

Climatic turning point for beech and oak under climate change in Central Europe

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Abstract. The growth behavior of coexisting tree species under climate change is important from an ecological, silvicultural and economic perspective. While many previous studies are concerned with climatic limits for species occurrence, we focus on climate related shifts in interspecific competition. A landmark for these changes in competition is the ‘climatic turning point’ (CTP): those climate conditions under which a rank reversal between key tree species occurs. Here, we used a common type of temperate mixed forest in Central Europe with European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) to explore the CTP under a future climate projection of increasing temperature and aridity. We selected a dry region where the prerequisite of differential climate sensitivity in mixed beech-oak forests was fulfilled: In-situ dendrochronological analyses demonstrated that the currently more competitive beech was more drought sensitive than sessile oak. We then used two complementary forest growth models, namely SILVA and LandClim, to investigate the climate induced rank-reversal in species dominance and to quantify it as the CTP from beech to oak by simulating future forest development from the WETTREG 2010 A1B climate projection. Utilizing two models allowed us to draw conclusions robust against the assumptions of a particular model. Both models projected a CTP at a mean annual temperature of 11–12°C (July temperature >18°C) and a precipitation sum of 500–530 mm. However, the change in tree species composition can exhibit a time-lag of several decades depending on past stand development and current stand structure. We conclude that the climatic turning point is a simple yet effective reference measure to study climate related changes in interspecific competition, and confirm the importance of competition sensitivity in climate change modeling.

Key words: climatic turning point; competitiveness; drought; *Fagus sylvatica*; forest growth models; LandClim; mixed forest; *Quercus petraea*; SILVA; species rank reversal; tree coexistence; tree-ring analysis.

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INTRODUCTION

Climatic extremes are increasing in intensity and frequency and their effect on global forest biomes are of particular interest to forest scientists. Precursors of a future climate posing a drier growing season (Schär et al. 2004, Barriopedro et al. 2011, IPCC 2012) are seen already today as main causes of changes in tree growth, tree death and even diebacks in temperate forests around the world (Gitlin et al. 2006, van Mantgem and Stephenson 2007, Worrall et al. 2008, Rehfeldt et al. 2009). Especially for mixed species forestry— one of the epitomes of climate change risk mitigation—such changes in the species' growth behavior are most important from an ecological, silvicultural and economic perspective, and may precede the decline of less drought-adapted species with severe ecological consequences (Carnicer et al. 2011, Hanewinkel et al. 2012).

In this study we investigate the 'climatic turning point' (CTP) as a measure for climate related changes in interspecific competition. Although the term has been used in some other contexts, here we define it as those climatic conditions under which a rank reversal between key tree species occurs with respect to their biomass or basal area share. So far, the concept of rank reversal has been applied to the establishment phase of tree species in relation to light conditions (Baltzer and Thomas 2007, Beaudet et al. 2007, Osada 2012) or to compare ontogenetic growth patterns (Boyden et al. 2009, Pérez-Ramos et al. 2012). Here, we focus on how changing climate alters species performance and thereby induces a rank reversal at the stand level. Sánchez-Gómez et al. (2008) and Gómez-Aparicio et al. (2011) projected climate-induced species rank reversals for tree species in mixed forests of Spain using statistical spatially explicit neighborhood models parameterized from National Forest Inventory data. Yet, there is no clear picture of the competitive response of trees along a climatic gradient of increasing temperature and aridity. Models like climatic species distribution models (SDMs) (e.g., Araújo and Guisan 2006, Morin et al. 2008, Czúcz et al. 2011) may be strong on species' climatic demands but they are usually not able to represent strongly size-structured population dynamics that determine species balances. Yet, a change of the dominant

tree species, even if the formerly dominant species is still present in the understorey, has great impact on the ecosystem and changes conditions for organisms at all trophic levels (Chapin 2003, Ellison et al. 2005). The search for the CTP aims at finding the point in the gradient of a possible future climate where such rank reversals in mixed forests occur.

Identifying the CTP is not trivial due to the complexity in tree species' climate-growth control, competition for light and the interaction with ontogenetic growth behavior. Particularly in long-lived ecosystems dominated by species with long generation periods, the slow and gradual response of forest structure and species composition to the changing climate might remain unnoticed. The two reasons are, first, the persistence of adult trees and, second, that the species' regeneration success takes effect only in the following generation (Sykes and Prentice 1996, Soja et al. 2007, Johnstone et al. 2010, Temperli et al. 2012). Clearly, the response of a forest to changing climate conditions cannot simply be projected by means of extrapolating regression functions or searching climate analogies (Fuhrer et al. 2006, Williams and Jackson 2007).

Here we apply the general concept of a climatic turning point to the particular case of mixed stands of European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). We employ an approach based on in-situ data on tree and stand growth under past and present climate in combination with two climate-sensitive dynamic forest simulation models. This forest type is of considerable relevance, and grows mainly on climatic and edaphically dry sites in Central Europe. Among the two species, beech is typically dominant, and the light-demanding oak can only compete under less favorable abiotic conditions than beech (i.e., warm and relatively dry sites, or wet and clayey soils or if oak is favored by silviculture). Ellenberg (2009) suggest that oak becomes more competitive than beech at July-temperatures >18°C and precipitation <600 mm/yr. For the chosen stands the present climate was already close to the above-mentioned limits, and climate change scenarios of higher magnitude such as the WETTREG 2010 A1B (Kreienkamp et al. 2009) project an even stronger summer aridity in that region. Under such conditions, both species can

Table 1. Stand parameters from surveys of the studied beech-oak stands near Schweinfurt by initial stand age, site, and survey year. Exp. = Experimental plot, N = Stem number per hectare, H100 = Upper canopy/ top height, G = Basal area, V = Merchantable wood volume, dg = Root of mean square diameter, B = Aboveground biomass (Schroeder et al. 1997).

Site	Survey year	All tree species					Beech		Oak		Other	
		N (ha ⁻¹)	H100 (m)	G (m ² /ha)	V (m ³ /ha)	B (t/ha)	dg (cm)	G (m ² /ha)	dg (cm)	G (m ² /ha)	dg (cm)	G (m ² /ha)
27 years												
Exp.	1995	3160	15.7	25.2	143.6	536	11.4	6.4	9.6	17.0	11.3	1.8
Exp.	2005	1751	19.9	28.4	233.2	824	15.1	9.1	14.3	18.0	11.4	1.3
54 years												
Exp.	1995	1935	22.1	34.4	311.4	715	15.7	15.2	19.1	9.9	12.1	9.3
Exp.	2005	1384	25.2	40.7	449.3	778	20.4	19.3	22.5	12.1	15.6	9.3
86 years												
Exp.	1995	1149	24.3	30.1	316.8	561	15.4	11.2	22.7	15.4	16.3	3.5
Exp.	2005	1037	26.8	36.9	443.2	636	18.5	14.2	25.7	18.8	18.6	3.9
106 years												
Exp.	1995	676	27.8	25.7	323.3	422	18.8	14.4	30.9	10.4	24.9	0.9
Exp.	2005	615	30.4	30.5	425.7	485	21.4	16.6	34.9	12.8	27.1	1.1
105 years												
Reserve	1978	723	25.8	30.4	355.1	472	27.2	12.9	35.6	6.4	18.0	11.1
Reserve	1996	531	30.5	37.0	528.1	644	34.6	18.5	42.8	7.5	22.3	11.0
Reserve	2010	396	33.8	38.6	622.4	593	40.7	22.4	44.5	6.5	26.0	9.7

be expected to experience a loss in productivity (Leuschner et al. 2001, Lebourgeois et al. 2005, Jump et al. 2006, Piovesan et al. 2008) and might be even prone to dieback (Bréda et al. 2006, Michelot et al. 2012). Yet, oak is considered to suffer less than beech due to a higher capability to resist adverse climatic conditions or to recover better after climatic extreme events (Peterken and Mountford 1996). Under drought, beech apparently down-regulates its photosynthesis earlier than sessile oak to avoid cavitation (Leuschner et al. 2001, Raftoyannis and Radoglou 2002, Bréda et al. 2006). Therefore, we expected a CTP at the study site under climate change. We further argue that a CTP will depend on the past stand development: Past climate conditions and forest management have shaped the stand structure and species composition. This might cause a time-delayed and gradual response in long-lived ecosystems with a slow generation turnover (Sykes and Prentice 1996, Temperli et al. 2012).

For the forest growth simulators we choose SILVA (Pretzsch et al. 2002) and LandClim (Schumacher and Bugmann 2006, Schumacher et al. 2006). Although the models were developed for different purposes, both have in common that they operate on the individual tree level—which allows changes in structural competition to be reproduced. In-situ data from repeated forest surveys and tree-ring analysis

were used to assess current tree growth and ensure the validity of the forest models. The models were then used to project the forest development under climate change.

With this combination of empirical evidence and modeling we investigate the following two hypotheses: (1) Projected future climate passes a climatic turning point where a rank reversal in the species' dominance occurs and (2) the rank reversal exhibits a time lag due to the legacy of past stand development.

