Ann. For. Res. 55(1): 113-124, 2012

ANNALS OF FOREST RESEARCH
www.e-afr.org

Temporally resolved intra-annual wood density variations in European beech (*Fagus sylvatica* L.) as affected by climate and aspect

E. van der Maaten, M. van der Maaten-Theunissen, H. Spiecker

van der Maaten E., van der Maaten-Theunissen M., Spiecker H., 2012. Temporally resolved intra-annual wood density variations in European beech (*Fagus sylvatica* L.) as affected by climate and aspect. Ann. For. Res. 55(1): 113-124, 2012.

Abstract. We investigated the temporal variability of intra-annual wood density variations in European beech (*Fagus sylvatica* L.) in a valley in south-western Germany. Samples were collected from 11 beech trees growing at north-west (NW) and south-west (SW) exposed slopes. High-frequency densitometry was used to obtain wood density profiles. We converted radial positions within these profiles to a seasonal time scale over automatic point dendrometer data for the period 2001–2006. Temporally resolved wood density data was analyzed both visually and statistically, using correlation analysis and multiple linear regressions. Water availability was found to be of major importance for wood formation. Further, our results suggest that climatic forcing of wood density is not necessarily restricted to the late growing season only, but that strong associations may exist during a major part of the growing season. Combining wood property data with point dendrometer measurements was demonstrated to be valuable for increasing the understanding on the effects of changing environmental conditions on wood formation.

Keywords point dendrometer, wood formation, water availability, vessel size

Authors. Ernst van der Maaten (Ernst.van-der-Maaten@iww.uni-freiburg.de) - Marieke van der Maaten-Theunissen, Heinrich Spiecker - Institute for Forest Growth, Albert-Ludwigs-University, Tennenbacher Str. 4, 79106 Freiburg, Germany.

Manuscript received March 29, 2012; revised April 16, 2012; accepted May 07, 2012; online first May 08, 2012.

Introduction

Wood density has been frequently studied as an indicator of wood quality (e.g., Erickson & Harrison 1974, Evans & Ilic 2001) and was demonstrated to provide additional information on climate–growth relationships of trees compared to radial growth data (Hughes et al. 1984). Variations in wood density originate from differences in wood anatomical characteristics, such as the proportion, size and distribution of woody tissues (Kramer & Kozlowski 1979, Zobel & van Buijtenen 1989), which occur amongst others due to variations in environmental factors. Especially for coniferous species, relationships between maximum latewood density and late summer temperature have been established, and are widely used for climate reconstructions (Briffa et al. 1990, D'Arrigo et al. 1992, Briffa et al. 2001). In contrast, only a few studies analyzed wood density variations of diffuse-porous tree species.

However, recent densitometric studies on European beech (*Fagus sylvatica* L.) showed that wood density variations accurately reflect changes in vessel size and frequency along the wood matrix, and that inter- and intra-annual density variations may provide valuable and additional information on growth responses of beech to climate (Z'Graggen 1992, Bouriaud et al. 2004, Skomarkova et al. 2006). Despite these evidences, and other histological studies (Sass & Eckstein 1995, Schmitt et al. 2000) that provided insight in the physiological mechanisms underlying tree ring formation in beech, our knowledge on direct effects of short-term climate fluctuations on wood anatomy and formation remains not well elucidated. The understanding on climatic forcing of wood formation could be significantly improved by analyzing intra-annual courses of wood density over longer time periods and under contrasting environmental conditions. Different methods may be employed to gain insight in the timing of wood formation, including pinning (cf. Seo et al. 2007) and micro-coring techniques (Rossi et al. 2006). Recently, however, dendrometers were demonstrated to be suitable tools for rescaling wood property data, like wood density, from a distance scale to a time scale (e.g., Wimmer et al. 2002, Bouriaud et al. 2005, Drew et al. 2009), as these instruments measure stem radius variations at high temporal resolution without disturbing the cambium.

In this study, we used automatic point dendrometers to convert wood density profiles of European beech to a seasonal time scale in order to gain deeper insight in the respective roles of climatic variables on wood density. We investigated temporally resolved wood density variations of 11 trees over six growing seasons (2001–2006). The trees grew at north-west (NW) and south-west (SW) exposed slopes of a valley in southwestern Germany. The objective was to investigate how intra-annual fluctuations in climate and water availability are influencing wood density of beech, and to see how these responses differ with aspect. In addition, we compared the courses of wood density with concurrent day-to-day stem radius variations. We expect that short-term variations in climate are reflected in the entire wood density profile, with wood density being positively related to water stress. Further, we assume a negative association between wood density and stem radius variations at an intra-annual level.

