

Stomatal conductance and intrinsic water use efficiency in the drought year 2003: a case study of European beech

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Abstract

Key message Beech trees were able to cope with the drought of 2003. Harmful water shortage has been avoided by an effective stomatal closure while use of carbon storage pools may have prevented carbon starvation and growth reduction.

Abstract We applied hydrodynamic modeling together with a tree ring stable isotope approach to identify the physiological responses of beech trees to changing environmental conditions. The drought conditions of the extreme hot and dry summer in 2003 were hypothesized to

significantly influence the radial growth of European beech mainly triggered by the stomatal response towards water scarcity leading, in turn, to a decline in carbon assimilation. The functional–structural single tree modeling approach applied, revealed in fact a strong limitation of water use and carbon gain during drought. However, tree ring width data did not show a clear drought response and no differentiation in radial growth during six subsequent years examined (2002–2007) has been observed. Using integrated results from mechanistic carbon–water balance simulations, tree ring carbon and oxygen isotope analysis and tree ring width measurements we postulate that the suggested drought-induced growth decline has been prevented by the remobilization of stored carbohydrates, an early onset in growth and the relatively late occurrence of

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the severe drought in 2003. Furthermore, we demonstrate that the stomatal response played a significant role in avoiding harmful water tension that would have caused xylem dysfunction. As a result of the combined investigation with physiological measurements (stable isotope approach) and hydrodynamic modeling of stomatal aperture, we could give insights into the physiological control of mature beech tree functioning under drought. We conclude that beech trees have been operating at their hydraulic limits and that the longer or repeated drought periods would have affected the growth considerably.

Keywords *Fagus sylvatica* · Intrinsic water use efficiency · Leaf physiology · Stomatal conductance · Carbon and oxygen stable isotopes · Hydrodynamic modeling

Introduction

An increasing vulnerability of forests in many regions worldwide towards climate change-induced drought stress has been described recently by various authors (Allen et al. 2010; Lindner et al. 2010; Anderegg et al. 2012; Choat et al. 2012; Cailleret et al. 2014; Rais et al. 2014; Anderegg et al. 2014; Doughty et al. 2015). Drought stress, e.g., induced by increased evaporation, has been identified as a reason for global forest dieback (Adams et al. 2009; Allen et al. 2010; Breshears et al. 2013). Moreover, even below the threshold of mortality, a general decline in productivity due to dry conditions can be expected from reduced assimilation and a relatively low sink priority for growth (e.g., Wiley and Helliker 2012) or due to drought-induced tissue damages decreasing their functionality and requiring additional carbon expenses for repair (e.g., Palacio et al. 2014). As an example, the extraordinary dry growing season in 2003 in Europe leads to an estimated reduction in gross primary productivity in ecosystems over Europe of about 30 % (Ciais et al. 2005). In forest ecosystems a reduction in annual radial growth has been observed in response to this drought year (e.g., Granier et al. 2007) but exceptions have also been noted (Hartl-Meier et al. 2014). In particular for European Beech (*Fagus sylvatica* L.), which is widespread in central Europe, growth decline has been demonstrated at various sites (Löw et al. 2006; Jump et al. 2006; van der Werf et al. 2007; Charru et al. 2010; Maxime and Hendrik 2011).

Two main hypotheses have been put forward to explain the reduction of tree growth and increased mortality: carbon starvation and hydraulic failure (McDowell et al. 2008). Carbon starvation summarizes the situation when the carbon demand for maintenance of cellular and defensive metabolism is not met owing to low

carbohydrate supply from photosynthesis and storage (McDowell et al. 2011). However, in several cases carbon starvation has been found to fail explaining growth decline and tree death (Körner 2003; Sala 2009). Nevertheless, the carbon supply status is likely to play an important role for repair and recovery as well as for secondary stress defense (Niinemets 2010). Hydraulic failure, however, seems to be the primary cause of plant mortality during drought due to xylem embolisms (Anderegg et al. 2012; Choat et al. 2012) but might be avoided under high availability of mobile soluble carbon compounds (Adams et al. 2009; McDowell 2011; Gruber et al. 2012; Sevanto et al. 2014).

While carbon starvation is expected to occur during prolonged drought periods in relatively isohydric plants closing their stomata at low xylem water tensions, hydraulic failure is expected to proceed more rapidly especially in relatively anisohydric plants keeping their stomata open during drought (Sevanto et al. 2014). However, because hydraulic functioning and carbohydrate and defense metabolism are strongly interdependent (McDowell et al. 2011), the explanation of growth decline and tree death may require a combination of these two hypotheses and supplementary explanations (Anderegg et al. 2012). While stomatal regulation in vascular plants is an efficient means for adjusting water use to changes in plant water supply and demand (e.g., Aranda et al. 2005; Sperry et al. 2003; Whitehead 1998), the question how the impact on tree metabolism can be described considering a simultaneously reduced CO₂ uptake is still open (Sala et al. 2010; Zeppel et al. 2013). For example, tree species-specific variations in the mobilization of non-structural carbohydrates in response to water shortage and critical thresholds for storage compounds in trees may play an important role for the actual carbon supply during drought (Palacio et al. 2014).

Because water shortage evokes a general predicament for plant gas exchange, i.e., the loss of water to gain carbon (Chaves et al. 2003), the mechanistic description of this tradeoff is essential for the estimation of tree vulnerability to drought stress and of forest growth under future climate conditions. In addition, the representation of relations between carbohydrate availability and hydraulic regulation seems to be fundamental to describe long-term drought responses (e.g., Galiano et al. 2011; Mitchell et al. 2013; Sevanto et al. 2014). We aim to reveal which physiological responses occur and to which degree stomatal closure can be made responsible for growth declines during drought. Therefore, we investigated mature trees of European beech and determined the ratio of H₂O and CO₂ exchange throughout years of contrasting water supply. The intrinsic water use efficiency (IWUE) as calculated by the ratio of assimilation (*A*) and stomatal conductance (*g_s*) is used here as an integrative measure of the carbon and water balance.

IWUE can be derived from the $\Delta^{13}\text{C}$ (carbon isotope discrimination) of tree rings allowing a retrospective view of the physiological responses under different environmental regimes (Farquhar et al. 1989; McCarroll and Loader 2004). The stable isotope composition of plant organic matter, in particular the carbon isotope ($\delta^{13}\text{C}$) and the oxygen isotope signatures ($\delta^{18}\text{O}$), has been widely used to address leaf level acclimation of A and g_s to environmental drivers (see for review Gessler et al. 2014 and Werner et al. 2012). Furthermore, the leaf water enrichment of ^{18}O depends on the ratio of the vapor pressures in the atmosphere and the intercellular spaces of the leaves (Dongmann et al. 1974). Thus, the $\delta^{18}\text{O}$ signature and the ^{18}O enrichment above source water ($\Delta^{18}\text{O}$) of tree rings can be associated to the stomatal sensitivity to changing evaporative conditions (Scheidegger et al. 2000). To capture the short- and long-term responses (c.f. Hentschel et al. 2014), the tree ring isotope composition and the tree ring width were determined throughout a period of six subsequent years (2002–2007), which includes the extremely dry year 2003. Furthermore, we relate our results to the findings of a long-term growth assessment conducted at our study site (see Poschenrieder et al. 2013) covering the period between 1970 and 2010.

