Ecosystems (2017) 20: 1494–1511
DOI: 10.1007/s10021-017-0128-x

ECOSYSTEMS

Recent Climate Warming-Related Growth Decline Impairs European Beech in the Center of Its Distribution Range

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ABSTRACT

Increasing summer droughts represent a major threat for the vitality and productivity of forests in the temperate zone. European beech, the most important tree species of Central Europe's natural forest vegetation, is known to suffer from increased drought intensity at its southern distribution limits, but it is not well known how this species is affected in the center of its distribution range in a sub-oceanic climate. We compared tree-ring chronologies and the climate sensitivity of growth (MS) in 11 mature beech stands along a precipitation gradient (855–576 mm y^{-1}) on two soil types with contrasting water storage capacity (WSC) in northwest Germany to test the hypotheses that recent warming is impairing beech growth also in the center of its distribution below a certain precipitation limit, and stands with low soil WSC are more susceptible. We found a threshold of about 350 mm of mean growing season precipitation below which basal area increment (BAI) showed a consistent decline since the 1970s. The frequency of negative pointer years and MS were highest in low-precipitation stands on sandy soil, but both parameters have increased during the last decades also in the moister stands. The factor with largest impact on BAI was precipitation in June, in combination with high mid-summer temperatures. Contrary to our hypothesis, the edaphic effect on growth dynamics was surprisingly small. We conclude that global warming-related growth decline is affecting European beech even in the center of its distribution below a hydrological threshold that is mainly determined by mid-summer rainfall.

Key words: basal area increment; climatic drought; edaphic drought; *Fagus sylvatica*; growth decline; mean sensitivity; negative pointer years; precipitation gradient; tree-ring chronology.

INTRODUCTION

Due to their longevity, trees are facing global warming and associated longer, hotter, and often drier summers (Parry and others 2007; Allen and others 2010). Regional climate models such as ECHAM5-MPIOM (Max-Planck Institute for Meteorology, Hamburg) project declining summer

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Received 8 July 2016; accepted 16 February 2017;

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-017-0128-x) contains supplementary material, which is available to authorized users.
Author contributions CL, ICM, and CD conceived and designed the research project. FK performed research. FK, CD, and ICM analyzed the data. All authors wrote the manuscript.

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precipitation by up to 40% in certain regions of Germany in conjunction with a temperature increase by up to 3°C (scenario A1B) until the end of this century (Jacob and others 2014). Even more relevant for biological systems are meteorological extremes such as summer heat waves that may increase in frequency and severity (Schär and others 2004; IPCC 2013). Rising temperatures have, on the one hand, extended the growing season length of European forests (Menzel and Fabian 1999), increased forest productivity (Spiecker 1999; Pretzsch and others 2014), and promoted the spread of thermophilic forest plants with more southerly distribution (van Herk and others 2002; Pócs 2011; Jantsch and others 2013). On the other hand, climate warming has reduced the vitality and productivity of various tree species, notably Scots pine (*Pinus sylvestris* L.; Rebetez and Dobbertin 2004) and European beech (*Fagus sylvatica* L.). In particular beech, the most important tree species of the natural forest vegetation of Central Europe, has been found to be affected by severe droughts as that in 2003 (Rennenberg and others 2004; Ciais and others 2005; Bréda and others 2006). Pre-senescent leaf abscission and growth decline have been observed at the southern and eastern limits of the beech range in Spain, Italy, and Hungary (for example, Jump and others 2006; Piovesan and others 2005, 2008; Lakatos and Molnár 2009; Garamszegi and Kern 2014). More alarming is that recent growth decline has been observed in dendrochronological studies also in the center of beech distribution, that is, in Switzerland, eastern France, Belgium, and Germany (Charru and others 2010; Kint and others 2012; Scharnweber and others 2011; Weber and others 2013; Zimmermann and others 2015; Dulamsuren and others 2016). Otherwise, there are reports that wood formation in beech is relatively insensitive to droughts (van der Werf and others 2007). In fact, *F. sylvatica* occurs in Europe at a wide range of precipitation amounts (*c.* 2000 to less than 450 mm y^{-1}, Ellenberg and Leuschner 2010). Moreover, various authors have emphasized the adaptation potential of beech to a drier climate (for example, Meier and Leuschner 2008; Rose and others 2009; Weber and others 2013; Carsjens and others 2014), but the bulk of adaptation studies were conducted with saplings, the results of which cannot simply be extrapolated to mature trees. Thus, considerable uncertainty remains with respect to the drought sensitivity of adult European beech. No doubt, more precise information on precipitation and soil moisture limits of beech is urgently needed, given the typical production cycle of beech in managed forests of about 100 years (Weber and others 2013).

One reason for the partly contradicting observations on the drought response of beech is that water shortage can arise from low precipitation, a small WSC of the soil, or a combination of both factors. Moreover, the timing of drought is of paramount importance for its biological significance (Zimmermann and others 2015). Although many earlier studies have produced empirical evidence that the drought limit of trees depends to a considerable extent on soil properties (for example, Rigling and others 2001; Lebourgeois and others 2005; Weber and others 2007), synchronous variation in precipitation and soil WSC, and its impact on tree growth has not been investigated in detail so far.

Climate change and new forest management goals render a deeper understanding of beech drought limits even more urgent. Before humankind began to reduce forest cover from Neolithic times onwards, beech covered roughly 66% of Germany's land surface area (BMEL 2014). Until recent time, this area has been reduced to 7%, which represents approximately 17% of the current forest area (BMU 2011; BMEL 2014). In a move to more natural forest management, in many regions of Central Europe, forestry has begun to convert conifer plantations into beech forests or mixed broad-leaved conifer forests (Tarp and others 2000; Metz and others 2013). However, especially in more subcontinental regions with relatively low summer precipitation, this goal may conflict with the assumed drought sensitivity of beech. The tendency for decreasing summer precipitation in various regions of Central Europe (Schönwiese and others 2003) will further increase the drought risk in future time.

With a comparative dendrochronological study in mature beech stands along a precipitation gradient (855–577 mm mean annual precipitation, MAP), we aimed to characterize climatic and edaphic drought effects on the radial growth of *F. sylvatica* in the center of its distribution range. As hydrological variables, we considered mid-summer, summer, and annual precipitation as well as two levels of soil WSC (sandy and sandy-loamy soil) to assess the influence of climatic and edaphic drought on radial growth in a 60-year investigation period (1951–2010). Main study aims were (1) to identify precipitation thresholds beyond which long-term growth trends are decreasing, (2) to analyze the patterns of growth decline (continuously or abruptly triggered by certain drought events), (3) to examine which precipitation component (spring, mid- or late-summer precipitation) has the largest influence on radial growth, and (4) to compare the effects of reduced precipitation with those of lowered soil WSC. The comparison of six sites along a precipitation gradient allowed to examine long-term adaptive responses to a permanent reduction in precipitation by nearly 300 mm and contrast it with short- to medium-term growth responses (years to a few decades) as visible in annual ring chronologies. Based on earlier research by our group and other authors, we hypothesized that (1) increases in summer drought and/or temperature reduce the radial growth of beech below a yet-to-be-defined precipitation threshold, (2) the climatic impact on beech has increased since about the 1970s, and (3) the growth decline is stronger on sandy soil with lower WSC than on loam-richer soil.

METHODS

Forest Site Selection

Eleven mature beech forests with comparable stand structure were selected for study in the center of the distribution range of *F. sylvatica* between 52 and 53°N and 9 and 11°E in the lowlands of northwestern Germany (Table 1). The forests were located along a 130-km-long NW–SE precipitation gradient in the Lüneburg Heath (Federal States of Lower Saxony and Saxony-Anhalt). Apart from the climate influence (precipitation, temperature) on tree growth, we examined the effect of soil texture by selecting each one stand with a sandy or a sandy-loamy soil texture at six locations along the gradient (except for the locations Oe and Go: only one stand with sandy texture, and the location Ca: one stand with sandy-loamy and two stands with sandy textures; Table 1). The stands on sandy-loamy soil were mostly located on sandy moraine deposits with elevated silt and clay content and, thus, in general have higher WSC. The stands on sandy soil grew on more coarse-grained meltwater sands with low silt and clay content and a smaller WSC. Additional stand selection criteria were: canopy closure (canopy cover >0.9 in the upper layer, additional tree or shrub layers mostly absent), mature and even-aged stand structure (85–125 years old; Table 2), no or low admixture of other tree species (SeS, UnS, KlS, CaL: 3–19% *Quercus petraea*, OeS 39%, GoS: 6% *Pseudotsuga menziesii*), last forest management activities at least ten years ago, and tree origin from natural regeneration (with the exception of Oe). For the sake of comparability with respect to soil chemical conditions, all stands were selected on similar geological substrate, Pleistocene glacial or fluvioglacial sandy deposits from the penultimate (Saalian) Ice Age. Soil types ranged from Haplic Arenosols to Stagnic Podzols, with 4- to 9-cm-thick organic layers.

