Tree-ring Growth Response of Scots Pine (*Pinus sylvestris* L.) to Climate and Soil Water Availability in the Lowlands of North-Eastern Germany

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Abstract

The relationships between the radial growth of Scots pine (*Pinus sylvestris* L.) and both temperature and precipitation were studied at 17 sites in the North-Eastern German lowlands. Furthermore, we investigated the influence of soil water availability on growth response to detect whether this integrative parameter better explains radial growth than climatic variables alone. Dendrochronological methods were applied to build tree-ring chronologies and calculate chronology statistics. Correlation coefficients, bootstrapped response functions, and pointer year analysis were used to analyse climate-growth relationships. Principal component analysis (PCA) was performed to explore differences in the strength of the climate signal. Chronology statistics showed similar radial growth patterns for the selected stands. Comparably low values for the expressed population signal (EPS) indicated a moderate common climate signal. The analyses revealed that radial growth is promoted primarily by a wet/warm February and secondarily by a wet/cool June. Although soil moisture availability in summer was not identified as the determining factor for radial growth, severe soil water stress can lead to substantial growth depression. Mean sensitivity and PCA suggest that climate sensitivity tends to slightly increase with increasing tree age. We conclude that the pine forests in North-Eastern Germany are far from being seriously threatened by inter-annual climatic variations in the near future.

Key words: Dendroclimatology, climate–growth relationships, relative extractable water, LWF-BROOK90

Introduction

For North-Eastern Germany, climate projections predict a general increase of the mean annual temperature (1.7 – 3°C) combined with decreasing precipitation sums during the vegetation period until 2100 (Spekat et al. 2007). In addition, extreme climatic events such as droughts, storms, or heat-waves are likely to occur more frequently (Schär et al. 2004, Beniston et al. 2007). There is some evidence that global warming already affects the water balance in North-Eastern Germany, which is one of the driest regions of the country (DWD 2012). During the last decades, scientists observed a decreasing groundwater recharge resulting in lower groundwater and lake levels (Germer et al. 2009). A modelling study revealed a decreasing trend in soil water content (SWC) up to the present day, which will likely continue through the middle of the 21st century (Holsten et al. 2009). These alterations in environmental conditions will presumably have noticeable effects on the vitality of forest stands. Against this backdrop, gathering knowledge about forests' ecological response to prevalent climate and soil moisture conditions in this region is a matter of high relevance.

Monocultural Scots pine (*Pinus sylvestris* L.) forests on poor sandy soils dominate the forested areas in North-Eastern Germany. Although the Scots pine is relatively well adapted to drought (Ellenberg and Leuschner 2010), changed climatic conditions have negatively influenced their vitality in Central Europe over the last decades (Rebetez and Dobbertin 2004, Lebourgeois et al. 2010). Dendroclimatic analyses provide an excellent basis to investigate the sensitivity of tree growth to climatic or other environmental factors. Researchers have widely described the impact of climatic parameters, especially precipitation and temperature, on the radial growth of Scots pine in different regions across Europe. However, most of the investigations were carried out in mountainous or highly elevated regions such as the Austrian (Oberhuber et al. 1998) and Swiss Alps (Weber et al. 2007), northern Spain (Bogino et al. 2009, Pasho et al. 2011), or the region of Provence in France (Thabeet et al. 2009, Lebourgeois et al. 2012). In all of these studies, precipitation from spring to early summer of the growing year determined tree-ring width significantly. The influence of temperature was generally less pronounced (Oberhuber et al. 1998, Bogino et al. 2009, Lebourgeois et al. 2012). However, a mild February promoted tree growth along the natural distribution area of Scots pine in northern Spain (Bogino et al. 2009) and in the mountainous regions of South-Eastern France (Lebourgeois et al. 2012).

Linderholm et al. (2010) give an excellent overview about dendroclimatic research in Fennoscandia. Studies of the Baltic region highlighted the positive influence of mild winter temperatures on the radial growth of Scots pine (Läänelaid and Eckstein 2003, Vitas 2008, Pärn 2009, Hordo et al. 2009, Dauškane et al. 2011). Here, the impact of precipitation on growth was generally less pronounced. Precipitation, in particular in early summer, seems to play a more important role further to the south, as results of a dendroclimatic analysis in North-Eastern Germany indicate (Perez et al. 2005). Nevertheless, there is a lack of information on the sensitivity of Scots pine to the alterations of soil moisture in the lowlands of Central Europe, where this tree species often dominates in the forests. To our knowledge, the relevance of soil moisture of the very sandy soils in the southern Baltic region on Scots pine's growth has not been analysed adequately so far.

Recent studies have revealed that (soil-) drought indices might explain more of the variability in tree-ring width than the isolated consideration of temperature or precipitation (Friedrichs et al. 2009, Scharnweber et al. 2011). Weber et al. (2007) and Bogino et al. (2009) applied a meteorological drought index, based on the difference between precipitation and potential evaporation. The (self-calibrated) Palmer Drought Severity Index (PDSI) (Palmer 1965, van der Schrier et al. 2006) considers soil moisture in addition to climatic parameters and is one of the most popular drought indices. Disadvantageous is its strong auto-correlative nature and low spatial resolution of 0.5°×0.5°, which does not allow the consideration of small-scale heterogeneities of the soil. To overcome these shortcomings, calibrated physically based soil water balance models on the plot scale provide excellent approaches to reflect the soil water availability more realistically.

In this study, we focused on the relationships between tree-ring width and precipitation, temperature, and soil water availability for 17 Scots pine stands in North-Eastern Germany over a period of 21 years. In particular, we aimed to identify the most influential factors affecting tree growth and analyse whether soil water availability better predicts tree growth than climatic variables alone. Finally, this paper will discuss differences in climate–growth relationships among the stands with regard to soil properties, vegetation characteristics and climatic conditions.

