Ann. For. Res. 56(1): 91-103, 2013

ANNALS OF FOREST RESEARCH
www.e-afr.org

Wood density variations of Norway spruce (*Picea abies* (L.) Karst.) under contrasting climate conditions in southwestern Germany

M. van der Maaten-Theunissen, S. Boden, E. van der Maaten

van der Maaten-Theunissen M., Boden S., van der Maaten E., 2013. Wood density variations of Norway spruce (*Picea abies* (L.) Karst.) under contrasting climate conditions in southwestern Germany. Ann. For. Res. 56(1): 91-103, 2013.

Abstract. We analyzed inter-annual variations in ring width and maximum wood density of Norway spruce (*Picea abies* (L.) Karst.) at different altitudes in Baden-Württemberg, southwestern Germany, to determine the climate response of these parameters under contrasting climate conditions. In addition, we compared maximum, average and minimum wood density between sites. Bootstrapped correlation coefficients of ring width and maximum wood density with monthly temperature and precipitation, revealed a different climate sensitivity of both parameters. Ring width showed strong correlations with climate variables in the previous year and in the first half of the growing season. Further, a negative relationship with summer temperature was observed at the low-altitude sites. Maximum wood density correlated best with temperature during the growing season, whereby strongest correlations were found between September temperature and maximum wood density at the high-altitude sites. Observed differences in maximum, average and minimum wood density are suggested to relate to the local climate; with lower temperature and higher water availability having a negative effect on wood density.
Keywords tree rings, climate–growth relationships, altitude, densitometry.

Authors. Marieke van der Maaten-Theunissen (marieketheunissen@gmail.com), Simon Boden, Ernst van der Maaten - Institute for Forest Growth, Albert-Ludwigs-University Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany.
Manuscript received October 23, 2012; revised November 05, 2012; accepted November 12, 2012; online first November 16, 2012.

Introduction

Norway spruce (*Picea abies* (L.) Karst.) is the most abundant coniferous tree species in the state of Baden-Württemberg, southwestern Germany, occupying an area of 483.236 hectares (36.5% of forestland) (BMELV 2008). The species is found under warm and dry climate conditions in lowlands (~400 m a.s.l.), as well as under more cool and humid conditions close to the timberline (~1400 m a.s.l.). However, without human intervention, the share of spruce would be small and restricted to high-mountainous areas only (>1100 m a.s.l.) (Volk 1969, Schlenker & Müller 1978).

Predicted changes in climate, with higher temperature and more frequent summer droughts (Beniston 2004, Meehl & Tebaldi 2004, Schär et al. 2004), might negatively affect tree growth and vitality of spruce. Especially trees growing at sites prone to drought, i.e., at low altitudes, and at sites outside the natural distribution area of the species are likely to be susceptible. As climate change may have considerably large ecological and economical impacts, e.g., in Baden-Württemberg, a close analysis of the effects of past changes in climate on the growth of spruce is needed, to increase our understanding on possible impacts of future changes in climate.

In dendroclimatological analyses, inter-annual variations in ring width are most commonly studied (e.g., Mäkinen et al. 2002, Lebourgeois 2007). However, maximum wood density was demonstrated to provide additional information on climate−growth relationships for a variety of tree species (e.g., Hughes et al. 1984, Schweingruber et al. 1993). Ring width and maximum wood density contain a different climate signal, with ring width being more sensitive to climate conditions in the first part of the growing season, and maximum wood density to climate conditions in late summer (Bouriaud et al. 2005, Skomarkova et al. 2006). The strong correlations between maximum latewood density and late summer temperature have often been applied for temperature reconstructions (e.g., Briffa et al. 1988, Jacoby & D'Arrigo 1989, Briffa et al. 2002, Wilson & Luckman 2003).

Also for spruce, strong correlations between latewood density and summer conditions were observed that might relate to increasing drought stress towards the end of the growing season (Bouriaud et al. 2005, Jyske et al. 2010). The intensity of water stress affects the diameter of simultaneously formed tracheids; under dry conditions, the tracheids will have small conduits and thicker walls (e.g., Von Wilpert 1991), thereby increasing wood density. In southwestern Germany, for example, wood density is suggested to differ between sites with different water availability in a study by Park & Spiecker (2005). They observed thicker cell walls and smaller radial cell diameters in Norway spruce trees on a warm and dry site compared to trees at a cool and humid site.

A majority of studies analyzing climate sensitivity of both ring width and wood density was conducted at extreme sites, e.g., in alpine environments (D'Arrigo et al. 1992, Frank & Esper 2005). Rather than maximizing the climate signal in measurement series, the focus of this study was to analyze annual ring width and wood density variations of more complacent trees at different altitudes in Baden-Württemberg. Our aim was to reveal site-specific differences in maximum, average and minimum wood density, and to determine the main climate factors responsible for variations in ring width and maximum wood density of Norway spruce. In particular, we wanted to identify possible differences in wood density and shifts in climate response between warm-dry sites vs. cool-humid sites. We hypothesized that absolute differences in wood density between sites relate to local environmental conditions, with wood density increasing in response to water stress. Further, we expect to find differences in climate sensitivity of ring width compared to maximum wood density, irrespective of altitude.

Materials and methods

Study sites and sampling

The study material consists of increment cores and stem discs of Norway spruce from five sites in southwestern Germany (Fig. 1; Table 1), which have been collected during former research projects. At sites HEI, ROT and OCH, 20 dominant or co-dominant trees were sampled in the winter of 2004/2005. With an increment borer, two cores were extracted from each tree, parallel to the slope and at breast height. They were air-dried, glued on wood holders and sanded. Some cores were excluded from the dataset as they were incomplete, broken or contained compression wood. At the high-altitude sites KUH and SIR, stem discs of five dominant or co-dominant spruce trees were extracted at breast height in the winter of 2010/2011. After drying and sanding these discs, two wedges were extracted from slope-parallel stem radii that were free from compression wood.