Materials and methods

Site description

The study area is located in a beech-dominated forest in the Swabian Alb, a low mountain range in southwestern Germany (altitude: 740-760 m a.s.l., latitude: 48°00'N, longitude: 8°50'E). Study sites support 80–100 year old beech and are situated at NW and SW exposed slopes of a valley, and are not more than 500 m apart. Slopes are steep and have inclinations ranging between 23 and 30°. Soils are limestone-derived Terra Fusca-Rendzinas (Chromo-Calcic Cambisol (FAO)) and shallow (< 20 cm) before becoming dominated by bedrock. Water availability is lowest at SW due to high radiation interception and evaporation rates (Mayer et al. 2002), as well as high rock content in the upper soil layer (Hildebrand et al. 1998). Rainfall does not vary significantly across the valley (Geßler et al. 2001).

The climate in the area can be characterized as semi-continental with a mean annual air temperature of 7.0°C and an annual rainfall sum of 900 mm over the period 1961–1990 (source: 1 × 1 km gridded climate surface of German Weather Service, WebWerdis 2011). Average air temperature and precipitation over the growing period April-August amounts to 12.3°C and 459 mm, respectively.

Dendrometric and ring density measurements

Stem radius variations of 11 dominant or co-dominant European beech trees ($n_{NW} = 5$; $n_{SW} = 6$) were monitored over the period 2001–2006 using automatic point dendrometers. These instruments measure the linear displacement of a sensing rod (Trans-Tek. Inc., Connecticut, USA) pressed perpendicularly against the bark (Hauser 2003). Variations in stem radius were recorded in millivolt (1 mV ≈ 0.001 mm) at 30-second intervals, and averaged to half hour values by dataloggers. Dendrometers were installed at 1.40 m and slope-parallel to avoid direct solar irradiation on the measurement devices and disturbing influences of reaction wood formation. Mean tree height and diameter breast height (DBH) of the study trees were higher at NW (25.9 ± 0.6 m and 37.5 ± 3.0 cm compared to 20.5 ± 0.6 m and 32.7 ± 1.3 cm at SW). With a mean age of ~100 years, trees are somewhat older at NW than at SW (~90 years).

After the six years of growth monitoring, all study trees were felled in the course of a more extensive dendroclimatological study (van der Maaten 2012). Wood samples were extracted following the point-dendrometer axis. These longitudinal wood strips were air-dried and smoothed with an ultra-precise diamond fly-cutter (Spiecker et al. 2000) to allow high-frequency densitometry analysis (Schinker et al. 2003). This latter method determines relative density variations (in Volt) over dielectric wood properties. We measured wood density using a probe of 91 μm width and 843 μm length, defining an integration area and wood sample volume (see Boden et al. 2012) that enable wood density measurements on the diffuse-porous tree species beech, which density is mainly determined by variations in vessel properties (Skomarkova et al. 2006). Measurements were taken in radial direction at an interval of 28 μm, implying a 70% overlap in scanned wood surface between adjacent measurements. We used specific software routines developed at the Institute for Forest Growth (Freiburg, Germany) to detect annual rings and to superimpose wood density profiles onto tree-ring series.

Meteorological and soil water content data

Daily weather data was gathered from meteorological towers that were installed in the valley within a large research project (for a complete description see Mayer et al. 2002, Holst et al. 2004). For the SW exposed site, on-plot meteorological records were available, whereas no meteorological data was collected at the NW aspect. We therefore relied on climate data that was measured on a nearby NE aspect, approximately 500 m south-southeast from the study trees at NW. In the analyses, we used the following environmental variables: daily air temperature (minimum, mean and maximum), solar radiation, precipitation sum, soil water content (SWC) and vapor pressure deficit (VPD). Soil water content was monitored for the uppermost soil layer using the time domain reflectometry (TDR) method. Per aspect, two probes with needle lengths of 30 cm (CS615, Campbell Scientific, Logan, USA) were buried vertically into the soil.

Rescaling and analyzing wood-property data

As wood samples for high-frequency densitometry analysis were extracted following the point-dendrometer axis, approximate dates of wood formation could be inferred over dendrometer measurements. To rescale the wood density profiles, we first standardized daily average dendrometer series as relative to total stem radius variation. Then, we eliminated effects of shrinkage on the alignment by transforming daily dendrometer data to monotonically increasing time series (Figure 1) (cf. Bouriaud et al. 2005). A routine was written in MATLAB (R2009b, the MathWorks, Inc., Natick, USA) to obtain these monotonic growth curves. The *round* function was then used to perform a tree- and year-specific rescaling of wood density profiles. Growth onset and cessation were defined as the dates when the study trees achieved 2.5 and 97.5% of the total stem radius variation, respectively.

To determine the extent to which temporal wood density fluctuations could be associated with changes in environmental variables, we calculated correlations between mean monthly wood density of the study trees and monthly averaged (or summed) climatic variables. Lagged effects were considered by correlating the average density of wood formed in a particular month with climate conditions in the previous month. Calculating these correlations for both aspects allowed the detection of possible differences in the climatic forcing of wood density between NW and SW. Correlations were calculated for the months May, June and July, and for the period May–July as growth is largely restricted to these months.