MATERIALS AND METHODS

Study site and current stands

The studied beech-oak forest stands were located in southeastern Germany on the 'Franconian plateau' at an altitude of 300–400 m asl. We used four sites of different stand age which belong to the Bavarian long-term experimental plot network, and a fifth site that is part of the forest reserve of the Bavarian state forest institute LWF (Table 1). The study sites belonging to the experimental plot network were installed in 1995 and surveyed in 1995 and 2005. The sites were even-aged and ranged from 27–106 years with merchantable wood volumes of 233–323 m³/ha in 1995. The basal area ratios of oak:beech:other species ranged from 25:67:7 to 56:40:4, with hornbeam (*Carpinus betulus* L.), lime (*Tilia cordata*

P. Mill.) and maple (*Acer pseudoplatanus* L.) covering minor percentages. No thinning occurred between 1995 and 2005. The site in the forest reserve was designated in 1978 and surveyed in 1978, 1996 and 2010. Since that time any forest management was forbidden. In 1978, stand age was 105 years, wood volume was 311 m³/ha and basal area ratio of oak:beech:other species was 42:21:37 (Table 1).

For retrospective growth analyses, increment cores were extracted in the direct vicinity of the 86-year experimental site in 2009. Two cores of each of 15 dominant oak and beech trees were sampled at breast height. After wood surface preparation, ring width of each sample was measured using a LINTAB linear table (Rinn 2003) to a precision of 0.01 mm. The software TSAP-Win (Rinn 2003) was used to cross-date the ring width curves visually and statistically. The biological age trend in the original tree-ring series was eliminated using the dplR library v 1.5.5 (Bunn 2008) in R v 2.15.1 (R Development Core Team 2012) by applying a cubic smoothing spline of 2/3 of the series length. Autoregressive modeling was used to remove first order autocorrelation. Residual chronologies of beech and oak were obtained by averaging the ring width series using a biweight robust mean (Cook and Peters 1997).

Climate data

Climate data (daily values of temperature and precipitation for the period 1 May 1958 to 31 December 2003) were obtained from a weather station close to the study site (DWD Station 4621 ‘Schweinfurt-Gartenstadt’, 50.06° N; 10.22° E; 240 m asl). These data were used for the retrospective growth analysis of SILVA and LandClim.

The WETTREG 2010 A1B ‘normal’ scenario for the same climate station from 1961–2100 (Kreienkamp et al. 2009) formed the basis for the projections of possible future forest development. For our study only one scenario was sufficient because the aim was not to compare forest succession across a large number of scenarios but to highlight whether there might be some difference between the two forest simulation models (Bugmann 1997). For this scenario, 10 realizations were available. These climate time series provided a climatic gradient from moderate temperature and soil moisture conditions in

the past and present to warmer and dryer conditions in the future, including a realistic temporal variability and autocorrelation (Appendix: Table A1). Compared to 1971–2000 the WETTREG scenario projects for 2071–2100 a significant increase in the mean annual and May–September temperatures from 9.0°C to 12.5°C and 15.9°C to 19.4°C, respectively. The growing season with mean temperatures above 10°C is thereby extended from 164 to 202 days (Fig. 1). Annual precipitation decreases from 558 mm to 523 mm and summer precipitation from 258 mm to 200 mm.

Definitions

In the present study a species was defined as dominant if its basal area (SILVA) or above-ground biomass (LandClim) was higher than any other species’ basal area/biomass (Pretzsch and Schütze 2009). The competitiveness of a species is indicated by the gain or loss in that species’ basal area or biomass share. Competitiveness (and ultimately dominance) results from the joint effect of the demographic processes establishment, growth and mortality.

We define the climatic turning point (CTP) as the climate where a rank reversal of the species’ dominance (i.e., basal area share (SILVA) and biomass share (LandClim)) occurs. A potential and actual CTP were distinguished, the first referring to hypothesis 1, the latter to hypothesis 2. The potential CTP was determined by simulating a forest developing *ex novo*, i.e., established from seed rain, under different, but stationary climate conditions derived from the WETTREG data (cf. ‘Simulations’). The actual CTP was assessed by prescribing forest succession of existing stands along the projected climatic gradient from moderate temperature and precipitation to warmer and dryer conditions (WETTREG time series). The difference between the potential and actual CTP is that the latter might be superposed by the past stand development.

Forest models

In order to identify the CTP, the two central model requirements were climate and competition sensitivity at adequate spatio-temporal scales (Bugmann 1997, Bugmann and Cramer 1998, Pretzsch et al. 2008). While climate change

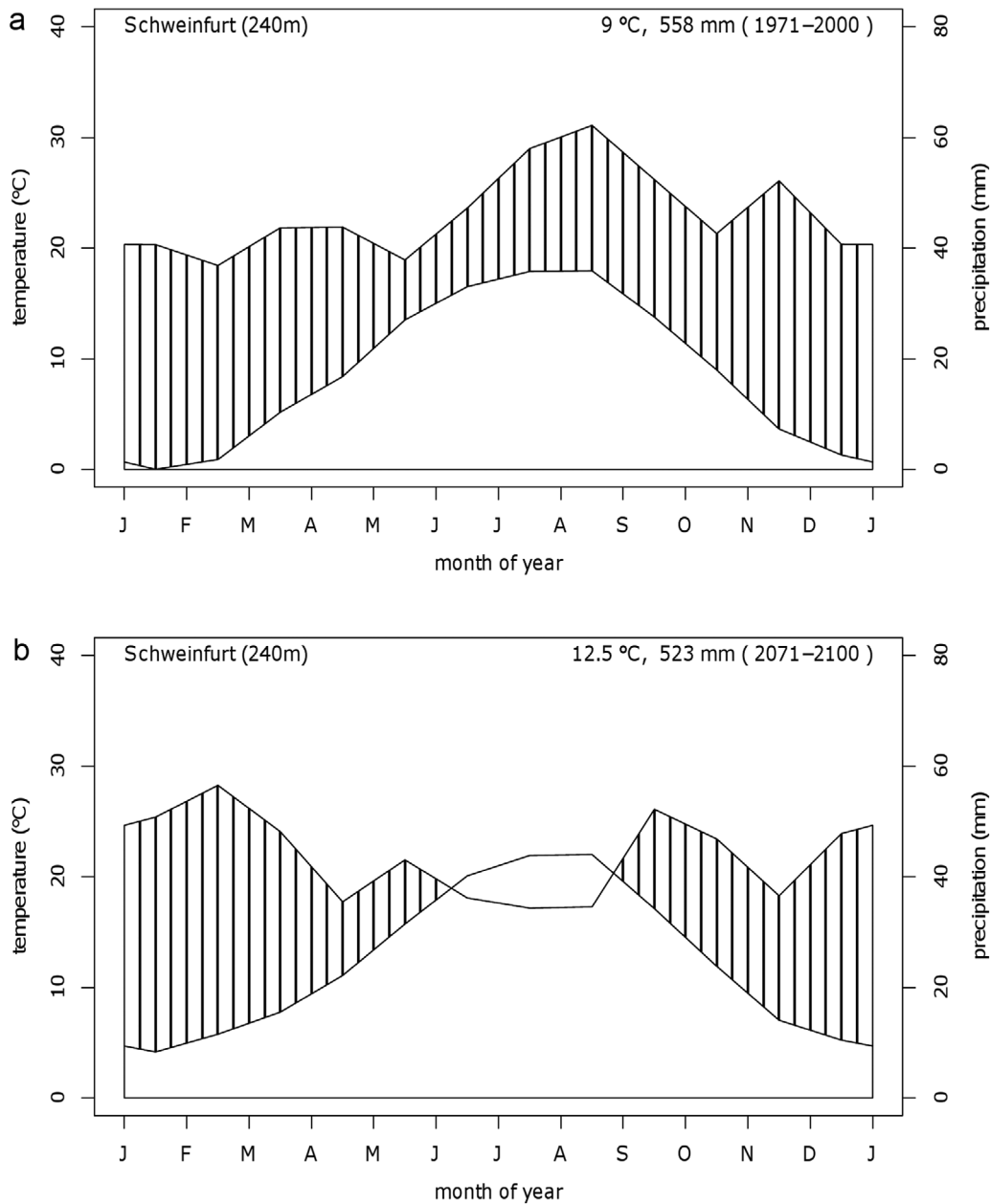


Fig. 1. Present and future climate of the study site Schweinfurt (southeastern Germany). (a) Present climate for the period 1971–2000 according to the DWD climate station Schweinfurt, (b) future climate from 2071–2100 according to the WETTREG 2010 A1B scenario. Hatched areas indicate moist periods; areas where the temperature curve exceeds the precipitation curve indicate dry periods (Walter and Lieth 1967).

modifies the growth potential of each species in a stand, it does not translate linearly into more or less growth. In particular, the resource light is asymmetrically distributed and leads to size-structured population dynamics in forests which

have to be taken into account in climate change modeling (Gómez-Aparicio et al. 2011). Our hypotheses implicitly include the assumption that the direct influence of climate is not the only factor but that also competition for light

plays a major role. This competition sensitivity is a strength of SILVA and LandClim.