All samples (cores and wedges) were prepared with an ultra-precise diamond fly cutter (Kugler F500, Kugler GmbH, Salem, Germany; for method, see Spiecker et al. 2000) to allow high-frequency densitometry analysis

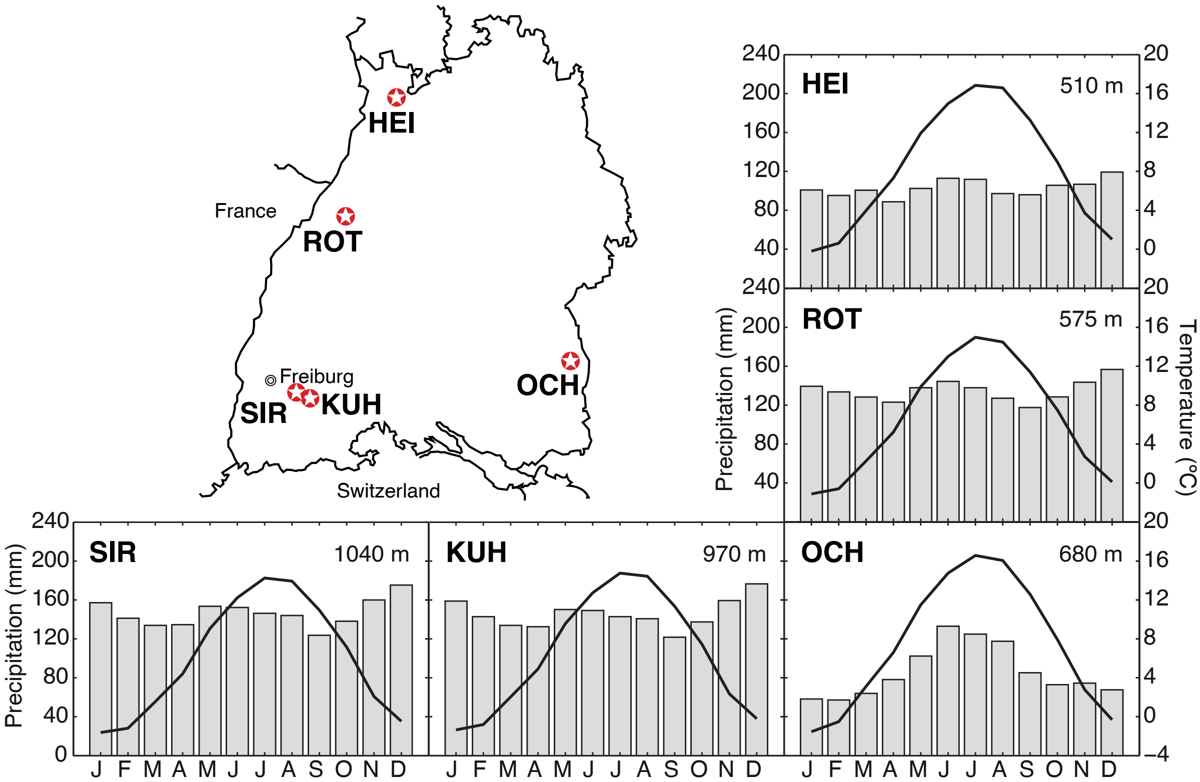

Figure 1 Geographical location of the five study sites in the state Baden-Württemberg in southwestern Germany. Climate diagrams show mean monthly temperature (lines) and precipitation (bars) over the period 1954–2003. Altitude of the site is indicated in m a.s.l.

Table 1 Description of sampling sites and trees. Age refers to age at breast height in 2003 (standard deviations in parentheses)

Site	Lat. (°N)	Long. (°E)	Altitude (m a.s.l.)	No. of trees (cores/radii)	Time span (all trees)	Age (years)
HEI	49.46	8.75	510	20 (35)	1940-2004	73.3 (4.4)
ROT	48.81	8.40	575	20 (36)	1923-2004	90.4 (4.4)
OCH	48.01	9.96	680	20 (34)	1938-2004	73.1 (3.1)
KUH	47.78	7.79	970	5 (10)	1903-2010	104.4 (3.5)
SIR	47.80	7.77	1040	5 (10)	1921-2010	87.6 (4.2)

(Schinker et al. 2003, Boden et al. 2012). This latter method determines relative density variations (in Volt) over dielectric wood properties. Within a single routine, we measured wood density and annual ring width (cores) or annual radial growth (discs). Hereafter, these latter two tree-growth measures are referred to as ring width. Wood density was assessed using a probe of 65 μm width and 980 μm length. Measurements were taken in radial direction, at an interval of 28 μm, implying a 43% overlap in scanned wood surface between adjacent measurements, and were automatically assigned to specific years using image analysis software developed at the Institute for Forest Growth. We determined maximum, average and minimum wood density for each annual ring. When two measurement series were available for a single tree, we calculated annual ring width and wood density values as arithmetic means.

Ring-width series and maximum wood density series were cross-dated visually and statistically (Gleichläufigkeit). We detrended each series by fitting a cubic smoothing spline with 50% frequency cut-off at 30 years to retain high-frequency variability (Cook and Peters 1981), using MATLAB's (V7.9.0, R2009b) Spline Toolbox function *csaps* (V3.3.7), in combination with the spline smoothing parameter function *splinep* (presented courtesy of J.L. Dupouey). Indices were calculated dividing the observed by the predicted values. Chronologies were constructed per site and inter-series correlations (*IC*), mean sensitivities (*MS*) and first-order autocorrelations (*AC*) were calculated over the common overlap period 1954−2003. The *IC* is a measure for the strength of the common signal in the chronologies, *MS* is the relative change in radial increment between consecutive years and *AC* assesses the previous years' influence on current years' growth (Fritts 1976). Expressed population signal (*EPS*) values were calculated to check whether the individual chronologies are representative for the site (Wigley et al. 1984) using the *wigley1* function (presented courtesy of D. Meko).