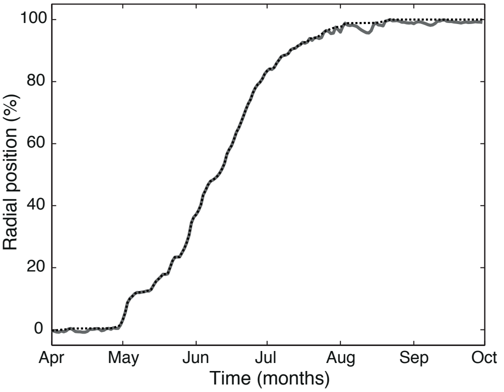

Figure 1 Example of a standardized daily dendrometer curve (gray line) with a monotonic increasing time series (black dotted line) used for rescaling of wood property data.

In addition, we calculated multiple linear regressions between mean monthly wood density and (lagged) environmental variables for the NW and SW aspect, using a forward stepwise variable selection method. From the available temperature variables, only monthly mean air temperature was included in these analyses. Further, we penalized overly complex models by using Akaike's Information Criterion (AIC) to select final models. Normality of model residuals was assured using Shapiro-Wilk tests, and multi-collinearity among regressors was examined. Variance inflation factors (*VIF*) indicated that dependencies among the environmental variables in the final models did not affect the regression estimates (VIF_{NW} = 2.135 and VIF_{SW} = 1.655). All statistical analyses were performed in SPSS (Version 19, IBM Statistics).

Results

Growth conditions differed over the study period 2001–2006 (Table 1). Over this period, differences in annual growth profiles were observed as well (Figure 2). Growth duration was particularly short in 2003 due to an early growth cessation, whereas the years 2001 and 2002 were characterized by comparably long growing seasons. Narrow error bars indicate that growth patterns of trees within a particular aspect are highly comparable. Also differences in growth profiles between both aspects were small, except for 2003 where trees at SW showed later growth cessation. Differences in achieved growth levels, however, are large between both aspects (Figure 3), as trees at SW showed higher growth levels in all years.

Intra-annual variations in wood density, arithmetically averaged over multiple trees for each aspect, are plotted over time in Figure 4. Temporal wood density profiles were quite comparable within, but also between both aspects. Strong density contrasts, defined as the difference between minimum and maximum wood density, were observed in all years and illustrate the suitability of European beech for high-frequency densitometry analysis. Lower wood density was formed in the beginning of each year, whereas higher wood densities were found in the second part of the growing season. Distinct intra-annual density fluctuations were observed in 2001 at NW, and in 2006 at both aspects. For this latter year, comparing time-mapped wood density (Figure 5d) with VPD (Figure 5c), SWC (Figure 5b) and day-to-day stem radius variation (SRV; Figure 5a) reveals relationships between these parameters, especially for the indicated periods P2 and P3. More specifically, in P2, a decrease in SWC and an associated increase in VPD coincide with an increase in growth and a decrease in wood density. Water availability remained

Table 1 Mean climate characteristics for the study years 2001–2006 calculated over the period from April till August (NE tower)

Year	T_{mean}	P
2001	13.0	416
2002	13.0	553
2003	15.6	333
2004	12.6	416
2005	13.0	457
2006	13.3	665

Note: T_{mean} mean air temperature (°C) and P precipitation sum (mm)

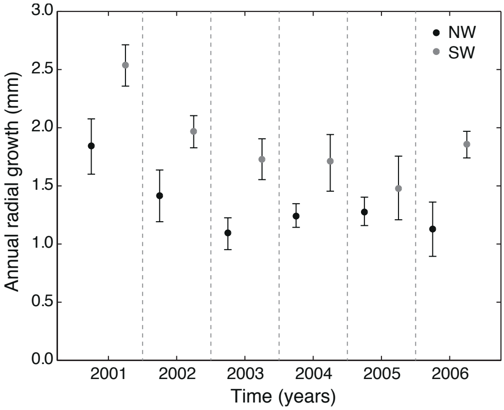

Figure 3 Mean radial growth and standard deviations of study trees at NW (black circles) and SW (gray circles) for the years 2001–2006.

