sci 70(4):329–343. doi:10.1007/s13595-013-0263-2

Bouriaud O, Bréda N, Le Moguédec G, Nepveu G (2004) Modelling variability of wood density in beech as affected by ring age, radial growth and climate. Trees 18(3):264–276. doi:10.1007/s00468-003-0303-x

Bouriaud O, Leban J, Bert D, Deleuze C (2005) Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Physiol 25:651–660

Crawley MJ (2007) The R book. Wiley, England

Cregg BM, Dougherty PM, Hennessey TC (1988) Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. f. Can J For Res 18(7):851–858. doi:10.1139/x88-131

DeBell DS, Singleton R, Harrington CA, Gartner BL (2002) Wood density and fiber length in young Populus stems: relation to clone, age, growth rate, and pruning. Wood Fiber Sci 34:529–539

Diaconu D, Kahle H, Spiecker H (2015) Tree- and stand-level thinning effects on growth of european beech (Fagus sylvatica L.) on a Northeast- and a Southwest-facing slope in Southwest Germany. Forests 6(9):3256–3277. doi:10.3390/f6093256

Dormann CF (2013) Parametrische Statistik: Verteilungen, Maximum Likelihood und GLM in R. Springer, Berlin

Eilmann B, Sterck F, Wegner L, de Vries SMG, von Arx G, Mohren GMJ, den Ouden J, Sass-Klaassen U (2014) Wood structural differences between northern and southern beech provenances growing at a moderate site. Tree Physiol 34(8):882–893. doi:10.1093/treephys/tpu069

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht: 170 Tabellen, 5., stark veränd. und verb. Aufl. UTB, vol 8104. Ulmer, Stuttgart

Fan Z, Bräuning A, Yang B, Cao K (2009) Tree ring density-based summer temperature reconstruction for the central Hengduan Mountains in southern China. Glob Planet Chang 65(1–2):1–11. doi:10.1016/j.gloplacha.2008.10.001

Filipescu CN, Lowell EC, Koppenaal R, Mitchell AK (2014) Modeling regional and climatic variation of wood density and ring width in intensively managed Douglas-fir. Can J For Res 44(3):220–229. doi:10.1139/cjfr-2013-0275

Franceschini T, Bontemps J, Gelhaye P, Rittie D, Herve J, Gegout J, Leban J (2010) Decreasing trend and fluctuations in the mean ring density of Norway spruce through the twentieth century. Ann For Sci 67(8):816. doi:10.1051/forest/2010055

Geßler A, Schrempp S, Matzarakis A, Mayer H, Rennenberg H, Adams MA (2001) Radiation modifies the effect of water availability on the carbon isotope composition of beech (Fagus sylvatica). New Phytol 150:653–664

Geßler A, Jung K, Gasche R, Papen H, Heidenfelder A, Börner E, Metzler B, Augustin S, Hildebrand E, Rennenberg H (2005) Climate and forest management influence nitrogen balance of European beech forests: microbial N transformations and inorganic N net uptake capacity of mycorrhizal roots. Eur J Forest Res 124(2):95–111. doi:10.1007/s10342-005-0055-9

Guilley E, Herve J, Huber F, Nepveu G (1999) Modelling variability of within-ring density components in Quercus petraea Liebl. with mixed-effect models and simulating the influence of contrasting silvicultures on wood density. Ann For Sci 56:449–458

Guilley E, Hervé J, Nepveu G (2004) The influence of site quality, silviculture and region on wood density mixed model in Quercus petraea Liebl. For Ecol Manage 189(1–3):111–121. doi:10.1016/j.foreco.2003.07.033

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126(4):457–461. doi:10.1007/s004420100628

Hackenberg J, Wassenberg M, Spiecker H, Sun D (2015) Non destructive method for biomass prediction combining TLS derived tree volume and wood density. Forests 6(4):1274–1300. doi:10.3390/f6041274

Hauser S (2003). Dynamik hochaufgelöster radialer Schaftveränderungen und des Dickenwachstums bei Buchen (FAgus sylvatica L.) der Schwäbischen Alb unter dem Einfluss von Witterung und Bewirtschaftung. Dissertation, Albert-Ludwigs Universität Freiburg