The nutrient-poor sandy soils had a pH(KCl) of 4.0–4.3 (mean 4.2), a C:N ratio of 13–26 mol mol^{-1} (mean 20), and a base saturation of 3–13% (mean 8) in the top mineral soil (data from Müller-Haubold and others 2013). The stands on sandy-loamy soil had a similar stand basal area as those on sandy

Table 1. Location and Climatic Data of 11 Investigated Beech Stands in Northwestern Germany

Site	Texture	Code	Latitude (N)	Longitude (E)	Elevation (m a.s.l.)	MAP (mm)	MGSP (mm)	MSP (mm)	MAT (°C)	Soil water (mm 120 cm^{-1})
Se	Loamy	Se L	53°10′	09°57′	127	855	419	237	8.7	111
	Sandy	Se S	53°10′	09°57′	130	855	419	237	8.7	90
Un	Loamy	Un L	52°50′	10°19′	120	816	394	223	8.7	95
	Sandy	Un S	52°50′	10°19′	117	816	394	223	8.7	79
Oe	Sandy	Oe S	52°59′	10°14′	90	786	384	217	8.9	59
Go	Sandy	Go S	53°09′	10°52′	85	707	365	212	9.0	78
Kl	Loamy	Kl L	52°37′	11°14′	102	656	343	195	9.0	124
	Sandy	Kl S	52°37′	11°15′	85	655	344	196	9.1	90
Ca	Loamy	Ca L	52°24′	11°16′	72	577	308	175	9.3	140
	Sandy	Ca S	52°23′	11°17′	75	576	307	174	9.4	81
	Sandy	Ca S II	52°22′	11°16′	105	594	315	179	9.3	46

Climate data refer to the period 1981–2010 and were derived from weather station data provided by the National Climate Monitoring of Deutscher Wetterdienst (DWD) which were corrected for elevation. Soil water: soil water storage capacity in the profile to 1.2 m depth. For additional edaphic and stand structural properties of the investigated beech stands, see Müller-Haubold and others (2013).

Climatic data: MAP, mean annual precipitation; MGSP, mean growing season precipitation (April–September); MSP, mean summer precipitation (June–August); MAT, mean annual temperature.

Sites: Se, Sellhorn; Un, Unterlüß; Oe, Oerrel; Go, Göhrde; Kl, Klötze; Ca, Calvörde. Code for textures: L, sandy-loamy; S, sandy.

Table 2. Descriptive Statistics for Unstandardized Tree-Ring Chronologies

Site code	n	Age (years)	DBH (cm)	MRW (mm)	MS	AC1	EPS > 0.85 since
Se L	20	106 ± 15^{c}	40.6 ± 3.7^{ab}	1.59 ± 0.13^{f}	0.34 ± 0.01^{bcd}	0.51 ± 0.03^{abc}	1930
Se S	20	108 ± 13^{c}	34.6 ± 2.3^{abc}	1.72 ± 0.13^{e}	0.28 ± 0.01^{d}	0.65 ± 0.03^{a}	1930
Un L	21	103 ± 15^{cd}	34.6 ± 2.6^{abc}	2.28 ± 0.19^{b}	0.32 ± 0.01^{cd}	0.45 ± 0.04^{abc}	1940
Un S	21	100 ± 11^{cd}	26.7 ± 2.1^{cd}	1.50 ± 0.16^{f}	0.32 ± 0.01^{cd}	0.57 ± 0.04^{ab}	1940
Oe S	35	82 ± 13^{e}	20.3 ± 2.0^{d}	1.50 ± 0.10^{f}	0.35 ± 0.01^{bcd}	0.56 ± 0.03^{abc}	1950
Go S	21	124 ± 12^{b}	32.8 ± 2.4^{bc}	1.33 ± 0.12^{g}	0.37 ± 0.01^{cb}	0.59 ± 0.03^{abc}	1920
Kl L	20	128 ± 10^{b}	46.7 ± 2.5^{a}	1.55 ± 0.10^{f}	0.38 ± 0.01^{cbd}	0.50 ± 0.05^{abcd}	1920
Kl S	21	108 ± 8^{c}	38.9 ± 3.1^{abc}	1.72 ± 0.19^{e}	0.32 ± 0.01^{cd}	0.59 ± 0.03^{ab}	1940
Ca L	12	99 ± 11^{cd}	40.1 ± 2.9^{ab}	2.11 ± 0.16^{c}	0.32 ± 0.02^{cbd}	0.62 ± 0.04^{d}	1950
Ca S	12	82 ± 4^{e}	31.2 ± 1.4^{bcd}	1.95 ± 0.13^{d}	0.45 ± 0.02^{a}	0.35 ± 0.05^{dc}	1970
Ca S II	12	83 ± 3^{e}	36.1 ± 1.5^{abc}	2.44 ± 0.13^{a}	0.39 ± 0.02^{b}	0.35 ± 0.04^{bcd}	1970

The 11 mature beech stands were located along a precipitation gradient in northwestern Germany. Tree age refers to the mean age at breast height (1.3 m). Mean ring width (MRW), mean sensitivity (MS), and first-order autocorrelation (AC1) were calculated for the period 1951–2010. Within a column, means followed by the same letter do not differ significantly (Ryan–Einot–Gabriel–Welsch multiple range test).
n, number of sampled trees; DBH, mean diameter at breast height; EPS, expressed population signal.

soil but were slightly older (13 years) and taller (4 m), whereas stem density was slightly higher in the latter (Table S1).

Climate Conditions and Meteorological Data

Mean annual temperature (averaged from climate data of the years 1981–2010) along the gradient was 9.0°C, with a tendency of slightly higher temperatures at the drier southeastern end of the gradient (Table 1). MAP decreased from 855 mm y^{-1} in the more sub-oceanic northwest to 575 mm y^{-1} in the more subcontinental southeast. The corresponding growing season rainfall (April to September) decreased from 405 to 295 mm y^{-1}.

For the analysis of the response of tree-ring width to monthly or yearly climate conditions, we used climate data (precipitation, temperature, sunshine duration) from the 1×1 km^2 grid data set provided by the German Meteorological Service (Deutscher Wetterdienst DWD, Offenbach, Germany). These data were regionalized by averaging climate data of the nine nearest grid fields of a study site and correcting for altitude. The DWD data were available from 1951 onwards. The close relation between the precipitation gradient and an associated soil moisture gradient was demonstrated by the measurement of volumetric soil water content with time domain reflectometry probes (TDR CS616; Campbell Scientific Inc., Logan, UT) installed at 20-cm soil depth in the center of each study site. The volumetric water content during the summer months (April to September) decreased from 11.5 to 6.0% v/v in the sandy-loamy soils and from 8.7 to 6.5% v/v in the sandy soils from the moistest to the driest study site (data from Müller-Haubold, personal communication).

Increment Core Sampling and Analyses of Tree-Ring Chronologies

The sampling of increment cores took place in a 30 × 30 m plot in the center of each forest stand. In December 2011, wood cores (5 mm in diameter) were taken with an increment corer (Suunto, Vantaa, Finland, 400 mm length) from 20 randomly selected trees per site (exceptions due to permission constraints: each twelve trees at the three sites in Calvörde, 35 at the single site in Oerrel), with at least ten dominant trees, resulting in 237 wood cores in total. All sampled trees had canopy access and diameters at breast height (DBH) of at least 15 cm. Permissions were granted for one increment core per tree only. Wood cores were taken at 1.3 m height at the northern side of the trunk, except for trees with reaction wood in this sector. The DBH of every cored tree was recorded. Cores with rotten segments or knobs were excluded from further analyses. Subsequently, the wood cores were air-dried, mounted on grooved boards, sanded, and polished. Every sample was scanned with an Epson perfection A4 or A3 scanner at a resolution of 1200 dpi and analyzed for tree-ring widths with the software LignoVision (version 1.38 m; Rinntech, Heidelberg, Germany). In case of questionable measurements, the increment cores were recut with a scalpel and reanalyzed using a movable object table (Lintab 6; Rinntech) and the software TSAP-Win (version 4.69 h; Rinntech). All measurements had a precision of 10 µm.