We restricted our analyses to the period 1954−2003 as this was the longest possible overlap period in which all trees were older than 15 years, not containing juvenile wood anymore. The year 2004 was excluded from the analyses to avoid erroneous measurements caused by the transition from wood to bark.

Statistical analysis

To determine the climate factors responsible for the inter-annual variations in ring width and maximum wood density, we calculated bootstrapped correlation coefficients between chronologies and mean monthly air temperature and monthly precipitation sums from June of the previous year till September of the current year, using the software package DENDROCLIM2002 (Biondi & Waikul 2004). Site-specific climate data were obtained from spatially interpolated gridded data (1 km × 1 km) of the German Weather Service (WebWerdis 2010).

We used the linear mixed model procedure in SPSS (Version 19, IBM Statistics) to identify differences in absolute values of the maximum, average and minimum wood density between study sites (fixed effect). Linear mixed models do not require independent observations with constant variance and are particularly useful for repeated measures studies (Norusis 2007). In our analyses, trees were specified as subjects and years as repeated variables, in effect defining a random variable at the lowest level. As we wanted to control for the variance in wood density accounted for by cambial age and annual ring width, these factors were included with tree-level random coefficients. We used an autoregressive-moving average model of order one ARMA(1,1) to account for residual autocorrelations.

Results

Chronology characteristics

Mean tree-ring widths were highest at the lower altitude sites (Table 2). At all sites, the *IC* for chronologies of ring width and maximum wood density over the period 1954–2003 is high (in the two ranges 0.607–0.772 and 0.565–0.688, respectively), indicating that strong common signals exist between trees from the same site (Fig. 2). Besides, all *EPS* values exceed the threshold of 0.85, indicating that site chronologies can be considered reliable (Wigley et al. 1984). Ring width at the lowest site HEI has the largest *MS* value, suggesting a higher climate-sensitivity of these trees.

We calculated Pearson correlation coefficients between site chronologies of ring width and maximum wood density and plotted them as a function of altitudinal distance (Fig. 3), to analyze whether chronologies of sites at short altitudinal distance have more in common than those of sites that are further apart. For ring width, the strength of the correlation significantly decreases with increasing distance, whereas the correlation coefficients for maximum wood density are higher and decrease only slightly with increasing altitudinal distance.

Climate response

Bootstrapped correlation coefficients of ring width and maximum wood density with monthly temperature and monthly precipitation show that both climate factors influence annual variability of these tree-ring parameters (Fig. 4).

Where the lower altitude sites HEI, ROT and OCH show negative correlations with summer temperature in the current year, variations in ring width at the high-altitude sites KUH and SIR are generally positively correlated with temperature from January till September. Previous-year summer temperature is negatively correlated with ring width at all sites, being significant for July at sites KUH and SIR. Further, previous-year October temperature shows significant positive correlations with ring width at sites HEI and OCH, whereas previous-year November temperature is negatively correlated with growth at all sites, being significant for ROT and OCH. No clear relations with precipitation are observed.

Maximum wood density shows negative correlations with temperature in previous-year July, which are significant for the high-altitude sites KUH and SIR, and in previous-year October, being significant for HEI and SIR. Further, all maximum wood density chronologies show positive correlations with temperature during the growing season. Strongest correlations exist between September temperature and growth at the high-altitude sites. For precipitation, strongest negative correlations are found for current-year July (HEI and OCH) or August and September (KUH and SIR).

Table 2 Chronology statistics of annual ring width and maximum wood density series. Statistics refer to the maximum common overlap period 1954–2003. *IC* inter-series correlation, *MS* mean sensitivity, *AC* first-order autocorrelation, *EPS* expressed population signal. Sites are ranked in order of increasing altitude

	Ring width					Maximum wood density			
Site	Mean (SD)	*IC*	*MS*	*AC*	*EPS*	*IC*	*MS*	*AC*	*EPS*
HEI	2.67 (0.93)	0.673	0.236	0.302	0.976	0.577	0.066	-0.012	0.965
ROT	2.75 (0.84)	0.734	0.188	0.302	0.982	0.619	0.077	-0.042	0.970
OCH	2.70 (0.83)	0.651	0.203	0.324	0.974	0.598	0.066	0.008	0.968
KUH	2.12 (0.46)	0.607	0.164	0.186	0.885	0.565	0.082	-0.201	0.867
SIR	2.56 (0.60)	0.772	0.165	0.282	0.944	0.688	0.069	-0.029	0.917

