

Modelling the impact of climate change on the productivity and water-use efficiency of a central European beech forest

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ABSTRACT: This scenario study is focused on the analysis and causal explanation of the effects of regional climate change on the productivity and water-use efficiency of a pure European beech *Fagus sylvatica* (L.) forest in western Germany. An ensemble of 9 regional climate model (RCM) simulation results based on the A1B emissions scenario from the ENSEMBLES project was used, along with local observations to drive the physiological forest growth model BALANCE for a 10 yr period. It simulates biomass increments, as well as productivity and efficiency, under different climatic conditions. Despite the RCM ensemble's large bandwidth, the results clearly indicate a decrease in total living biomass under future climate conditions compared to initial conditions and BALANCE control simulations. Net primary productivity was significantly reduced by 30 % and water-use efficiency — though more uncertain — by 13 % for end-of-the-century climate conditions compared to the control runs. In the A1B scenario, the lowered productivity and efficiency of the beech stand under future climate conditions are caused by higher mortality rates, lower water availability and higher drought stress, though partly counterbalanced by longer growing seasons.

KEY WORDS: Regional climate change · Impacts · Forest productivity · Water-use efficiency · Forest growth · Regional modelling · Ensemble data set

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1. INTRODUCTION

Over the past 100 yr the average global temperature has increased by roughly 0.7°C (IPCC 2007). The average temperature in Europe has increased by 0.95°C during the same period. Over the next 100 yr, the average global temperature is expected to rise by 1.4–5.8°C, while the expected rise in temperature in Europe is estimated to be between 2.0 and 6.3°C (IPCC 2007).

Forests are seriously affected by local climatic conditions (e.g. van der Meer et al. 2002). Many studies

show a rise in photosynthesis and net primary productivity under elevated temperatures and higher CO₂ concentrations (e.g. Hamilton et al. 2002). Studies in Finland (e.g. Garcia-Gonzalo et al. 2007) have shown that climate change will alter the growth patterns of important tree species. Evaluation of long-term observation plots revealed positive growth trends for most regions in Europe, and negative trends for some regions in the east and south, in the last decades (e.g. Spiecker et al. 1996, Pretzsch 1999). While drought and heat stress increase forest mortality in response to climate change (Allen et al.

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2010), higher temperatures will extend the length of the growing season (e.g. Chmielewski & Rötzer 2002, Menzel et al. 2006) and thereby the time for carbon fixation. Chmielewski & Rötzer (2001) for example reported an 8 d earlier onset of spring across Europe within the last 3 decades of the 20th century.

In an expected warmer and dryer future climate, growth and competitiveness of trees will be influenced e.g. by higher temperatures, a more restricted water supply and longer and more frequent drought events (Gebler et al. 2007), and/or changed frost periods (Kreyling et al. 2012). In addition, other environmental parameters such as stand structure, soil characteristics, or the level of stress may change in a changing climate and possibly influence growth and yield of forest stands. Feedback reactions of trees could modify the environment of a tree and thus alter stand growth. In a simulation study, Rötzer (2013) demonstrated that drought stress decreases leaf biomass and photosynthesis in mixed forest stands. Because of less leaf biomass, however, radiation conditions are improved, which increases photosynthesis. Despite the fact that in many studies single aspects of these issues have been examined (e.g. Bergh et al. 2003, Garcia-Gonzalo et al. 2007, Rötzer et al. 2009), the cause and effect relationships are not yet fully understood.

European beech *Fagus sylvatica* (L.) is one of the main tree species in Central Europe; without anthropogenic impact it would dominate forests in the region (Ellenberg & Leuschner 2009). For example, in Germany, beech covers approximately one-third of all forested areas (BMELF 2005). How beech will be affected by climate change is still open to debate (Rennenberg et al. 2004), but this species' fate is of high relevance for forest ecosystem management.

For our study we chose a European beech stand which is located at the periphery rather than the centre of the real niche and ecological amplitude of beech. Stands in this range of the ecological amplitude are widely held to be negatively susceptible to climate change via drought stress. We investigated the impacts of regional climate change with a physiological tree growth model that is driven by regional climate model (RCM) simulation results as part of a dynamical downscaling of Emissions Scenario A1b-driven global climate model (GCM) runs. Physiological growth models are particularly applicable tools for examining the reaction patterns, feedback loops and sensitivities of individual trees or forest stands, e.g. in response to modified climatic conditions (Fontes et al. 2010). Prominent examples of such models are 3-PG (Landsberg & Waring 1997), Biome-

BGC (White et al. 2000), Tree-BGC (Korol et al. 1995) and BALANCE (Grote & Pretzsch 2002, Rötzer et al. 2010a). For our simulations we use the physiological model BALANCE. However, the potential adaptation processes of beech to future drought stress are not considered in our scenario analysis, as sound knowledge for implementation of such effects in growth models is still scarce (e.g. Aitken et al. 2008). Another measure of stress prevention not considered by the scenario analyses is the possibility of species mixing, e.g. the mixing of beech with sessile oak. Drought stress in beech can be alleviated through inter-specific association with oak (Pretzsch et al. 2013), which is characteristic in the dry and warm northwest area of its range.

Our goal was to analyze and understand how regional climate change, as represented by an ensemble RCM data set, affects the productivity and efficiency of an European beech stand in southwestern Germany. In detail, the objectives of the study were (1) to estimate growth development and productivity, (2) to quantify changes of water-use efficiency and (3) to show the sensitivity to and give prognoses for the productivity and efficiency changes of a beech stand under present and possible future climate conditions.

2. DATA AND METHODS

2.1. Site description

Our study site was located in the Pfälzerwald, one of the largest forests in NW Europe, with an area of 1798 km² (Fig. 1). The Pfälzerwald is located in the south of the federal state of Rhineland Palatinate (49° 02'–49° 37' N, 7° 30'–8° 09' E) in a low-mountain region. The site was located near Merzalben in the Südwestpfalz district (7° 48' E, 49° 18' N, elevation: 550 m above sea level), 1 of about 90 Level II plots around Germany that are part of the ICP-Forests program (<http://icp-forests.net/>).

The climate of the region can be described as fully humid and warm temperate, with warm summers (Cfb according to the Köppen-Geiger climate classification system; Kottek et al. 2006). Originally, the dominant tree species in this region were oak and beech. For economic reasons, pine and spruce have been planted during the last 150 yr.