Tree-ring chronologies were derived for the 60-year period between 1951 and 2010. In a first step, the ring widths were cross-dated with TSAP-Win software based on three parameters: the coefficient of agreement (''Gleichläufigkeit'' GL; Eckstein and Bauch 1969), the cross-dating index (CDI; Dobbertin and Grissino-Mayer 2004), and Student's *t*-value (TVBP; Baillie and Pilcher 1973). Tree-ring series used for the calculation of mean tree-ring chronologies had a GL ≥ 65%, a CDI ≥ 20, and a TVBP ≥ 3.5. For the determination of tree age, ten years were added to the age determined by coring at 1.3 m height. The coherence within the tree-ring chronologies was examined with the expressed population signal (EPS; Wigley and others 1984), using the software ARSTAN (version 41d; Cook 1985). Chronologies were split into 30-year intervals with a running window overlap of 15 years. EPS was calculated for each interval. Chronologies were considered reliable if EPS exceeded the 0.85 threshold. Longer time series were also plotted for inspecting the age-related growth trend, but data prior to 1951 were not analyzed for climate sensitivity. Before averaging the tree-ring series from the individual trees to site chronologies, raw data were standardized using the formula $z_i = w_i/m_i$ with m_i being the 5-year moving average of year *i*. Standardization was applied to remove the long-term age-related growth trend from the data.

Analysis of Climate–Growth Relationships

The standardized site chronologies were also used to quantify the influence of temperature, precipitation and sunshine duration in individual months on tree-ring width in the climate response analysis. Climate data used for the climate response analysis were *z*-transformed using the equation $z_i = (x_i - \mu)/\sigma$, where x_i is the tree-ring width of year *i*, μ is the mean of the time series, and σ is the standard deviation of the time series.

The mean sensitivity (MS) of a tree-ring width series was calculated from the year-to-year variability in unstandardized tree-ring widths with $\mathrm{MS} = \frac{200}{N}\sum_{1}^{N}\left|\frac{a_n - a_{n-1}}{a_n + a_{n-1}}\right|$, where *N* is the length of the series (years), *a* is the tree-ring width, and *n* is the year. MS characterizes the inter-annual fluctuation of stem increment in a forest stand. The first-order autocorrelation (AC1, autocorrelation lag of 1 year) was calculated from the influence of the increment of the previous year on the increment of the current year. AC1 can be seen as the degree of similarity between a time series and a lagged version of itself. Both MS and AC1 were calculated for different time periods within the period 1951–2010.

For identifying pointer years, we quantified the extent of growth deviation from the mean with $\delta p_i = (p_i - m_i)/\sigma_c \times 100$, where p_i is the tree-ring width of year *i*, m_i is the 5-year moving average of year *i*, and σ_c is the standard deviation (SD) of the whole chronology. A year was defined as pointer year if the difference between p_i and m_i was larger than one SD of the chronology and if 85% of the trees of a chronology showed the same growth trend (compare Zimmermann and others 2015). Because of the focus on drought effects on increment in this study, only negative pointer years were considered ($\delta p_i \leq -50$).

We calculated three coefficients that characterize the tolerance of a tree's radial increment, (1) resistance Rt (the ratio between BAI during a drought year and the pre-drought period), (2) recovery Rc, which expresses the ability to recover growth relative to the increment reduction experienced during drought (that is, the ratio between the BAI in the post-drought period and in the drought year), and (3) resilience Rs, that is, the ability to re-reach the performance level observed prior to drought (the ratio between the BAI of the post-drought period and the pre-drought period), following Lloret and others (2011) and Zang and others (2014). A two-year period was chosen for the post-drought and pre-drought periods in order to avoid interference when investigating the two pan-European drought years 2000 and 2003.

The de-trending of ring widths into normalized ring width indices for eliminating growth trends largely removes information on long-term climate change influences on growth (Cook and others 1990; Briffa and others 1996, 2001; Jump and others 2006). Thus, we also calculated mean unstandardized BAI for the stands, because this parameter is less affected by uneven stem geometry (Biondi and Qeadan 2008; Weber and others 2008) and differences in tree age and stem diameter (Biondi 1999; Hogg and others 2005; Nakawatase and Peterson 2006) than ring width. The BAI of dominant trees can be seen as an indicator of forest productivity and a negative trend in BAI as strong indication of a true decline in radial growth (Jump and others 2006).

Competition and also social position may alter the climate response of trees (for example, Piutti and Cescatti 1997), and the strongest climate signals are expected in dominant trees. Thus, we considered only the ten dominant trees sampled in each stand for the investigation of the climate response, while all sampled trees entered the pointer year analysis conducted for the climate response analysis to the extremely dry years 2000 and 2003.

Statistical Analyses

Arithmetic means and standard errors (SE) were calculated either for the ten investigated dominant trees or for all twenty sampled trees per stand. Probability of fit to normal distribution was tested with a Shapiro–Wilk test using the software SAS, version 9.3 (SAS Institute, Cary, NC, USA). The stand means were compared with the Ryan–Einot–Gabriel–Welsch multiple range test. The number of climatic, edaphic, and stand structural parameters to be considered in subsequent analyses was reduced by three independent principal components analyses (PCA; Table S2), using the package CANOCO, version 5.03 (Biometris, Wageningen University and Research Centre, The Netherlands). Those PCA axes that explained at least 75% of the cumulative variance were used as independent variables in subsequent multiple regression analyses with forward variable selection to test whether the PCA-derived variables were significant predictors of BAI, using SAS software (Table 3). Subsequently, we analyzed for multivariate relationships by calculating general linear models (proc GLM) for predicting BAI by annually resolved precipitation amounts and tree age. We further calculated multiple regression analyses with forward variable elimination to test the influence of different monthly climate variables (precipitation, temperature, and sunshine duration) of the year before and during the year of ring production on standardized tree-ring width. Finally, linear regression analyses were conducted for quantifying the influence of precipitation on BAI, AC1, and MS using the software Xact, version 8.03 (SciLab, Hamburg, Germany). Significance was determined at $P \leq 0.05$; in one case, a marginal significant effect at $P \leq 0.10$ was also reported (Table 4).

RESULTS

Precipitation and Temperature Trends

The climate record evidenced significant change during the last decades (Figure 1). The amount of precipitation in mid-season (June) decreased during the last 60 years, especially in the drier part of the transect (Figure 1A). At the moistest location Se, the amount of June precipitation remained almost unchanged with about 78–79 mm, whereas at the driest location Ca, the amount decreased from 76 mm in 1950 to 51 mm in 2010, that is, by about 30%. By contrast, the amount of precipitation in the late season (September) increased from 1950 to 2010 in particular at the moister sites (Figure 1B) with the result that the September precipitation changed only little in the driest forest stand but increased from 67 to 75 mm in the moistest stand. Similar to the trend for September precipitation, MAP also showed a larger increase at the moister than the drier sites (Figure 1C), with the result that the absolute difference in MAP was only approximately 200 mm along the transect in the 1950s, but nearly 300 mm in the 2000s. Consequently, the slope of the precipitation gradient has increased during the lifetime of the trees.

Mean temperature increased in all forest stands in both June and September as well as during the whole year from the 1950s to the 2000s (Figure 1D–F). The average temperature increase during the last 60 years was 0.5°C in June and 0.8°C in September. Mean annual temperature increased by even 1.4°C in 1950–2010.