Measurements were applied to challenge the current knowledge about stomatal behavior and carbon assimilation by simulating g_s based on a mechanistic, hydrodynamic modeling approach (xylem water flow model, XWF). In the model, the hydraulic conductance of the soil–leaf continuum is functionally linked to the stomatal control of water loss—a fact that might furthermore dictate the limits of a species' tolerance to water stress (Sperry et al. 2002). In the XWF model, g_s is expressed as a function of leaf water potential, which in turn depends on the evaporative demand and the water relations within the soil–leaf continuum (e.g., Bohrer et al. 2005). According to the cohesion–tension theory (Tyree and Zimmermann 2002) and in consideration of tree anatomy and individual branching systems (see for review Cruiziat et al. 2002), the water transport in the soil–leaf continuum can be calculated on a solid physical basis (Hacke and Sperry 2001; Schulte and Brooks 2003; Tyree et al. 1994). Finally, we model the photosynthesis of the individual trees using a biochemical approach established by Farquhar et al. (1980) which has been linked to the XWF model via its dependency on g_s . Therefore, the individual hydraulic pathways of nine mature beech trees were parameterized from terrestrial laser scanning (TLS) images. Thus, the whole tree hydraulic conductance could be linked with transpiration flux, carbon gain and growth rate.

Since various authors have demonstrated a drought-induced growth decline in European beech as mentioned

above, we hypothesized for the drought in 2003 (a) that limited soil water supply should have caused a reduction of the annual radial growth as a major indication of a distinct drought response. Moreover, we assumed (b) that a mismatch between plant available water and evaporation demand occurred, leading to stomatal regulation and reduced H_2O and CO_2 exchange at the leaf level. As a consequence, we expected (c) that a shift in the A -to- g_s ratio towards increasing water use efficiency occurred. The first impact should be visible in the tree ring dimensions, the second should be reflected in the simulation of whole tree hydraulic conductance, and the third in an increased IWUE.

Materials and methods

This study has been designed to examine the IWUE ($\mu\text{mol mol}^{-1}$) of individual trees derived by a hydrodynamic model approach (IWUE_{XWF}) and a tree ring stable isotope approach (IWUE_{iso}). We examined nine mature trees of a closed beech stand in Southwest Germany. The study trees ranged in diameter at breast height between 21.9 and 41.0 cm and in tree height between 25.4 and 34.7 m. To examine the physiological response towards water shortage, we analyze six subsequent years of varying soil water supply (2002–2007) including the drought year 2003.

To evaluate the growth response of the trees, we additionally considered a long-term growth assessment conducted at the same study site that included the nine beech trees mentioned above (Poschenrieder et al. 2013). These authors analyzed a stratified sample of 27 mature beech trees covering the years 1970–2010. The annual radial growth of the individual trees (DBH_i) was determined by two tree cores taken with an angular distance of 90° from each other and one of the cores was taken from the uphill side.

Furthermore, Poschenrieder et al. (2013) contrasted their findings of the NE-exposed study site with a similar growth analysis of an SW-exposed beech stand in close vicinity. To compare the growth and the intrinsic water use efficiency at the two different sites, we conducted an additional tree ring stable isotope analysis at the SW-exposed study site. The study trees selected ($n = 9$) had similar DBH as the trees of the NE-exposed study site. For a direct comparison of the beech trees analyzed for stable isotope composition, we present the mean annual DBH_i of the particular nine beech trees in this study. Due to the availability of TLS images and XWF simulations, however, our study focuses on the NE-exposed study site and the physiological response towards drought of the respective trees (Fig. 1).



Fig. 1 Terrestrial laser scan image of the individual study trees at the NE-exposed study site displayed in *different grey shading*

Study site

The forest where all measurements and the XWF simulations have been conducted is a beech-dominated stand (>90 % *Fagus sylvatica* L.) on the Swabian Alb in Southwest Germany (790 m a.s.l., 8°45'E, 47°59'N), stocking on a steep NE-exposed slope (58–100 %). The trees are 80–90 years old and the stand density is 28 m² ha⁻¹. The soil profile has been characterized as a shallow Rendzic Leptosol derived from limestone associated with a low water holding capacity (Gessler et al. 2005). The soil properties and the hydraulic parameters used for the simulation of the soil water balance can be found in Hentschel et al. (2013).

The study site is located in a narrow valley. Both sites of the valley are covered by old-growth beech-dominated forest and various studies have been conducted to assess

the impact of differences in mesoclimate of the NE- and SW-exposed slope on water fluxes (Holst et al. 2010) and stomatal conductance (Keitel et al. 2003) of beech trees. While both study stands are comparable in structure and age, the SW-exposed study site is characterized by a generally warmer and drier mesoclimate compared to the NE study site (Holst et al. 2004b) and shows lower volumetric soil water contents in 2002–2007 (Holst et al. 2010; Table 1). The soil of the SW-exposed study site is shallower and has less water storage capacity (Gessler et al. 2001, 2004a). A detailed site and forest stand description of both study sites can be found in Holst et al. (2004a), Gessler et al. (2005) and Poschenrieder et al. (2013).

Environmental conditions

The meteorological data have been recorded at the top of a forest walk-up tower (1.5 times the stand height) located within the study stand on the NE-exposed slope. The soil moisture was determined continuously on both study sites (NE and SW slope) with two probes each using the time domain reflectometry method (TDR, CS615, Campbell Scientific). Detailed information on the instrumentation used for the measurements is given by Mayer et al. (2002) and Holst et al. (2004b, 2010).

The drought year 2003 showed the highest seasonal values of air temperature (T ; °C), global radiation (G ; W m⁻²) and vapor pressure deficit of the air (VPD; kPa) and lowest values of precipitation (P ; mm) during the observation period. For the analysis of the tree ring isotope signature we also compared the NE- with the SW-exposed study site. The SW-exposed stand is known to be more prone to drought (Holst et al. 2010), which is indicated by lower volumetric soil water contents (Θ ; %) compared to the NE-exposed site.

To determine different levels of drought stress, the relative extractable soil water (REW; %) was calculated by division of the actual soil water content and the maximal extractable soil water content according to Granier et al. (2007). These authors suggested a threshold of 0.4 REW

Table 1 Meteorological data including air temperature (T), precipitation (P), water vapor pressure deficit (VPD), global radiation (G) and the average volumetric water content in 0–30 cm soil depth (Θ) at the NE-exposed study site

Year	T (°C)	P (mm)	VPD (kPa)	G (W/m ²)	Θ (%)
2002	13.9 ± 4.1	568	0.49	190 ± 95	47 ± 8 (33 ± 9)
2003	16.9 ± 5.0	258	0.88	215 ± 76	37 ± 1 (28 ± 8)
2004	13.7 ± 4.2	416	0.56	199 ± 86	43 ± 8 (27 ± 6)
2005	14.3 ± 4.5	413	0.58	195 ± 85	45 ± 9 (32 ± 7)
2006	15.0 ± 4.5	441	0.62	202 ± 84	45 ± 9 (41 ± 11)
2007	13.8 ± 3.9	414	0.37	198 ± 93	49 ± 7 (34 ± 8)

Except of P , all values are given as arithmetic mean and respective standard deviation of the growing season (01.05–30.09). P is given as sum of the growing season. The *values in brackets* in the last column illustrate Θ of the SW-exposed study site

when soil drought conditions start to induce stomatal regulation. Since the TDR soil water measurements available obtained minor data gaps, we were using the modeled soil water data for the XWF simulation and the REW calculation. The evaluation of soil water simulations resulted in a normalized root mean square error (NRMSE) ranging between 16 and 30 % for particular years (2002–2007), thus, providing a reliable estimate of REW over the whole growing season.