Our test plot, with an area of 4250 m², was a pure stand of European beech *Fagus sylvatica* (L.) planted around 50 yr ago and comprised 262 trees with an average diameter at breast height of 15.7 cm and an

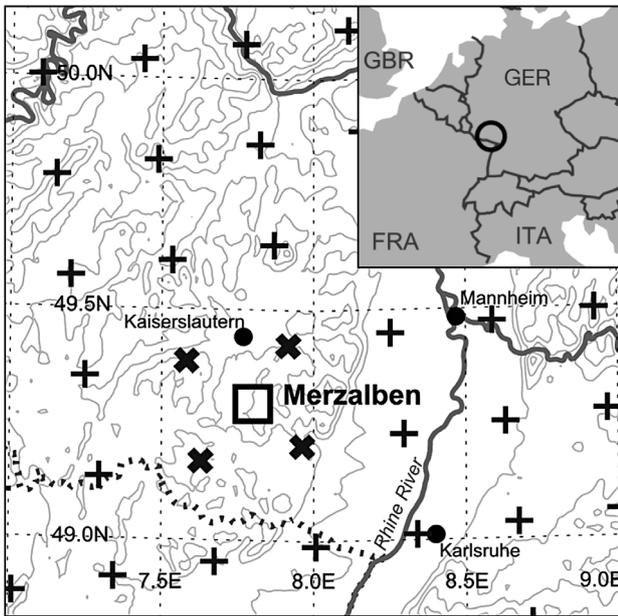


Fig. 1. Geographical overview of the Pfälzerwald study area (circled in the inset). Rectangle: Merzalben study site. +: spatial distribution of 25 km resolution regional climate model grid points (shown here: ENSEMBLES RT2B REMO model grid from MPI-M); ✖: 4 grid elements used to derive the meteorological data time series for the Merzalben site

average height of 18.3 m. These characteristics of the beech stand were used as initial conditions for all scenario simulations.

The soils of the Pfälzerwald are generally nutrient-poor sands derived from red bed sandstones and limestones. For the test plot, Merzalben soil information was determined in December 2008 by the Research Institute for Forest Ecology and Forestry

Rheinland-Pfalz. The soil is a cambisol developed from sandstone. Field capacity and wilting point of 4 layers (0–6 cm, 6–25 cm, 25–55 cm, 55–80 cm) were assessed with 39.5, 33.5, 24.5 and 23.5 vol% and 15.5, 11.5, 7 and 7 vol%, respectively.

2.2. *In situ* meteorological observations

Local quality-controlled and error-corrected meteorological observations in close vicinity to the forest research site were available from a standard weather station operated by the Research Institute for Forest Ecology and Forestry Rheinland-Pfalz (ICP Level 2 site). Data were accessible from 1991 to 2000; we used temperature, global radiation, wind speed, humidity and precipitation at a daily resolution to drive the reference simulations with the BALANCE tree growth model.

2.3. Regional climate change projections

All RCM simulation results used came from the Research Theme 2B of the ENSEMBLES project (van der Linden & Mitchell 2009) (see Table 1 for a listing of the GCM–RCM downscaling combinations included in our ensemble). They were used to assess future climate change and to provide input data for the BALANCE tree growth model. The spatial resolution of the RCMs was 25 × 25 km; the models covered an overall time span from 1961 to 2099 at a daily temporal resolution. All modelling chains used were based on the A1B emissions scenario (see special

Table 1. Listing of regional climate model (RCM) simulations used and their driving global climate model (GCM). In all cases a SRES A1b emissions scenario drives the GCM from 2001 onwards. Total time span covered: 1961–2099, daily temporal resolution (means and totals), spatial resolution 25 × 25 km

Model abbreviation	Driving GCM	Downscaling RCM	Downscaling institution
M1	ECHAM5	RCA3	Met Éireann, Ireland
M2	ECHAM5-r3	HIRHAM5	Danish Meteorological Institute, Denmark
M3	HadCM3Q0 (normal sensitivity)	CLM	Swiss Federal Institute of Technology, Switzerland
M4	HadCM3Q0 (normal sensitivity)	HadRM3	Hadley Centre, Great Britain
M5	ECHAM5-r3	RegCM3	The Abdus Salam International Centre for Theoretical Physics, Italy
M6	ECHAM5-r3	RACMO	Royal Netherlands Meteorological Institute, Netherlands
M7	ECHAM5-r3	REMO5	Max Planck Institute for Meteorology, Germany
M8	BCM	RCA3	Swedish Meteorological and Hydrological Institute, Sweden
M9	ECHAM5-r3	RCA3	Swedish Meteorological and Hydrological Institute, Sweden

report on emissions scenarios [SRES]; Nakićenović & Swart 2000). The time span up to the year 2000 was the control period, with a reference time span (1961–1990) based on 20th century observed emissions, followed by a projection time span up to 2100, split into the near (2021–2050) and far future (2071–2100). Time slices considered in the growth model were from 1991 to 2000 and 2090 to 2099. RCM variables selected were daily mean air temperature, relative humidity, sea-level pressure, wind speed, global radiation, daily minimum and maximum air temperature, as well as daily total precipitation. The time series for the Merzalben site were extracted from a neighbourhood of 4 RCM grid elements using inverse-distance-weighting averaging with a weighing factor of 1.

Regionally downscaled climate projections are prone to many uncertainties (Giorgi 2005). An indication of these uncertainties is the bandwidth of our 9 RCM member ensemble where no weighing is applied, following recommendations for good practice from Knutti et al. (2010).

Because the RCM simulations reveal systematic biases when for example driven by re-analysis data in a validation run and compared to observations, bias corrections are necessary (Piani et al. 2010). We used simple linear scaling as described by Lenderink et al. (2007), which mainly corrects errors in the mean values. Correction factors were determined using 30 yr long-term monthly means for each RCM data set at each model grid point separately based on a reference time span from 1961 to 1990 using the E-OBS v3.0 gridded (25 × 25 km) observational reference data set (Haylock et al. 2008). As part of the bias correction, RCM air temperature time series (mean, min. and max.) were height corrected with a temperature gradient of 0.65 K/100 m throughout the year up to the altitude of the Merzalben study site. This correction was carried out after extraction of the temperatures from the RCM results and before spatial averaging. Due to data availability, only precipitation could be bias-corrected in addition to the aforementioned temperature variables.

2.4. The physiological tree growth model

BALANCE

This section only provides an overview of the model processes relevant to this study; a comprehensive description of the model BALANCE can be obtained from Grote & Pretzsch (2002) or Rötzer et al. (2005, 2009, 2010a).

2.4.1. Structure

BALANCE simulates the 3-dimensional development of individual trees and estimates the consequences of environmental influences such as competition, stand structure, species mixture and management impacts. It includes simulations of the microclimates for every tree and represents total water and carbon flows. Individual tree development is described in response to its environmental conditions, which change with individual tree development (Grote & Pretzsch 2002). Thus, each individual tree is structured in crown and root layers, which are in turn divided up into 8 crown and root segments. In this way, tree growth can be simulated for spruce, beech, pine, oak and Douglas fir in any kind of species mixture or stand structure.