Materials and Methods

Study sites

The study area comprises the entire Federal State of Brandenburg in North-Eastern Germany (Fig. 1) and is characterized by a mainly flat topography with gentle slopes. 35.3% of the region is covered by forests, in which Scots pine predominates with 72%, followed by oak (5%), and beech (3%) (BMELF 2002). 17 Scots pine stands from the Forest Condition Control Program (ÖWK) in East Germany, run by the Eberswalde Forestry State Center of Excellence (LFE), were chosen for the analyses. One plot (KH1203) of the European Level-II-monitoring network (Lorenz 1995) with perennial measurements of the volumetric SWC was used as a reference stand to calibrate the soil water balance model. Soil and vegetation data from the selected stands were obtained through observations by the LFE in 1988, 1993, and 2006.

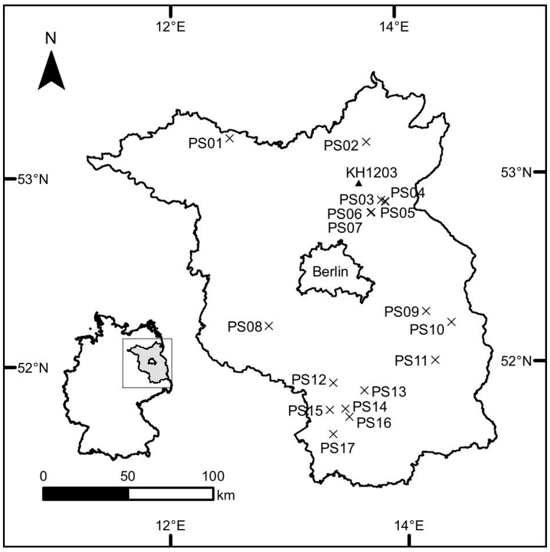

Figure 1. Location of selected forest stands (crosses) and reference plot (triangle)

Table 1 illustrates the characteristics of the individual sites. Trees were between 58 and 97 years old in 2006. Stand densities and leaf area indices ranged between 323 and 2,283 stems/ha and from 2.0–3.4 m²/m², respectively, and generally decreased with increasing tree age. Prevailing soil types are Cambisols and Podzols (WRB 2006). The average sand content of the sites amounted to approximately 93%, whereas the portions of silt (approx. 5%) and clay (approx. 2%) played only a minor role in particle size distribution. As a consequence, available water capacities, which were calculated by a pedotransfer function based on particle size distribution, bulk density, and soil organic matter (Renger et al. 2008), were comparably low and ranged between 145 and 227 mm for the rooting zone. The depth of the rooting zone was set to 160 cm for all stands on the basis of measurements by the LFE. The soil moisture classes (SMC) are derived by a combination of available water capacity and soil texture (Konopatzky 2012). The investigated sites comprise the full range of SMC from 1 to 7, where 1 is the driest and 7 is the wettest class.

Climate data with a daily resolution from the nearest weather stations of the German Weather Service formed the basis to build climate–growth relationships and served as input variables for the model. The climate stations provided data on temperature (mean, minimum, maximum), wind speed, relative humidity, and sunshine duration. In addition, the dense net of precipitation stations yielded precipitation data. The distances from study sites to meteorological stations were relatively short, ranging from 1–7 km for precipitation stations and from 4–23 km for climate stations. Stand-specific mean annual temperature and precipitation totals during the observation period ranged from 8.7–9.5 °C and from 541–603 mm, respectively. While the amount of precipitation was more or less evenly distributed throughout the year with maxima in summer and minima in winter, the annual temperature course showed the typical seasonal fluctuations for Central Europe with minima in January (0.1 °C) and maxima in August (18.6 °C) (Figure 2).

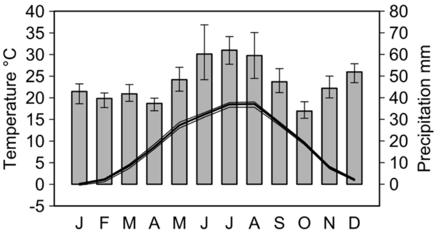

Figure 2. Climate diagram of the study sites. Thick line and bars represent mean monthly temperatures and precipitation totals. Thin lines and whiskers indicate site-specific minima and maxima

Table 1. Soil properties of the main rooting zone (160 cm) and vegetation characteristics of the selected stands. *BD* bulk density, K_{sat} saturated hydraulic conductivity, *AWC* available water capacity, *SMC* soil moisture class, *N* number of trees per hectare, *DBH* diameter at breast height, *H* tree height, *LAI* maximum leaf area index

Stand	Soil									Vegetation				
	Sand (%)	Silt (%)	Clay (%)	Gravel (%)	C_{org} (%)	BD (g/cm³)	K_{sat} (m/d)	AWC (mm)	SMC	Age (2006) (years)	N (No./ha)	DBH (cm)	H (m)	LAI (m²/m²)
PS01	96.8	2.1	1.1	3.4	0.3	1.57	3.09	154.0	1	86	614	28.0	24.3	2.8
PS02	92.3	4.8	2.9	1.4	0.3	1.34	3.49	149.0	2	74	695	31.0	26.5	3.1
PS03	95.6	2.1	2.3	1.0	0.1	1.62	1.35	147.6	2	63	2283	14.7	15.2	3.4
PS04	90.3	6.1	3.6	25.4	0.2	1.64	2.23	165.8	1-2	95	323	35.2	25.8	2.0
PS05	95.7	2.0	2.3	2.0	0.2	1.60	2.03	150.6	1	90	565	31.9	26.4	2.9
PS06	94.9	3.7	1.4	12.7	0.2	1.63	2.61	149.1	1	97	385	32.2	25.5	2.1
PS07	96.1	2.0	1.9	0.0	0.2	1.54	2.20	147.6	1	95	498	28.8	25	2.2
PS08	96.5	2.3	1.2	9.3	0.2	1.63	2.77	155.4	1	84	952	22.5	17.9	2.7
PS09	89.8	8.1	2.1	3.3	0.3	1.52	2.47	165.7	2-3	86	393	31.2	24.3	2.0
PS10	95.6	2.8	1.7	3.8	0.3	1.47	3.49	153.4	1	68	920	25.1	20.5	2.6
PS11	95.4	2.7	1.9	1.6	0.3	1.47	3.49	147.5	1	67	1010	18.1	17.2	2.7
PS12	81.2	15.1	3.8	5.5	0.2	1.34	1.33	210.0	4-5	68	920	25.8	20.1	3.3
PS13	86.0	11.7	2.3	4.1	0.2	1.45	2.72	168.5	4	80	760	27.1	20.7	2.9
PS14	79.0	17.3	3.7	0.5	0.2	1.32	2.18	226.7	7	64	906	21.6	18.7	2.7
PS15	93.8	4.4	1.7	1.7	0.3	1.50	2.21	170.2	4	74	563	25.8	20.7	2.7
PS16	97.5	1.5	1.0	0.0	0.2	1.30	3.49	144.6	2	58	1160	22.4	18.0	3.1
PS17	92.6	5.2	2.2	49.0	0.2	1.42	3.49	147.6	1	85	989	21.5	17.8	2.8
KH1203	96.0	2.9	1.1	0.0	0.3	1.51	3.49	151.5	1	96	394	31.0	20.6	2.7