Furthermore, the water deficit within the forest stand was characterized by the actual soil water deficit (Wd; mm) calculated as the cumulative difference of daily precipitation and potential evapotranspiration (pET; mm). The latter was modeled by the Penman–Monteith equation at hourly time steps according to ASCE-EWRI (2005).

XWF modeling

The xylem water flow (XWF) model is based on a functional–structural single tree approach with a detailed representation of the soil–leaf continuum and is implemented within the modeling framework *Expert-N 3.0* (Priesack and Bauer 2003; Priesack et al. 2006; Priesack 2006). The explicit information of the hydraulic pathway of the individual tree is used to determine the maximal water flow rates within the trees on a solid physical basis (Hacke and Sperry 2001; Schulte and Brooks 2003; Tyree et al. 1994). In previous studies, the XWF model has shown a good match with sap flow density measurements (e.g., Janott et al. 2010; Bittner et al. 2012a; Hentschel et al. 2013) and is supposed to provide reliable estimates of stomatal responses. At our study site, in particular, the XWF simulation of twelve individual beech trees resulted in a normalized root mean square error ranging between 12 and 31 % (Hentschel et al. 2013). The Nash–Sutcliffe model efficiency, given as dimensionless value with 1.0 indicating a perfect fit of the model (Nash and Sutcliffe 1970), amounted on average to 0.7 at our study site and 0.75 at the study site of Bittner et al. (2012a).

The water flow in porous media, such as the xylem tissue of trees, can be described by the cohesion–tension theory (Tyree and Zimmermann 2002) and has been calculated as a function of the gradient in water potential following Darcy’s law (Chuang et al. 2006). The pressure drop between the atmosphere and the soil is driven by the evaporative demand of the atmosphere and the water availability of the soil. In the XWF model, a sink/source term is added to the hydraulic pathway to represent the water loss of the crown due to transpiration and the water inflow due to the root water uptake and to solve the one-dimensional Richards equation as suggested by Chuang et al. (2006) and Früh and Kurth (1999),

$$\frac{\partial \theta(\psi)}{\partial t} = \frac{\partial}{\partial l} \left[k(\psi) \cdot \left(\frac{\partial \psi}{\partial l} + \cos(\alpha) \right) \right] - S \quad (1)$$

where θ denotes the volumetric water content ($\text{m}^3 \text{m}^{-3}$) at the time step t (s) for the individual cylinder element with the axial hydraulic conductivity k (mm s^{-1}) as function of the xylem water potential ψ (mm). The vertical position of the cylinder element is given by the height above (positive upward) or the depth below the soil surface (negative downward); the axial length of the element l (mm) and the respective zenith angle α (–). The sink-source term S (s^{-1}) represents the water loss of the outer branches (transpiration) and the soil water uptake by the root elements.

The aboveground tree architectures of nine trees on the NE slope were obtained by TLS conducted in the year 2011 (Hentschel et al. 2013). The point clouds obtained have been further processed into a tree skeleton consistent of connected cylinders with exact position and orientation (Xu et al. 2007). The belowground tree architecture has been modeled according to a beech-specific distribution of coarse and fine roots (Meinen et al. 2009). The XWF model operates at hourly basis and includes a mechanistic description of physiological response derived by the individual tree water status.

A detailed description of the XWF model has been published by Janott et al. (2010), Bittner et al. (2012a) and Hentschel et al. (2013). The parameters applied for the simulations of the carbon–water balance of individual beech trees can be found in the appendix (Table 3).

Stomatal conductance

The stomatal conductance g_s ($\text{mol m}^{-2} \text{s}^{-1}$) can be calculated by Fick’s law in proportionality with the water vapor pressure gradient between the leaf intercellular air spaces and the ambient air (Ewers and Oren 2000),

$$g_s = \frac{E}{\delta_w} \quad (2)$$

where E is the actual transpiration per leaf area ($\text{mol m}^{-2} \text{s}^{-1}$) and δ_w is the water vapor pressure gradient (mol mol^{-1}). Under the assumption of similarity in leaf and air temperature and water vapor saturation inside the leaf, δ_w can be described by the water vapor deficit of the air (Ewers and Oren 2000). The stomatal conductance equation is, however, restricted to a range of environmental variables examined by Phillips and Oren (1998). Therefore, Eq. 2 can be only applied under conditions of $\text{VPD} > 0.1 \text{ kPa}$, $\text{PAR} > 0 \text{ } \mu\text{mol m}^{-2} \text{s}^{-1}$ and for time periods without rain. Following Phillips and Oren (1998), the daily mean of g_s was only calculated for days with a minimum of six suitable estimates at an hourly basis.

In this study, E was simulated by the XWF model (Janott et al. 2010; Bittner et al. 2012a; Hentschel et al. 2013) where the actual transpiration is controlled by the stomatal activity that is driven by the water potential at the leaf level as suggested by Bohrer et al. (2005). Calibrated on beech-specific vulnerability curves (Köcher et al. 2009), the relative reduction f_s of the potential leaf transpiration due to stomatal closure is described as follows,

$$f_s = \max \left[0.1, \exp \left(- \left(\frac{-\psi}{St_b} \right)^{St_c} \right) \right] \quad (3)$$

where St_b (mm) and St_c (–) are curve-fitting parameters and ψ (mm) is the leaf water potential. In the hydrodynamic model, each outer branch of the canopy represents the hydraulic state of the connected leaves (Hentschel et al. 2013) and determines the leaf physiological control of water loss.

Photosynthesis

The XWF simulation of the actual assimilation rate at the leaf level A followed conceptually the modeling of E in a way that the potential CO_2 influx of each leaf segment is limited by g_s . This assumption was made to account for the diffusional restriction of carbon uptake in addition to the biochemical limitation by species-specific maximal rates of carboxylation and electron transport (e.g., Wullschleger 1993).

In a first step, photosynthesis was calculated according to the widely applied photosynthesis model by Farquhar et al. (1980). Here, the CO_2 assimilation rate A_{Farq} is given by the gross rates of photosynthesis determined by the ribulose biphosphate carboxylase–oxygenase (Rubisco) activity A_c , the rate of ribulose biphosphate (RuP_2) regeneration A_j and the rate of CO_2 evolution from processes other than photorespiration Rd :

$$A_{\text{Farq}} = \min \{ A_c | A_j \} - Rd \quad (4)$$

A summary of how the assimilation rate is modeled can be found in Leuning (1995) while the determination of Rd is described in Falge et al. (1996). A_{Farq} is calculated as a function of air temperature (K), atmospheric CO_2 concentration (mol mol^{-1}) and the intercepted photosynthetic active radiation PAR ($\text{mol m}^{-2} \text{s}^{-1}$). The parameter values applied are provided in the appendix (Table 3). In a second step, A_{Farq} was corrected by multiplication with f_s (Eq. 3) representing the reduced gas exchange at leaf level due to stomatal closure (A_{XWF} , $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Intrinsic water use efficiency

IWUE_{XWF} ($\mu\text{mol mol}^{-1}$) was determined by the ratio of the simulated A_{XWF} and g_s . The seasonal average of

IWUE_{XWF} was weighted by the daily assimilation rate to estimate the amount of carbon incorporated into the tree ring archive during the growing season from May to September (IWUE_w). According to dendrometer measurements by Offermann et al. (2011), however, the period from the 31st May to 10th August [day of the year (DOY) 151–222] has been shown most important for of beech growth. Hence, we additionally calculated IWUE_w for this period (IWUE_g).