2.4.2. Water balance

To calculate water balance, the soil conditions in different layers are considered for every individual tree. Soil water can be exchanged between the rooted and un-rooted soil layers of a tree. The change in soil water content for each layer is derived from precipitation, percolation, interception and actual evapotranspiration. While both throughfall precipitation and interception are estimated, stem flow is not regarded explicitly. Potential evapotranspiration (et_p) is calculated by using the Penman-Monteith approach (e.g. Allen et al. 1998). Actual evapotranspiration is calculated considering potential evapotranspiration and maximum water uptake, which is derived from the water content within the soil volume that contains fine roots.

2.4.3. Physiological processes

The daily resource availabilities per layer of each individual tree are summed up for 10 d, the period for which the physiological processes and the biomass changes are calculated. These processes are photosynthesis, respiration, nutrient availability, carbon allocation and growth of the compartments. Photosynthesis is computed as a function of the absorbed photosynthetically active radiation (PAR), air temperature and internal CO₂ concentration for each segment of a tree (Haxeltine & Prentice 1996). Relative light consumption is calculated according to the competition algorithm of the growth simulator SILVA (Pretzsch 1992) and extended by a light extinction

function of a Lambert-Beer type. Photosynthesis depends on leaf surface area and can be reduced by the lack of water and nutrients, as well as by pollutants. The internal CO_2 supply depends on the stomata conductivity which is a non-linear function of the soil water supply. Thus, water balance is linked with photosynthesis by reducing the net assimilation of the segment via stomatal closure. For the scenarios in this study, the trees' soil water and nutrient status was assessed at their optimum at the beginning of the simulations. Maintenance respiration and growth respiration comprise the total respiration, whereby maintenance respiration is calculated as a function of biomass, specific respiration rate and temperature, and growth respiration is estimated as a constant fraction of the maximum photosynthesis (Penning de Vries et al. 1989).

2.4.4. Allocation and biomass increment

The carbon available for allocation is distributed between the single compartments foliage, branches, stem, coarse and fine roots depending on their growth and respiration demands, which are defined by the relationships between the compartments according to the functional balance theory (Mäkela 1990) and the pipe model theory (Chiba 1998). Biomass increase is the result of the interaction of physiological processes which depend on the physical and chemical microenvironment that is itself influenced by the stand structure. Above-ground biomass is calculated from stem biomass and the sum of the foliage, twig, branch and bud biomass of all segments and layers. Below-ground biomass is the sum of fine and coarse root biomass of segments and layers.

2.4.5. Foliage development

To illustrate the relationships between environmental influences and growth, the annual cycle of foliage development must be known. With the beginning of bud burst, the foliage, biomass, leaf area, light availability and radiation absorption change. Thus, the date of foliage emergence in a tree determines its assimilation and respiration rate, but also affects the environmental conditions of the trees in its vicinity. In BALANCE, the beginning of bud burst is modelled by using a temperature sum model (Rötzer et al. 2004), while foliage senescence is estimated in dependence on cumulative respiration (Rötzer et al. 2010a).

2.4.6. Validation

Validation studies of the model BALANCE have already been done for several species, sites and climate regimes in Central Europe. It has been shown that fundamental processes and variables such as the photosynthesis, micro-climate, or foliage senescence of an individual tree can be reproduced realistically (Rötzer et al. 2010a). For example, the correlation between measured and modelled assimilated carbon for beech showed an r^2 between 0.7 and 0.8 (Rötzer et al. 2010a). Furthermore, simulated parameters of the stand dynamics, like water balance, growth and annual development, closely match those measured (Grote & Pretzsch 2002, Rötzer et al. 2005, 2010a). A model validation has also been performed successfully for the Merzalben study site (Liao 2011). Figs. 2 & 3 depict comparisons of the independent data sets of beeches in Merzalben and the simulated results. The specific leaf areas of 2 randomly chosen individual trees corresponded well with the simulated values (Fig. 2). The results were similar when the simulated diameter at breast height and height data were compared to measured data (Fig. 3), which were based on stem disc samples from the Merzalben site and their recalculations for 20 yr.

Because site-independent base processes of the model are validated sufficiently, and site-dependent growth variables have been validated based on independent data, BALANCE is able to realistically simu-

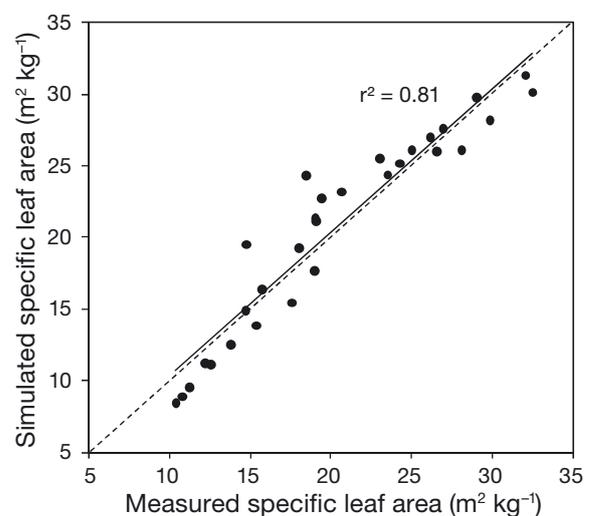


Fig. 2. *Fagus sylvatica*. Simulated and measured specific leaf area of 2 beech trees from the Merzalben site in the year 2009 (measured data: University of Trier, Faculty of Geography and Geosciences, unpubl. data)

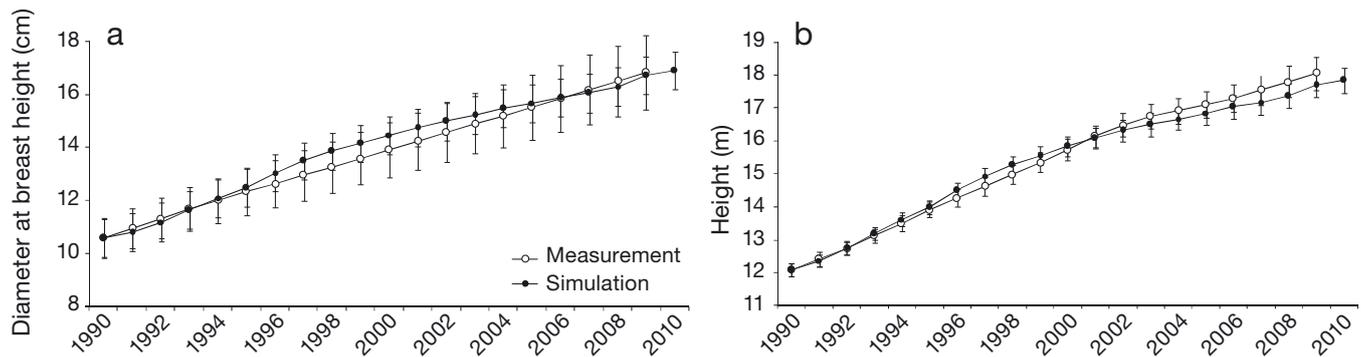


Fig. 3. *Fagus sylvatica*. Simulated and measured data based on stem disc samples of (a) the mean diameter at breast height and (b) mean height for a beech stand at the Merzalben site over 20 yr. Error bars: \pm SD

late beech stand growth for the Merzalben site. Due to the availability of observational reference data and computational constraints for the impact study, 10 yr time spans from 1991 to 2000 and 2090 to 2099 were used.