Tree-ring data

21 to 30 dominant trees at each site were chosen and one core per tree was extracted at breast height in 2005. After mounting and sanding the cores, ring widths were measured with an accuracy of 10 μm by using a LINTAB measuring table and the software TSAP-Basic (Rinn 2003). For this study, we analysed the last 21 years (1984-2004) of the cores beginning with the onset of the ÖWK-Program. Site-specific

chronologies were built by using the package dplr (Bunn 2008) for R (R Development Core Team 2012) as follows: to remove age-related trends, we detrended the individual raw ring series by using a cubic spline with a frequency response of 50% at 2/3 of the series length (Cook and Peters 1981) resulting in a dimensionless tree-ring width index (RWI). First-order autocorrelation was then removed from the detrended series to calculate residual chronologies (Fritts 1976). Eventually, site-specific chronologies were built by averaging the individual series with a robust mean. The master chronology was calculated by averaging site chronologies. To assess the signal strength and the quality of each site chronology, we calculated the mean sensitivity (MS, average year-to-year change in ring width), the inter-series correlation (Rbar), and the expressed population signal (EPS, the deviation from the ideal chronology).

Modelling approach

The water balance model LWF-BROOK90 (Hammel and Kennel 2001), an improvement on the BROOK90 model (Federer 2002), was applied to estimate soil moisture dynamics. LWF-BROOK90 is process-based and has been applied to forest stands in various studies (Wellpott et al. 2005, Holst et al. 2010, Bauwe et al. 2012). Details about model algorithms and functionalities can be found in the online model documentation (Federer 2002). The model is driven by daily climatic parameters. The vertical water flux is calculated layer-wise iteratively by solving the Richards equation. Evaporation and transpiration are calculated using the Shuttleworth-Wallace equation (Shuttleworth and Wallace 1985), a modification of the Penman-Monteith formula (Monteith 1965), which determines transpiration and evaporation rates separately. Soil hydraulic properties were characterized employing the Mualem-van-Genuchten approach (Mualem 1976, van Genuchten 1980).

The model was calibrated using measured data from the reference plot KH1203 of the Level-II-network (see Figure 1 for location). This plot is a monocultural Scots pine stand on sandy soil and resembles the other sites in our study in terms of climate, soil, and vegetation (see Table 1 for details). Volumetric SWC was measured using TDR-probes at soil depths of 10, 20, 30, 40, 60, 100, and 150 cm in two replicates during the period from 2006 to 2009. Several pedotransfer functions (Wösten et al. 1999, Teepe et al. 2003, AG Boden 2005, Puhlmann and von Wilpert 2012) to obtain Mualem-van-Genuchten parameter values from soil texture, bulk density, and soil organic matter content were tested for suitability. Measured SWC was best portrayed by Teepe's approach, which eventually formed the basis for the water balance simulations of the 17 Scots pine stands. The most important model input variables with respect to climate, soil, and vegetation were measured and have been described previously. For additional parameters, we applied values for comparable Scots pine stands provided by Hammel and Kennel (2001).

The relative extractable water (REW) (Granier et al. 1999, Bréda et al. 2006) of the rooting zone served to characterize soil moisture conditions. It was calculated from the volumetric SWC as follows:

$$REW = \frac{\theta_{act} - \theta_{pwp}}{\theta_{fc} - \theta_{pwp}}$$

where θ_{act} is the actual volumetric SWC, θ_{pwp} is the volumetric SWC at permanent wilting point, and θ_{fc} is the volumetric SWC at field capacity. REW values of 1 and 0 indicate field capacity and permanent wilting point, respectively. Soil water shortage occurs when REW drops below the threshold of 0.4 and stomata begin to close (Granier et al. 1999, Bréda et al. 2006). Two variables derived from REW were used to characterize soil drought (Bréda et al. 2006): drought duration (DD) as the annual number of days with REW<0.4 and drought intensity (DI) (0.4-REW)/0.4 as the annual sum of days with REW<0.4.

Statistical analysis

Monthly values for precipitation, mean temperature, and REW were calculated over a 14-month period running from September of the year before ring formation through October of the growing year. Drought duration and drought intensity were determined annually for the observation period. To analyse climate–growth relationships, we calculated Pearson's correlation coefficients on a monthly basis between residual tree-ring width and climatic data and REW and on an annual basis for drought duration and drought intensity. In addition, response function coefficients were calculated for the variables above using the principal components regression approach (Fritts 1976), including a permutation-based significance test (Biondi and Waikul 2004). Since the number of observations was comparably low in our dataset, it was not possible to build a combined response model for all variables. Instead, we calculated separate response functions for monthly precipitation, temperature, and REW. Pointer years represented years with an extraordinary growth response (positive or negative) and were defined as being higher than one standard deviation from the mean RWI of the master chronology. Principal Component Analysis (PCA) was performed to discuss differences in site-specific climate sensitivity with regard to potential influencing factors. PCA was calculated by using the package stats (version 2.14.0) for R (R Development Core Team 2012).