SILVA is a single-tree based, spatially explicit forest growth model (Pretzsch et al. 2002). The growth functions were statistically parameterized from data of long-term experimental plots across Central Europe. The parameterizations for beech were based on 13,000 trees of 89 plots; the parameterizations for oak were based on 3,000 trees of 37 plots. SILVA was developed as a growth simulator for operational forest management planning of the Bavarian state forest management, for educational and scientific purposes (Pretzsch et al. 2008). Due to its site-sensitivity, SILVA simulations have been included in the analysis of climate change effects on forest growth and the development of forest carbon stocks under different climate and management scenarios (Köhl et al. 2010, Rötzer et al. 2010). Growth and mortality depend on a site (i.e., climate and soil) dependent growth potential, the individual trees' competitive situation and a stochastic component. The crown competition index searches for competing crowns with a size dependent circle around the target tree.

LandClim is a spatially explicit forest landscape model that was developed to assess the importance of climatic effects, wildfire, and management on forest dynamics (Schumacher 2004, Schumacher and Bugmann 2006, Schumacher et al. 2006). It incorporates patch level processes of climate-dependent tree regeneration, growth and mortality, and landscape level processes such as forest disturbances and seed dispersal. Climatic aridity causes drought stress for tree individuals by a reduction of available soil water mainly determined by the difference between precipitation and evapotranspiration in monthly time steps. Available soil water cannot exceed the maximum available soil water capacity, but can be larger than the precipitation of a given month due to carry-over of soil water from previous months. The demographic rates of individual trees within the patches are modified by light availability which is determined by the number of larger trees in their neighborhood. Thereby, several stand generations can be simulated and the influence of variables changing with time or space (such as climate and stand density) on forest dynamics can be assessed. LandClim operates at a relatively fine scale (grid

cells of 25×25 m, monthly weather data), and has been tested and adapted to the European Alps, the North American Rocky Mountains, and Mediterranean forests (Schumacher et al. 2006, Colombaroli et al. 2010, Henne et al. 2011, 2013, Briner et al. 2012, Elkin et al. 2012, Temperli et al. 2012). Species parameters were taken from Schumacher (2004) and Henne et al. (2011) except for an increase in the drought tolerance of *Quercus petraea* from 3.0 to 3.5 to reflect the slightly higher drought tolerance than *Fagus sylvatica* (drought tolerance = 3.0) reported in the literature (Leuschner et al. 2001, Raftoyannis and Radoglou 2002, Bréda et al. 2006, Scharnweber et al. 2011).

Model validation

For model validation SILVA was initialized with the first survey of the experimental sites. Simulated stand development for the 1981–2020 was compared to the data from the experimental sites. The simulated basal area growth matched the actual basal area well, except for 10–15% underestimation in the case of the 54- and 86-year-old stands. The difference was due to an underestimation of the increment of the 'other species' that cluster several species with different growth characteristics. The growth ratio of oak to beech was generally estimated correctly; oak increment was slightly overestimated in the 27-year-old stand (Appendix: Fig. A1).

LandClim was validated by comparing simulations with current climate (DWD data) starting from bare ground to the empirical stands of the corresponding age. The empirical tree diameter data of the five experimental sites were translated into biomass using the allometric function implemented in LandClim (Schroeder et al. 1997). As the LandClim simulations did not include the past silviculture which favored oak, stand biomass was dominated by beech, which is more competitive under the current climate as shown by the empirical data and reported in the literature (Appendix: Fig. A2).

Overall, model performance was acceptable for our purposes; a perfect match of observed data is unrealistic since stochastic environmental events such as late frost or other climate hazards, insect calamities, mast years all have a very unpredictable pattern and are essentially smoothed in the model parameterizations.

Table 2. Definition of simulation runs for potential climatic turning point (simulation with quasi-constant climate conditions) by model. The SILVA model used the experimental stand in the initial age; the LandClim model used establishment from ‘global seed rain’ in the initial age. Temperature and precipitation are given per annum (Temp.a, Prec.a) and per growing season (Temp.v, Prec.v), i.e., May–September of a respective year.

Initial age (yr)	Sim. period (yr)	Final age (yr)	WETTREG A1B period	Temp.a (Temp.v) (°C)	Prec.a (Prec.v) (mm)
SILVA					
27	120	147	1961–1980 [CLIM1]	8.9 (15.6)	546 (256)
27	120	147	1981–2000 [CLIM2]	8.9 (15.9)	553 (251)
27	120	147	2001–2020 [CLIM3]	9.3 (16.4)	561 (245)
27	120	147	2021–2040 [CLIM4]	10.3 (17.2)	534 (219)
27	120	147	2041–2060 [CLIM5]	11.1 (18.2)	512 (227)
27	120	147	2061–2080 [CLIM6]	11.9 (19.0)	500 (200)
27	120	147	2081–2100 [CLIM7]	12.6 (19.4)	516 (195)
LandClim					
0	150	150	1961–1980 [CLIM1]	8.9 (15.6)	546 (256)
0	150	150	1981–2000 [CLIM2]	8.9 (15.9)	553 (251)
0	150	150	2001–2020 [CLIM3]	9.3 (16.4)	561 (245)
0	150	150	2021–2040 [CLIM4]	10.3 (17.2)	534 (219)
0	150	150	2041–2060 [CLIM5]	11.1 (18.2)	512 (227)
0	150	150	2061–2080 [CLIM6]	11.9 (19.0)	500 (200)
0	150	150	2081–2100 [CLIM7]	12.6 (19.4)	516 (195)

Simulations of future stand dynamics

Mixed beech-oak forest growth under climate conditions from the WETTREG 2010 A1B scenario was simulated in order to determine the potential CTP between both species (Table 2). Climate had to be stationary during the simulated succession so that forests developed in equilibrium with climate. To create such climate scenarios the WETTREG 2010 A1B time-series covering the period 1961–2100 was split into 20-year periods (for each of 10 available realizations). Seven climate scenarios named CLIM1, CLIM2, . . . , CLIM7 (Table 2) were generated by repeating each 20-year time-series as often as needed (for 150 years succession 7.5 times).

To investigate the potential CTP we simulated a forest succession uninfluenced by the past. Accordingly, SILVA was initialized with the 27-year old stand since this was the youngest available (Table 1). LandClim was initialized on bare ground with a beech-oak ‘global seed rain’ in which beech and oak had equal shares.

For the actual CTP, beech-oak stand development was simulated with the projected WETTREG 2010 A1B climate scenario until 2100 for each of 10 available realizations (Table 3). Again, SILVA and LandClim were initialized differently. SILVA was initialized with each of the forest sites resulting in five simulated successions influenced by the legacy of past stand development. LandClim stands were initialized with a global seed rain in 1921. Since no climate data was available

for this time period, we used the same climate conditions for the first 40 years (1921 to 1960) as those from 1961 to 1980. From then on the WETTREG 2010 A1B time series was used. In 2000, the LandClim stand was approximately as old as the 106-year-old experimental stand and the forest reserve (105 years) and used as starting point for the simulation of the ‘actual succession’ under a gradually changing climate.

Forest structure and species composition were evaluated at a stand age of 150 years. We choose 150 years for the evaluation of the CTP because this is the upper limit for beech rotation and lower limit for oak rotation and thereby relevant for (managed) forests in Central Europe. At this age none of the species suffers from age-dependent mortality as the main driver of forest dynamics is competition. The time of stand evaluation certainly influences the CTP. As Rohner et al. (2012) showed beech is more competitive in later successional stages and is able to out-compete oak in the long term by inhibition of oak regeneration by shading also under increased drought stress. Under more favorable conditions for oak the rank reversal in favor of beech is postponed to a later point of time within the succession. However, we seek no equilibrium with a hypothetical climate and/or disturbance regime (e.g., Fyllas and Troumbis 2009)—a state that SILVA is not suited for without a regeneration module. We attempted to stay close to the situation of the existing forest

Table 3. Definition of simulation runs for actual climatic turning point (continuous simulation acc. to WETTREG scenario). For temperature and precipitation data of the WETTREG A1B time series cf. Table 2.

Model	Initial age (yr)	Sim. period (yr)	Final age (yr)	Simulation span	Data
SILVA	27 (experimental stand)	100	127	2001–2100	WETTREG A1B time series
SILVA	54 (experimental stand)	100	154	2001–2100	WETTREG A1B time series
SILVA	86 (experimental stand)	100	186	2001–2100	WETTREG A1B time series
SILVA	106 (experimental stand)	100	206	2001–2100	WETTREG A1B time series
SILVA	105 (forest reserve)	120	205	1981–2100	WETTREG A1B time series
LandClim	0 (establishment from 'global seed rain')	180	180	1921–2100	From 1921 to 1960 WETTREG A1B time series '1961–1980' was repeated twice, afterwards WETTREG A1B time series

sites, be coherent with the empirical growth data, and employ relevant time horizons for today's forests management.