3. RESULTS

3.1. Past climatic conditions

Although the BALANCE model uses a number of meteorological inputs, we limited the discussion of past and future climatic conditions to air temperature and precipitation. The average annual cycles of air temperature and precipitation at the Merzalben weather station site during the tree growth model reference period from 1991 to 2000 are shown in Fig. 4.

The annual cycles derived from the RCM control runs are plotted along with observations to allow a qualitative comparison. Actual observations rather than statistical properties could only be reproduced by the RCM if they were driven by re-analysis data in a validation run setup. A comparison of empirical distributions of daily data on a monthly basis for 10 yr from 1991 to 2000 revealed fairly good agreement between the RCMs and local observations (data not shown). Within this time span, the multi-model mean provided a close match with the respective E-OBS reference data (not plotted) used for determining the bias-correction factors (1961–1990). The long-term mean annual cumulative precipitation was 818 mm in the models versus 800 mm in the E-OBS data, average air temperatures were 8.5°C (multi-model mean) versus 8.2°C (E-OBS). Note that the multi-model mean is only used for easier interpretation, it is not used to drive the BALANCE growth model.

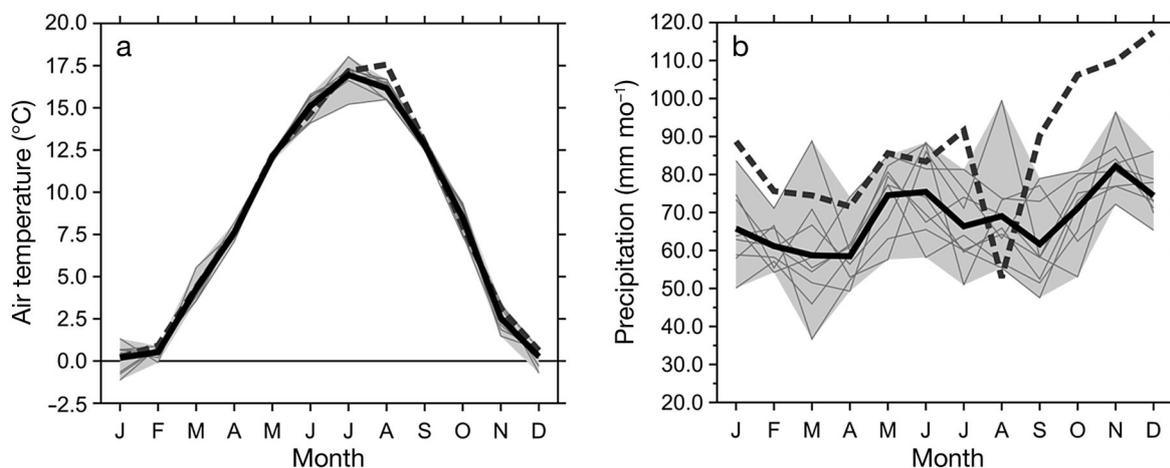


Fig. 4. *Fagus sylvatica*. Annual cycles of (a) 2 m mean air temperature ($^{\circ}$ C) and (b) total precipitation (mm mo^{-1}) long-term monthly means (1991–2000); local meteorological observations (dashed line) and RCM simulations multi-model mean (9 ensemble members) (black line); and overall multi-model bandwidth (grey shading) including individual model realizations (M1 to M9) (grey lines). Data source: Merzalben weather station; ENSEMBLES RT2B RCMs, linear-scaling bias correction

3.2. Future climate change

Fig. 5 summarizes the regional climate change and associated bandwidths that effectively drive the impacts. It shows the relative change in 10 yr seasonal means of near- and far-future projections with reference to the past control time span for the total ensemble (box-whisker plots) and the individual modelling chains.

There was an obvious tendency towards higher air temperatures throughout all meteorological seasons, associated with a strong temperature signal (Fig. 5a). There was no overlap of the near- and far-future distributions between the lower and upper quartile. The multi-model mean during winter changed from an increase of about 1.2°C (median = 0.9°C) in the near to about 3.0°C (median = 2.7°C) in the far future. In summer, a change from about 1.1°C (median = 0.6°C) to about 3.1°C (median = 2.7°C) of the multi-model means was projected, whereas the ensemble bandwidth increased from 1.9°C during winter to 3.5°C in summer for the far future. The individual model results were fairly equally distributed over the ensemble bandwidth. Each of the modelling chains was considered as equally likely in the present experimental setup.

The change signals for precipitation (Fig. 5b) were less well defined than those for temperature, with a tendency towards slightly more clustered results. For meteorological winter, there was a clear tendency towards higher precipitation amounts from a multi-

model mean of 12.6% (median = 12.2%) to 27.4% (median = 26.3%). Spring and autumn exhibited no clear tendency in the near future. In the far future, the increases in the multi-model means were about 14.6 and 13.3%, respectively. Summer showed slightly positive tendencies for the near future, with a median of 4.1%; in the far future all but 1 RCM ensemble member projected negative change tendencies, albeit with a multi-model mean of -20% (median = -21.4%) and a minimum of up to about -40%. These results are well in line with previous studies for Europe based on similar model results (e.g. Christensen & Christensen 2007).

3.3. Tree growth, productivity and efficiency

The development of the total living biomass (b_{tot}) at the Merzalben site for the 10 yr simulation time slices driven by the 9 control and scenario RCM runs and the meteorological reference observations exhibited intra-annual ups and downs—mainly caused by the leaf and fine root biomass—as well as a steady increase in the living biomass (Fig. 6).