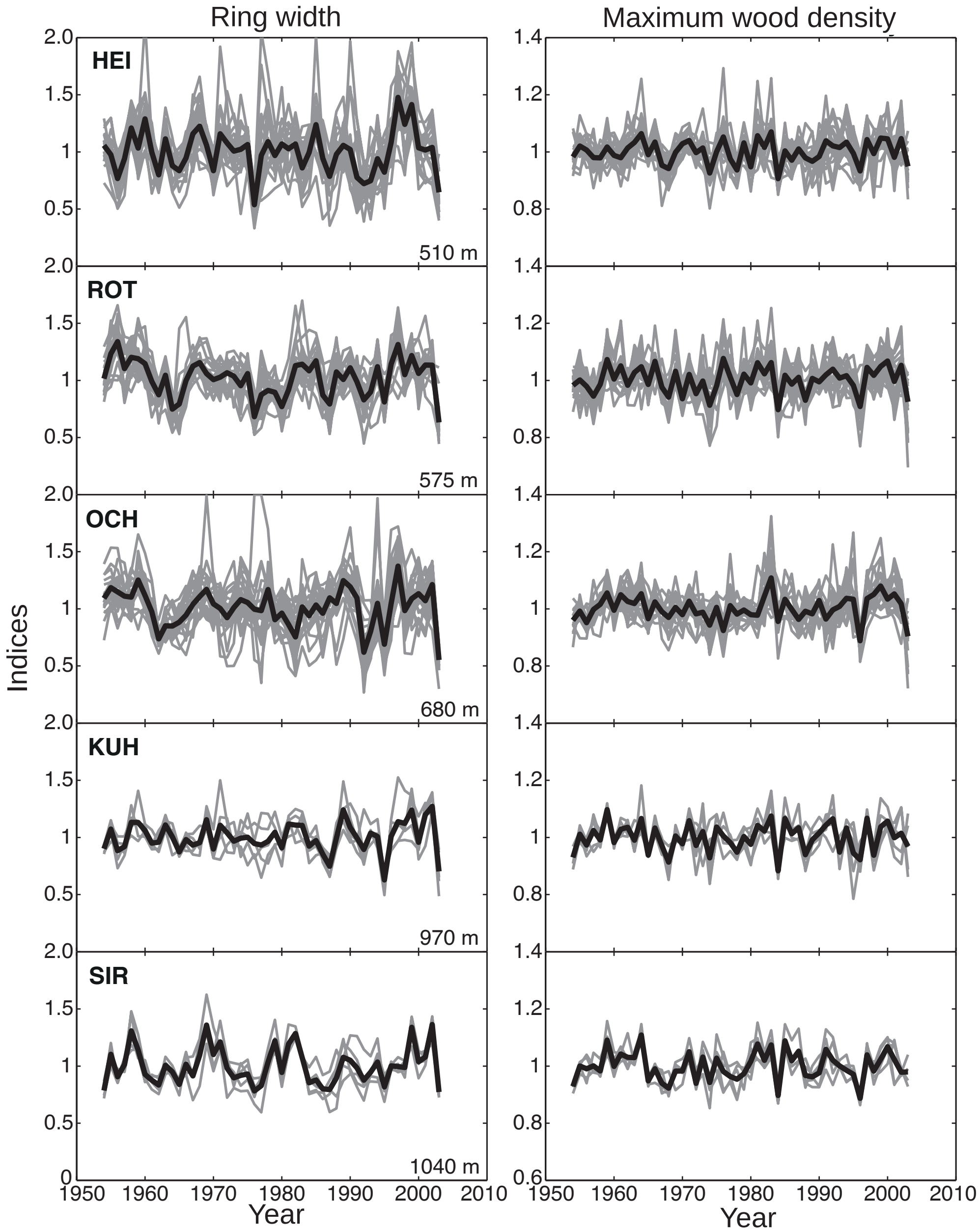

Figure 2 Individual (grey) and mean (black) standardized chronologies of the study sites for annual ring width and maximum wood density. Sites are ranked in order of increasing altitude

Differences in wood density

The results of the linear mixed models, which were performed to analyze differences in maximum, average and minimum wood density between sites, are shown in Fig. 5. Although a decrease in absolute wood density values is suggested with increasing altitude, the low-altitude site ROT blurs this pattern. Average climate conditions at site ROT (1954−2003 means for April−September: 12.8°C, 789 mm), however, are comparable with those at the high-altitude sites KUH (12.6°C, 837 mm) and SIR (12.1°C, 854 mm) rather than with those at the other low-altitude sites HEI (14.7°C, 609 mm) and OCH (14.3°C, 641 mm). Hence, an

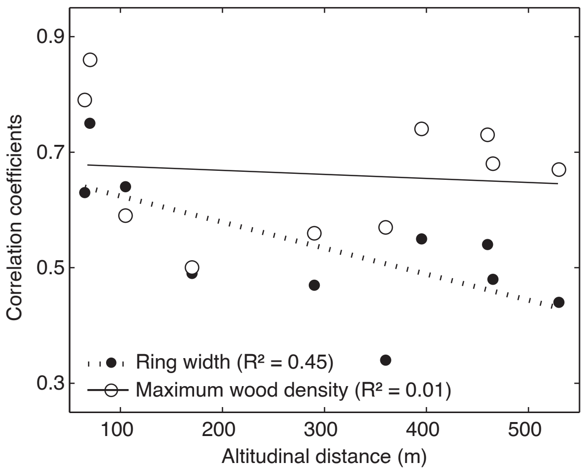

Figure 3 Pearson correlation coefficients between site chronologies of ring width and maximum wood density as a function of altitudinal distance

alternative ranking of sites in order of decreasing temperature means and increasing precipitation sums would clearly indicate that sites with relatively high temperature and low precipitation amounts, i.e., HEI and OCH, display higher wood densities compared to sites with relatively low temperature and high precipitation amounts.

Discussion

The objective of our study was to compare the climate response of ring width and maximum wood density of Norway spruce at sites with contrasting climate conditions in Baden-Württemberg, and to reveal site-specific differences in maximum, average and minimum wood density of this tree species. Although our observation period was restricted to 50 years, we were able to observe major climate constraints in the climate response analyses.

Climate response

In general, higher temperature and lower precipitation amounts limit tree growth at lower altitudes, whereas at higher altitudes low temperature and higher precipitation amounts are limiting factors (e.g., Dittmar & Elling 1999, Wilson & Hopfmüller 2001). At our low-altitude sites, we found positive correlations with precipitation during summer, but only significant for August at site ROT. The absence of close relationships with precipitation at low elevation is rather unusual for spruce. However, we did find negative correlations between summer temperature and ring width at the warm-dry low-altitude sites HEI and OCH, and positive tendencies between summer temperature and radial growth at the high-altitude sites KUH and SIR. This latter finding is in accordance with other studies that reported positive effects of summer temperature on tree growth at high elevation (e.g., Savva et al. 2006, Di Filippo et al. 2007, Leal et al. 2007).