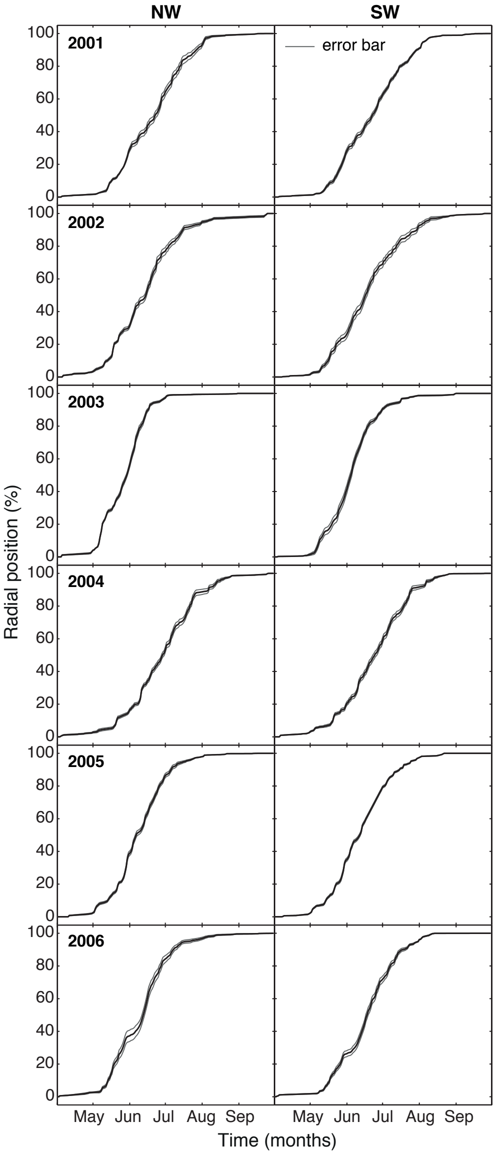

Figure 2 Monotonic increasing dendrometer curves presented as averages for NW (left; n = 5) and SW (right; n = 6) for the years 2001–2006; error bars denote standard errors.

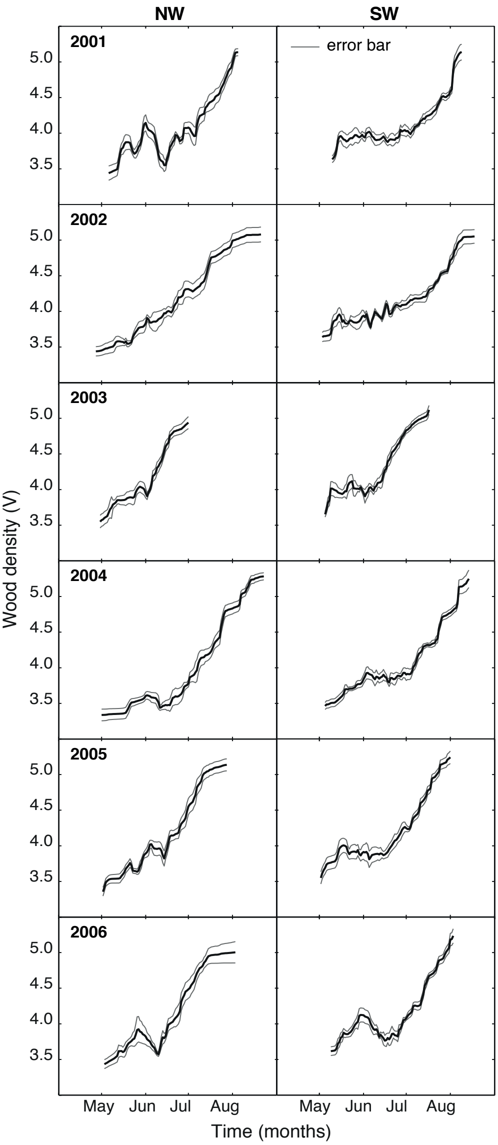

Figure 4 Intra-annual variations in wood density presented as averages for NW (left; n = 5) and SW (right; n = 6) for the years 2001–2006; error bars denote standard errors.

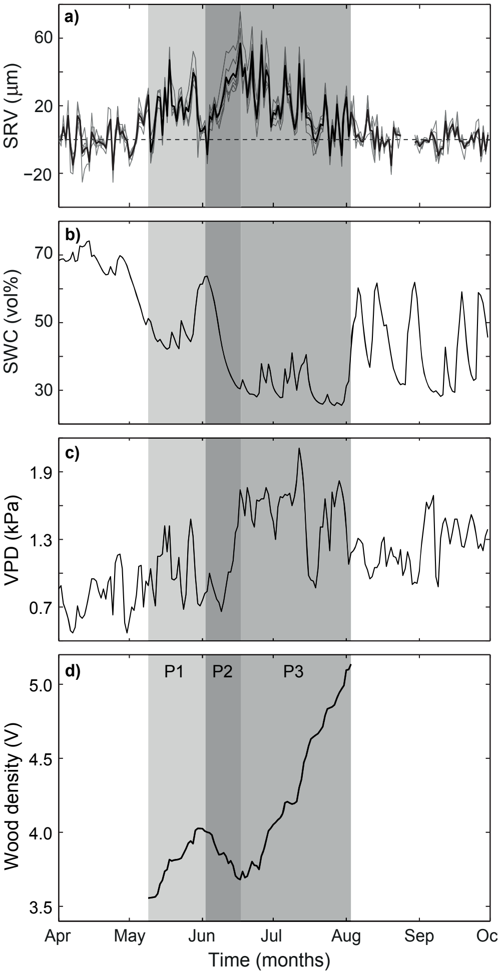

Figure 5 a) Individual (gray lines) and average (black line) day-to-day stem radius variations SRV (μm) of study trees at SW in 2006, and accompanying b) soil water content (vol%), c) vapor pressure deficit (kPa) and d) average wood density (V). P1, P2 and P3 denote characteristic periods as discussed in the text.

low over P3, and is accompanied by a gradual decrease in growth and an increase in wood density. For period P1, (negative) associations between growth and wood density were not obvious. In other years, negative associations between SRV and wood density were mainly restricted to the second half of the growing season.