The initial total biomass of 58.1 t, based on the measured Merzalben climate, increased to 76.4 t at the end of the 10 yr period, while b_{tot} based on the 9 control runs reached values between 65.6 and 84.0 t in the last year of the simulation. Under the future climate conditions of Scenario A1B, the simulations displayed a wide range of values for the total living bio-

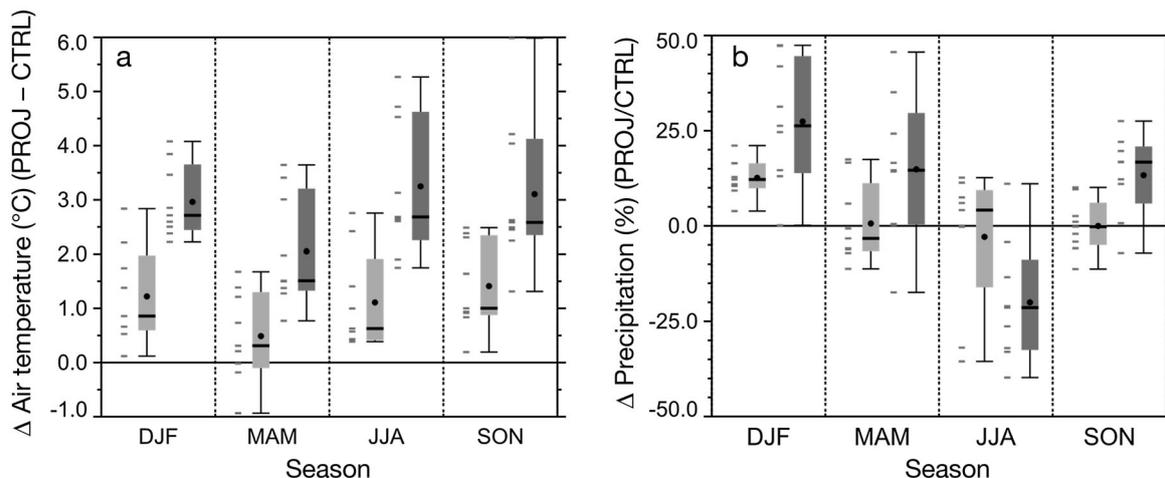


Fig. 5. Seasonal changes of (a) the mean near-surface air temperature (°C) (projection minus control) and (b) the average precipitation (%) (projection/control) during the meteorological seasons (DJF: December–February; MAM: March–May; JJA: June–August; SON: September–November) for the Merzalben forest site from 2041 to 2050 (light grey) and 2090 to 2099 (dark grey), with reference to 1991–2000. The spread of the 9 model combinations is represented by the short horizontal lines. The box-whisker plot summarizes this distribution statistically—whiskers: minimum and maximum; box: lower and upper quartile; horizontal line in box: median; black dot: arithmetic mean, i.e. multi-model mean. Data source: ENSEMBLES RT2B, linear-scaling bias correction

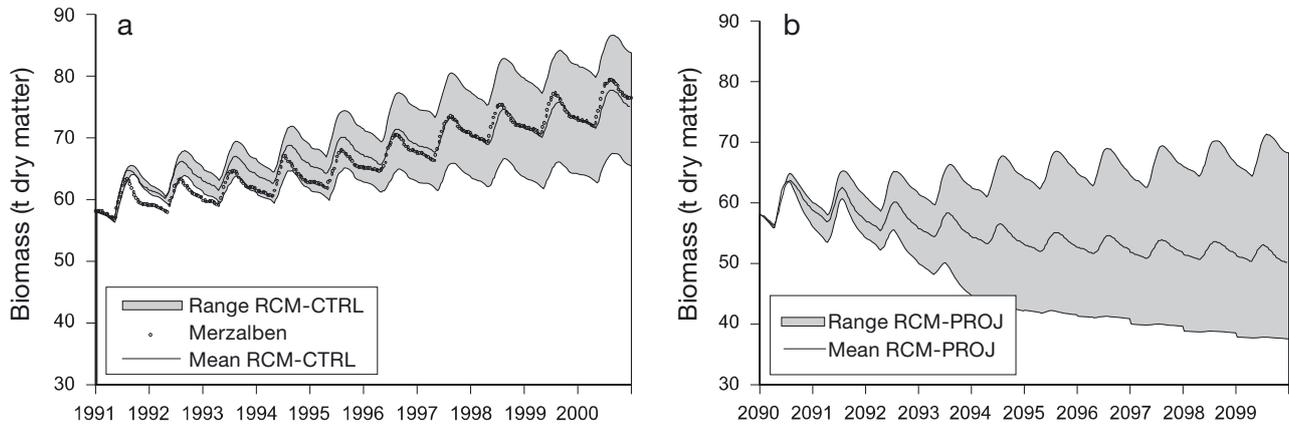


Fig. 6. *Fagus sylvatica*. Total living biomass development for the beech stand based on reference climate data (Merzalben) and range compared to mean b_{tot} under simulated climate conditions of the SRES A1b emissions scenario for (a) the regional climate model (RCM) control period (1991–2000) and (b) the projected period (2090–2099)

mass. The boundaries, i.e. the highest and lowest b_{tot} values at the end of the simulation period, were found for M8 and M1, respectively. Under the M8 scenario, b_{tot} increased to 68.3 t. Conversely, under the M1 scenario, b_{tot} decreased to 37.6 t. On average, a total living biomass of 49.8 t was simulated for the 9 scenarios, which amounted to a decrease of 8.3 t for the *Fagus sylvatica* stand after 10 yr.

The productivity of a forest stand can be effectively described by the net primary productivity (npp) based on the stand area. All 9 climate scenarios displayed higher npp values for the control runs than for the projected periods (Fig. 7a). Annual npp ranged from 8.5 to 12.1 t C ha⁻¹ yr⁻¹ under the climate conditions of the control runs and from 3.9 to 10.9 t C ha⁻¹ yr⁻¹ under the climate conditions of the projected future periods.

Based on the reference data for Merzalben, a mean annual npp of 10.0 t C ha⁻¹ yr⁻¹ was calculated (Fig. 7b). The annual npp for the control period averaged over the 9 climate scenarios was 10.5 t C ha⁻¹ yr⁻¹, which was close to the reference value. For the projected period, a significant drop in the average annual npp to 7.5 t C ha⁻¹ yr⁻¹ was observed ($p < 0.01$), revealing a decrease of 3 t C ha⁻¹ yr⁻¹. Compared to the reference this was a reduction of 30%.