Tree ring stable isotopes

The carbon and oxygen tree ring isotopic composition ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of the nine beech trees at the NE-exposed study site have been measured for the observation period from 2002 to 2007 (Table 2). The tree cores analyzed were taken from the downhill facing side of the trunk at breast height using an increment borer (Haglöfs, Sweden, 5.2 mm core diameter, 300 mm core depth). The sample cores have been stored in straw pipes and softly placed for transport. The cores were not sanded to avoid isotopic cross-contamination over year rings, carefully dated and separated into different years under a high-resolution (0.7–7.0) microscope (SZH 10, Olympus, Germany) using a sharp razor blade. The samples were milled (ZM1000, Retsch, Germany) and cellulose was extracted according to Boettger et al. (2007).

The determination of $\delta^{18}\text{O}$ in cellulose was performed by high-temperature pyrolysis in a Flash HT elemental analyzer (ThermoFisher, Bremen, Germany) coupled to a Delta V advantage isotope ratio mass spectrometer (ThermoFisher, Bremen, Germany). The precision was <0.2 ‰. For $\delta^{13}\text{C}$ measurements the samples were combusted in the elemental analyzer and the produced CO_2 was transferred to the isotope ratio mass spectrometer. The precision was <0.1 ‰. The oxygen and carbon stable isotope composition was expressed using the small delta notation in per mill, relative to the international Vienna Standard Mean

Table 2 Carbon and oxygen isotopic composition ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of tree ring cellulose ($n = 9$) and oxygen isotopic composition of the altitude corrected precipitation ($\delta^{18}\text{O}_p$) of the NE-exposed study site in 2002–2007

Year	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)	$\delta^{18}\text{O}_p$ (‰)
2002	-26.82 ± 0.93	28.09 ± 0.65	-8.89 ± 2.57
2003	-26.01 ± 0.91	28.71 ± 0.76	-6.77 ± 2.68
2004	-25.97 ± 1.18	29.19 ± 0.69	-7.03 ± 2.59
2005	-25.90 ± 1.07	28.98 ± 0.65	-7.92 ± 2.01
2006	-26.38 ± 1.32	28.23 ± 0.85	-8.06 ± 3.51
2007	-26.88 ± 1.49	28.03 ± 0.74	-8.15 ± 1.89

Ocean Water (VSMOW) and the Vienna Pee Dee Belemnite (VPDB) standards, respectively.

The depletion of the tree ring cellulose in ^{13}C in comparison with the CO_2 in the air ($\Delta^{13}\text{C}$) was calculated according to Farquhar et al. (1989),

$$\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{atmo}} - \delta^{13}\text{C}_{\text{cell}}}{1 + \delta^{13}\text{C}_{\text{cell}}} \quad (5)$$

where $\delta^{13}\text{C}_{\text{atmo}}$ represents the ratio of ^{13}C to ^{12}C in the atmosphere (-8‰) and $\delta^{13}\text{C}_{\text{cell}}$ is the carbon isotopic composition of the extracted cellulose. To correct the oxygen isotope signature for the impact of changing oxygen isotope signatures of the source water we calculated the evaporative enrichment of cellulose $\Delta^{18}\text{O}$ according to Barnard et al. (2007),

$$\Delta^{18}\text{O} = \frac{\delta^{18}\text{O}_{\text{cell}} - \delta^{18}\text{O}_{\text{source}}}{1 + \delta^{18}\text{O}_{\text{cell}}} \quad (6)$$

where $\delta^{18}\text{O}_{\text{cell}}$ is the oxygen isotopic composition of the tree ring cellulose and $\delta^{18}\text{O}_{\text{source}}$ is the isotopic composition of average growing season precipitation.

The precipitation $\delta^{18}\text{O}_p$ data were obtained from Global Networks of Isotopes in precipitation (GNIP) of the International Atomic Energy Agency (IAEA, <http://www.naweb.iaea.org>) from a GNIP station (Buchs AG, Switzerland, 380 m a.s.l.) in approx. 100 km distance. Saurer et al. (2012) showed that oxygen isotope signatures in precipitation only negligibly varied within this distance range. However, to determine a reliable estimate of the source water signal, we have conducted an additional altitudinal correction of the $\delta^{18}\text{O}_p$ (http://wateriso.utah.edu/waterisotopes/pages/data_access/oipc.html). The monthly mean values of the corrected $\delta^{18}\text{O}_p$ have been aggregated to the growing season average of the particular years (Table 2).

We are aware of the fact that the isotopic composition of precipitation is only an approximation for plant source water. Holst et al. (2010), however, showed that trees at our site take up water mainly from 10 to 15 cm soil depth and thus ground or aquifer water with a potentially different isotopic signature should not strongly affect the isotopic composition of the tree source water. Moreover, soil water from 10 to 15 cm depths is normally strongly related to the isotopic composition of precipitation water (e.g., Brandes et al. 2007). Differences between years might, however, occur especially when water from initial rainfall events after dry summers is locked tightly into small pores with low matric potential (Brooks et al. 2010). Depending on the water availability in the next summer, transpiration might empty these pores more or less intensively. The rates of carbon fixation and stomatal conductance are the primary factors determining carbon isotopic discrimination and thus

the intrinsic water use efficiency (IWUE_{iso}) can be derived from $\Delta^{13}\text{C}$ according to Farquhar et al. (1982) and Seibt et al. (2008),

$$\text{IWUE}_{\text{iso}} = \frac{c_a}{1,6} \left[\frac{b - \Delta^{13}\text{C}}{b - a} \right] \quad (7)$$

where a (4.4 ‰) is the carbon isotope fractionation during diffusion through the stomata, b (27 ‰) is the discrimination during carboxylation of Rubisco and c_a is the ambient CO_2 concentration.

Because the SW-exposed study stand is more prone to drought (“Study site”), the trees of this site were assumed to carry a stronger climate signal in the tree ring stable isotope archive. Therefore, we have included the $\Delta^{13}\text{C}$ -derived IWUE (Farquhar et al. 1982; Seibt et al. 2008) of the SW-exposed beech stand in our study ($\text{IWUE}_{\text{iso_NE}}$ and $\text{IWUE}_{\text{iso_SW}}$; raw data of ^{13}C and ^{18}O are shown for the NE slope only).

Statistical analyses

Statistical analyses were carried out using R (R Development Core Team 2010). The stand variables assessed were expressed as the arithmetic mean and standard deviation of the single tree values determined by the XWF modeling and stable isotope approach. We used the non-parametric Wilcoxon rank-sum test to assess significance in differences of the tree population in varying years and in comparison between the NE- and SW-exposed study stands. For the ^{13}C and ^{18}O isotope values we have used a paired t test to compare the year 2003 with the other years. For a comparison of the individual years at both study sites we used an unpaired t test.