While climate data were identical, SILVA and LandClim used different data aggregations and time windows. For SILVA the temperature and precipitation data were translated into length of growing season, average temperature May–September, temperature amplitude January–July, precipitation May–September and the Martonne aridity index, each of the parameters averaged over 20 year periods (Pretzsch 2009). In contrast, LandClim worked with monthly mean temperatures and precipitation sums to calculate seasonal and annual indices for water availability (drought index in Bugmann and Cramer 1998, Bugmann and Solomon 2000) and energy availability (degree-day-sum in Bugmann 1994) as well as temperature of the coldest month.

Soil descriptions for the five study sites were translated into the model requirements. Soil properties influence the CTP since the available soil water can compensate precipitation deficiency for some time. Specifically, for the SILVA simulations a low soil water availability was assumed (0.3 on a scale between 0 and 1) and further reduced as the climate became warmer and drier. For LandClim, the maximum available soil water capacity (model parameter 'bucket size') was set to 80 mm.

RESULTS

Current stand dynamics

In all but the 106-year-old stands, beech expanded its basal area while oak remained unchanged or declined (Fig. 2). Beech expansion was particularly strong in the young 27- and 86-year-old stands and in the forest reserve which

had the longest time period between surveys. Here, from 1978 to 2010, the beech basal area share increased from 42% to 58%, partly at the expense of oak (decline from 21% to 17%), but mainly due to the decline of other species (37% to 25%).

A closer look at the 86-year-old experimental site emphasized the effect of stand structure on basal area growth (DBH-distributions in Appendix: Fig. A3): The tree-ring analysis showed an increase of mean DBH of dominant beech from 31.6 to 37.5 cm (+5.9 cm) and oak from 26.0 to 29.8 cm (+3.8 cm). Diameter increase of beech trees thus exceeded oak trees by 40–60% in the upper canopy. However, the majority of beech trees still grew in the subcanopy and was strongly suppressed so that, in total, the basal area share remained unchanged (Appendix: Fig. A3).

Correlations between tree-ring indices and climate data revealed that beech was much more sensitive to climate than oak. While oak showed significant positive correlations with precipitation during the growing period, beech tree-ring indices were positively correlated with precipitation during spring and the growing season as well as during September and December of the previous year. For beech, correlations with temperature were negative for most months except for October of the previous year (Appendix: Fig. A4). In the driest summer of 2003 (100 mm precipitation from May–September), beech ring-width index dropped to 0.5 while that for oak only decreased to 0.7.

Future stand dynamics

Potential climatic turning point.—In almost all scenarios, beech extended its initially low basal

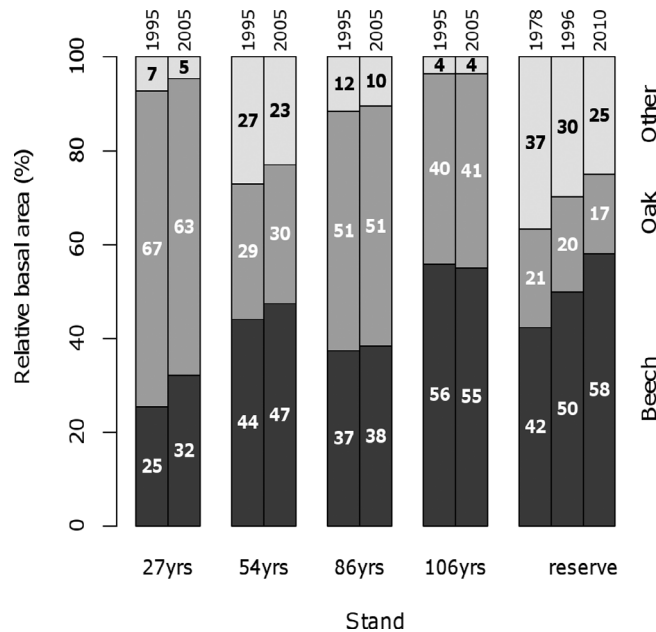


Fig. 2. Basal area share of beech, oak and other tree species of the four experimental sites (in 1995 and 2005) and the forest reserve (in 1978, 1996, and 2010) according to field surveys.

area share in SILVA simulations (Fig. 3a). However, the beech expansion decreased along the climatic gradient. While in CLIM6 (2061–2080) beech still slowly expanded, in CLIM7 (2081–2100) beech basal area did not further expand. In these last two scenarios CLIM6-7 (2061–2100) beech did not reach dominance. Notably, not only species composition changed, but also the final basal area value decreased from almost 38 m²/ha in CLIM1 (1961–1980) to 26 m²/ha in CLIM7 (2081–2100).

Focusing on the economically most interesting target trees, dominant beech trees grew higher than oak in SILVA simulations. Oak reached only larger diameters in the last three scenarios CLIM5-7 (2041–2100) (Fig. 4). Both diameter and height of the dominant trees decreased with increasing aridity. This negative climate effect was even more apparent in the survival of the initially dominant beech and oak trees. From CLIM1-5 (1961–2060), more dominant beech than oak trees survived. In CLIM6-7 (2061–2100) significant upper canopy mortality caused death of almost all of the initially dominant beech trees.

LandClim simulations (Fig. 3b) were generally in agreement with those of SILVA. From CLIM1-3 (1961–2020) beech dominated in all realizations,

with biomass shares of 75–89%. In CLIM4 (2021–2040) one out of 10 climate realizations resulted in oak dominance, in CLIM5 (2041–2060) already five out of 10. Finally, in CLIM6 (2061–2080) and CLIM7 (2081–2100) LandClim predicted mixed stands with a share of oak of 64% in CLIM6 and 96% in CLIM7, and a share of beech of 34% in CLIM6 and 11% in CLIM7 (medians of 10 realizations). Beech experienced higher mortality and was mainly restricted to the understory owing to its shade tolerance. Oak dominated the upper canopy, which led to a considerable increase in the biomass of large trees above 50 cm DBH: 168 t/ha in the CLIM1 (1961–1980) scenario vs. 225 t/ha in the CLIM7 (2081–2100) scenario. Consequently, total stand biomass varied only little between the scenarios, contrasting with SILVA results, where basal area declined with progressing climate change (SILVA –34%; Fig. 3a CLIM7 vs. CLIM1).

Actual climatic turning point.—In SILVA, basal area peaked around the year 2050 in the continuous WETTREG 2010 A1B climate scenario (Fig. 5a). This pattern was mainly caused by changes in beech basal area while oak basal area remained almost constant. The beech expansion in the first half of the 21st century was lowest in

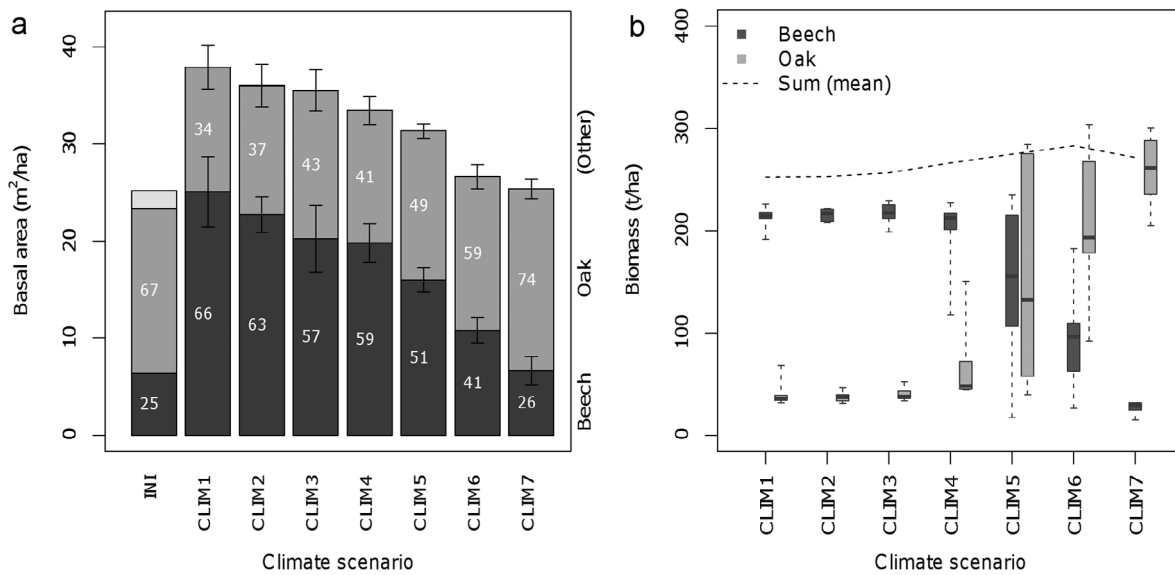


Fig. 3. Predicted species composition of ~150-year-old beech-oak stands in (a) SILVA and (b) LandClim under seven climate conditions which correspond to periods of the WETTREG 2010 A1B scenario (CLIM1 = 1961–1980, CLIM2 = 1981–2000, . . . CLIM7 = 2081–2100). (a) Initial (INI) stand 27-year-old experimental site, simulation span 120 years (final age: 147 yr). Error bars indicate range of simulation results. (b) Initial beech-oak seed rain (age 0) on bare ground, simulation span 150 years (cf. Table 2 for details). Whiskers indicate the range of simulation results.

the 27-year-old stand where oak competition was high due to its early growth climax. Beech expansion was highest in the 54-year-old stand where beech has its growth climax. As a consequence, in 2050 beech occupied the upper canopy so effectively that in the second half of the 21st century oak still did not exceed its initial share (with exception of the 27-year-old stand). In the forest reserve, only minor changes occurred in the absolute basal area and basal area shares.