Water-use efficiencies (wue) for the beech stand defined as the ratio between npp and the sum of the actual evapotranspiration (et_a) were calculated from the annual values for the 9 climate scenarios (Fig. 8) and varied greatly depending on the RCM used. Under RCM control conditions, wue ranged from 4.6 (M6) up to 7.2 (M8) or 7.4 g kg⁻¹ (M9). For the scenarios of the projected future period efficiencies, be-

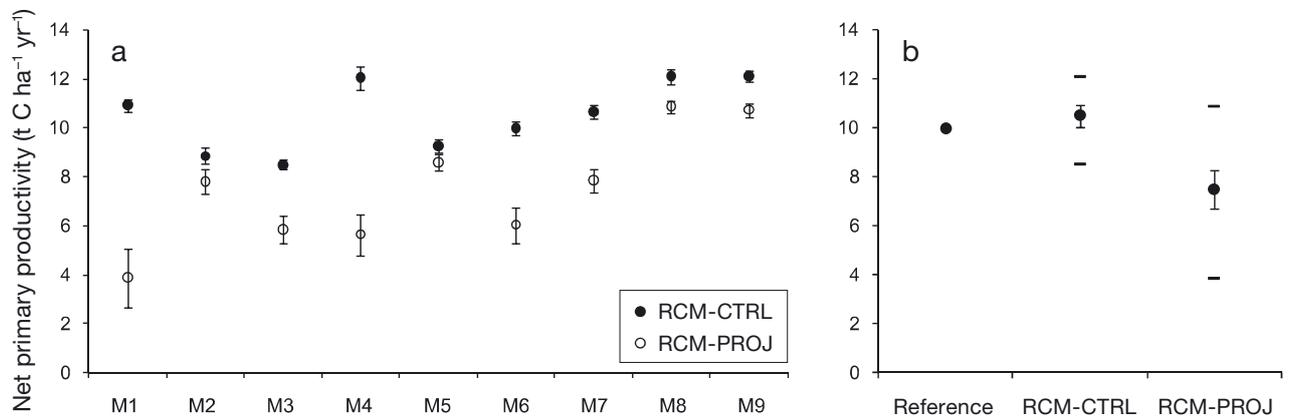


Fig. 7. *Fagus sylvatica*. Average annual net primary productivities of the beech stand (a) based on the 9 climate simulations, M1 to M9, for the control (RCM-CTRL) and projected periods (RCM-PROJ) (SRES A1b emissions scenario) and (b) based on measured climate records for the period 1991–2000 (reference) and averaged for the 9 climate scenarios for both the control and projected periods (means, SE, min., max.)

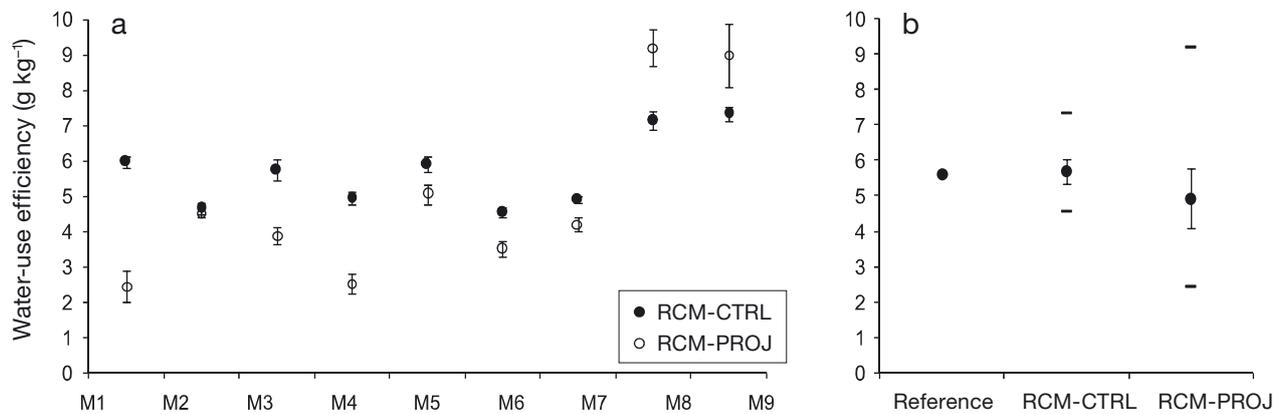


Fig. 8. *Fagus sylvatica*. Average water-use efficiencies for the beech stand (a) based on the 9 climate simulations, M1 to M9, for the control (RCM-CTRL) and projected periods (RCM-PROJ) (SRES A1b emissions scenario) and (b) based on measured climate records for the period 1991–2000 (reference) and averaged for the 9 climate scenarios for both the control and projected periods (means, SE, min., max.)

tween 2.5 (M1) and 9.2 (M8) or 9.0 g kg⁻¹ (M9) were calculated. Compared to the control runs, the latter 2 efficiencies were higher for the future, while for all other climate scenarios *wue* was lower or equal under projected future climate conditions. Averaged over the 9 climate simulations, the *wue* of the RCM control was 5.7 g kg⁻¹, which was very close to the value calculated for the reference, i.e. for the measured climate data (5.6 g kg⁻¹; Fig. 8). The mean for the projected future climate was clearly lower (4.9 g kg⁻¹), indicating a 13% reduction compared to the reference. Hence, the beech trees were less efficient under future climate conditions. However, the values were not significantly different ($p > 0.1$) because, particularly under the projected future climate conditions, considerable fluctuations in *wue*, between 2.5 and 9.2 g kg⁻¹, were noted.

3.4. Causal explanations for changed productivities and efficiencies

In order to find causal explanations for the productivity and efficiency changes of the beech stand, the outputs based on the growth model BALANCE were analyzed in more detail. With the changing climate, the growing season became longer under projected future climate conditions (Table 2). A clear but not significant ($p > 0.1$) difference of 9 d in growing season length was evident between the reference and control runs. This was caused by a greater delay in the end of the growing season (13 d) than in the beginning (4 d). Compared to the control runs, the projections showed significant elongation ($p < 0.02$) of the growing season by a total of 12 d. This was

Table 2. *Fagus sylvatica*. Average simulated start, end and length of the growing season for the beech forest in Merzalben for the reference, control (CTRL) and projected (PROJ) periods of the 9 regional climate models (RCM)

Scenario	Growing season		
	Beginning	End	Length (d)
Reference	29 Apr	8 Oct	162
RCM-CTRL	3 May	21 Oct	171
RCM-PROJ	25 Apr	25 Oct	183

based on an earlier beginning of 8 d along with a later end of 4 d.

Competition between individuals, stress, aging, etc. are responsible for tree mortality. For the reference period from 1991 to 2000, BALANCE simulated the death of 45 out of 262 trees (mortality rate: 17%). In simulations based on the RCM control runs, 47 trees died (mortality rate: 18%), which was not significantly different from the reference run ($p > 0.1$). On average, the mortality in the projected future periods was significantly higher than in both the reference and control periods ($p < 0.02$), with 59 dead trees (mortality rate: 22%).