Results

In the following, we present seasonal (2002–2007) and intra-seasonal (daily) variations of leaf stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) and CO_2 assimilation rates (A_{XWF} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) as estimated with the XWF model (“XWF modeling” in “Materials and methods”). As an integrated record of A_{XWF} and g_s , IWUE has been derived from the XWF simulations (IWUE_{XWF} , IWUE_w and IWUE_g ; “Intrinsic water use efficiency”) and from the tree ring cellulose $\delta^{13}\text{C}$ signature results (IWUE_{iso} ; “Tree ring stable isotopes”). Furthermore, tree ring cellulose $\Delta^{18}\text{O}$ analyses were used to determine the stomatal sensitivity towards changing evaporative conditions. Tree growth (DBH_i) has been derived from the tree ring width of the study trees and is, furthermore, substantiated by a long-term chronology conducted by Poschenrieder et al. (2013). All tree data have been aggregated to the stand average based on nine

mature beech trees at each site. The occurrence of drought stress is expressed as the ratio between soil water availability and evaporative demand (REW and Wd; “Environmental conditions”).

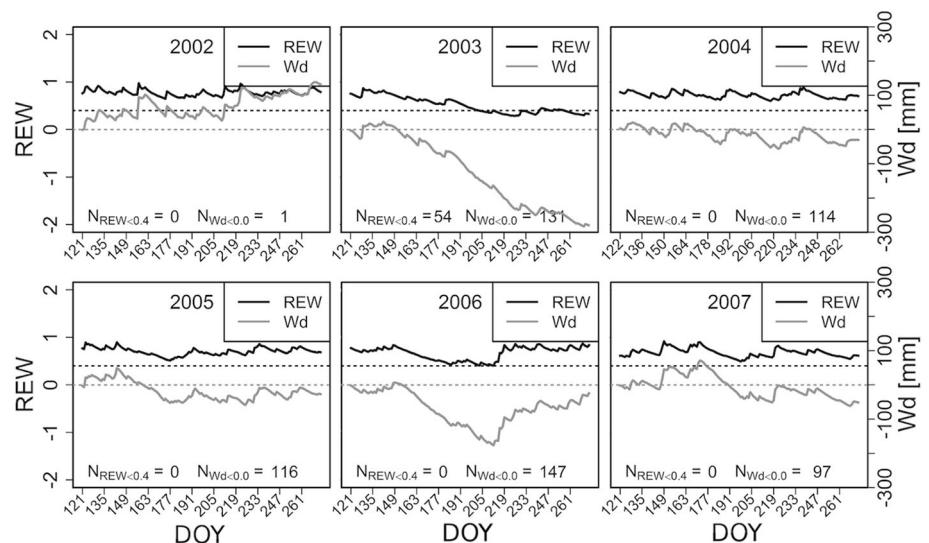
Drought stress

The calculated drought indices REW and Wd indicate severe drought conditions in 2003. After the 20th of July 2003, REW dropped below 0.4 (DOY 201; Fig. 2), the threshold indicating drought stress for European forest trees as suggested by Granier et al. (2007). Wd then continuously declined to negative values down to -300 mm, indicating an increasing water deficit towards the end of the growing season. A comparable, though less intensive decline in Wd was calculated for 2006, with lowest values close to -200 mm at DOY 205 and the highest number of days with negative Wd of all examined years. In the other years examined, Wd was around zero and did not fall below -100 mm. Severe drought, as defined by REW below 0.4, has been observed only in 2003 on more than 50 days. In June, the most important period for beech seasonal radial growth (Lebourgeois et al. 2005), Wd did not fall below zero in the years 2002 and 2007.

Tree growth

The mean radial growth is shown in Fig. 3. No significant differences were apparent neither between years nor sites. At both sites, a decreasing growth trend could be observed approximately until 2005. However, while DBH_i remained relatively constant at the NE site in 2006 and 2007, the DBH_i increased again at the SW site. The largest difference in DBH_i between both sites (1.1 cm) was thus observed for the year 2007.

Fig. 2 Relative extractable soil water (REW) in the upper soil layers (0–30 cm) and the actual soil water deficit (Wd; mm) calculated as the cumulative difference of daily precipitation and potential evapotranspiration for the growing season (May to September) of the years 2002 to 2007. $N_{REW<0.4}$ and $N_{Wd<0.0}$ indicate the number of days below the respective threshold of water stress



Tree ring stable isotopes

Figure 4 shows the time series of $\Delta^{13}\text{C}$ and $\Delta^{18}\text{O}$ in tree ring cellulose of the NE-exposed site (2002–2007). $\Delta^{18}\text{O}$ has been corrected for the inter-annual variation of $\delta^{18}\text{O}$ in source water given by the seasonal average of $\delta^{18}\text{O}_p$ (see Appendix Table 3). The altitude correction between Buchs AG, Switzerland (380 m a.s.l.) and the present study site (790 m a.s.l.) resulted in a -0.6 ‰ difference. The tree ring $\Delta^{18}\text{O}$ signature in 2003 was significantly lower compared to the other years of the time series (Fig. 4). No significant differences between the years have been observed in the tree ring $\Delta^{13}\text{C}$ signature.

The mean tree ring isotope values of the nine examined beech trees varied from 18.4 (in 2005) to 19.4 ‰ (in 2007) for $\Delta^{13}\text{C}$ and from 35.7 (in 2003) to 37.3 ‰ (in 2002) for $\Delta^{18}\text{O}$. The mean standard deviation for the whole time series was 1.18 ‰ for $\Delta^{13}\text{C}$ and 0.73 ‰ for $\Delta^{18}\text{O}$. The lowest ^{18}O enrichment in tree ring cellulose has been observed in 2003, when the source water oxygen isotopic signature ($\delta^{18}\text{O}_p$) was lowest (-6.77 ± 2.68 ‰; Table 2). Highest values in tree ring $\Delta^{18}\text{O}$ occurred in 2002 and 2005. The $\Delta^{13}\text{C}$ isotopic signature in tree ring cellulose was highest in 2002 and 2007 and stayed approximately constant from 2003 to 2005 at a slightly lower level.

XWF modeling

The intra-seasonal H_2O and CO_2 exchange in the examined beech forest (NE site) for the growing season (May to September) of the years 2002–2007 are shown in Fig. 5. The results are illustrated as average daily values derived from hourly XWF simulation results of nine study trees.

The panels on the left hand site show the average of the daily sum of the potential and actual stand transpiration,

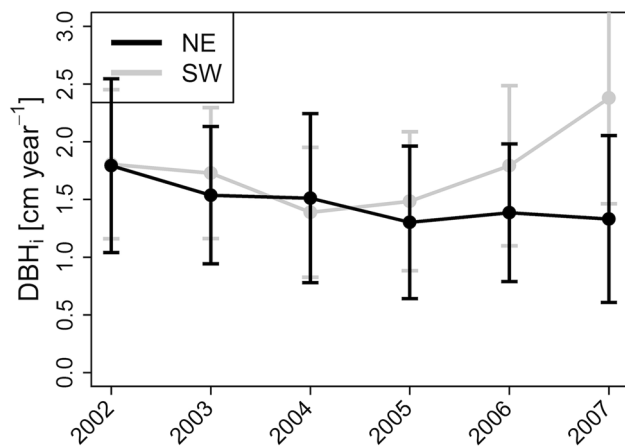


Fig. 3 Mean annual radial growth (DBH_i ; cm year^{-1}) of nine beech trees at the NE (black)- and the SW (grey)-exposed study site. Dots are measured mean values and error bars denote the standard deviations ($n = 9$)