In the LandClim simulations, which were best comparable to the SILVA simulations of the 27-year-old stand, beech dominated the stand during the entire simulated succession (Fig. 5b). However, a decrease in beech biomass could be observed. Notably, there was considerable variability among the 10 climatic realizations. When the simulations of the succession were run for longer (assuming CLIM7 from 2100 on), oak gained dominance in about 2150–2200, while beech was not able to regenerate under such arid conditions and gradually declined until 2500 (not shown).

DISCUSSION

Beech dominates oak under current climate

We found evidence for the occurrence of a climatic turning point (CTP) for a beech-oak system. The rationale was that under current conditions beech was more competitive but less drought tolerant than oak. This is in line with former studies on the drought sensitivity of beech (Leuschner et al. 2001, Friedrichs et al. 2009) and with findings on the competitive balance in beech-oak forests. Scharnweber et al. (2011) reported dominant beech trees to perform a superior diameter growth in beech compared to oak under dryer conditions until annual precipitation falls below 540 mm in a 100-year-old mixed beech-oak forest. An extensive review by Bolte et al. (2007) lists sources of empirical evidence for beech dominance down to 550 mm and 18–19°C July temperatures, but also highlights several other limiting factors such as winter temperatures and late frost. Notably, these values are more arid than the climate suggested by Ellenberg (2009) to foster the dominance of oak over beech (July temperatures >18°C and

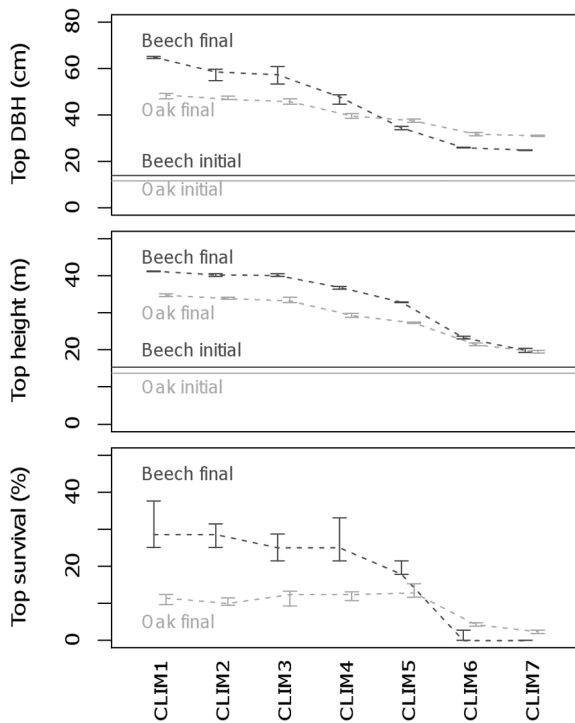


Fig. 4: DBH, height and survival of the dominant ('top') beech and oak trees in a SILVA simulation for the 27-year-old experimental site (simulation span 120 years). The climate conditions correspond to periods of the WETTREG 2010 A1B scenario (CLIM1 = 1961–1980, CLIM2 = 1981–2000, ... CLIM7 = 2081–2100). Top diameter and top height defined as the 90% percentile of the diameter and height distribution of each species; top survival the survival of dominant 20% of each species in the initial stand (at age 27 years). Final age: 147 years.

precipitation <600 mm/yr).

However, the CTP does not reflect the species range of tolerated site conditions. Species usually tolerate a wider range of conditions and can remain as minor components in the community. According to Kölling's (2007) climate envelopes, beech tolerates annual precipitation as low as 500 mm at 10°C mean annual temperature (but requires 650 mm at temperatures of 12.5°C). With 450 mm sessile oak needs less annual precipitation even at annual mean temperatures up to 12°C. At the southern limits of beech distribution, the Spanish inventory contains records of beech even down to 587 mm and up to 13.7°C and of sessile oak down to 540 mm and

up to 16.2°C (Gómez-Aparicio et al. 2011). Nevertheless, in the Mediterranean mountains, both Jump et al. (2006) and Piovesan et al. (2008) document declining beech populations as a consequence of increasing summer aridity.

Rank reversal between beech and oak under future climate

Our results confirmed both hypotheses: As formulated in H1, simulations for the potential CTP of forests developing ex novo projected that the dominance of beech begins to deteriorate when mean annual temperature exceeds 11.1°C and the annual precipitation drops below 510 mm (temperature May–September 18.2°C, temperature July 20.9°C, precipitation May–September 230 mm; cf. Table 3). The WETTREG 2010 A1B scenario projected such climate conditions for the second half of the 21st century. Yet, as hypothesized in H2, in the continuous succession of present forests along the climatic gradient no such rank reversal occurred, thus beech still remained dominant in 2100, due to the suppression of oak regeneration by shading and the slow life cycles of trees.

The simulations demonstrated the importance of the interplay of climatic factors together with structural competition. In the models, climate determines the species-specific growth potential which is then modified by the individual trees' competition situation. Since the competition situation is determined by structure, climate-induced changes of the species' growth potential do not translate linearly into more or less growth. This becomes obvious in the abrupt change in the LandClim simulations from beech to oak dominance between CLIM4 and CLIM6 (Fig. 3b, potential CTP) which does not occur in the gradually changing scenario (Fig. 5b, actual CTP). This could be explained by a higher sensitivity of beech seedlings to drought which favored oak in bare ground establishment scenarios. Older beech trees, which established under conditions more favorable for beech, tolerated drought to some degree and additionally impeded oak regeneration due to their strong shading. The changes in SILVA—which can only represent established stands—are accordingly more gradual (Figs. 3a and 5a). Both species grow less in height and diameter and experience an increase in mortality. So, neither

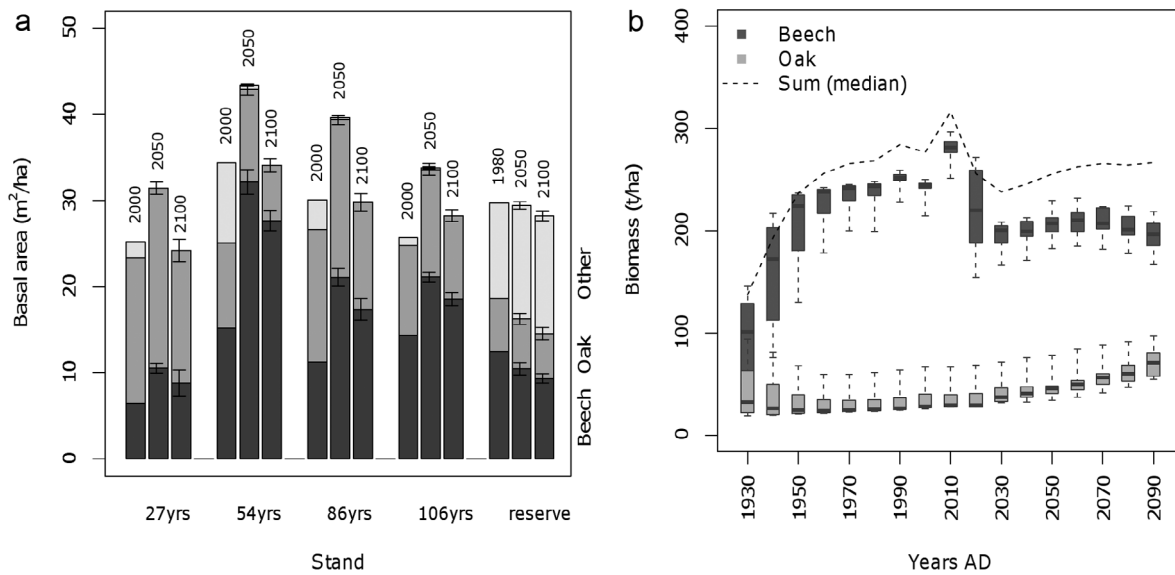


Fig. 5. Predicted development of beech-oak stands under the WETTREG 2010 A1B scenario until 2100 (a) in SILVA for five stands evaluated in 2050 and 2100 and (b) in LandClim for one stand, entire succession shown. (a) SILVA was initialized with four experimental sites (age 27 to 106 years in 2000), and one forest reserve (age ~105 in 1980); (b) LandClim started with beech-oak seed rain on bare ground in 1921, thus stand age is comparable with SILVA simulations ‘106 years’ and ‘reserve’. (cf. Table 3 for details).

species is a true winner of climate change, yet oak is less affected than beech. The time lag in the climate adaption of the forest species composition can be described as a legacy of the past stand development.