Results

Model performance

LWF-BROOK90 reproduced the temporal dynamics of measured soil moisture quite well (Figure 3). The grey bands illustrate the large degree of soil moisture heterogeneity within the soil profile. For all depths, the predicted SWC lay mostly within the range of observed values. Average deviations between the simulated SWC and mean measured values were relatively low and ranged from 0.3–1.9%. This was confirmed by high correlation coefficients. However, under very dry conditions, the lowest simulated SWC was equivalent to the residual water content of the applied pedotransfer function and, therefore, did not always reproduce the short-term dynamics of the measured values. Under wet conditions, the degree of fit was lower in the upper soil layer (20 cm) compared to deeper soil layers.

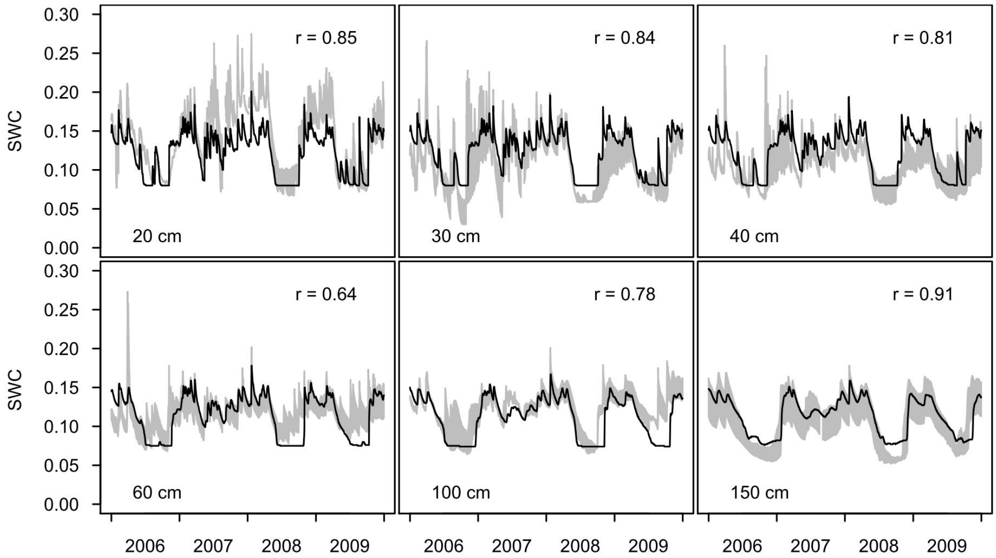

Figure 3. Daily measured (upper and lower limit of grey areas) and simulated (black lines) volumetric soil water contents (SWC) at different soil depths for the reference stand (KH1203) from 2006–2009, with correlation coefficients between r=0.64 and r=0.91

Tree-ring statistics and chronologies

The analysed chronologies showed variable growth characteristics (Table 2, Figure 4). For 14 out of the 17 chronologies, the expressed population signal was above the 0.85 threshold value (Wigley et al. 1984), which indicates a good representation of the ideal chronology for the Scots pine stands under investigation. The lower EPS-values for the remaining three chronologies (PS09, PS10, PS13) were accompanied by comparatively low inter-series correlation values. Average annual growth rates ranged between 1.13 mm and 1.65 mm, whereby growth rates decreased with increasing age (r = -0.416, p < 0.1). An age dependency was also observed for mean sensitivity (r = 0.421, p < 0.1). The inter-annual variability (0.233 – 0.319) of the chronologies was generally higher for older trees. First-order autocorrelation ranged from 0.242 to 0.550 and was more pronounced in the younger stands, which suggests a stronger dependency of current growth rates on the growth of the preceding year at these stands. However, this relationship was statistically not significant.

Relationships between radial growth and environmental factors

The most frequent significant correlations between monthly climatic parameters and tree-ring width were calculated for February and June of the growing year. Radial tree growth was aided by a mild/wet February and a cool/wet June. In general, precipitation had a greater impact than temperature on tree-ring width (Table 3). In February, six and ten out of 17 Scots pine stands showed significant positive correlations for temperature and precipitation, respectively. Correlations between temperature and RWI were significantly negative at three stands (PS06, PS10, PS17) in June, while these stands had no significant relationships in February. In terms of precipitation, there were significantly positive correlations with RWI for five stands in June. A wet September of the previous year promoted tree growth at three stands (PS01, PS15, PS17). The number of significant relationships with regard to temperature and precipitation for the other months was lower and seemed to have only a minor influence on tree growth.

Table 2. Chronology statistics for individual stands. *N* number of trees, *AGR* average growth rate (mm/year), *AC(1)* first-order autocorrelation, *MS* mean sensitivity, *Rbar* inter-series correlation, *EPS* expressed population signal

Stand	N	raw ring data		residual ring data		
		AGR	AC(1)	MS	Rbar	EPS
PS01	30	1.26	0.266	0.294	0.281	0.922
PS02	28	1.35	0.388	0.266	0.294	0.921
PS03	30	1.28	0.355	0.235	0.262	0.914
PS04	25	1.60	0.374	0.305	0.301	0.915
PS05	29	1.39	0.455	0.268	0.201	0.880
PS06	30	1.26	0.385	0.319	0.168	0.859
PS07	24	1.14	0.338	0.277	0.260	0.894
PS08	27	1.13	0.251	0.298	0.437	0.954
PS09	21	1.25	0.305	0.233	0.145	0.781
PS10	26	1.44	0.419	0.249	0.123	0.785
PS11	30	1.43	0.495	0.296	0.486	0.966
PS12	28	1.26	0.338	0.298	0.332	0.933
PS13	26	1.12	0.247	0.285	0.176	0.848
PS14	27	1.55	0.407	0.265	0.312	0.924
PS15	27	1.54	0.242	0.287	0.299	0.920
PS16	30	1.65	0.550	0.270	0.460	0.962
PS17	23	1.30	0.333	0.318	0.265	0.893