Results of the correlation analysis between monthly wood density and environmental variables stress the importance of water availability for wood density (Table 2). From the three variables related to water-availability, being precipitation, SWC and VPD, strongest correlations were found for VPD. This parameter, which can be considered a major driver of evapotranspiration, was positively related to wood density. A negative effect was only suggested for a lagged effect of April VPD on May wood density. Similarly, opposing lagged effects of April temperature (minimum, mean and maximum) on wood density were observed. Negative associations for this month were suggested for both aspects, and might be explained by a stimulation of growth with high April temperatures, likely reducing wood density. Although no significant negative correlation between average SRV and wood density could be observed for May, strong positive correlations between growth onset and April temperature ($r_{NW} = –0.554$, $r_{SW} = –0.715$; $P < 0.001$) suggested a release of growth-limiting temperature constraints, with growth onset advancing under high April temperatures.

The importance of VPD for wood density is substantiated in the multiple regression models. For both aspects, this factor was included as a regressor (Table 3). At NW, a linear model using VPD and lagged air temperature explained 86.7% of the average density of wood formed each month, whereas on the SW aspect VPD and solar radiation explained 65.5% of the variation in wood density.

Discussion

Rescaling of wood density

In this study we successfully rescaled wood density profiles for beech to a temporal scale over high-resolution point dendrometer data. A limited number of previous studies have used dendrometers to temporally resolve and ana-

Table 2 Pearson correlation coefficients between mean monthly wood density and monthly environmental variables

Environmental factor	Wood density							
	NW				SW			
	May	June	July	May-July	May	June	July	May-July
Minimum air temperature	0.70	0.85*	0.51	0.84**	0.88*	0.85*	0.29	0.76**
lagged	-0.73	0.27	0.73	0.87**	-0.48	0.46	0.82*	0.87**
Mean air temperature	0.86*	0.87*	0.48	0.83**	0.84*	0.84*	0.42	0.73**
lagged	-0.48	0.50	0.73	0.88**	-0.43	0.43	0.81	0.86**
Maximum air temperature	0.84*	0.88*	0.48	0.81**	0.83*	0.83*	0.38	0.72**
lagged	-0.55	0.49	0.74	0.88**	-0.33	0.46	0.80	0.86**
Solar radiation	0.04	0.81*	0.04	0.36	-0.02	0.61	0.04	0.22
lagged	-0.13	-0.39	0.73	0.82**	-0.21	-0.32	0.66	0.81**
Soil water content	-0.02	-0.91*	-0.44	-0.85**	0.56	-0.28	0.08	-0.64**
lagged	0.42	0.39	-0.77	-0.74**	0.55	-0.08	-0.27	-0.65**
Vapor pressure deficit	0.96**	0.89*	0.37	0.86**	0.97**	0.87*	0.21	0.76**
lagged	-0.32	0.76	0.64	0.90**	-0.20	0.74	0.81	0.89**
Precipitation sum	0.20	-0.38	-0.08	-0.18	0.18	-0.14	-0.31	-0.13
lagged	0.27	0.26	-0.75	-0.08	0.36	-0.04	-0.68	-0.15

Note: Asterisks denote significant correlations, * $P < 0.05$, ** $P < 0.01$

Table 3 Results of multiple regression analysis of monthly averaged wood density in relation to environmental variables

Variable	Coefficient	SE	*t* statistic	Significance
NW				
Constant	1.89	0.32	5.9	0.000
Vapor pressure deficit	1.35	0.37	3.7	0.002
Mean air temperature (lagged)	0.06	0.01	4.2	0.001
$R^2_{adj} = 0.867$				
SW				
Constant	3.25	0.45	7.3	0.000
Vapor pressure deficit	1.86	0.33	5.7	0.000
Solar radiation	-0.07	0.03	-2.4	0.033
$R^2_{adj} = 0.655$				

lyze wood property data, e.g., for *Eucalyptus* species (Wimmer et al. 2002, Drew et al. 2011) and Norway spruce (*Picea abies* (L.) Karst.) (Bouriaud et al. 2005). Skomarkova et al. (2006) used weekly stem diameter measurements from girth bands to rescale wood properties onto a time axis. However, point dendrometers were suggested to be most appropriate for rescaling purposes as these instruments allow a reasonable accurate estimation of the timing when radially sequential portions of wood were formed (Drew & Downes 2009).