However, that correlations in our study were largely not significant probably relates to the fact that trees at the high-altitude sites KUH and SIR are not as close to the upper tree line as those in the other studies.

Growth at all sites was positively correlated with previous October temperature, being significant for sites HEI and OCH. In contrast, previous November temperature negatively affected growth at all sites, being significant for ROT and OCH. Positive effects of previous year October temperature upon growth may be explained by an increased storage of energy reserves for growth of spruce in the next year. However, when warm conditions persist in November, an increased production of growth hormones may take away carbohydrate reserves for next years' cambial reactivation, when temperature (suddenly) drops in December. Cambial dormancy may be stimulated too rapidly then, limiting the time for storage and preparation (Perry 1971, Fritts 1976, Biermann 2009).

In contrast to the findings for ring width, temperature during the growing season was found to have a positive effect on maximum wood density, both at low- and high-altitude sites. Correlation patterns for maximum wood

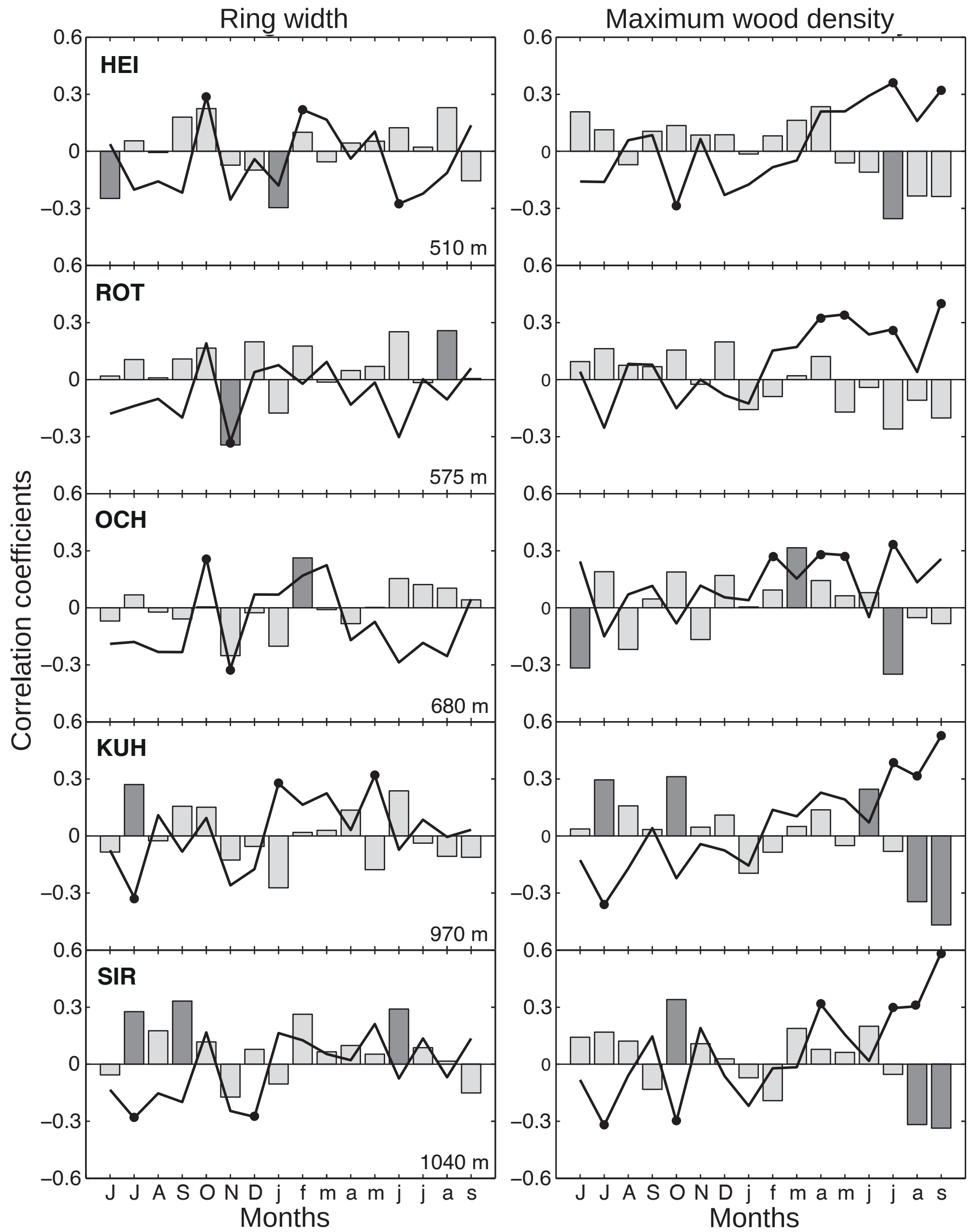

Figure 4 Bootstrapped correlation coefficients with monthly temperature (*lines*) and precipitation (*bars*) for annual ring width and maximum wood density. Dots and darker colored bars indicate significant correlations at $P < 0.05$. Sites are ranked in order of increasing altitude

density were consistent between sites, similar to findings of Levanič et al. (2009) in the southeastern European Alps. The relation between temperature and maximum wood density was strongest for September at the two high-altitude sites. Also Splechtna et al. (2000) observed a stronger correlation between temperature and maximum wood density with increasing elevation (700 vs. 1950 m a.s.l.) in British Columbia, whereas Frank & Esper (2005) found none, when comparing sites between 1500 and 2000 m a.s.l. in the European Alps. Although cambial activity has generally stopped in September in the region, the