The individual Scots pine stands responded differently to soil water availability. Significant positive correlations between RWI and REW were mainly observed between June and August of the growing year. Six stands showed significant correlations during this period, with a predominance of the sites with lowest of soil moisture classes (4 × SMC = 1, 1 × SMC = 1-2, 1 × SMC = 4). Significant correlations usually extended over several consecutive months (PS01, PS04, PS06,

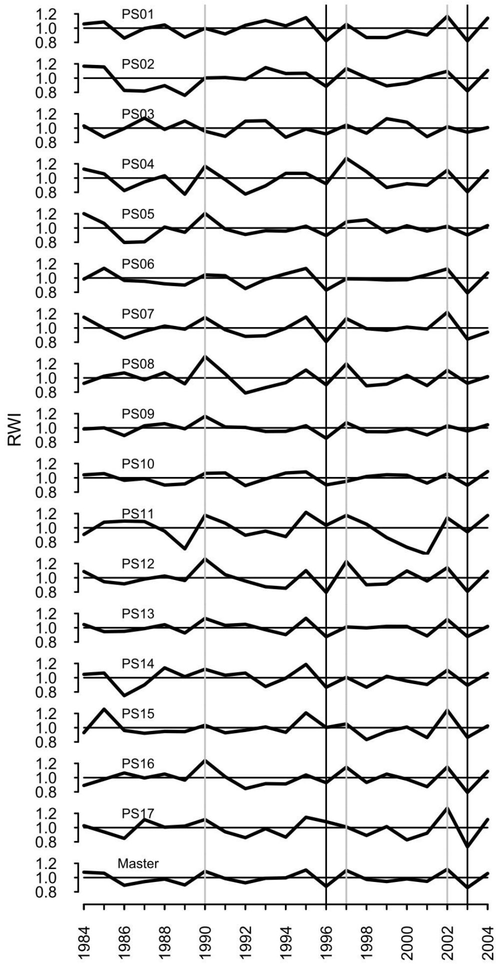

Figure 4. Residual chronologies of the 17 Scots pine stands and the master chronology. Vertical lines indicate negative (black) and positive (grey) pointer years

Table 3. Pearson's correlation coefficients between temperature, precipitation, relative extractable water (REW) and ring-width index (RWI) for the period from September of the previous year through October of the growing year. Only months with significant correlations ($p<0.05$) are shown. * - $p<0.01$, ** - $p<0.001$

	PS01	PS02	PS03	PS04	PS05	PS06	PS07	PS08	PS09	PS10	PS11	PS12	PS13	PS14	PS15	PS16	PS17
Temperature																	
Nov-1	0.456																
Feb					0.533		0.609*		0.588*			0.620*	0.578*	0.541			
Jun						-0.567*				-0.453							-0.490
Precipitation																	
Sep-1	0.443														0.554*		0.437
Feb	0.438						0.583*	0.503	0.439			0.523	0.595*	0.505	0.526	0.556*	0.688**
Mar											-0.477						-0.474
May			-0.436														
Jun					0.441	0.441			0.465		0.532						0.627*
Aug						0.456											
REW																	
Feb	0.608*					0.521											
Jun						0.478									0.471		0.530
Jul	0.461			0.624*		0.477					0.449						0.555*
Aug	0.567*			0.535		0.471											0.485
Sep				0.464		0.452											
Oct				0.444		0.425											

PS17), which is due to the high auto-correlative nature of REW.

Response function analysis confirmed the results obtained from simple correlations and reduced the number of significant variables (Table 4). Response function coefficients were lower than correlation coefficients and indicate that the climate sensitivity varied strongly among the Scots pine stands. For 6 out of 17 stands, climatic parameters could not significantly explain variances among the individual chronologies. For the remaining sites, the explained variance was higher for precipitation (19.4% to 68.9%) than for temperature (11.9% to 36.0%). Soil water availability expressed by REW influenced radial growth significantly at only one stand (PS01) with an explained variance of 52%.

Table 4. Response function coefficients and explained variances (R^2) for temperature, precipitation, and relative extractable water (REW) calculated separately covering the period from September of the previous year through October of the growing year. Only months with significant coefficients ($p<0.05$) are shown

	PS01	PS02	PS03	PS04	PS05	PS06	PS07	PS08	PS09	PS10	PS11	PS12	PS13	PS14	PS15	PS16	PS17
Temperature																	
Feb							0.353					0.334	0.363				0.438
Jun		-0.359				-0.366				-0.339							
R²		**0.119**				**0.252**	**0.354**			**0.221**		**0.360**	**0.344**				**0.155**
Precipitation																	
Feb							0.342					0.439	0.432	0.368		0.375	0.366
Mar																	-0.318
Jun						0.334					0.377						0.393
Jul	0.395												-0.386				
Oct	-0.354																
R²	**0.354**					**0.194**	**0.317**				**0.283**	**0.274**	**0.547**	**0.255**		**0.391**	**0.689**
REW																	
Feb	0.510																
R²	**0.520**																

The relationships between soil water deficit and tree growth are illustrated in Figure 5. Strong significant negative correlations between the residual chronologies and the annual number of drought days and drought intensity were found for five Scots pine stands (PS02, PS04, PS06, PS16, PS17), of which three stands exceeded the 99% significance level. The individual stands responded quite similarly to these two drought indices because of the indices' strong relationship to each other (r=0.98, p<0.0001). Nevertheless, the absolute values of r were generally slightly higher for drought intensity, which could be an indication that drought severity influences tree growth more than drought duration alone. Drought duration (15 to 137 days) and drought intensity (6 to 75) varied greatly among the stands, which could be attributed to different amounts of stand precipitation (see also Table 1). The relationships between precipitation and drought indices were statistically significant (r = -0.63 for drought duration and r = -0.65 for drought intensity, p < 0.0001).