Hildebrand E, Augustin S, Schack-Kirchner H (1998) Bodenkundliche Charakterisierung der Kernflächen. In: Rennenberg H (ed) Buchendominierte Laubwälder unter dem Einfluß von Klima und Bewirtschaftung: Ökologische, waldbauliche und sozialwissenschaftliche Analysen - Vorcharakterisierung der Untersuchungsflächen. Eigenverlag der Universität Freiburg, Freiburg, pp 7–12

Jozsa LA, Brix H (1989) The effects of fertilization and thinning on wood quality of a 24-year-old Douglas-fir stand. Can J For Res 19(9):1137–1145. doi:10.1139/x89-172

Kahle HP, Karjalainen T, Schuck A, Å GI, Kellomäki S, Mellert K, Prietzel J, Rehfuess KE, Spiecker H (2008) Causes and consequences of forest growth trends in Europe: Results of the Recognition project. In: European Forest Institute Research Report, vol 21. Brill, Leiden

Kuznetsova A, Brunn Brockhoff P, Haubo Bojesen Christensen R (2014). lmerTest: Tests in Linear Mixed Effects Models. r package version 2.0-29. https://cran.r-project.org/web/packages/lmerTest/index.html. Accessed 22 May 2015

Le Goff N, Ottorini J (1993) Thinning and climate effects on growth of beech (Fagus sylvatica L.) in experimental stands. For Ecol Manage 62:1–14

Le Goff N, Ottorini J (1999) Effects of thinning on beech growth. Interaction with climatic factors. Rev For Fr 51:355–364

Mäkinen H, Jaakkola T, Piispanen R, Saranpää P (2007) Predicting wood and tracheid properties of Norway spruce. For Ecol Manage 241(1–3):175–188. doi:10.1016/j.foreco.2007.01.017

Mayer H, Holst T, Schindler D (2002) Microclimate within beech stands - part I: photosynthetically active radiation. Forstwiss Cent 121(6):301–321. doi:10.1046/j.1439-0337.2002.02038.x

Montwé D, Spiecker H, Hamann A (2014) An experimentally controlled extreme drought in a Norway spruce forest reveals fast hydraulic response and subsequent recovery of growth rates. Trees 28(3):891–900. doi:10.1007/s00468-014-1002-5

Niklas KJ, Spatz H (2010) Worldwide correlations of mechanical properties and green wood density. Am J Bot 97(10):1587–1594. doi:10.3732/ajb.1000150

Piispanen R, Heinonen J, Valkonen S, Mäkinen H, Lundqvist S, Saranpää P (2014) Wood density of Norway spruce in uneven-aged stands 1. Can J For Res 44(2):136–144. doi:10.1139/cjfr-2013-0201

Pinheiro JC, Bates DM (2000) Mixed-Effects Models in S and S-PLUS. Statistics and computing, Springer, New York

Preston KA, Cornwell WK, Denoyer JL (2006) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. New Phytol 170(4):807–818. doi:10.1111/j.1469-8137.2006.01712.x

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Available online at http://www.R-project.org/

Rennenberg H (1998) Buchendominierte Laubwälder unter dem Einfluß von Klima und Bewirtschaftung: Ökologische, waldbauliche und sozialwissenschaftliche Analysen - Vorcharakterisierung der Untersuchungsflächen. Eigenverlag der Universität Freiburg, Freiburg

Sass U, Eckstein D (1995) The variability of vessel size in beech (Fagus sylvatica L.) and its ecophysiological interpretation. Trees 9:247–252

Schinker MG, Hansen N, Spiecker H (2003) High-frequency densitometry - a new method for the rapid evaluation of wood density variations. IAWA J 24(3):231–239

Shchupakivskyy R, Clauder L, Linke N, Pfriem A (2014) Application of high-frequency densitometry to detect changes in early- and latewood density of oak (Quercus robur L.) due to thermal modification. Eur J Wood Wood Prod 72(1):5–10. doi:10.1007/s00107-013-0744-x