Variability of Stem Increment During the Last Decades

Mean tree-ring width varied between 1.3 and 2.4 mm per year among the 11 mature beech stands investigated (Table 2), and decadal means of BAI derived from the tree-ring chronologies varied

Table 3. Multiple Regression Analysis (Forward Variable Selection) on the Effects of PCA Parameter Groups on BAI of Dominant Beech Trees

Y	Model			Predictor	F	P
	R^2	P				
BAI	0.46	0.08	+	Climate 1	6.5	0.03
			−	Climate 2	0.7	0.44

Mean basal area increment (BAI) of 110 dominant beech trees from 11 mature beech stands located along a precipitation gradient in northwestern Germany. The tested parameter groups climate, soil, and stand structure are derived from principal components analyses (cf. Table S2). Values given are the determination coefficient R^2 and the probability of error P for the model and the F value and probability of error P for the selected predictors. The + or − signs at the predictor variables indicate positive or negative relationships.

Table 4. GLM Analyzing the Influence of MAP and Tree Age on BAI

Y	Period	Predictor			
		Precipitation		Age	
		F	*P*	*F*	*P*
BAI	1951–1960	64.0	***	409.5	***
	1961–1970	0.3		5.9	*
	1971–1980	14.8	***	1.3	
	1981–1990	0.1		3.9	
	1991–2000	5.2	*	0.1	
	2001–2010	6.1	*	0.5	

*Mean basal area increment (BAI) of 110 dominant beech trees from 11 mature beech stands located along a precipitation gradient in northwestern Germany. The ANCOVAs were conducted separately for each decade between 1951 and 2010. Values given are the F value and probability of error P. Significance is indicated at P ≤ 0.05 and ≤ 0.001 as * and ***, respectively.*

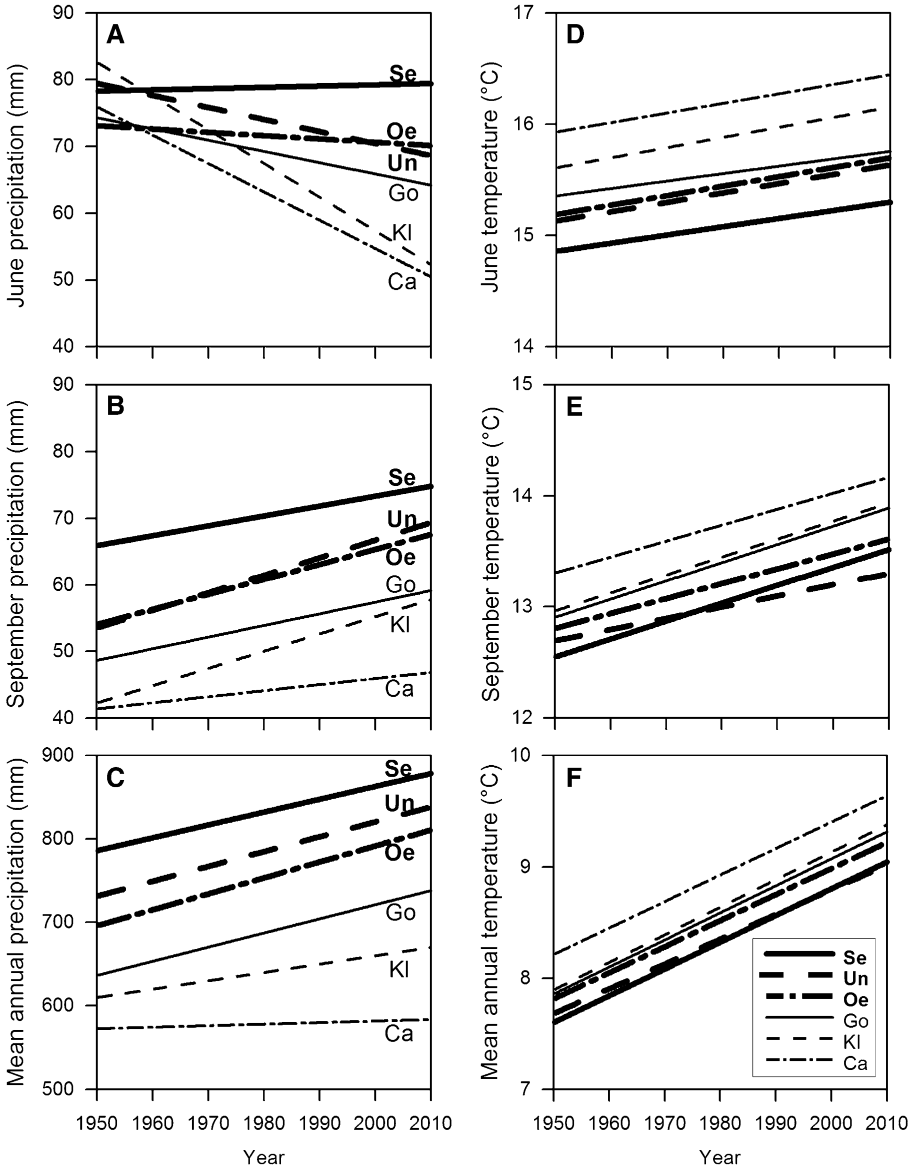

Figure 1. Trends in **A** precipitation in mid-season (June), **B** precipitation in late season (September), and **C** MAP, as well as **D** temperature in June, **E** temperature in September, and **F** MAT from 1951 to 2010 in 11 mature beech stands at six locations along the investigated precipitation gradient in northwestern Germany.

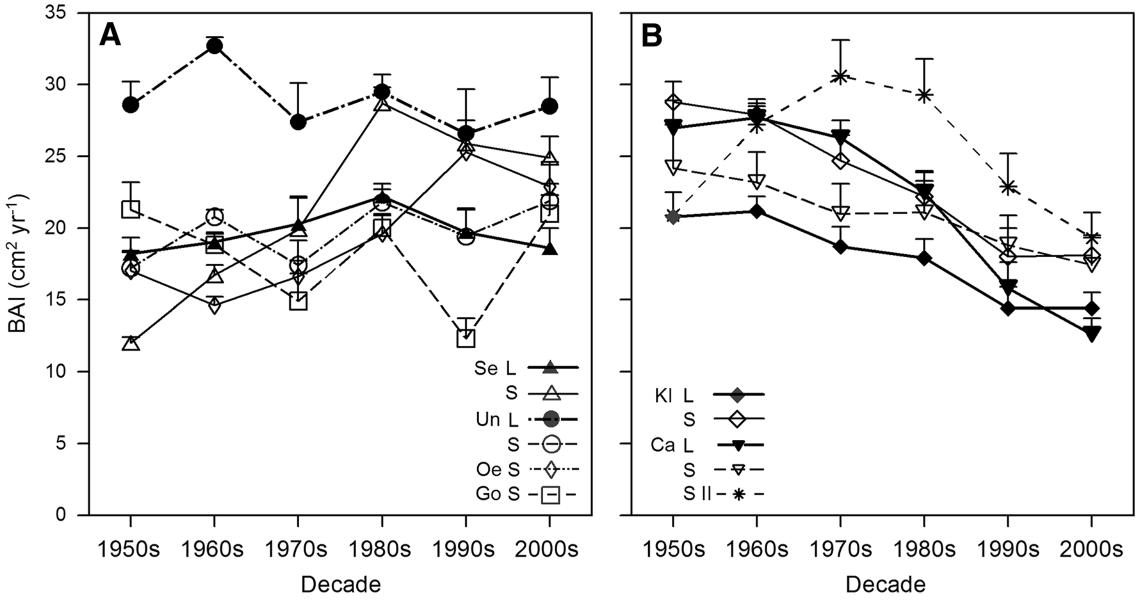

Figure 2. BAI of each ten dominant beech trees per stand from 1951 to 2010 (decadal means and SE of 10 trees per stand) in **A** the 6 stands with MGSP > 350 mm (or MSP > 200 mm) and **B** the 5 stands with MGSP < 350 mm (or MSP < 200 mm).

between 12 and 33 $cm^2 y^{-1}$ (Figure 3). BAI remained relatively constant (sites: SeL, UnL, UnS) or increased (sites: SeS, Oe, GoS) in the moister beech stands (>700 mm y^{-1}) over the last six decades (Figure 2A), whereas it decreased in all five drier beech stands (<660 mm y^{-1}) since the 1970s from about 24 to 16 $cm^2 y^{-1}$ (Figure 2B and S3 in Appendix). According to a multiple regression analysis, the main factors influencing BAI were PCA Climate 1 (which is related to precipitation and temperature) and PCA Climate 2 (related to WSC), but not any other PCA axis, which were related to parameters of nutrient availability, tree age, or stand structure (Table 3). The trend of a decline in BAI at the drier sites was significant since the 1970s, when the underlying age effect on the variance of BAI became insignificant and the climate signal dominated the variation in BAI (Table 4; Figure S1a-c). Negative growth deviations in pointer years appeared until the 1973 pointer year mainly at the driest forest site (MAP < 600 mm y^{-1}), whereas growth was depressed at all sites in the strong pointer years 1976 and 2000. In addition, the frequency of pointer years increased at the moister sites (Table 5, Figure S3). Although the number of negative pointer years increased from one event (1951–1970 interval) to three (1971–1990 interval) and seven events (1991–2010 interval) in the forest stands with MGSP >345 mm, the number of negative pointer years remained more or less constant with four to six events in the drier stands.