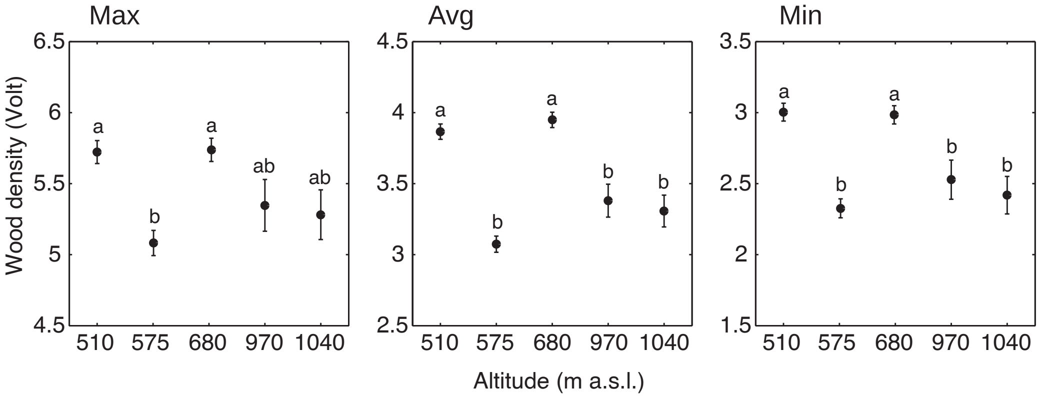

Figure 5 Estimated marginal means with error bars of maximum, average and minimum wood density for the five study sites for the period 1954–2003. Different superscripts (e.g., a, b) indicate a significant ($P < 0.05$) difference in wood density between the sites. Sites are ranked in order of increasing altitude

strong correlation between maximum wood density and temperature in this month may be explained by lignification of the latest formed tracheids, which may persist long after radial expansion has stopped (e.g., Gindl et al. 2000).

Although correlations between maximum wood density and temperature were strongest in (late) summer, we also found significant positive correlations for April and May. A positive influence of spring temperature on maximum (latewood) density was observed in earlier studies as well (Kienast et al. 1987, D'Arrigo et al. 1992, Schweingruber et al. 1993), and may be explained by an increased supply of photosynthates under warm spring conditions (Conkey 1979), needed for the building of cell wall material (Larson 1964, Antonova & Stasova 1993, 1997).

In accordance with numerous other studies, we observed differences in climate sensitivity of ring width and maximum wood density (e.g., Bouriaud et al. 2005, Skomarkova et al. 2006, Kirdyanov et al. 2007, Büntgen et al. 2010). These differences are assumed to relate to the different climate conditions occurring during the formation of earlywood (which mainly determines ring width) – in the first half of the growing season, and latewood (in which maximum wood density generally occurs) – in the second half of the growing season. Therefore, ring width is likely to be especially sensitive for climate variations in spring, whereas maximum wood density shows strongest correlations with summer temperature (Wang et al. 2002, Kirdyanov et al. 2007).

Differences in wood density

Although we observed similarities in maximum wood density variations (Fig. 2,3) and in their response to climate between the sample sites (Fig. 4), absolute wood densities were rather different (Fig. 5). Maximum, average and minimum wood densities were lower at sites characterized by low temperature and high precipitation amounts (ROT, KUH and SIR). This finding is confirmed by another study in the same region (Park & Spiecker 2005), comparing tracheid characteristics of spruce trees at a warm-dry and cool-humid site. Trees from the warm-dry site contained smaller cells, with thicker cell walls compared to trees from the cool-humid site, and are thus characterized by higher wood densities. A reducing effect of water availability on wood density is suggested as well in irrigation experiments on *Eucalyptus* species (Wimmer et al. 2002, Drew et al. 2011). Similarly, water availability was reported to influence tracheid diameters of, e.g., *Juniperus thurifera* L. (DeSoto et al. 2011), *Cryptomeria japonica* D. Don. (Abe & Nakai 1999, Abe et al. 2003) and Norway spruce (Von Wilpert 1991, Dünisch & Bauch 1994). Further, changes in water availability during wood formation have been shown to induce false ring formation in numerous coniferous species (Wimmer et al. 2000, Rigling et al. 2002, Rozenberg et al. 2002, Bouriaud et al. 2005, Vieira et al. 2009, Olivar et al. 2012). It is suggested that adaptations in xylem structure (e.g., cell diameter and wall thickness) are a response to drought in order to increase the resistance against cavitation (Hacke et al. 2001, Martinez-Meier et al. 2008, Fonti et al. 2010, DeSoto et al. 2011).

Following shifts in climate limitations over altitudinal gradients, a decrease in cell wall thickness and, consequently, in wood density is generally observed over such gradients as well (e.g., Lassen & Okkonen 1969, Lingg 1986, Gindl et al. 2001). Also in our study region, wood density measurements by Schweingruber & Nogler (2003), suggested decreasing wood density with altitude. In this study, the general pattern was blurred by the inclusion of the low-altitude site ROT, which climate is characterized by low temperatures and high precipitation amounts that are typically found at higher altitudes. Differences in wood density over climatic characteristics, however, are uniform. They are in accordance with studies showing reductions in wood density with decreasing temperature (and increasing precipitation amounts) in other areas (Schweingruber et al. 1993, Splechtna et al. 2000).

Conclusions

In our study, we found differences in climate response between ring width and maximum wood density of Norway spruce in southwestern Germany. Climate sensitivity also varied between high- and low-altitude sites. Besides, we revealed differences in absolute wood density values, whereby maximum, average and minimum wood density were generally lower at sites with low temperature and high precipitation amounts. In a future warmer climate, with higher temperature and reduced precipitation during the growing season (Maracchi et al. 2005), growth of spruce is likely to be negatively affected in the area, whereas wood density might increase.