Sykes and Prentice (1996) reported similar findings for a study site in Sweden. Under climate warming, beech was expected to be the long-term replacement for spruce (in pine-spruce forests), but in simulations its dominance was delayed for centuries due to the persistence of old-growth spruce stands. Under such conditions disturbances can initiate succession and thereby function as catalysts for ecosystem change following climate change (Soja et al. 2007, Johnstone et al. 2010). In a modelling study of Hanewinkel et al. (2012) on the economic value of future forests a considerable decline of beech was found, while oak remained unchanged or even increased in their study. Indeed, the forest simulator 4C projected a decline in both, beech and oak, with decreasing precipitation (Lasch et al. 2002), but at the same time, the range of possible climate projections differed to such degree that it remained unclear if beech and oak will actually suffer a loss in productivity at a

particular site. Increased diebacks of upper canopy trees as simulated by SILVA, are one of the severest consequences of climate change and have received high attention (Bigler et al. 2006, McDowell et al. 2008, Allen et al. 2010). For example, Hlásny et al. (2011) projected a dieback for beech forests in lower altitudes of Hungary during the 21st century. Far-reaching consequences of increases in drought induced mortality have been documented for forest ecosystems of the southwestern United States (Allen and Breshears 1998): A rapid and persistent shift of the ecosystem boundary between semiarid ponderosa pine forest and pinon-juniper woodland followed a drought-induced dieback in the 1950s. Whereas in the drought of the 1950s mainly trees older than 100 years were affected, widespread tree mortality was observed across size and age classes in the drought of 2000–2003 in the same region (Breshears et al. 2005). Our simulations did not show such dramatic consequences of climate change. However, SILVA and LandClim only regarded climate effects on establishment, growth and mortality. In reality, major diebacks can only seldom be attributed directly to climate events (e.g., in McDowell et al.

2008), mostly the factors are more complex (e.g., Bigler et al. 2006). Droughts are for example a main cause of fires that entail tree death, occasionally at large areas. Moreover, droughts are regarded as an inciting mortality factor (sensu Manion 1981), while secondary agents take advantage of the weakened tree defense and kill the trees in the end. For example, in the ponderosa pine forest, drought weakened tree defense against cambium-feeding beetles (*Dendroctonus* sp. and *Ips* sp.), which caused additional mortality (Allen and Breshears 1998).

Implications for management

For more than 30 years, forest management in Central Europe has pursued a more sustainable and stable productivity through conversion of coniferous forest to broadleaf forest and propagation of species mixtures (Spiecker et al. 2004, Pretzsch et al. 2013). As climate change moved into the focus of attention, species suitability decisions had to take into account future climate trends (Linder 2000, Bolte et al. 2009, Lindner et al. 2010). For dry and warmer sites, the decision is between beech and oak. Temperature and precipitation are the most commonly used factors to guide such decisions. Our study demonstrated that beech is currently not drought-limited in southeastern Germany, even at the driest sites. These values remain within the climate envelopes of Kölling (2007) for beech existence, but fall below the typical values given for beech dominance (Bolte et al. 2007). Based on these values, there is still a buffer for beech forests: on the dryer sites in southeastern Germany at least until 2050 even under ‘worst-case’ assumptions like the WETTREG 2010 A1B scenario.

However, in view of the projected beech decline in both SILVA and LandClim in the second half of the 21st century, the promotion of oak already today seems advisable due to the superior resistance and resilience of oak (pedunculate oak even more than sessile oak) to drought (Leuschner et al. 2001, Friedrichs et al. 2009, Scharnweber et al. 2011). Also the high value of oak wood might make oak more profitable than beech if stand productivity decreases as projected. Additionally, the facilitative behavior of oak in mixed stands is a strong argument for a preferential choice of this species as stabilizing component of ecosystems under climate change.

Only recently, independently of each other, Zapater et al. (2011) and Jonard et al. (2011) found evidence for hydraulic lift of oak in young mixed beech-oak stands. This could be the cause for a lower sensitivity of beech to water scarcity in mixed beech-oak stands than in pure stands. Further, Pretzsch et al. (2012) found that growth of beech in mixture with spruce decreased less than in monoculture and thereby improved its competitive strength. This stress release by mixing is an important emergent property implying that the realized climatic niche of beech in mixed stands might be wider than in pure stands (Pretzsch et al. 2013).

Conclusion

We demonstrated that a rank reversal of key forest species is to be expected under projected climate change, but that established forest structures introduce considerable inertia in the climate change adaptation of forests. The climatic turning point proved a simple yet effective reference measure to study climate related changes in interspecific competition. Competition sensitivity—a strength of the models employed here—is needed to account for the strongly size-structured population dynamics and therefore imperative in climate change modelling.

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LITERATURE CITED

- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences* 95:14839–14842.

- Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33:1677–1688.
- Baltzer, J. L., and S. C. Thomas. 2007. Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *Journal of Ecology* 95:1208–1221.
- Barriopedro, D., E. M. Fischer, J. Luterbacher, R. M. Trigo, and R. Garcia-Herrera. 2011. The hot summer of 2010: Redrawing the temperature record map of Europe. *Science* 332:220–224.
- Beaudet, M., J. Brisson, D. Gravel, and C. Messier. 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest. *Journal of Ecology* 95:458–467.
- Bigler, C., O. U. Bräker, H. Bugmann, M. Dobbertin, and A. Rigling. 2006. Drought as an inciting mortality factor in scots pine stands of the Valais, Switzerland. *Ecosystems* 9:330–343.
- Bolte, A., T. Czajkowski, and T. Kompa. 2007. The north-eastern distribution range of European beech: A review. *Forestry* 80:413–429.
- Bolte, A., C. Ammer, M. Löf, P. Madsen, G.-J. Nabuurs, P. Schall, P. Spathelf, and J. Rock. 2009. Adaptive forest management in Central Europe: Climate change impacts, strategies and integrative concept. *Scandinavian Journal of Forest Research* 24:473–482.
- Boyden, S. B., P. B. Reich, K. J. Puettmann, and T. R. Baker. 2009. Effects of density and ontogeny on size and growth ranks of three competing tree species. *Journal of Ecology* 97:277–288.
- Bréda, N., R. Huc, A. Granier, and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* 63:625–644.
- Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences* 102:15144–15148.
- Briner, S., C. Elkin, R. Huber, and A. Grêt-Regamey. 2012. Assessing the impacts of economic and climate changes on land-use in mountain regions: A spatial dynamic modeling approach. *Agriculture Ecosystems and Environment* 149:50–63.
- Bugmann, H. 1994. On the ecology of mountainous forests in a changing climate: A simulation study. Dissertation. Swiss Federal Institute of Technology Zurich, Zurich, Switzerland.
- Bugmann, H. 1997. Sensitivity of forests in the European Alps to future climatic change. *Climate Research* 8:35–44.
- Bugmann, H., and W. Cramer. 1998. Improving the behaviour of forest gap models along drought gradients. *Forest Ecology and Management* 103:247–263.
- Bugmann, H. K. M., and A. M. Solomon. 2000. Explaining forest composition and biomass across multiple biogeographical regions. *Ecological Applications* 10:95–114.
- Bunn, A. G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26:115–124.
- Carnicer, J., M. Coll, M. Ninyerola, X. Pons, G. Sánchez, and J. Peñuelas. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences* 108:1474–1478.
- Chapin, F. S. 2003. Effects of plant traits on ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. *Annals of Botany* 91:455–463.
- Colombaroli, D., P. D. Henne, P. Kaltenrieder, E. Gobet, and W. Tinner. 2010. Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. *Journal of Ecology* 98:1346–1357.
- Cook, E. R., and K. Peters. 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *Holocene* 7:361–370.
- Czúcz, B., L. Gálhidy, and C. Mátyás. 2011. Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. *Annals of Forest Science* 68:99–108.
- Dalgaard, P. 2002. *Introductory statistics with R*. Springer, New York, New York, USA.
- Elkin, C., B. Reineking, C. Bigler, and H. Bugmann. 2012. Do small-grain processes matter for landscape scale questions? Sensitivity of a forest landscape model to the formulation of tree growth rate. *Landscape Ecology* 27:697–711.
- Ellenberg, H. 2009. *Vegetation ecology of Central Europe*. Fourth edition. Cambridge University Press, Cambridge, UK.
- Ellison, A. M., et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486.
- Friedrichs, D. A., V. Trouet, U. Büntgen, D. C. Frank, J. Esper, B. Neuwirth, and J. Löffler. 2009. Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees* 23:729–739.
- Fuhrer, J., M. Beniston, A. Fischlin, C. Frei, S. Goyette, K. Jasper, and C. Pfister. 2006. Climate risks and their impact on agriculture and forests in Switzerland. Pages 79–102 in H. Wanner, M. Grosjean, R. Rötthlisberger, E. Xoplaki, editors. *Climate variability, predictability and climate risks*. Springer, Dordrecht, The Netherlands.
- Fyllas, N. M., and A. Y. Troumbis. 2009. Simulating vegetation shifts in north-eastern Mediterranean