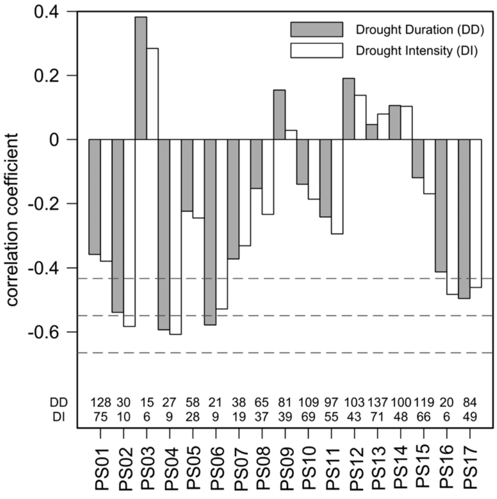

Figure 5. Pearson's correlation coefficients between drought indices and RWI. Numbers are mean annual drought duration in days and drought intensity. Dashed lines indicate 95%, 99%, and 99.9% significance levels

Soil and vegetation parameters played only a minor role in causing different soil water deficits and did not show any significant correlations to drought indices (data not shown). The severity of the modelled soil water deficit appeared to have no effect on tree growth response. For instance, the soil water deficit was highest at PS13 (Figure 5), but no significant relationship with RWI was observed. At the same time, significant relationships were calculated between RWI and drought parameters for PS04, although soil water stress was relatively low at this stand. However, significant correlations between radial growth and drought indices were only found in the stands with the lowest soil moisture classes (SMC = 1 and 2) and low available water capacities (AWC < 166 mm).

Pointer year analysis

According to pointer year calculations, two negative and three positive pointer years were identified (Table 5). The year with the largest growth depression (-0.133 deviation from the mean) was 2003. This extraordinary negative departure from the average could be attributed clearly to a prolonged drought period from summer to fall. Relevant drought indicators (DD, DI, REW7) showed remarkable deviations from the 21-year mean. In contrast, data indicate that narrow tree rings in 1996 were not induced by summer drought, since drought duration, drought intensity, and REW7 reflect an above-average wet summer. Precipitation in June that year was indeed considerably below average, but the main trigger for growth depression in 1996 was presumably a very cold February. 1990, 1997, and 2002 were positive pointer years, which were commonly characterized by an above-average warm February. A mild February combined with significant rainfall in February (2002) and June (1990) favoured growth conditions. Aside from February temperature, relevant parameters varied around the mean in 1997. Therefore, we can assume that growth was mainly promoted by warm February temperatures that year.

Table 5. Values for ring-width index (RWI), temperature (T), precipitation (P), drought duration (DD), drought intensity (DI), and relative extractable water (REW) for pointer years averaged over all Scots pine stands. Numbers indicate February (2), June (6), and July (7). Arithmetic mean refers to the entire observation period 1984-2004 through all Scots pine stands

	RWI	T2	T6	P2	P6	DD	DI	REW7
Negative pointer years								
1996	0.901	-3.3	16.0	35	33	14	6	0.84
2003	0.859	-2.2	18.7	8	41	169	109	0.19
Positive pointer years								
1990	1.125	6.5	16.6	50	130	93	50	0.62
1997	1.092	4.1	16.7	51	50	60	28	0.77
2002	1.125	5.2	17.1	83	48	5	1	0.71
Arithmetic mean								
	0.992	1.1	16.1	40	60	73	37	0.60

Factors controlling climate sensitivity

The analysis of climate–growth relationships revealed that the Scots pine stands responded differently to environmental factors. A principal component analysis (PCA) was performed to explore the main influencing factors inducing a site-specific sensitivity to climatic parameters. Potential controlling factors for climate (temperature and precipitation in February and June), as well as AWC and tree age (see Table 1) as integrative soil and vegetation parameters, were included into the model. The explained variances for temperature and precipitation, obtained by response function analysis, and mean sensitivity (see Table 2) served as measures of climate sensitivity.

The first and the second axis explained 41.3% and 22.1% of the total variance in the data. PC1 was controlled solely by climatic parameters (Figure 6). Temperature in February and June had high positive loadings on PC1 (0.48 and 0.46), while precipitation in February and in June had high negative loadings on this axis (-0.42 and -0.39). Figure 6 illustrates that higher temperatures are accompanied by lower precipitation totals, and vice versa. Climatic parameters had low loadings on PC2. Instead, this axis was controlled by parameters explaining tree age and climate sensitivity. Tree age (loading: -0.49), mean sensitivity (-0.56), and the explained variances for precipitation (-0.39) and temperature (-0.43) had high negative loadings on that axis. These similar values imply a positive relationship to each other, which suggests increasing climate sensitivity for older trees. The relatively low loadings of climatic parameters on PC2 indicate that the variability of temperature and precipitation across the study area (see Figure 2) did not considerably influence the radial growth of the Scots pine stands. Available water capacity had low loadings on both axis one (0.29) and axis two (0.16) and was therefore of minor relevance in explaining variations in stand-specific climate sensitivity.