Acknowledgements

The authors are grateful to Klaus von Wilpert (Forest Research Institute Baden-Württemberg (FVA), Department of Soils and Environment) for the kind provision of increment cores on Norway spruce. Further, they would like to thank Hans-Peter Kahle for maintaining contacts with the FVA. Felix Baab and Clemens Koch are thankfully acknowledged for technical assistance in the lab. Comments of Heinrich Spiecker, Andreas Hamann and two anonymous reviewers helped on improving earlier versions of this manuscript. MMT and SB received a PhD scholarschip from the Landesgraduiertenförderung Baden-Württemberg.

References

Abe H., Nakai T., 1999. Effect of the water status within a tree on tracheid morphogenesis in *Cryptomeria japonica* D. Don. Trees – Structure and Function 14: 124-129.

Abe H., Nakai T., Utsumi Y., Kagawa A., 2003. Temporal water deficit and wood formation in *Cryptomeria japonica*. Tree Physiology 23: 859-863.

Antonova G.F., Stasova V.V., 1993. Effects of environmental factors on wood formation in Scots pine stems. Trees – Structure and Function 7: 214-219.

Antonova G.F., Stasova V.V., 1997. Effects of environmental factors on wood formation in larch (*Larix sibirica* Ldb.) stems. Trees – Structure and Function 11: 462-468.

Beniston M., 2004. The 2003 heat wave in Europe: A shape of things to come? An analysis based on Swiss climatological data and model simulations. Geophysical Research Letters 31: 2022-2026.

Biermann C.P., 2009. Twentieth century changes in the climate response of yellow pines in Great Smoky Mountains National Park, Tennessee, U.S.A., University of Tennessee.

Biondi F., Waikul K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers and Geosciences 30: 303-311.

BMELV, 2008. Bundeswaldinventur 2. Web: http://www.bundeswaldinventur.de. Accesed: 2 Jun 2011.

Boden S., Schinker M.G., Duncker P., Spiecker H., 2012. Resolution abilities and measuring depth of high-frequency densitometry on wood samples. Measurement 45: 1913-1921.

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: 651-660.

Briffa K.R., Jones P.D., Schweingruber F.H., 1988. Summer temperature patterns over Europe: A reconstruction from 1750 A.D. based on maximum latewood density indices of conifers. Quaternary Research 30: 36-52.

Briffa K.R., Osborn T.J., Schweingruber F.H., Jones P.D., Shiyatov S.G., Vaganov E.A., 2002. Tree-ring width and density data around the Northern Hemisphere: Part 1, local and regional climate signals. The Holocene 12: 737-757.

Büntgen U., Frank D., Trouet V., Esper J., 2010. Diverse climate sensitivity of Mediterranean tree-ring width and density. Trees – Structure and Function 24: 261-273.

Conkey L.E., 1979. Response of tree-ring density to climate in Maine, U.S.A. Tree-Ring Bulletin 39: 29-38.

Cook E.R., Peters K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bulletin 41: 45-53.

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

DeSoto L., De la Cruz M., Fonti P., 2011. Intra-annual patterns of tracheid size in the Mediterranean tree *Juniperus thurifera* as an indicator of seasonal water stress. Canadian Journal of Forest Research 41: 1280-1294.

Di Filippo A., Biondi F., Cufar K., de Luis M., Grabner M., Maugeri M., Saba E.P., Schirone B., Piovesan G., 2007. Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. Journal of Biogeography 34: 1873-1892.

Dittmar C., Elling W., 1999. Radial growth of Norway spruce and European beech in relation to weather and altitude. Forstwissenschaftliches Centralblatt 118: 251-270.

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

Dünisch O., Bauch J., 1994. Influence of soil substrate and drought on wood formation of spruce (*Picea abies* (L.) Karst) under controlled conditions. Holzforschung 48: 447-457.

Fonti P., von Arx G., García-González I., Eilmann B., Sass-Klaassen U., Gärtner H., Eckstein D., 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytologist 185: 42-53.

Frank D., Esper J., 2005. Characterization and climate response patterns of a high-elevation, multi-species tree-ring network in the European Alps. Dendrochronologia 22: 107-121.

Fritts H.C., 1976. Tree Rings and Climate. Academic Press, London.

Gindl W., Grabner M., Wimmer R., 2000. The influence of temperature on latewood lignin content in treeline Norway spruce compared with maximum density and ring width. Trees – Structure and Function 14: 409-414.

Gindl W., Grabner M., Wimmer R., 2001. Effects of altitude on tracheid differentiation and lignification of Norway spruce. Canadian Journal of Botany 79: 815-821.

Hacke U.G., Sperry J.S., Pockman W.T., Davis S.D., McCulloh K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457-461.

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: 341-344.

Jacoby G.C., D'Arrigo R., 1989. Reconstructed Northern Hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America. Climate Change 14: 39-59.

Jyske T., Hölttä T., Mäkinen H., Nöjd P., Lumme I., Spiecker H., 2010. The effect of artificially induced drought on radial increment and wood properties of Norway spruce. Tree Physiology 30: 103-115.

Kienast F., Schweingruber F.H., Bräker O., Schär E., 1987. Tree-ring studies on conifers along ecological gradients and the potential of single-year analysis. Canadian Journal of Forest Research 17: 683-696.

Kirdyanov A.V., Vaganov E.A., Hughes M.K., 2007. Separating the climatic signal from tree-ring width and maximum latewood density records. Trees – Structure and Function 21: 37-44.

Larson P.R., 1964. Some indirect effects of environment on wood formation. In: Zimmermann M.H. (ed.), The formation of wood in forest trees. Academic Press Inc., New York, pp. 345-365.