Water consumption of a tree—expressed here as its actual cumulative evapotranspiration—is closely linked with its productivity. An average annual actual evapotranspiration of 356 mm was simulated for the beech stand for the reference climate data set. For the control runs of the 9 climate models, the average et_a summed up to 378 mm, which was not significantly higher than the value for the reference ($p > 0.1$). However, et_a for the projected future periods (321 mm) was significantly ($p < 0.1$) lower than the value for the control runs.

A simple way of identifying drought periods is to calculate drought indices, for example, the Martonne index, which is defined as precipitation divided by temperature plus 10. We analyzed this index for the period April–October. An average index of 24.4 was calculated for the reference period. This is not significantly different from the value computed for the mean of all control periods (21.6; $p > 0.1$). Compared to reference and control periods, the index for the projected future periods was lower (18.8), which indicates an increase in drought stress in the 10 yr period. Due to strong inter-model differences, the indices of the control and projected periods were not significantly different ($p > 0.1$).

4. DISCUSSION AND CONCLUSIONS

By using the physiological growth model BALANCE, tree growth was simulated for a beech stand in Merzalben, located in the southwestern part of Germany. The simulations were done for a 10 yr period based on daily meteorological observations and 10 yr time series from control runs and future climate projections of a 9 model RCM ensemble. In terms of background information, regional climate change was assessed by analyzing air temperature and precipitation changes on a seasonal basis. Despite the large, albeit desired, bandwidth of the far-future projections with reference to the control runs, the ensemble was in line with many previous results showing wetter winters and dryer summers on average, with an overall air temperature increase in all seasons (e.g. Christensen & Christensen 2007).

4.1. Productivity and efficiency under present and future climate conditions

After the end of the last glaciation around 5000 BC (Atlantic/Subboreal periods), beech occupied no more than approximately 50% of the area occupied today. The species colonized the remainder of today's native range during the following millennia, with expansion of the beech area still going on (Bradshaw et al. 2010). Since human influence on European forests began, beech has been severely decimated by clearings for agricultural land or, during the last centuries, by replacement in the forest by faster and straighter growing conifers such as spruce, fir and pine species (Mantel 1961). Without human interference, beech would probably cover more than two-thirds of the forest area in Central Europe (Bohn et al.

2003) instead of their current share of less than one-fifth (Fischer & Fischer 2012).

When the impact of the current climate was compared to the influence of future climate conditions, net primary productivity of beech decreased by 30% (Fig. 7). The mean annual *npp* values of 10.0 t C ha⁻¹ yr⁻¹ for the reference and 10.5 t C ha⁻¹ yr⁻¹ under the climate conditions of the control runs correspond well with the known data for beech (e.g. Bergh et al. 2003, Pretzsch et al. 2012). The productivity values for the Merzalben site were somewhat higher than those Rötzer et al. (2010b) estimated for beech stands in western Germany (between 5.2 and 8.6 t C ha⁻¹ yr⁻¹). Differences could either be due to the considered periods, altered stand structures (e.g. stand age, stand density), or different site conditions (precipitation, soil conditions, light regimes). Mund et al. (2010) calculated a mean *npp* value of 7.3 t C ha⁻¹ yr⁻¹ for an old-growth mixed beech forest in central Germany for the period 2000–2005, but emphasized that the mean inventory-based *npp* was 30% higher, i.e. around 9.5 t C ha⁻¹ yr⁻¹.

The average drop in the *npp* to 7.5 t C ha⁻¹ yr⁻¹ for the projected periods based on the RCM ensemble was probably caused by the more frequent and intensive extreme climate events, like droughts or heat waves, but also by the higher mean temperatures and lower cumulative precipitation, particularly during the summer months, of the projected time spans. Because beech trees were not precipitation-limited at the study site under the present climate conditions (the mean cumulative precipitation was approximately 1000 mm yr⁻¹), the effect of climate change on beech productivity was representative of many central European beech forest stands.

The climate scenarios used for this study indicated clear decreases in the amounts of precipitation in summer months (Fig. 5), which, together with higher temperatures, induced drought. The very low Martonne indices and very low et_a/et_p ratios that we found for single years of the climate scenarios were the result of intense drought periods in the summer months; this was also reported by the IPCC (2012) for future climate scenarios. Ciais et al. (2005) calculated a mean reduction in productivity of 0.2 t C ha⁻¹ mo⁻¹ for European forests in the hot and dry summer of 2003, compared to the period 1998–2002. This was a decrease of 16% for the entire year. Based on eddy flux measurements, the same authors found particularly large reductions in the net ecosystem productivities of beech forests in Hesse/France and Hainich/Germany for the year 2003 when compared with 2002.

Studies on the behaviour of beech trees under water-stress conditions within (Gärtner et al. 2008) or close to the border (Fotelli et al. 2008) of its natural range often ignore the species-specific and site-specific stress tolerance. Anisohydric species such as beech continue transpiring and growing despite drought stress until water runs out (Hartmann 2011). Therefore, their growth rates decrease less, but the risk of morphological changes or losses of fine roots and leaves due to cavitation of the water-conducting pipes increases. Río et al. (2013) showed for several common tree species in Europe that facilitation effects can reduce water-stress in harsh environments, while competition can aggravate stress even in mild environments.

Kölling et al. (2007) stated that beech is able to withstand annual mean temperatures of up to 13°C if there is sufficient water supply. In the present study, the annual mean temperatures for the projected periods were above this threshold for some scenarios. Additionally, precipitation was—particularly in the summer season—clearly limited. Both these factors contributed to a reduction in the *npp* of 30%. Notably, Geßler et al. (2007) found that an increase in drought frequency reduces the growth of beeches. This outcome highlights the *npp* decrease found in this study for the future climate projections in which more drought stress was observed than in control periods.