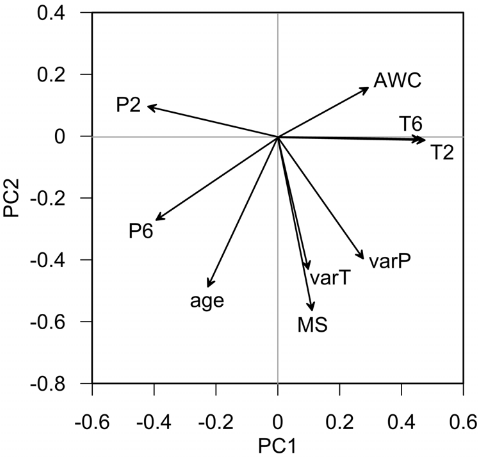

Figure 6. Biplot of the Principal Component Analysis (PCA) comprising 17 Scots pine stands. Variables are precipitation (P) and temperature (T) in February (2) and June (6), available water capacity (AWC), tree age (age), mean sensitivity (MS), explained variances for precipitation (varP) and temperature (varT)

Discussion

Chronology statistics

The chronology statistics indicate that the 17 Scots pine stands exhibited similar radial growth patterns. Expressed population signal (EPS) values were relatively low – seven stands <0.9 – suggesting a moderately pronounced common climate signal on tree growth. In contrast, EPS-values calculated for Scots pine throughout Europe mostly exceeded the 0.9 level (Linderholm et al. 2003, Bogino et al. 2009, Friedrichs et al. 2009). First-year autocorrelation of ring width was rather low compared to studies from Atlantic regions in Western and Northern Europe (Linderholm 2001, Lebourgeois et al. 2010), but more in line with observations from Central Europe (Friedrichs et al. 2009). Therefore, we assume that prior-year growth conditions do not have a sustaining impact on the current-year growth of Scots pine in the North-Eastern German lowlands. This behaviour can at least partly be explained by a recent experimental study (Eilmann et al. 2010), according to which Scots pine can quickly recover from drought stress. However, observations within the Brandenburg region have shown that needle losses of Scots pine are clearly influenced by weather conditions up to three preceding years (MLUR 2003). Mean sensitivity fell within in the range of other studies (Bogino et al. 2009, Bouriaud and Popa 2009, Pasho et al. 2011) and seemed to increase with tree age.

Climate–growth relationships

The analysis of climate–growth relationships revealed common patterns of climatic variables influencing tree growth. The correlation analysis, response functions, and analysis of pointer years performed in this study draw a consistent picture about the climate sensitivity of Scots pine in North-Eastern Germany. Generally, radial growth was more affected by precipitation than by temperature. Correlation analysis and response functions showed that temperature and precipitation in February have a crucial impact on the formation of tree rings. Also, but to a lesser extent, high precipitation in combination with low temperatures in June had a significant positive relation to tree-ring width. The relevant impact of June precipitation on the tree-ring growth of Scots pine is in agreement with many studies conducted in different European regions (Oberhuber et al. 1998, Perez et al. 2005, Friedrichs et al. 2009, Thabeet et al. 2009, Pasho et al. 2011, Michelot et al. 2012). However, the marked influence of February precipitation seems to be a particular feature of the North-Eastern German lowlands. A possible explanation for this could be improved soil water availability in early spring (Lingg 1986, Oberhuber et al. 1998), which was supported by soil water balance simulations. Hence, we found significant ($p<0.05$) site-specific positive correlations between February precipitation and REW in March for 12 of the analysed stands. However, the influence of February precipitation was restricted to March, since no significant relationships were found in April and May. Michelot et al. (2012) also mentioned a lagging effect of climatic conditions on tree growth finding that for three Scots pine stands in a temperate forest in Central France a warm December in combination with abundant precipitation promoted early wood formation in the following spring.

The impact of temperature on tree growth is consistent with other studies in similar ecotones in Germany (Perez et al. 2005, Friedrichs et al. 2009), as well as in lowland and mountain forests in France (Lebourgeois et al. 2010), in which February and June temperatures played an important role. High temperatures in winter support an early onset for the cambial reactivation of conifers (Friedrichs et al. 2009, Lebourgeois et al. 2010), while cool summers limit evapotranspiration rates and – in combination with sufficient rain – prevents depletion of the soil. The climate signal affecting the radial growth of Scots pine in the North-Eastern German lowlands seems to be limited. No significant response coefficients for either precipitation or temperature could be calculated for five stands. The low explained variance of the response functions for the remaining stands together with moderate EPS values indicate a weak climate forcing on tree growth. In contrast, the climate signal is much stronger in mountainous regions (Oberhuber et al. 1998) or at the distribution limit (Bogino et al. 2009).

Six Scots pine stands showed significant correlations between the soil water deficit index (REW) and tree-ring width primarily between June and August. Several studies have pointed out the importance of soil moisture and concluded that soil water availability is the driving force behind ring formation (Lebourgeois et al. 2005, Friedrichs et al. 2009, Michelot et al. 2012). In contrast to these observations, our results indicate a lesser importance of soil water availability for the formation of tree rings, since a significant response coefficient for REW was only calculated for PS01. This assumption is supported by the fact that stands susceptible to soil dryness with a large number of drought days and high drought intensities do not necessarily show significant relationships between drought indices and tree-ring width (Figure 5). Therefore, it can be assumed that growth response is not primarily affected by a moderate summer soil water deficit. Rather, February weather conditions seem to predominantly determine the radial growth of Scots pine in North-Eastern Germany's lowland forests.

The analysis of pointer years completed the investigations of climate–growth relationships and refined their results. The hot, dry year of 2003 was the year with the largest growth depression, which was eventually induced by a severe summer soil moisture deficit. The negative effect of this exceptional summer drought on tree growth had been observed for different tree species throughout Europe (Ciais et al. 2005, Bréda et al. 2006, Granier et al. 2007, Pichler and Oberhuber 2007). In contrast, a very cold February (the third coldest within the observation period) in combination with low rainfall in June (the third driest within the observation period) seems to be responsible for the growth depression in 1996. Favourable growth conditions emerged through the analysis of the three positive pointer years with exceptionally high temperatures in February. The results of the pointer year analysis stress the importance of weather conditions in February, which seem to have more influence on radial growth than the soil water availability in summer. Nevertheless, if the summer soil water deficit is too severe, Scots pine trees respond with substantial growth depression.