Although over-bark dendrometer measurements include both irreversible growth and reversible changes in stem hydration (Kozlowski & Winget 1964, Herzog et al. 1995, Panterne et al. 1998, Deslauriers et al. 2003), reversible changes in tissue width external to the xylem seem less strong for beech when compared to coniferous tree species, which likely relates to the thin bark of beech. Whereas reductions in stem size lasting over several days are frequently observed in species like Norway spruce (Bouriaud et al. 2005, Zweifel et al. 2005), daily dendrometer series for beech largely increase (Figure 1). This suggests that dendrometer data for beech closely reflect radial growth. We therefore used monotonically increasing time series directly derived from daily dendrometer data in the rescaling of wood density profiles, instead of sigmoid functions like Gompertz to describe intra-annual growth patterns (Rossi et al. 2003). We averaged wood density profiles over multiple beech trees ($n_{NW} = 5$; $n_{SW} = 6$), assuming that this allows an accurate detection of intra-annual wood density variations (cf. Drew et al. 2009).

Growth and wood density fluctuations

Growth profiles were highly comparable within and between aspects for individual years (Figure 2). Only for 2003, we observed a major difference in growth pattern at NW and SW, as trees at SW showed later growth cessation. Nevertheless, growth duration was extremely short at both aspects, and likely relates to the extreme dry conditions in this year. An early growth cessation of beech in 2003 is consistent with observations in other areas in Europe (e.g., Ježík et al. 2011). Differences in achieved annual growth levels between both aspects (Figure 3) are in contrast with a long-term study in the area (van der Maaten 2012). This latter study reported higher growth levels at NW compared to SW over the period 1934–1998. The difference between both studies is explained by a gradually increasing growth trend observed in tree-ring chronologies for SW, suggesting a stand development with late differentiation. We assume that differences in annual radial growth over the study period 2001–2006 (Figure 3) relate to climate variability, as well as to negative effects of masting, which occurred in the area in 2004 and 2006 (Meining and von Wilpert 2006), and to effects of previous-year conditions upon growth.

Also wood density profiles were characteristic for individual years, but quite comparable between both aspects (Figure 4). It was remarkable that maximum wood densities were rather constant over the six-year study period with contrasting climate conditions. This finding is in contrast with a long-term study on beech that reported positive correlations between maximum wood density and late summer temperatures (Skomarkova et al. 2006). Strong density contrasts observed in all years substantiated the suitability of high-frequency densitometry for beech. Reported wood density profiles, with lower wood density formed in the beginning and higher wood density towards the end of each growing season, well reflected typical vessel distribution patterns as described by Sass and Eckstein (1995). They observed that vessel frequency was nearly constant throughout the tree ring, but that vessel size distribution changed. More than half of the tree ring consists of both large and small vessels, whereas the remaining part of the ring comprises only small vessels.

Effects of water availability and temperature

Our results suggest links between temporal courses of wood density, day-to-day stem radius variation, soil water content and vapor pressure deficit (Figure 5). As illustrated for 2006, wood density seemed unrelated to growth (SRV) in the beginning of the growing season (period P1). However, it displayed a negative relationship throughout the rest of the growing season (P2 and P3). Besides, a shift in climatic forcing of growth over time was indicated. Initially, reductions in water availability were suggested to induce a stimulation of growth (P1 and P2), whereas growth gradually decreased when water stress conditions persisted (P3), assuming a shift from temperature- towards water-limitation over the growing season in this year. The absence of unambiguous wood density responses in period P1 probably relates to the influence of internal factors, e.g., plant hormones, as these factors were suggested to explain a major part of vessel size variation in the beginning of the growing season, whereas the importance of external (or: environmental) factors increased over time (Sass & Eckstein 1995). Similarly, Z'Graggen (1992) reported that minimum wood density is explained less by climate than maximum wood density found towards the end of the growth period. Also Bouriaud et al. (2004) suggested that a major part of the inter-annual variability in wood density in beech is due to internal factors. By temporally resolving wood density profiles, we could elucidate these findings and illustrate that climatic forcing of wood density is not per se solely restricted to the late growing season, but that associations may be present during a major part of the growing season (Figure 5).

The importance of water availability for wood density was not only stressed in our temporally resolved wood density profiles (Figure 5), but also in the correlation analysis by negative correlations with SWC and positive correlations with VPD (Table 2), as well as in the multiple regression models by the inclusion of VPD for both aspects (Table 3). These results are consistent with the general understanding that water stress has a major impact on various aspects of wood formation through direct effects of cell turgor as well as changes in hormonal balances and carbohydrate storage (cf. Kramer 1964, Zahner 1968, Cosgrove 1986). Similar effects of water availability on wood density were also observed for other species. In Norway spruce and Aleppo pine (*Pinus halepensis* Mill.), for example, wood density was found to increase in association with increased drought stress, creating a false ring (e.g., Rozenberg et al. 2002, Bouriaud et al. 2005, Olivar et al. 2012). Various studies on *Eucalyptus* species (Wimmer et al. 2002, Drew et al. 2011) reported density decreases in response to water stress releases that were accompanied by acceleration in daily increment. However, sometimes these responses appeared to be out of phase, which was explained by a delayed expression in mature wood through the cambial region. In contrast to findings from an irrigation-experiment on *Eucalyptus globulus*, which showed differences in overall wood density in response to treatment / water availability (Drew et al. 2011), our results did not indicate clear differences in wood density between the two aspects despite of climatically more extreme and water-limited conditions at SW. However, tree-ring analyses of beech growing in the same area did not reveal large differences in climate-response between both aspects either (van der Maaten 2012), suggesting possible adaptations in tree architecture and dimension to prevailing local climate conditions.