Climate Response of Radial Growth

The multiple regression models for climate–growth relationships of dominant trees showed significant effects for the amount of precipitation in June of the current year as well as for the amount of precipitation and heat intensity in September of the preceding year of tree-ring formation (Figure 3). In all stands except for Ca, the positive influence of June precipitation was larger than that of other months, or of summer (June–August) or growing season precipitation (April–September). The radial growth of trees on sandy soil was mostly influenced by June precipitation, while the growth of trees on sandy-loamy soil was not only affected by June precipitation but also by other climatic factors like June temperature (Tables S3a and S3b). Generally, sunshine duration had only a minor influence on radial growth. A remarkable finding is that the negative influence of temperature in both June and September of the previous year on ring width became increasingly important toward the driest sites (Kl and Ca), while June temperature had no effect in the moister stands (Se, Un, and Oe).

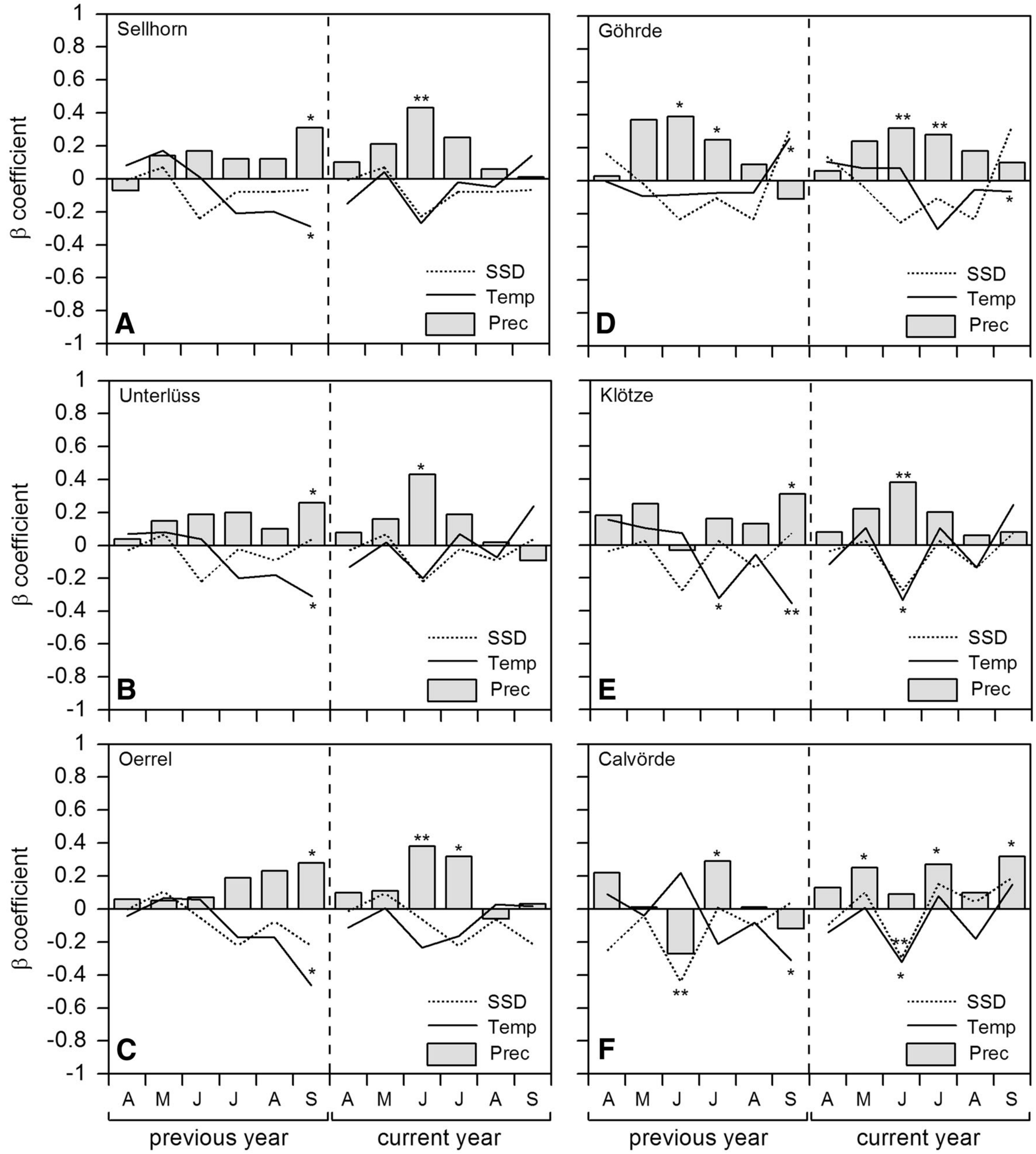

Figure 3. Standardized coefficients of the response of tree-ring width of 20 (in Calvörde 30) dominant trees to monthly precipitation (Prec), temperature (Temp), and sunshine duration (SSD) of the year before ring production and during the year of tree-ring production for **A** Sellhorn (MGSP 419 mm), **B** Unterlüss (MGSP 394 mm), **C** Oerrel (MGSP 384 mm), **D** Göhrde (MGSP 365 mm), **E** Klötze (MGSP 344 mm), and **F** Calvörde (MGSP 310 mm). The trees on the sandy and sandy-loamy plots of a site were pooled. Significance is indicated at $P \leq 0.05$, ≤ 0.01, and ≤ 0.001 as *, **, and ***, respectively.

Climate Change Responses of Ring Width and BAI Across the Precipitation Gradient

Apart from radial growth responses to climate at the monthly or annual time scales, we also investigated decade-long growth trends in their relation to climate warming and summer drying. Across the gradient, mean June precipitation had a significant positive effect on mean BAI in the 1990s ($R^2 = 0.18$, $P = 0.08$) and in the 2000s ($R^2 = 0.38$, $P = 0.02$; Figure 4). In the latter period, mean BAI

Table 5. Negative Growth Deviations in Pointer Years Between 1951 and 2010

Site MGSP (mm)	Se 419	Un 394	Oe 384	Go 365	Kl 344	Ca 310
1954						–121
1957						–51
1959						–108
1960		–105		–80		
1963						–70
1973						–51
1976	–94	–97	–58	–55	–85	–71
1983	–78				–59	
1989					–55	–92
1992$^{L\ S}$	–59	–79				–85
1995$^{L\ S}$		–70			–56	
1996						–73
1998$^{L\ S}$						
2000$^{L\ S}$	–101	–159	–95	–112	–119	–108
2002^{S}						
2004$^{L\ S}$	–70	–98	–93		–69	
2006$^{L\ S}$						
2009$^{L\ S}$						

Negative growth deviations δp_i in 11 mature beech stands at six locations along a precipitation gradient in northwestern Germany. Masting year in Lower Saxony (L) and Saxony-Anhalt (S) with at least 40% fruiting beech trees (according to Niedersächsische Landesforsten, data available since 1991).