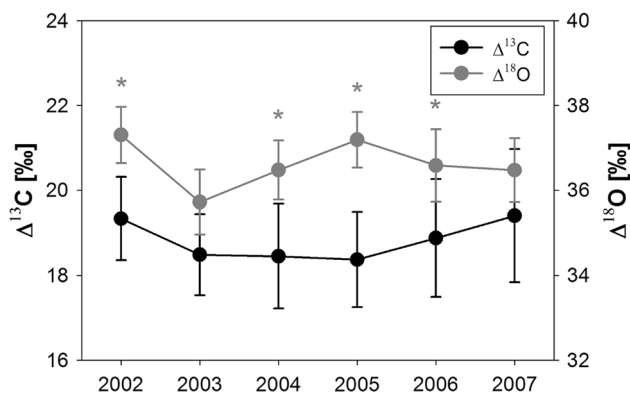


Fig. 4 Carbon isotopic discrimination and oxygen isotopic enrichment of tree ring cellulose at the NE site in 2002 to 2007. The tree ring isotopic discrimination of carbon ($\Delta^{13}\text{C}$) is indicated by the black line and $\Delta^{18}\text{O}$ is depicted by a grey line. Dots are mean values and error bars denote the standard deviations ($n = 9$). The grey stars denote significant differences ($p \leq 0.05$) between $\Delta^{18}\text{O}$ in 2003 compared to the other years

respectively (ST_{pot} and ST_{act}) and the average of the daily mean of the stomatal conductance (g_s). ST_{pot} in 2003 was about 16–25 % higher compared to the other years. The seasonal average of g_s in 2003 was about 27–44 % lower compared to the other years. The XWF model performed a general reduction of ST_{pot} so that ST_{act} was ranging in the seasonal sum to between 47 and 63 % of ST_{pot} . The highest reduction of ST_{pot} and the lowest seasonal g_s has been observed in 2003. The longest period of the daily average of g_s close to zero appeared between DOY 214 and DOY 224 of this year.

The panels on the right-hand site show the mean CO_2 assimilation rate of the beech trees, derived by the biochemical photosynthesis model (A_{Farq}) and additionally

corrected for diffusional limitation (A_{XWF}). The seasonal mean of A_{XWF} ranged between 69 and 85 % of the respective seasonal mean of A_{Farq} . The intrinsic water use efficiency ($IWUE_{\text{XWF}}$) shown at the bottom of the panels is given as ratio of A_{XWF} and g_s . A decrease in g_s was mirrored by an increase of $IWUE_{\text{XWF}}$. The highest seasonal average of $IWUE_{\text{XWF}}$ occurred in 2003 ($144 \mu\text{mol mol}^{-1}$) and the lowest in 2007 ($78 \mu\text{mol mol}^{-1}$).

IWUE changes

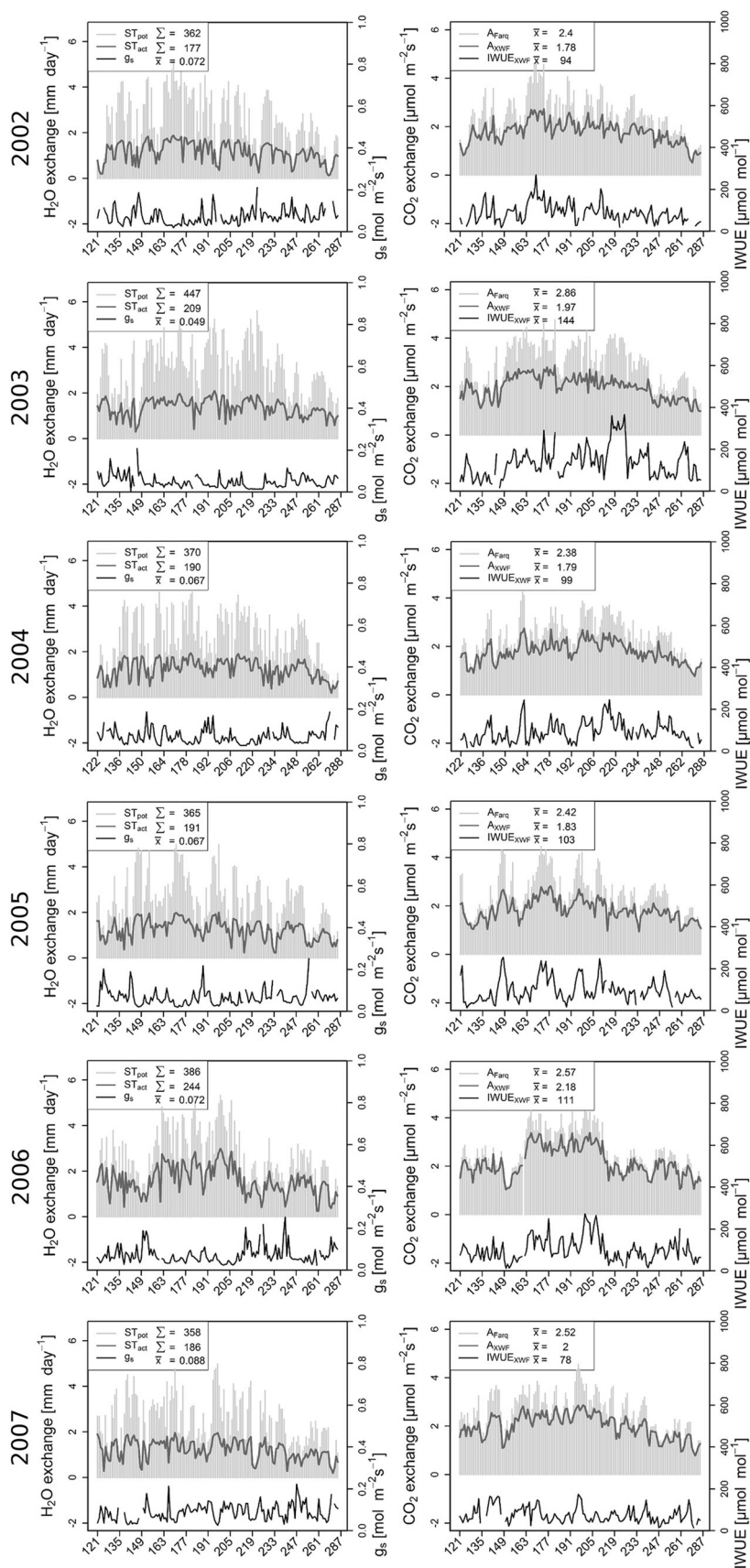
IWUE derived from the tree ring cellulose carbon isotope composition ($IWUE_{\text{iso_SW}}$ and $IWUE_{\text{iso_NE}}$) showed no significant differences between single years (2002–2007). At the SW site, characterized by a generally warmer climate and lower volumetric soil water contents between 2002 and 2007 (Holst et al. 2010), $IWUE_{\text{iso_SW}}$ was approx $15 \mu\text{mol mol}^{-1}$ higher than at the NE site (Fig. 6): $IWUE_{\text{iso_NE}}$ ranged between $92 \mu\text{mol mol}^{-1}$ in the year 2003 and $81 \mu\text{mol mol}^{-1}$ in the year 2007 and $WUE_{\text{iso_SW}}$ ranged between $106 \mu\text{mol mol}^{-1}$ in the year 2003 and $92 \mu\text{mol mol}^{-1}$ in the year 2007. The unpaired t test revealed a significant difference between $WUE_{\text{iso_SW}}$ and $WUE_{\text{iso_NE}}$ in 2003. The XWF simulations of IWUE (only done for the NE slope) generally resulted in higher values compared to $IWUE_{\text{iso}}$ (Fig. 6). Both aggregates of $IWUE_{\text{XWF}}$, weighted by the assimilation rate of the whole growing season ($IWUE_w$, 1st May to 30th September) and weighted by the assimilation rate of the stem growing season of European beech ($IWUE_g$, 31st May to 10th August), showed distinctly lower values compared to $IWUE_{\text{XWF}}$. All estimates derived by the XWF model ($IWUE_{\text{XWF}}$, $IWUE_w$, $IWUE_g$) indicate a significant increase in the drought year 2003. $IWUE_{\text{XWF}}$ decreased continuously until 2007 whereas $IWUE_w$ and $IWUE_g$ increased again in the relatively dry year 2006 (indicated by negative Wd throughout the whole growing season; Fig. 2) followed by a sharp decline in 2007. The highest agreement between the XWF simulation and the tree ring stable isotope approach was found for $IWUE_w$ with no significant differences to $IWUE_{\text{iso_NE}}$ in the years 2002, 2004, 2005 and 2007.