Correlations between temperature and wood density were generally positive (Table 2). Negative relationships were only observed between April temperature and May wood density, and might relate to a release of temperature constraints with high April temperatures. Positive associations between wood density and temperature were also found in inter-annual wood density studies on beech. Skomarkova et al. (2006) found positive correlations between maximum wood density and temperature during the second half of the growing season, whereas maximum wood density decreased in years with a moist September.

Conclusion

In this study, we rescaled wood density measurements of beech over high-resolution dendrometer data to provide insight in the effects of changing environmental conditions on tree growth. Following previous studies, we demonstrated that dendrometers could play an important role to increase our understanding on wood formation when possible errors inherent to the rescaling approach are acknowledged by analyzing data at a realistic temporal resolution. For the year 2006, a year with a strong drought cycle, we showed strong negative associations between growth and wood density during a major part of the growing season, which suggests that climatic forcing of wood density is not necessarily restricted to the late growing season only. Water availability was found to be of major importance for wood formation in beech.

Acknowledgements

The authors are greatly indebted to Helmut Mayer (Meteorological Institute, Albert-Ludwigs-University, Freiburg, Germany) for the kind provision of forest-meteorological data. They would like to thank Stadtwald Tuttlingen for supporting the research activities in the area. Felix Baab is acknowledged for long-term maintenance of the dendrometer plots and Martin Schinker for discussions on high-frequency densitometry. Comments of Olivier Bouriaud and an anonymous reviewer were helpful to improve an earlier version of this manuscript. EM was financially supported by the EU-FP7 project MOTIVE (‘Models for adaptive forest management’, grant No. 226544) and MMT received a PhD scholarship from the Landesgraduiertenförderung Baden-Württemberg.

References

Boden S., Schinker M.G., Duncker P., Spiecker H., 2012. Resolution abilities and measuring depth of high-frequency densitometry on wood samples. Measurement. doi: 10.1016/j.measurement.2012.03.013

Bouriaud O., Bréda N., Moguédec G., Nepveu G., 2004. Modelling variability of wood density in beech as affected by ring age, radial growth and climate. Trees -

Structure and Function 18(3): 264-276.

Bouriaud O., Leban J.M., Bert D., Deleuze C., 2005. Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Physiology 25(6): 651-660.

Briffa K.R., Bartholin T.S., Eckstein D., Jones P.D., Karlén W., Schweingruber F.H., Zetterberg P., 1990. A 1,400-year tree-ring record of summer temperatures in Fennoscandia. Nature 346(6283): 434-439.

Briffa K.R., Osborn T.J., Schweingruber F.H., Harris I.C., Jones P.D., Shiyatov S.G., Vaganov E.A., 2001. Low-frequency temperature variations from a northern tree ring density network. Journal of Geophysical Research 106(D3): 2929-2941.

Cosgrove D., 1986. Biophysical control of plant cell growth. Annual Review of Plant Physiology 37(1): 377-405.

D'Arrigo R.D., Jacoby G.C., Free R.M., 1992. Tree-ring width and maximum latewood density at the North American tree line: parameters of climatic change. Canadian Journal of Forest Research 22(9): 1290-1296.

Deslauriers A., Morin H., Urbinati C., Carrer M., 2003. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). Trees - Structure and Function 17(6): 477-484.

Drew D., Downes G., Evans R., 2011. Short-term growth responses and associated wood density fluctuations in variously irrigated *Eucalyptus globulus*. Trees - Structure and Function 25(2): 153-161.

Drew D.M., Downes G.M., 2009. The use of precision dendrometers in research on daily stem size and wood property variation: a review. Dendrochronologia 27(2): 159-172.

Drew D.M., Downes G.M., O'Grady A.P., Read J., Worledge D., 2009. High resolution temporal variation in wood properties in irrigated and non-irrigated *Eucalyptus globulus*. Annals of Forest Science 66(4): 406.

Erickson H.D., Harrison A.T., 1974. Douglas-fir wood quality studies part I: effects of age and stimulated growth on wood density and anatomy. Wood Science and Technology 8(3): 207-226.

Evans R., Ilic J., 2001. Rapid prediction of wood stiffness from microfibril angle and density. Forest Products Journal 51(3): 53-57.

Geßler A., Schrempp S., Matzarakis A., Mayer H., Rennenberg H., Adams M.A., 2001. Radiation modifies the effect of water availability on the carbon isotope composition of beech (*Fagus sylvatica*). New Phytologist 150(3): 653-664.

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. PhD-thesis, Institute for Forest Growth, Albert-Ludwigs-University, Freiburg, 218 p.