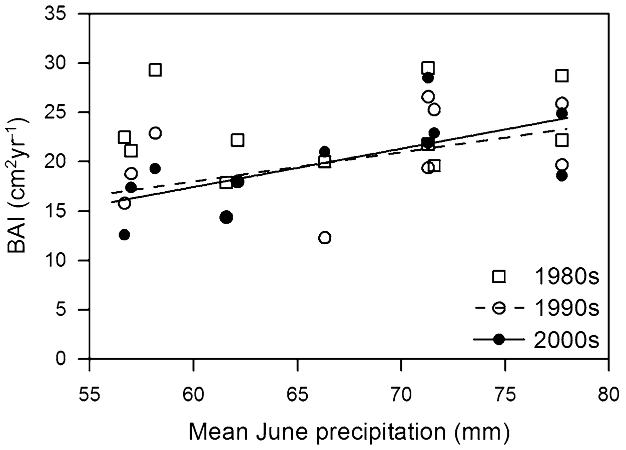

Figure 4. Relationship of mean BAI of each ten dominant beech trees per stand with mean June precipitation in the 11 mature beech stands along the precipitation gradient in northwestern Germany for the periods 1981–1990, 1991–2000, and 2001–2010. The relationship between mean BAI and MGSP was not significant in the period 1981–1990, but significant in the periods 1991–2000 ($y = 0.29 - 0.30x$, $R^2 = 0.24$, $P = 0.03$) and 2001–2010 ($y = -5.9 + 0.39x$, $R^2 = 0.45$, $P = 0.005$). Similar relationships existed for mean summer rainfall (June–August) and MGSP (April–September).

increased by 6 cm^2 y^{-1} with an increase in MGSP by 100 mm.

On sandy soil, the level of autocorrelation in the beech tree-ring chronologies for the period 1951–2010 increased significantly from the dry to the moist stands (Figure 5A), indicating decreasing growth dependence on precipitation and other external factors. Correspondingly, the mean sensitivity of radial growth increased from the moister to the drier stands (Figure 5B).

Splitting the considered 60-year period into three 20-year intervals showed that mean AC1 was 0.32 ± 0.05 between 1951 and 1970. This was comparable to the period from 1971 to 1990 (mean 0.4 ± 0.03), but dropped to 0.2 ± 0.03 in the most recent period (1991–2010) (Figure 6). MS in-

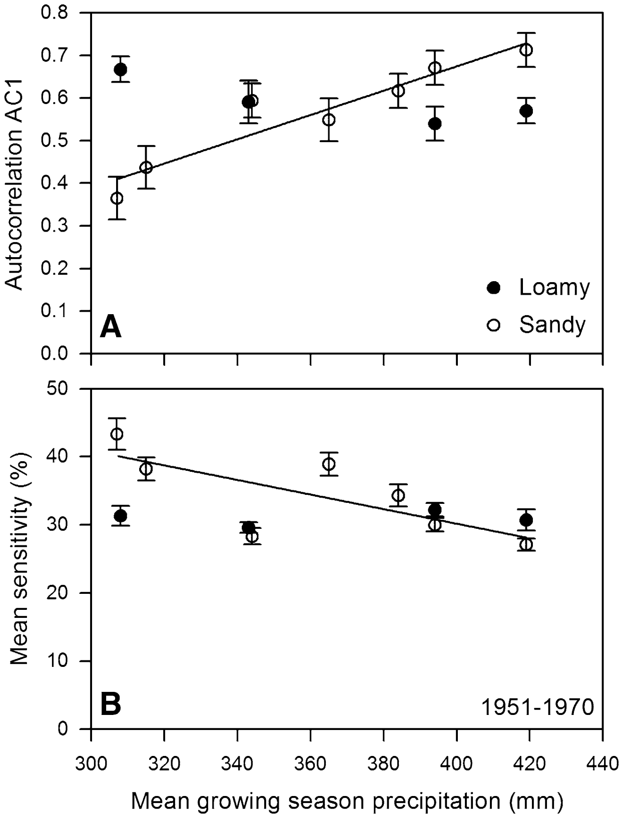

Figure 5. Relationship of **A** AC1 and **B** mean sensitivity of each ten dominant beech trees with MGSP (April–September) in 11 stands on sandy-loamy or sandy soil in the period 1951–2010. At the sandy sites, the correlations of both AC ($y = -0.47 - 0.003x$, $R^2 = 0.90$, $P < 0.001$) and MS ($y = 73.0 - 0.11x$, $R^2 = 0.53$, $P = 0.03$) with MGSP were significant.

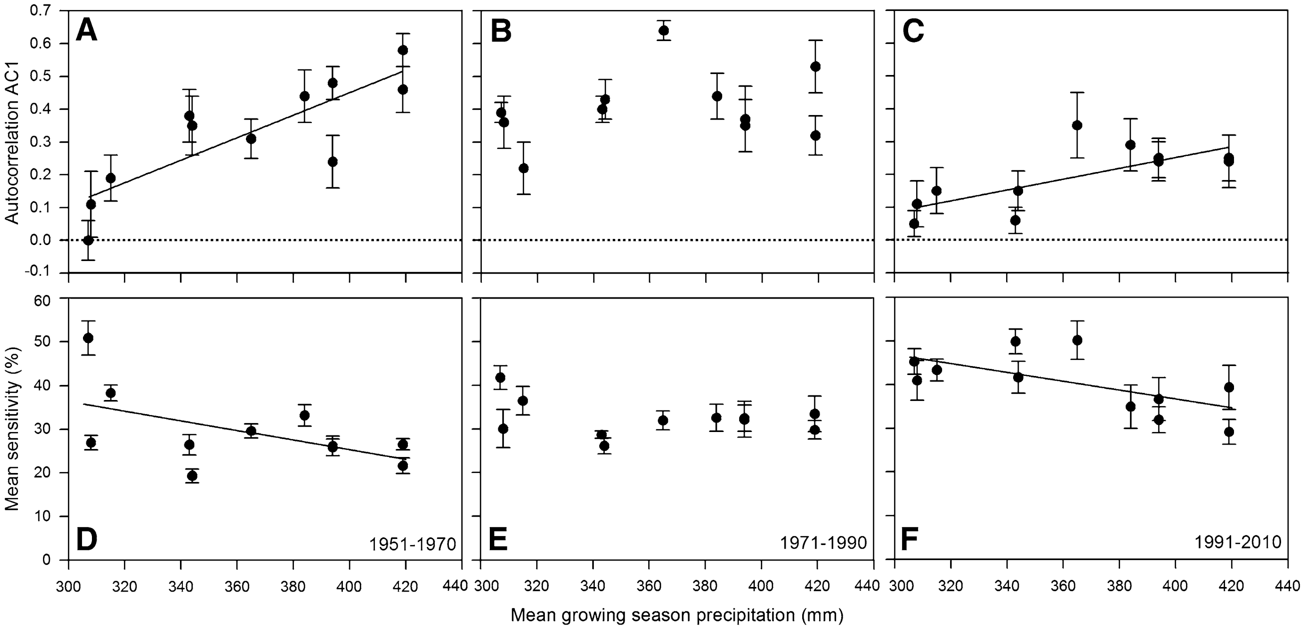

Figure 6. Relationship of **A**–**C** AC1 and **D**–**F** mean sensitivity of each ten dominant beech trees with mean MGSP (April–September) in 11 mature beech stands for the periods **A**, **D** 1951–1970, **B**, **E** 1971–1990, and **C**, **F** 1991–2010. The correlations of both AC1 and MS with MGSP were significant in the earliest (AC1: $y = -0.9 - 0.003x$, $R^2 = 0.71$, $P < 0.001$; MS: $y = 72.7 - 0.12x$, $R^2 = 0.33$, $P = 0.02$) and latest period (AC1: $y = -0.41 - 0.002x$, $R^2 = 0.52$, $P < 0.006$; MS: $y = 77.3 - 0.10x$, $R^2 = 0.40$, $P = 0.02$).