Discussion

Growth response

The year 2003 has been pointed out as an extraordinary dry year associated with a reduction in gross primary productivity in several forest types in large parts of Europe, including European beech ecosystems (Ciais et al. 2005). Despite the generally documented growth decline of forest

Fig. 5 Seasonal courses of environmental conditions and XWF simulations for the years 2002 to 2007 as indicated at the left hand side of the figure. The panels on the left hand side show the potential and actual transpiration at stand level (ST_{pot} and ST_{act}) and stand average of the stomatal conductance at leaf level illustrated at the bottom of the panels (g_s). The panels on the right-hand side show CO_2 assimilation rate derived by the Farquhar model (A_{Farq}) and A_{Farq} under consideration of the restriction of CO_2 diffusion by stomatal conductance derived by the XWF model (A_{XWF}). The intrinsic water use efficiency ($IWUE_{XWF}$) was calculated as the ratio of A_{XWF} and g_s and is illustrated at the bottom of the panels ($IWUE$). The legend of the panels show the arithmetic means (\bar{x}) and sums (Σ) of growing season values of the examined beech trees ($n = 9$)



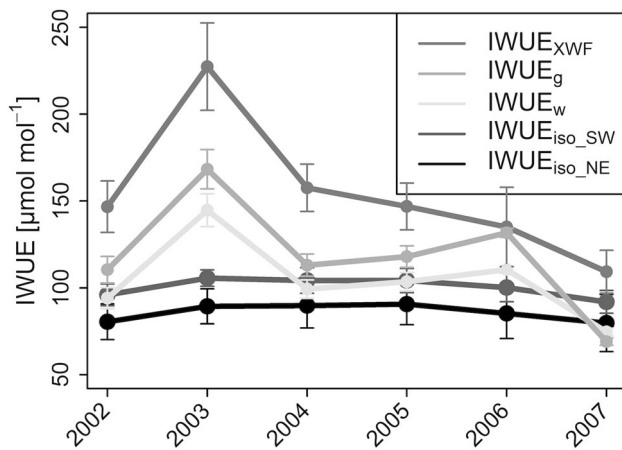


Fig. 6 The intrinsic water use efficiency in $\mu\text{mol mol}^{-1}$ derived from XWF simulation (IWUE_{XWF} grey line), weighted by the seasonal assimilation rate (IWUE_w light grey line) and calculated for the expected growing season of beech trees from DOY 151–122 (IWUE_g medium grey line). IWUE_{iso} was derived from the tree ring carbon isotopic composition of the SW-exposed (IWUE_{iso_SW} dark grey line) and the NE-exposed study stand (IWUE_{iso_NE} black line). Note that XWF simulations correspond to IWUE_{iso_NE}. Dots are measured mean values and error bars denote the standard deviations ($n = 9$)

trees in the year 2003 (Ciais et al. 2005) and the particular sensitivity of European beech (Granier et al. 2007), the decline in diameter growth has not been homogenous throughout Europe. For example, no decline was observed in Northern Greece (Fotelli et al. 2009; Nahm et al. 2006) and in the Catalanian mountains (Jump et al. 2006). In fact, the most severe and long-lasting declines have been observed at sites, already at the edge of the species natural distribution (Jump et al. 2006; Charru et al. 2010; Maxime and Hendrik 2011), while the decreases in other regions seem to be relatively small and short lived (Löw et al. 2006; van der Werf et al. 2007). In other cases, only dominant trees had been considered (Weemstra et al. 2013), which are known to be more susceptible to drought than understory trees (Pretzsch and Dieler 2011).

In this study, however, beech trees of different DBH classes and from two study sites of different soil water holding capacity did not show a significant growth response in 2003. This is against our expectations (a) since the occurrence of drought stress has been indicated by two drought indices (Fig. 2). Furthermore, the SW-exposed study site has been suggested to be generally prone to drought (Holst et al. 2010).

Since growth decline is directly related to stress intensity (Granier et al. 2007), the most likely explanation for the relatively small difference to other years at our site in Tuttlingen is a moderate stress occurrence in 2003. Indeed, less water depletion than in Central Germany or Eastern France beech stands has been documented at this site (Nahm et al. 2007). The moderate stress originates from

relatively high precipitation at Tuttlingen in May as well as in July (Nahm et al. 2007). Although surprising, this weather pattern is not unrealistic given that the anomalously high temperatures and low precipitation were by no means equally distributed across Central Europe (Fink et al. 2004; Rebetez et al. 2006).

In fact, a severe drought as indicated by REW below 0.4 is only observed in late summer 2003 starting at the 20th of July (DOY 201; Fig. 2). Assuming that most of the growth has already occurred before this period (e.g., Lebourgeois et al. 2005) radial increment might not have been affected by reduced carbon assimilation due to limited soil water supply. It should also be noted that relatively warm spring temperatures result in early leaf flushing and longer overall growth periods (Capdevielle-Vargas et al. 2015). Such an effect has been shown for 2003 at sites in Switzerland (Leuzinger et al. 2005) and may also apply for Tuttlingen. Finally, the high minimum temperatures in August and September as documented for Southern Europe up to Southwest Germany (Rebetez et al. 2006) might have provoked wide latewood tree rings as has been found at beech sites in Belgium (Lebourgeois et al. 2005), masking actual biomass growth declines.

From a more general point of view, other potentially mitigating effects might also be considered. For example, Tuttlingen is exposed to relatively high ozone concentrations (Fiala et al. 2003; Solberg et al. 2008) that might lead to a continuously decreased growth level (Grünhage et al. 2012; Subramanian et al. 2015). The uptake of ozone is decreased by closed stomata at low water supply which reduces growth losses by ozone and partly compensates for drought stress losses (Matyssek et al. 2006). Similarly, a fraction of the drought stress impact is related to a decreased nitrogen uptake (Grassi et al. 2005; Kreuzwieser and Gessler 2010). Therefore, sites with good nitrogen supply that enable a sufficient uptake are also less prone to drought stress effects. Indeed, the nitrogen supply at Tuttlingen was relatively good in 2003 (Nahm et al. 2007).

In principle it might also be assumed that trees growing on weathered limestone might have access to deeper water from karst caves as shown for example by Jackson et al. (1999) and thus could sustain growth even when the availability of water in shallower soil layers decreases. Previous research at the same site gave, however, good indication that the trees did not have access to such deep water sources. Holst et al. (2010) compared the oxygen isotope composition of soil and xylem water at the study site and concluded that the beech trees took up water mainly from the upper 10–15 cm of the soil layer. In agreement with this finding, Gessler et al. (2001) observed that $\delta^{13}\text{C}$ in the phloem organic matter (which immediately responds to changing environmental conditions), sap flow densities and twig water potential directly responded to

changes in soil water potential in the upper 60 cm of the soil profile. Thus, the measured and simulated soil water contents at our study site are suggested to represent the actual water availability and, in turn, to be a reliable indicator for the occurrence of drought stress.