Herzog K.M., Häsler R., Thum R., 1995. Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. Trees - Structure and Function 10(2): 94-101.

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. Antrag auf Finanzierung eines Sonderforschungsbereiches - Anlage. Freiburg, pp. 7-12.

Holst T., Mayer H., Schindler D., 2004. Microclimate within beech stands - part II: thermal conditions. European Journal of Forest Research 123(1): 13-28.

Hughes M.K., Schweingruber F.H., Cartwright D., Kelly P.M., 1984. July-August temperature at Edinburgh between 1721 and 1975 from tree-ring density and width data. Nature 308(5957): 341-344.

Ježík M., Blaženec M., Střelcová K., Ditmarová L., 2011. The impact of the 2003-2008 weather variability on intra-annual stem diameter changes of beech trees at a submontane site in central Slovakia. Dendrochronologia 29(4): 227-235.

Kozlowski T.T., Winget C.H., 1964. Diurnal and seasonal variation in radii of tree stems. Ecology 45(1): 149-155.

Kramer P.J., 1964. The role of water in wood formation. In Zimmermann M.H. (ed.), The formation of wood in forest trees. Academic Press, New York, London, pp. 519-532.

Kramer P.J., Kozlowski T.T., 1979. Physiology of woody plants. Academic Press, New York, 811 p.

Mayer H., Holst T., Schindler D., 2002. Microclimate within beech stands - part I: photosynthetically active radiation. Forstwissenschaftliches Centralblatt 121(6): 301-321.

Meining S., von Wilpert K., 2006. Waldzustandsbericht 2006 der Forstlichen Versuchs- und Forschungsanstalt Baden-Württemberg. FVA, Freiburg, p. 57.

Olivar J., Bogino S., Spiecker H., Bravo F., 2012. Climate impact on growth dynamic and intra-annual density fluctuations in Aleppo pine (*Pinus halepensis*) trees of different crown classes. Dendrochronologia 30(1): 35-47.

Panterne P., Burger J., Cruiziat P., 1998. A model of the variation of water potential and diameter within a woody axis cross-section under transpiration conditions. Trees - Structure and Function 12(5): 293-301.

Rossi S., Anfodillo T., Menardi R., 2006. Trephor: a new tool for sampling microcores from tree stems. IAWA Journal 27(1): 89.

Rossi S., Deslauriers A., Morin H., 2003. Application of the Gompertz equation for the study of xylem cell development. Dendrochronologia 21(1): 33-39.

Rozenberg P., van Loo J., Hannrup B., Grabner M., 2002. Clonal variation of wood density record of cambium reaction to water deficit in *Picea abies* (L.) Karst. Annals of Forest Science 59(5-6): 533-540.

Sass U., Eckstein D., 1995. The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. Trees - Structure and Function 9(5): 247-252.

Schinker M.G., Hansen N., Spiecker H., 2003. High-frequency densitometry - A new method for the rapid evaluation of wood density variations. IAWA Journal 24(3): 231-239.

Schmitt U., Möller R., Eckstein D., 2000. Seasonal wood formation dynamics of beech (*Fagus sylvatica* L.) and black locust (*Robinia pseudoacacia* L.) as determined by the ‘‘pinning’’ technique. Journal of Applied Botany 74: 10-16.

Seo J., Eckstein D., Schmitt U., 2007. The pinning method: from pinning to data preparation. Dendrochronologia 25(2): 79-86.

Skomarkova M., Vaganov E., Mund M., Knohl A., Linke P., Boerner A., Schulze E.D., 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 - Structure and Function 20(5): 571-586.

Spiecker H., Schinker M.G., Hansen J., Park Y.I., Ebding T., Doll W., 2000. Cell structure in tree rings: novel methods for preparation and image analysis of large cross sections. IAWA Journal 21(3): 361-373.

van der Maaten E., 2012. Climate sensitivity of radial growth in European beech (*Fagus sylvatica* L.) at different aspects in southwestern Germany. Trees - Structure and Function 26(3): 777-788.

WebWerdis (2011) German Weather Serivce (DWD): Web-based Weather Request and Distribution System. www.dwd.de/webwerdis [Accessed on: 15.03.2011].

Wimmer R., Downes G., Evans R., 2002. High-resolution analysis of radial growth and wood density in *Eucalyptus nitens*, grown under different irrigation regimes. Annals of Forest Science 59(5-6): 519-624.

Z’Graggen S., 1992. Dendrohistometrische-klimatologische Untersuchung an Buchen (*Fagus sylvatica* L.). Dissertation, University of Basel, Basel, 167 p.

Zahner R., 1968. Water deficits and growth of trees. In Kozlowski T.T. (ed.), Water deficits and plant growth. Academic Press, New York, London, pp. 191–254.

Zobel B.J., van Buijtenen J.P., 1989. Wood variation: its causes and control. Springer-Verlag, Berlin, xv + 363 p.

Zweifel R., Zimmermann L., Newbery D.M., 2005. Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiology 25(2): 147-156.