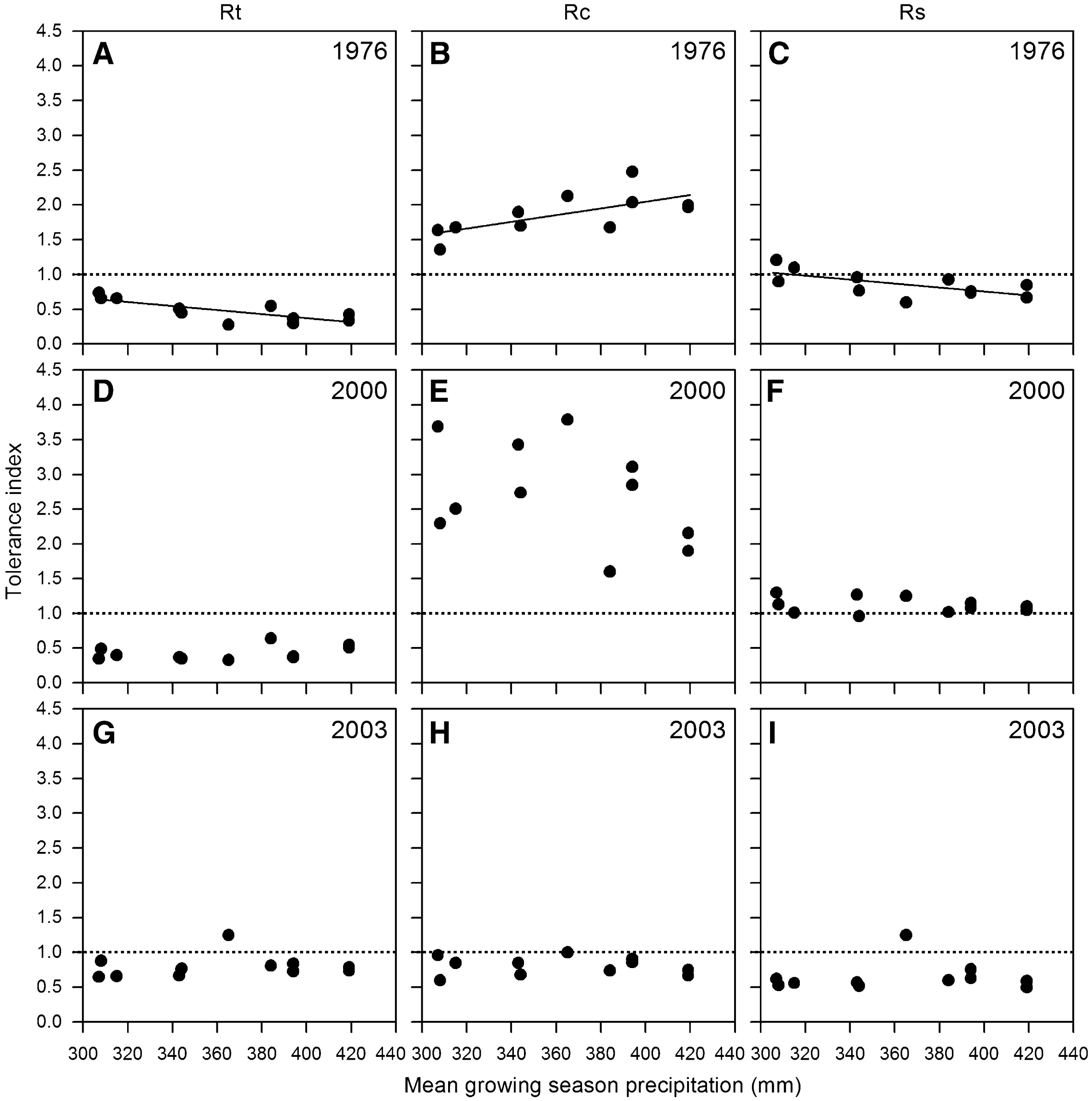

Figure 7. Relationship of the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) with MGSP (April–September) in each ten dominant beech trees per stand in 11 mature forest stands during the pan-European drought years 1976 (**A**–**C**), 2000 (**D**–**F**), and 2003 **(G–I)**. A 2-year period was chosen for the pre-drought and post-drought periods. The relationships between the tolerance indices Rt ($y = 1.53 - 0.003x$, $R^2 = 0.61$, $P = 0.002$), Rc, ($y = 0.12 - 0.005x$, $R^2 = 0.46$, $P = 0.01$), and Rs ($y = 1.89 - 0.003x$, $R^2 = 0.43$, $P = 0.01$) with MGSP were significant for the drought year 1976 ($P \leq 0.05$) but not significant for the drought years 2000 and 2003 (*cf.* Table S5). The *dashed lines* indicate unity.

creased from 29.5 to 32.3 and 40.3% in 1991–2010. MS was negatively related to MGSP in the first and last intervals (steeper slope in the first period), but no relation existed in the intermediate interval (Figure 6D–F). Nearly all sites showed an increase in MS during the last decades (Figure S1a-c). The relationship of AC1 with MGSP was highly significant before the 1970s with a slope of 0.003 (Figure 6A). In the subsequent time period (1971–1990), the relationship was not significant (Figure 6B). In the most recent period from 1991 to 2010, the relationship between MAP and AC1 was significant, but with a smaller slope (0.002) than in the 1951–1970 period and smaller AC1 values across the whole precipitation gradient.

In the three pan-European summer droughts in 1976, 2000, and 2003, the drought tolerance indices Rt, Rc, and Rs showed significant growth decreases (negative Rt values) at all sites during the three events (Figure 7). However, a much higher recovery (Rc index) in 2000 and 1976 than in 2003 and a reduction in resilience (Rs values) was observed. This reflects the growth decline in the last decades, whereas in 1976 moister stands suffered more but recovered faster after drought than drier stands. This relation had disappeared in the 2000 and 2003 events.

DISCUSSION

Global Warming Effects on Beech Radial Growth

The results of this study indicate that recent global warming causes a radial growth decline in European beech even in the center of the species' distribution range when water is deficient. We found a consistent decrease in BAI since the 1970s in the five stands with MGSP of <345 mm (Figure 2). This growth decline in the eastern part of the transect was more pronounced on sandy-loamy soil with higher WSC than on sandy soil and cannot be explained by a tree age effect, because the multiple regression analysis showed precipitation and soil WSC to be the only determinants of BAI variation but detected no tree age or stand structure effect (Table 3). An age-dependent growth decline can be excluded also because any age effect visible on radial growth disappeared after the 1960s according to the GLM (Table 4). Finally, most trees of our study were 80–120 years old which is younger than the age when a senescence-driven BAI decrease may begin in beech (Jump and others 2006).

Our results match earlier findings on a recent growth decline in Central European beech populations as reported from northern Switzerland (Weber and others 2013: on shallow soil at $\sim$1100 mm y^{-1}), in the lowlands of northeast Germany (Scharnweber and others 2011: on sandy soil at <595 mm y^{-1}) and in the uplands of central Germany with relatively low summer precipitation (Zimmermann and others 2015: 600–640 mm y^{-1}). In the present study, summer precipitation thresholds (June–August) were identified at about 200 mm (Zimmermann and others 2015: 190 mm), beyond which a negative growth trend was observed. Thus, the turning point is found in a relatively narrow precipitation range given that the edaphic conditions are quite diverse and the climate ranges from sub-oceanic to subcontinental in the three studies.

Our study has produced convincing evidence that climate warming gains increasing importance as a stressor in beech stands in the lowlands of northwestern Germany. Apart from the long-term growth reduction in the east of the gradient, we found (1) increasing MS of radial growth to climate variation at four of the six sites since the 1950s, whereas (2) the degree of autocorrelation decreased. This finding is in line with other studies that reported a marked increase in MS of growth of beech since about 1990 (for example, Beck 2009; Scharnweber and others 2011; Beck and Heußner 2012). Even though some controversy exists with respect to the interpretation of sensitivity data (for example, Bunn and others 2013), the increase in this parameter at most of our sites is obvious. The picture of an increasing climate warming impact is further supported by the observation that (3) a dependence of BAI on MGSP across our gradient was absent before 1990 but developed since then. Strong indication of increased climate stress is also (4) the more frequent occurrence of negative pointer years since 1976 at all sites except for the driest one (Ca) where they were relatively frequent already before 1976 (Table 5). Today, stands in moister climates are showing symptoms of climate sensitivity that were characteristic for the driest stands already 40 years ago. One future scenario for the moister stands can be that the more frequent negative pointer years are leading to a similar growth decline as observed in the drier stands since the 1980s.

Extreme summer droughts like in 1976, 2000, and 2003 will probably occur with increasing frequency in the decades to come (for example, Schär and others 2004; Bréda and Badeau 2008). In 1976, all major tree species in Central Europe were affected by a cold and long winter and cool spring, which was followed by a hot and dry summer. These two harmful events resulted in an outstanding negative pointer year in all our stands and elsewhere (Beck 2011). The drought years 2000 and 2003 also impacted on all stands irrespective of the mean precipitation level, but the two events differed strongly in their index of beech growth recovery (Rc). In 2003, the index was particularly low (0.5–1.0). We speculate that this may either be caused by the short time interval between the 2000 and 2003 events, or related to the fact that both the year 2000 and the year after the 2003 drought event were masting years.