Lassen L.E., Okkonen E.A., 1969. Effect of rainfall and elevation on specific gravity of coast Douglas-fir. Wood Fiber 1: 227-235.

Leal S., Melvin T.M., Grabner M., Wimmer R., Briffa K.R., 2007. Tree-ring growth variability in the Austrian Alps: The influence of site, altitude, tree species and cli-

mate. Boreas 36: 426-440.
Lebourgeois F., 2007. Climatic signal in annual growth variation of silver fir (*Abies alba* Mill.) and spruce (*Picea abies* Karst.) from the French Permanent Plot Network (RENECOFOR). Annals of Forest Science 64: 333-343.
Levanič T., Gričar J., Gagen M., Jalkanen R., Loader N.J., McCarroll D., Oven P., Robertson I., 2009. The climate sensitivity of Norway spruce [*Picea abies* (L.) Karst.] in the southeastern European Alps. Trees – Structure and Function 23: 169-180.
Lingg W., 1986. Dendroökologische Studien an Nadelbäumen im alpinen Trockental Wallis (Schweiz). [Dendroecological studies on conifers in the alpine dry valley of Valais (Switzerland)] Berichte / Eidgenössische Anstalt für das Forstliche Versuchswesen, vol 287.
Mäkinen H., Nöjd P., Kahle H.P., Neumann U., Tveite B., Mielikäinen K., Röhle H., Spiecker H., 2002. Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. Forest Ecology and Management 171: 243-259.
Maracchi G., Sirotenko O., Bindi M., 2005. Impacts of present and future climate variability on agriculture and forestry in the temperate regions: Europe. In: Salinger J., Sivakumar M.V.K., Motha R.P., (eds.) Increasing Climate Variability and Change. Springer Netherlands, pp. 117-135.
Martinez-Meier A., Sanchez L., Pastorino M., Gallo L., Rozenberg P., 2008. What is hot in tree rings? The wood density of surviving Douglas-firs to the 2003 drought and heat wave. Forest Ecology and Management 256: 837-843.
Meehl G.A., Tebaldi C., 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305: 994-997.
Norusis M.J., 2007. SPSS 15.0 Advanced Statistical Procedures Companion. Prentice Hall Press, 380 p.
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: 35-47.
Park Y.I., Spiecker H., 2005. Variations in the tree-ring structure of Norway spruce (*Picea abies*) under contrasting climates. Dendrochronologia 23: 93-104.
Perry T.O., 1971. Dormancy of trees in winter. Science 171: 29-36.
Rigling A., Bräker O., Schneiter G., Schweingruber F., 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). Plant Ecology 163: 105-121.
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: 533-540.
Savva Y., Oleksyn J., Reich P.B., Tjoelker M.G., Vaganov E.A., Modrzynski J., 2006. Interannual growth response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains, Poland. Trees – Structure and Function 20: 735-746.
Schär C., Vidale P.L., Lüthi D., Frei C., Häberli C., Liniger M., Appenzeller C., 2004. The role of increasing temperature variability for European summer heat waves. Nature 427: 332-336.
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: 231-239.
Schlenker G., Müller S., 1978. Erläuterungen zur Karte der Regionalen Gliederung von Baden-Württemberg III. Teil (Wuchsgebiet Schwarzwald). [Notes to the regional map of Baden-Württemberg III. Part (growth area Black Forest)] Mitteilungen des Vereins für Forstliche Standortskunde und Forstpflanzenzüchtung Nr. 26.
Schweingruber F.H., Briffa K.R., Nogler P., 1993. A tree-ring densitometric transect from Alaska to Labrador. International Journal of Biometeorology 37: 151-169.
Schweingruber F.H., Nogler P., 2003. Synopsis and climatological interpretation of Central European tree-ring sequences. Botanica Helvetica 113: 125-143.
Skomarkova M.V., Vaganov E.A., 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: 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: 361-373.
Splechtna B.E., Dobry J., Klinka K., 2000. Tree-ring characteristics of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in relation to elevation and climatic fluctuations. Annals of Forest Science 57: 89-100.
Vieira J., Campelo F., Nabais C., 2009. Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate. Trees – Structure and Function 23: 257-265.
Volk H., 1969. Untersuchungen zur Ausbreitung und künstlichen Einbringung der Fichte im Schwarzwald. Schriftenreihe der Landesforstverwaltung Baden-Württemberg [Studies on the distribution and artificial introduction of spruce in the Black Forest], Schriftenreihe der Landesforstverwaltung Baden-Württemberg 28.
Von Wilpert K., 1991. Intraannual variation of radial tracheid diameters as monitor of site specific water stress. Dendrochronologia 9: 95-113.
Wang L., Payette S., Bégin Y., 2002. Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec. Canadian Journal of Forest Research 32: 477-486.
WebWerdis, 2010. German Weather Service (DWD): Web: based Weather Request and Distribution System. www.

dwd.de/webwerdis. Accessed: 2 September.

Wigley T.M.L., Briffa K.R., Jones P.D., 1984. On the average value of correlated time-series, with applications in dendroclimatology and hydrometeorology. Journal of Climate and Applied Meteorology 23: 201-213.

Wilson R.J.S., Hopfmüller M., 2001. Dendrochronological investigations of Norway spruce along an elevational transect in the Bavarian Forest, Germany. Dendrochronologia 19: 67-69.

Wilson R.J.S., Luckman B.H., 2003. Dendroclimatic reconstruction of maximum summer temperatures from upper tree-line sites in interior Britisch Columbia. The Holocene 13: 853-863.

Wimmer R., Downes G.M., 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: 519-524.

Wimmer R., Strumia G., Holawe F., 2000. Use of false rings in Austrian pine to reconstruct early growing season precipitation. Canadian Journal of Forest Research 30: 1691-1697.