The efficiencies (based on water consumption) of the beech forest stand in Merzalben for the reference and average control runs (5.6 and 5.7 g kg⁻¹ respectively), were similar to each other and matched the literature data well (e.g. Polster 1950). Pretzsch et al. (2012) found *wue* values of 4.3 and 7.5 g kg⁻¹ (for Central European regions under current climate conditions), which decreased clearly in dry years. Under future climate conditions, which imply warmer and dryer conditions, we calculated lower efficiencies for most of the climate projections. The *wue* for all future climate projections was, on average, 4.9 g kg⁻¹, which denoted a drop of 13%. The reduction in *wue* under (drought) stress conditions within a year (e.g. 2003) compared to a year with favourable growing conditions was also found by Reichstein et al. (2007). This has also been reproduced in the published productivity and evapotranspiration data for an aspen forest (Barr et al. 2007) and for a temperate spruce forest (Grünwald & Bernhofer 2007). Consequently, productivity and efficiency of beech stands will decrease under the warmer and—in the summer months—drier climate conditions predicted for the future. Lower mean annual *wue* in our case led to

lower *npp* values and/or higher *et_a* values cumulated for the entire year. Higher temperatures and a sufficient water supply in the spring months may, for example, enhance *et_a* more than *npp*, while drought periods in summer may reduce *npp* more strongly than *et_a*, both patterns leading to a drop in *wue* for beech under the climate scenarios used here. These are species-specific reactions as beech respond in an anisohydric way (Lyr et al. 1992). Rötzer et al. (in press) found in another simulation study that the *wue* of a spruce and a pine stand in southern Germany increased under climate change conditions compared to that under present climate conditions. Note that in the simulation studies shown here, higher CO₂ concentrations were not considered. Taking higher CO₂ concentrations into account, the mean annual *wue* values of forest stands may also increase, particularly for isohydric species like spruce. First simulations with the model BALANCE support this assumption (authors' unpubl. data), which is also presented by Penuelas et al. (2011) in their review paper for 47 study sites worldwide.

4.2. Causal explanation for the expected changes

To provide causal explanations for the productivity and efficiency changes that were found for the beech stand in Merzalben under the possible future climate conditions of 9 RCMs, we analyzed possible changes in the length of the growing season, the mortality rate, the trees' water consumption and drought stress.

Growing season length increased by about 12 d under future climate conditions. The simulated lengths based on measured data and control runs of 162 or 171 d corresponded with the range of observed lengths for the beech stand in Merzalben for the years 2008–2010, with values between 166 to 179 d (H. W. Schroeck unpubl. data). Chmielewski & Rötzer (2001) found an increase in the length of the growing season for Europe of 5 d if temperature increases by 1°C. This finding is close to our results, i.e. an increase of 4.0 d per 1°C temperature increase based on the multi-model mean of the temperature increase for Merzalben of 3.0°C and an elongation in the growing season of 12 d. Assuming an increase of the annual mean temperature in Europe of 0.3°C per decade (Jones & Moberg 2003) and assuming that the increase in the length of the growing season is mainly determined by the earlier beginning of the growing season (Chmielewski & Rötzer 2001), the earlier leaf onsets of 2.2 and 2.3 d decade⁻¹—found by Schwartz et al. (2006) and Parmesan & Yohe (2003), respec-

tively—are equal, respectively, to elongations of the growing season of 7.3 and 7.7 d per temperature increase of 1°C. Elongation of the growing season lengthens the duration of photosynthesis for the deciduous tree species beech. The direct climate effect could thus be mitigated but not completely compensated.

Mortality can diminish the productivity of a forest stand and with it the stand's efficiency. As a consequence, photosynthetically active biomass is reduced. In our study, the mortality rate was significantly higher ($p < 0.02$) under future climate conditions than in the control runs, reducing the productivity of the entire stand. Geßler et al. (2007) report that a changing climate affects the vitality and growth of beech trees, as well as their competitive ability. In our simulations, this effect results in higher mortality rates. As a response to climate change, recently increased drought periods and/or higher temperatures may have already produced higher tree mortality in Europe (Allen et al. 2010). The same authors stated further that short drought periods may cause higher mortality rates in deciduous temperate forests than in evergreen temperate forests. These findings are in line with our simulated higher mortality rate under the warmer and dryer future conditions expected for the beech stand in Merzalben. The stand's productivity decline, induced by changed climate conditions and a higher mortality rate, could not be compensated for, despite the higher growth rates of trees which grow close to dead trees and should therefore be more productive because their resource supplies, i.e. light, water and nutrients, are increased.

The average annual actual evapotranspiration of the beech stand was simulated with 356 mm for the measured climate period and 378 mm for the control runs of the 9 climate models. These values correspond well with the modelled annual evapotranspiration of 387 mm in Merzalben for the same period calculated by Karl et al. (in press). A significantly lower ($p > 0.1$) average evapotranspiration of 321 mm for the projected future periods may result in lower C-assimilation rates, as lower transpiration values mean lower CO₂ supply for the leaves via stomatal closure (assuming a constant CO₂ concentration in the atmosphere, but see the next subsection). Consequently, under future climate conditions, the productivity and efficiency of beech is lower because the productivity decrease is higher than the decrease in evapotranspiration.

Drought stress, predominantly within the growing season, can decrease the productivity and efficiency

of a forest stand (e.g. Ciais et al. 2005, Geßler et al. 2007). The climate-based Martonne index indicates the drought stress of trees under future climate conditions, i.e. limited water supply for an individual tree, which leads via lower transpiration rates (see previous paragraph) to lower productivity and also lower *wue* values. As a consequence of lower productivity, leaf biomass in the next period will be reduced, which again lowers productivity but also decreases the tree's transpiration, i.e. lowers drought stress.

4.3. Future challenges

With respect to future climate change impact studies, higher resolution model results are being developed (e.g. Giorgi et al. 2009). In combination with more sophisticated non-linear RCM bias-correction methods like quantile mapping (e.g. Themeßl et al. 2011) and new, more complete reference data sets, larger ensembles and forcing data sets will evolve that are more suited to local impact assessments.

A major challenge in forest growth modelling will also be to include the rising CO₂ concentration of the atmosphere in addition to changed climate conditions. Process-based growth models like BALANCE can explicitly simulate the underlying physiological processes, i.e. they allow a mathematical description of the environmental regulations that affect mesophyll conductance. Thus, the impact of the CO₂ concentration in the chloroplast and, consequently, the rate of photosynthesis can be calculated. For example, Norby et al. (2005) and Körner et al. (2005) found increasing growth rates in the first years of CO₂ enrichment, followed by decreasing increments in subsequent years. However, it is still controversial how altered CO₂ concentrations in the atmosphere influence physiological processes and, in turn, tree and stand growth (e.g. Körner 2006, Bugmann & Bigler 2011). In addition, the nutrient cycles of nitrogen or phosphorus have to be considered when modelling tree growth because feedback and feed-forward reactions may remarkably change growth rates (e.g. Magnani et al. 2007).

The revealed stress reactions to climate change reflect the specific challenges which lie ahead for forest ecosystem managers. With the decrease in productivity, the forests' contribution to carbon storage and climate change mitigation will diminish. Productivity loss is closely linked with a reduction of fitness and competitive strength, in comparison with more drought-stress-tolerant species such as oak (Pretzsch

et al. 2013, Rigling et al. 2013). The latter will expand their range, narrowing the range of beech and thus jeopardizing the broad range of functions and services unique to beech ecosystems worldwide. Therefore, a future challenge will be to stabilize beech stand growth under climate change.

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