Climatic Factors Likely Driving the Growth Decline

It is likely that declining summer precipitation is one driver of the observed growth decline at the drier sites of our study region. This is suggested by the marked decrease in mid-summer precipitation especially at the sites Ca and Kl, where radial growth declined since about the 1960s and 1970s. The response analysis in Figure 3 indicates that June rainfall exerts the largest influence on radial growth of beech in our study region. At five of the six sites, the effect of June rainfall was more relevant than that of summer rainfall (June–August) or MGSP (April–September). Only at the driest site (Ca), the April–September rainfall was more influential than June rainfall (Figure 3F). The outstanding role of mid-summer precipitation is in accordance with other studies on the climate–growth relation in temperate trees (for example, Bouriaud and others 2005; Lebourgeois and others 2005; Hacket-Pain and others 2015; Zimmermann and others 2015). According to Čufar and others (2008), June can be considered as the most important month for tree-ring formation in beech in Central Europe, where up to 35% of the entire tree ring is normally formed. By the end of June, 75% of the tree ring is typically completed followed by cambial cell division stagnation until mid-August. Scharnweber and others (2011) found for northeastern Germany also the closest correlation between seasonal climatic parameters and ring width for current year's June. Similarly, other studies on the cambial activity and xylogenesis of beech from stands all over Europe showed that drought in April and June had the strongest negative effect on growth (for example, Michelot and others 2012; Prislan and others 2013; Vavrčík and others 2013; Rozas and others 2015) which is explained by the onset of cambial activity in April and highest radial growth rates in June. Drought in early summer could also impair nutrient supply through a negative effect on decomposition rate and ion diffusion in the soil, but we have no precise data in support of this hypothesis. Nevertheless, the principal role played by June rainfall has important implications for the likely future of beech forests in the lowlands of central–northern Germany: June rainfall is the precipitation component with the largest decrease in the past decades at four of the six sites, implying further growth decline when this trend continues in the twenty-first century as predicted by regional climate scenarios. Our finding that warmer temperatures in the previous year's September have a negative effect on radial growth can perhaps be explained with the observed latewood cell wall thickening in this month (Lebourgeois and others 2005) which consumes resources that are not available for next year's radial growth.

The response analysis evidences a negative effect of elevated mid-summer temperatures (in particular of current year's June) and of previous year's autumn (September) on radial growth, and this effect was more pronounced at the driest sites (Figures 2A, B, 3). A direct negative effect of elevated summer temperatures on the photosynthesis or growth of temperate trees has only rarely been proven so far (for example, Garcia-Plazaola and Becerril 2000; Alvarez-Uria and Körner 2007). Köcher and others (2013) proved that elevated air humidity is a main driver of higher radial growth in beech. Drier air in a warmer summer could therefore negatively impact on cambial growth.

In other regions of Europe, different climate–growth relationships may exist in beech than found in this study (for a review, see Babst and others 2013). Although water availability in summer is also a major driver of radial growth in southwestern Europe, May temperature and precipitation during winter are playing important roles as well, other than in Central Europe (for example, Biondi 1993; Piovesan and others 2005; Lebourgeois and others 2005). In colder regions, low winter temperatures often affect tree growth through freezing embolism (Lemoine and others 1999), which was not detectable in our study. At higher elevation, the temperature dependence of growth turns into a positive relation and cloudiness is often an important factor limiting photosynthesis (for example, Dittmar and others 2003; Graham and others 2003; Di Filippo et al. 2007; Peñuelas and others 2008; Rozas and others 2015; Dulamsuren and others 2016).

Another factor that may influence radial growth is mast fruiting of beech, which is influenced in a complicated manner by climate warming (Müller-Haubold and others 2015). Full mast in beech greatly reduces stem radial growth and thus is often responsible for negative pointer years (Schweingruber 1996; Mund and others 2010; Hacket-Pain and others 2015). Because the frequency of beech masting has increased during the last decades in Central Europe (Hilton and Packham 2003; Övergaard and others 2007), long-term growth decline could in theory also result from a tree-internal allocation shift from stem growth to fruit production. In our study region, information on masting events was available for the last 20 years (1991–2010), that is, a third of the observation period (Table 5). In this period, eight mast years occurred, four of which were negative pointer years. Because only one negative pointer year was not a masting year, it seems that masting plays an important role in the explanation of growth reductions in pointer years and probably for long-term growth trends as well. Müller-Haubold and others (2015) showed that masting likely is triggered by an extraordinarily high radiation input (and probably high temperatures) in the year prior to a mast, whereas drought itself is not influential. Climate warming with reduced precipitation and elevated temperatures and sunshine duration during mid-summer thus may act on stem growth through at least two pathways: (1) directly via reduced soil moisture availability (and possibly increased VPD) and (2) indirectly through a higher masting frequency. This could explain why both reduced precipitation and elevated temperature in mid-summer (which is related to higher sunshine duration) are negatively influencing radial growth in recent time.

The Role of Edaphic Factors

A remarkable result of our study is that the stands on sandy-loamy soil did not differ significantly from those on sandy soil with respect to mean annual ring width and also mean sensitivity of growth (Table S1), even though the former have a higher soil WSC. Even more astonishing is that the sandy-loamy sites had an on average stronger growth decline since the 1980s at the drier sites than the corresponding sandy sites. However, the dry stands on sandy soil had the highest MS and lowest AC1 of all 11 stands and thus may be particularly vulnerable to climate warming. In contrast, no relation between MGSP and MS (and AC1) existed across the loamy sites. The rather similar growth performance of stands on sandy and more loam-rich substrate is remarkable because it seems to indicate that the effect of soil WSC is relatively minor in our study region. This could result from the fact that all investigated Pleistocene substrates have similar profile depths (>1 m) and that the soil texture differences between sandy and sandy-loamy profiles are only moderate.

CONCLUSION

Our study produced convincing evidence that global warming is already acting as a major stressor in beech stands even in the center of the species' distribution range. Our first hypothesis that recent global warming is locally causing a growth decline in beech in northwestern Germany was confirmed. The results of this gradient study and other published dendrochronological studies in beech in central and northern Germany allow for the first time to define a minimum summer precipitation level which seems to be necessary for vital beech growth in the center and north of its distribution range. This threshold is located close to 660 mm of MAP, 350 mm of MGSP (April–September), or 200 mm of summer precipitation (June–August).

Our second hypothesis of an increasing climatic impact on the growth of beech since about the 1970s was also supported; but different criteria revealed different time frames of this response. Unexpected is that our third hypothesis of a soil moisture effect on the extent of growth decline was not supported. Although MS showed a dependence on precipitation only on the sandy, but not on the loam-richer sites, the BAI decline at the drier sites was stronger on the loam-richer than the sandy soils indicating clear priority for the climatic over the edaphic effect. The role of soil water storage for the growth dynamics of beech requires further study by considering other geologic substrates and soil types.

Given that regional climate change scenarios predict a further decrease in summer precipitation for parts of central and eastern Germany and beyond (Jacob and others 2014), the above-defined summer precipitation thresholds for vital beech growth may even be too low for safeguarding beech stands until their harvest time 100–120 years from now. It is likely that not only beech stands in regions with currently <200 mm of summer precipitation will face growth decline in the future, but stands in currently moister regions as well. The results of our study call for careful tree species selection by foresters in all those Central European beech forest regions where precipitation is already below the precipitation thresholds elaborated here. Beech may lose part of its range in the managed and natural forest area of Central Europe upon climate warming. These findings suggest that other mesophytic tree species of the temperate forests in North America and Eurasia might also be at drought risk, even though the climate is oceanic or sub-oceanic, notably other *Fagus* or *Acer* species which dominate large forest areas in the eastern USA, Japan, southwestern Asia, and elsewhere.

ACKNOWLEDGEMENTS

We are grateful to H.-H. Leuschner, H. Müller-Haubold, and J. Zimmermann for valuable comments on the data. This work was supported by grants provided by the Ministry for Science and Culture of Lower Saxony (Germany) in the context of the program ''Klimafolgenforschung in Niedersachsen'' (KLIFF; climate response research in Lower Saxony) (Grant #MWK 11-76102-51, subproject #FT54).

Compliance with Ethical Standards

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

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