- mountain forests under climatic change scenarios. *Global Ecology and Biogeography* 18:64–77.
- Gitlin, A. R., C. M. Stultz, M. A. Bowker, S. Stumpf, K. L. Paxton, K. Kennedy, A. Munoz, J. K. Bailey, and T. G. Whitham. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology* 20:1477–1486.
- Gómez-Aparicio, L., R. García-Valdés, P. Ruiz-Benito, and M. A. Zavala. 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. *Global Change Biology* 17:2400–2414.
- Hanewinkel, M., D. A. Cullmann, M. J. Schelhaas, G. J. Nabuurs, and N. E. Zimmermann. 2012. Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change* 3:203–207.
- Henne, P. D., et al. 2011. Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *Journal of Biogeography* 38:933–949.
- Henne, P. D., C. M. Elkin, B. Reineking, H. Bugmann, and W. Tinner. 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: Insights from paleoecology and dynamic modeling. *Landscape Ecology* 28:819–833.
- Hlásny, T., Z. Barcza, M. Fabrika, B. Balázs, G. Churlina, J. Pajtk, R. Sedmák, and M. Turčáni. 2011. Climate change impacts on growth and carbon balance of forests in Central Europe. *Climate Research* 47:219–236.
- IPCC. 2012. Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of working groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.
- Johnstone, J. F., E. J. McIntire, E. J. Pedersen, G. King, and M. J. Pisaric. 2010. A sensitive slope: Estimating landscape patterns of forest resilience in a changing climate. *Ecosphere* 1:14.
- Jonard, F., F. André, Q. Ponette, C. Vincke, and M. Jonard. 2011. Sap flux density and stomatal conductance of European beech and common oak trees in pure and mixed stands during the summer drought of 2003. *Journal of Hydrology* 409:371–381.
- Jump, A. S., J. M. Hunt, and J. Penuelas. 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology* 12:2163–2174.
- Köhl, M., et al. 2010. Combating the effects of climatic change on forests by mitigation strategies. *Carbon Balance and Management* 5:1–9.
- Kölling, C. 2007. Klimahüllen für 27 Waldbaumarten. *AFZ-DerWald* 23:1242–1245.
- Kreienkamp, F., A. Spekat, and W. Enke. 2009. Sensitivity studies with a statistical downscaling method: The role of the driving large scale model. *Meteorologische Zeitschrift* 18:597–606.
- Lasch, P., F. W. Badeck, M. Lindner, and F. Suckow. 2002. Sensitivity of simulated forest growth to changes in climate and atmospheric CO₂. *Forstwissenschaftliches Centralblatt* 121:155–171.
- Lebourgeois, F., N. Bréda, E. Ulrich, and A. Granier. 2005. Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees* 19:385–401.
- Leuschner, C., K. Backes, D. Hertel, F. Schipka, U. Schmitt, O. Terborg, and M. Runge. 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management* 149:33–46.
- Linder, M. 2000. Developing adaptive forest management strategies to cope with climate change. *Tree Physiology* 20:299–307.
- Lindner, M., et al. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259:698–709.
- Manion, P. D. 1981. *Tree disease concepts*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- McDowell, N., W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams, and E. A. Yezpez. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* 178:719–739.
- Michelot, A., N. Bréda, C. Damesin, and E. Dufrière. 2012. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *Forest Ecology and Management* 265:161–171.
- Morin, X., D. Viner, and I. Chuine. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology* 96:784–794.
- Osada, N. 2012. Crown exposure to light and tree allometry of 11 tree species in a snowy cool-temperate forest in Japan. *Plant Ecology* 213:783–794.
- Pérez-Ramos, I. M., I. R. Urbieto, M. A. Zavala, and T. Marañón. 2012. Ontogenetic conflicts and rank reversals in two Mediterranean oak species: Implications for coexistence. *Journal of Ecology* 100:467–477.

- Peterken, G., and E. P. Mountford. 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry* 69:125–136.
- Piovesan, G., F. Biondi, A. D. Filippo, A. Alessandrini, and M. Maugeri. 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14:1265–1281.
- Pretzsch, H. 2009. *Forest dynamics, growth, and yield. From measurement to model.* Springer, Berlin, Germany.
- Pretzsch, H., and G. Schütze. 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: Evidence on stand level and explanation on individual tree level. *European Journal of Forest Research* 128:183–204.
- Pretzsch, H., P. Biber, and J. Durský. 2002. The single tree-based stand simulator SILVA: Construction, application and evaluation. *Forest Ecology and Management* 162:3–21.
- Pretzsch, H., R. Grote, B. Reineking, and T. H. Rötzer. 2008. Models for forest ecosystem management: A European perspective. *Annals of Botany* 101:1065–1087.
- Pretzsch, H., J. Dieler, T. Seifert, and T. Rötzer. 2012. Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) in stands with different spatial mixing patterns. *Trees* 26:1343–1360.
- Pretzsch, H., K. Bielak, J. Block, A. Bruchwald, J. Dieler, H.-P. Ehrhart, U. Kohnle, J. Nagel, H. Spellmann, M. Zasada, and A. Zingg. 2013. Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *European Journal of Forest Research* 132:263–280.
- Raftoyannis, Y., and K. Radoglou. 2002. Physiological responses of beech and sessile oak in a natural mixed stand during a dry summer. *Annals of Botany* 89:723–730.
- R Development Core Team. 2012. *R: A language and environment for statistical computing.* Reference index version 2.15.2. R Foundation for Statistical Computing, Vienna, Austria.
- Rehfeldt, G. E., D. E. Ferguson, and N. L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecology and Management* 258:2353–2364.
- Rinn, R. 2003. *TSAP-Win (time series analysis and presentation for dendrochronology and related applications).* Version 0.53. Rinntech, Heidelberg, Germany.
- Rohner, B., C. Bigler, J. Wunder, P. Brang, and H. Bugmann. 2012. Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. *Journal of Vegetation Science* 23:892–905.
- Rötzer, T., J. Dieler, T. Mette, R. Moshhammer, and H. Pretzsch. 2010. Productivity and carbon dynamics in managed Central European forests depending on site conditions and thinning regimes. *Forestry* 83:483–496.
- Sánchez-Gómez, D., M. A. Zavala, D. B. Van Schalkwijk, I. R. Urbieto, and F. Valladares. 2008. Rank reversals in tree growth along tree size, competition and climatic gradients for four forest canopy dominant species in central Spain. *Annals of Forest Science* 65:605.
- Schär, C., P. L. Vidale, D. Lüthi, C. Frei, C. Häberli, M. A. Liniger, and C. Appenzeller. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature* 427:332–336.
- Scharnweber, T., M. Manthey, C. Criegee, A. Bauwe, C. Schröder, and M. Wilmking. 2011. Drought matters: Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management* 262:947–961.
- Schroeder, P., S. Brown, J. Mo, R. Birdsey, and C. Cieszewski. 1997. Biomass estimation for temperate broadleaf forests of the United States using inventory data. *Forest Science* 43:424–434.
- Schumacher, S. 2004. *The role of large-scale disturbances and climate for the dynamics of forested landscapes in the European Alps.* Dissertation. Swiss Federal Institute of Technology Zurich, Zurich, Switzerland.
- Schumacher, S., and H. Bugmann. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Global Change Biology* 12:1435–1450.
- Schumacher, S., B. Reineking, J. Sibold, and H. Bugmann. 2006. Modeling the impact of climate and vegetation on fire regimes in mountain landscapes. *Landscape Ecology* 21:539–554.
- Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin, III, and P. W. Stackhouse, Jr. 2007. Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56:274–296.
- Spiecker, H., J. Hansen, E. Klimo, J. Skovsgaard, H. Sterba, and K. von Teuffel, editors. 2004. *Norway spruce conversion: Options and consequences.* EFI Research Report 18, Brill, Leiden, The Netherlands.
- Sykes, M., and C. I. Prentice. 1996. Climate change, tree species distributions and forest dynamics: A case study in the mixed conifer/northern hardwoods zone of northern Europe. *Climatic Change* 34:161–

177.
 Temperli, C., H. Bugmann, and C. Elkin. 2012. Adaptive management for competing forest goods and services under climate change. *Ecological Applications* 22:2065–2077.
 van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* 10:909–916.
 Walter, H., and H. Lieth. 1967. *Klimadiagramm-Weltatlas*. Gustav Fischer Verlag, Jena, Germany.
 Williams, J. W., and S. T. Jackson. 2007. Novel climates,

no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
 Worrall, J. J., L. Egeland, T. Eager, R. A. Mask, E. W. Johnson, P. A. Kemp, and W. D. Shepperd. 2008. Rapid mortality of *Populus tremuloides* in south-western Colorado, USA. *Forest Ecology and Management* 255:686–696.
 Zapater, M., C. Hossann, N. Bréda, C. Bréchet, D. Bonal, and A. Granier. 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using ¹⁸O soil water labelling. *Trees* 25:885–894.