Shmulsky R, Jones PD (2011) Hardwood Structure. In: Forest Products and Wood Science An Introduction, Sixthth edn. Wiley-Blackwell, Oxford. doi:10.1002/9780470960035.ch5

Skomarkova MV, Vaganov EA, Mund M, Knohl A, Linke P, Boerner A, Schulze E (2006) Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (Fagus sylvatica) growing in Germany and Italy. Trees 20(5):571–586. doi:10.1007/s00468-006-0072-4

Spiecker H (2002) Tree rings and forest management in Europe. Dendrochronologia 20(1–2):191–202. doi:10.1078/1125-7865-00016

Spiecker H, Mielikäinen K, Köhl M, Skovsgaard JP (1996) Growth Trends in European Forests: Studies from 12 Countries. Springer, Berlin, Heidelberg

Spiecker H, Ebding T, Park Y, Hansen J, Schinker MG, Döll W (2000) Cell structure in tree rings: novel methods for preparation and image analysis of large cross sections. IAWA J 21(3):361–373. doi:10.1163/22941932-90000253

Spiecker H, Kahle H, Hauser S (2001) Klima und Witterung als Einflußfaktoren für das Baumwachstum in Laubwäldern: retrospektiven Analysen und

Monitoring. In: Rennenberg, H. (ed) Buchendominierte Laubwälder unter dem Einfluß von Klima und Bewirtschaftung: Ökologische, waldbauliche und sozialwissenschaftliche Analysen - Vorcharakterisierung der Untersuchungsflächen; Abschlußbericht des SFB 443. Eigenverlag der Universität Freiburg, Freiburg, pp 307–333.

Torgovnikov GI (1993) Dielectric Properties of Wood and Wood-Based Materials. Springer, Berlin, Heidelberg

van der Maaten E (2012) Intra- and interannual growth responses of European beech (Fagus sylvativa L.) to climate, aspect and thinning in the Swabian Alb - southwestern Germany. Dissertation, Albert-Ludwigs-Universität Freiburg

von Arx G, Kueffer C, Fonti P (2013) Quantifying plasticity in vessel grouping – added value from the image analysis tool ROXAS. IAWA J 34(4):433–445. doi: 10.1163/22941932-00000035

Walsh C, Mac Nally R (2013) hier.part: Hierarchical Partitioning: Variance partition of a multivariate data set. https://cran.r-project.org/web/packages/hier.part/hier.part.pdf. Accessed 21 May 2015

Wassenberg M, Montwé D, Kahle H, Spiecker H (2014) Exploring high frequency densitometry calibration functions for different tree species. Dendrochronologia 32(3):273–281. doi:10.1016/j.dendro.2014.07.001

Wassenberg M, Chiu H, Guo W, Spiecker H (2015a) Analysis of wood density profiles of tree stems: incorporating vertical variations to optimize wood sampling strategies for density and biomass estimations. Trees 29(2):551–561. doi:10.1007/s00468-014-1134-7

Wassenberg M, Schinker M, Spiecker H (2015b) Technical aspects of applying high frequency densitometry: Probe-sample contact, sample surface preparation and integration width of different dielectric probes. Dendrochronologia 34:10–18. doi:10.1016/j.dendro.2015.03.001

Wickham H (2007) Reshaping data with the reshape package. J Stat Softw 21:1–20

Wickham H (2009) Ggplot2: Elegant graphics for data analysis. In: Gentleman R, Hornik K, Parmigiani G (eds) Use R! Springer, New York. doi:10.1007/978-0-387-98141-3

Wickham H (2011) The split-apply-combine sttrategy for data analysis. J Stat Softw 40:1–29

Z'Graggen S (1992) Dendrohistometrisch-klimatologische Untersuchung an Buchen (Fagus silvatica L.). Dissertation, University of Basel

Zhang SY (1995) Effect of growth rate on wood specific gravity and selected mechanical properties in individual species from distinct wood categories. Wood Sci Technol 29:451–465