The analysed period of 21 years was comparably short for a dendroclimatic analysis. The obtained results are, however, believed to be justified and significant because the performed soil water balance simulations reflected the actual soil moisture conditions realistically. Model uncertainty would have increased drastically with longer time periods. In particular, silvicultural practices such as thinning in the more distant past influencing the soil water balance are difficult to identify retrospectively adding to the uncertainty in model outcome. Furthermore, there are good indications that our results reflect general relationships, because correlations between temperature and precipitation and radial growth of Scots pine over a longer time period in the same region were very similar (Perez et al. 2005).

Site-specific factors controlling climate sensitivity

Climate–growth relationships suggest that site-specific factors control the strength of the climate signal on tree growth. Relevant potential influencing factors with respect to soil, climate, and vegetation were included in a PCA to explore the controlling mechanisms. The biplot of the PCA (Figure 6) indicates that differences in available water capacity were only slightly reflected in a variable growth response. This result is in line with the study of Michelot et al. (2012), according to which differences in available water capacity did not influence the strength of climate–growth relationships. However, Lebourgeois et al. (2012) reported highest mean sensitivities for the lowest values of soil water availability. The PCA also revealed that varying weather conditions across the study area did not substantially cause different growth responses. In contrast to a dendroclimatic study performed for beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) trees along a climatic gradient in North-Eastern Germany, according to which climate sensitivity increases with decreasing precipitation (Scharnweber et al. 2011), the climatic gradient across our study area seems to be too small to induce different growth responses. The most straightforward explanation for a varying climate forcing, are differences in tree age. According to the PCA, there is a positive relationship between tree age and climate sensitivity, expressed by mean sensitivity and the explained variances for temperature and for precipitation. The results provide reasons to believe that climate sensitivity tends to increase with increasing tree age. Several studies observing different tree species have shown that tree-ring growth response to climate signals may vary with tree age (e.g., Szeicz and MacDonald 1994, Rossi et al. 2008, Yu et al. 2008, Vieira et al. 2009), whereby older trees tend to demonstrate a higher climate sensitivity (e.g., Carrer and Urbinati 2004, Wang et al. 2009, Copenheaver et al. 2011). Various authors have attributed the age-dependent climate sensitivity to physiological processes such as lower photosynthetic rates (Ryan et al. 1997, Bond 2000) and an increased hydraulic resistance in older trees (Szeicz and MacDonald 1994, Ryan et al. 1997). An age-dependent climate sensitivity of Scots pine was also observed in other European regions. Martinez-Vilalta et al. (2012) reported a lower resiliency to drought for older pine trees in North-Eastern Spain. A Scandinavian study (Linderholm and Linderholm 2004) revealed differences in the growth response of Scots pine to climate with higher climate sensitivity for older trees (> 250 years) in comparison to middle-aged trees (100–250 years). The maximum age difference (39 years) in our study was relatively small. Therefore, possible age-specific growth responses should be considered as an indication rather than evidence.

Conclusions

The obtained relationships between environmental variables and radial growth and the large sample size allow us to draw a precise picture of Scots pine's growth response to climate and soil water availability in North-Eastern Germany. The results of our study indicate a moderate impact of climate on the radial growth of Scots pine in North-Eastern Germany, which can be attributed to optimal growth conditions in a physiological sense within its natural distribution area (Ellenberg and Leuschner 2010). We conclude that the pine forests in question are far from being seriously threatened by inter-annual climatic variations in the near future. Climate–growth relationships revealed that tree growth is promoted primarily by a warm/wet February and secondarily by a cool/wet June. Although soil moisture availability is not the driving force for radial growth, severe soil water stress in summer may lead to substantial growth depression. The implications of regional climate change predictions (Spekat et al. 2007) may be twofold. On the one hand, warmer winters in combination with increased precipitation may favour tree growth. On the other hand, more frequent heat waves and droughts in summer may lead to notable growth reductions. Older trees tend to be more climate sensitive than younger trees. This indication should be investigated further by including trees with a wider age range.

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ЗАВИСИМОСТЬ РАДИАЛЬНОГО ПРИРОСТА СОСНЫ ОБЫКНОВЕННОЙ (*PINUS SYLVESTRIS* L.) ОТ КЛИМАТИЧЕСКИХ УСЛОВИЙ И ВОДНОГО РЕЖИМА ПОЧВ ВОСТОЧНОЙ ЧАСТИ СЕВЕРО-ГЕРМАНСКОЙ НИЗМЕННОСТИ

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Резюме

На 17 опытных участках восточной части Северо-Германской низменности были проведены исследования по выявлению взаимосвязи между радиальным приростом сосны обыкновенной и некоторыми климатическими факторами – температурным режимом и количеством осадков. Кроме того, было изучено влияние наличия доступной почвенной влаги на радиальный прирост, с целью сравнения влияния этого интегративного параметра по сравнению с климатическими переменными. Для построения дендрохронологической шкалы и хронолигической статистики были применены дендрохронологические методы. Коэффициент корреляции, бутстрэп, анализ экстремальных значений были использованы для объяснения взаимосвязи “климат-прирост”. Для анализа различий в интенсивности климатического сигнала применяли метод главных компонент. Результаты дендрохронологической статистики показывают сходные модели радиального прироста и незначительное влияние на него климатических факторов на всех опытных участках. Сравнительно низкие значения выраженного сигнала популяции (EPS) свидетельствовали об умеренном общем климатическом сигнале. Было также установлено, что радиальному приросту способствуют главным образом теплый/влажный февраль и влажный/холодный июнь. Несмотря на то, что наличие доступной почвенной влаги не является определяющим фактором для радиального прироста, значительный недостаток влаги может привести к существенному уменьшению толщины годичных колец. Значения средней чувствительности и результаты метода главных компонент подтверждают, что восприимчивость к климатическим условиям незначителъно повышается с увеличением возраста деревьев. Мы пришли к заключению, что в ближайшее время сосновые леса восточной части Северо-Германской низменности не подвержены угрозе исчезновения в результате годичных климатических колебаний.

Ключевые слова: дендроклиматология, взаимосвязь “климат-прирост”, относительное количество извлекаемой воды, LWF-BROOK90