SUPPLEMENTAL MATERIAL

APPENDIX

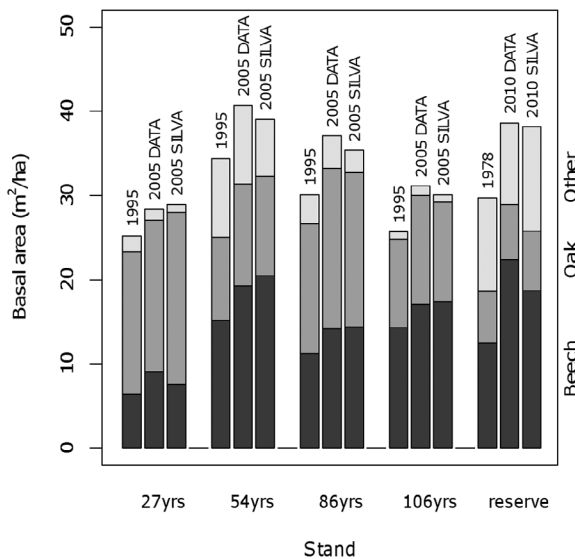


Fig. A1. Validation of SILVA vs. survey data. 10-years basal area development of the four experimental sites and the forest reserve. Comparison of the surveys 1995–2005 (1978–2010 in the case of the reserve) and SILVA simulation over 10 years (30 years in the case of the reserve) with the average climate from 1981–2000 (DWD station Schweinfurt).

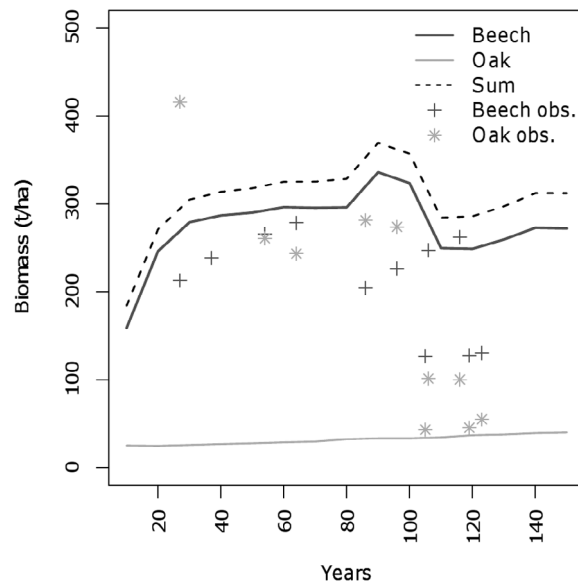


Fig. A2. Validation of LandClim vs. survey data. Simulations were run with the actual climate (DWD data) and results were compared to the real stands. A dominance of beech from c. 100 years onwards and lower biomass shares of beech in young stands and are well reproduced.

Table A1. Comparison of DWD and WETTREG 2010 A1B climate data for DWD weather station Schweinfurt from 1971 to 2000. T.a = mean annual temperature, T.v = mean temperature May–September (vegetation period), Prec.a = annual precipitation sum, Prec.v = precipitation sum May–September (vegetation period). Mean testing with Welch’s t-test and standard deviation testing with an F-test on the ratio of the group variances (functions t.test and var.test in R statistics, cf. Dalgaard 2002:86–89). DWD and WETTREG values different on a 0–0.001 error level (***), 0.05–0.1 error level (†).

Metric	Mean			SD		
	DWD	WETTREG	p	DWD	WETTREG	p
T.a (°C)	9.04	9.06	0.8703	0.72	0.32	5.705e ⁻¹⁴ (***)
T.v (°C)	15.95	15.97	0.875	0.87	0.42	5.506e ⁻¹¹ (***)
Prec.a (mm)	555	589	0.0886(†)	102	84	0.1276
Prec.v (mm)	261	279	0.1397	63	57	0.438

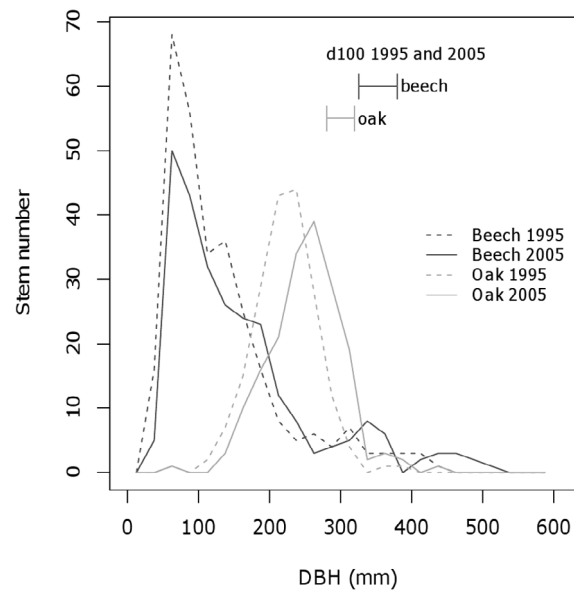


Fig. A3. Diameter at breast height (DBH) distribution of the 86-years-old mixed beech-oak stand in 1995 and 2005. d100 = average diameter of the 100 dominant trees per hectare. The DBH distribution in the 86-year-old stand displays that the stand structure consists of a dominant oak layer while beech mainly forms the subcanopy. However, the beech trees in the upper canopy layer expand stronger than oak: From 1995 to 2005, beech d100 increased from 32.58 cm to 37.98 cm (+5.40 cm) while oak d100 only increased from 28.02 cm to 31.96 cm (+3.94 cm).

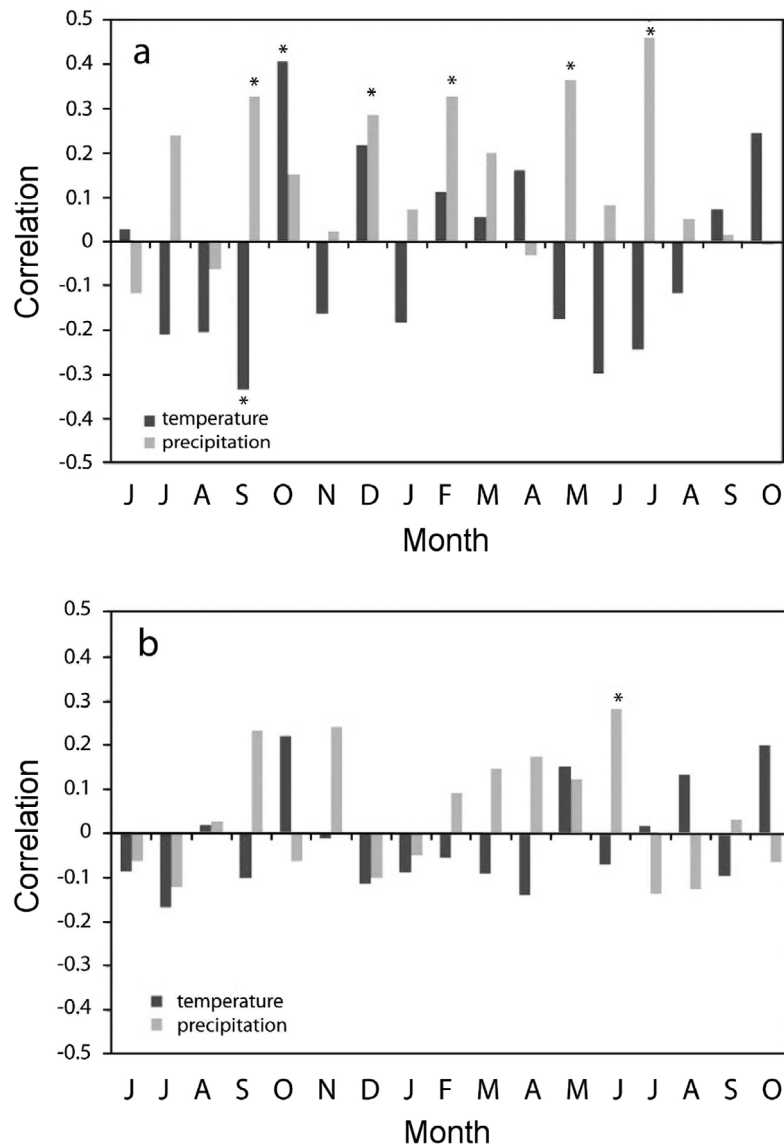


Fig. A4. Correlation coefficients for a 16-month period from June of the year prior to growth until October of the growth year between (a) beech and (b) oak tree-ring index curves and monthly climate data from Schweinfurt meteorological station for the period 1959–2003. Correlations significant at the $p < 0.05$ level are marked with an asterisk. Climate-growth relationships for both studied species were calculated as correlation functions between monthly climate data from Schweinfurt climate station and the dimensionless tree-ring indices as well as the raw ring-width data. The latter include the differences in the species' growth levels, so possible effects of tree age and size on the impact of climate on growth have to be regarded.