In fact, drought effects on radial growth might last for several years depending on the timing of drought periods during the growing season (Eilmann and Rigling 2012). Several investigations have addressed the impact of the drought in 2003 on beech and observed a delayed and dampened radial growth reduction (Bréda et al. 2006; Granier et al. 2007; Skomarkova et al. 2006). These authors suggested that the usage of stored carbohydrates might have played a significant role for trees to cope with drought and to maintain growth which might be applied to our study.

In fact, we observed no water-limiting conditions in 2002 (Fig. 2; Table 1, see also Holst et al. 2010) and may assume well-stocked carbon storage pools of the beech trees in 2003. Furthermore, Poschenrieder et al. (2013) showed a relatively high DBH_i at both study sites in 2001 and 2002. Due to the greater sink priority of carbon storage compared to growth (Wiley and Helliker 2012) this may also indicate a well-stocked carbon storage. Since the tree ring chronology shows a thinning induced growth peaks in 1997 and a continuous decrease in DBH_i until the year 2000 (Figure 6 in Poschenrieder et al. 2013), the increase of DBH_i in the following years strongly endorses this assumption.

If we further on assume the usage of stored carbohydrates in the year 2003, the refilling of carbon storage pools used in 2003 might have diminished the radial growth in the following years. In fact, at the SW site, the lowest annual DBH_i was observed one year after the drought (2004), which is in agreement with findings by Granier et al. (2007). However, given that the drought stress at the investigation site was less intense than at other Central European regions, it is unlikely that the lacking recovery is due to a particularly severe impact. This is underlined by the fact that beeches at other sites have performed a fast recovery in the following year (van der Werf et al. 2007). In correspondence, we observe a continuous increase in DBH_i at the SW-exposed study site from the years 2005–2007.

Form the growth assessment only, the lack of a significant growth response in 2003, which has been also shown by Poschenrieder et al. (2013) with a larger samples size, might be explained by three arguments: first, the beech trees in Tuttlingen experienced rather moderate drought stress, in particular due to the seasonal timing of the drought events at the end of the growing season. Second, the use of storage reserves during periods of limited carbon uptake supported the maintenance of growth. Third, the

refilling of the carbon storage pools (at least) in 2004 may have masked a distinct growth response.

Tree ring stable isotopes

In agreement with a study of Saurer et al. (1997), we observe a significant decrease in $\Delta^{18}\text{O}$ in 2003 (Fig. 4). However, when looking at $\delta^{18}\text{O}$ of tree ring cellulose, no clear difference appeared among years (Table 2). The reduction of the ^{18}O enrichment in tree ring cellulose might be explained by the Pécelet effect, which causes a reduction of lamina leaf water ^{18}O enrichment and thus $\Delta^{18}\text{O}$ of new assimilates with increasing transpiration (Farquhar and Lloyd 1993). Thus, the oxygen isotope results indicate increased transpiration rates in 2003. They might have overcompensated the effect of increased VPD, which would have led to higher leaf water evaporative enrichment. In fact, the highest ST_{pot} and with exception of 2006 the highest St_{act} has been observed in this particular year (Fig. 5).

From carbon stable isotope analysis ($\delta^{13}\text{C}$) at the NE-exposed site, no significant drought response between the year 2003 and the following years could be identified (Table 2). Various authors show clear responses towards changing environmental conditions (Libby et al. 1976; Francey and Farquhar 1982), which has not been observed in our study. However, the lack of a tree ring isotope signal to drought is not uncommon in literature (e.g., Galle et al. 2010; Michelot et al. 2011; Peñuelas et al. 2008) and might have various reasons.

As mentioned already in “Growth response”, the seasonal timing of drought events has a great influence on the tree growth pattern and, in turn, on the stable isotope composition incorporated in the tree ring archive. In agreement with findings of Helle and Schleser (2004), we suggest that the early growing season, which was not that much prone to drought stress compared to the late summer of 2003 (Fig. 2), significantly influenced both DBH_i and the tree ring stable isotope composition. Thus, the overall seasonal climate signal might not be mirrored by the whole tree ring assessment.

Furthermore, Skomarkova et al. (2006) derived from a stable isotope approach that about 10–20 % of a tree ring of European beech in spring is built from remobilized storage compounds while additional 10–20 % of the tree ring is affected by storage processes in autumn. In fact, from a multi-scale (leaf, phloem, xylem) stable isotope approach conducted at the NE study site, Offermann et al. (2011) postulated that the deposition of carbon derived from starch (relatively enriched in ^{13}C) in spring and the gradually increasing incorporation of newly assimilated C (relatively depleted in ^{13}C) in the tree ring during the rest of the growing season, most likely prevented tree ring $\delta^{13}\text{C}$

signatures from being closely related to intra-annual variations in environmental drivers. Taking into account an early growth onset in 2003 followed by a late onset in 2004 at our study site as found by van der Maaten et al. (2013), the usage of storage products for tree ring formation has probably been higher in 2003 than in 2002 or 2004. Thus, the isotopic results of 2003 are partly reflecting the conditions of 2002 while those of 2004 are including the drought responses from 2003. Indeed, several authors suggest the separation of tree rings for isotope analysis into early- and latewood (Helle and Schleser 2004, Barnard et al. 2012; Battipaglia et al. 2014; Voltas et al. 2013) or high-resolution isotope measurements (Michelot et al. 2011; Schulze et al. 2004; Skomarkova et al. 2006) to detect a stronger relationship between the environmental drivers and the physiological responses imprinted in the tree ring archive.

We suggest that the use of storage reserves and the late onset of the severe drought period have impacted the whole tree ring isotopic signature in our study diminishing the drought response. In agreement with the lack of a radial growth response towards the drought in 2003 (“Growth response”) the isotope signatures in the tree ring archive indicate that the growth conditions might not have been that much influenced by limited soil water supply as expected.

XWF modeling

The XWF simulation results, in particular the simulated stomatal closure, show a significant physiological response of individual trees towards the drought events in 2003 (Fig. 5). The most distinct drought response occurred for a 14-day period (DOY 212–225) when g_s dropped close to zero. During this period, a high evaporative demand ($ST_{pot} > 3 \text{ mm day}^{-1}$) coinciding with low soil water availability ($REW < 0.4$) resulted in very low leaf water potentials down to -2.7 MPa as obtained by the hydraulic maps of the individual trees (data not shown). The latter is in agreement with lowest leaf water potentials measured in sun-crown leaves of mature beech trees by Aranda et al. (2000) and Köcher et al. (2009).

The low values of the leaf water potential in 2003 suggest that beech trees already operated near the point of catastrophic xylem dysfunction. For example, Hacke and Sauter (1995) showed that about 50 % of the vessels of European beech branches experienced embolism at a water potential of -2.9 MPa . In fact, the critical hydraulic threshold of European beech as measured by pressure applications causing a loss of 50 % of hydraulic conductivity of the xylem may range between -2.5 MPa for shade-grown branches and -3.15 MPa for sun-exposed branches, respectively (Cochard et al. 2005; Lemoine et al.

2002). Thus, the simulated stomatal regulation can be seen as a plausible reaction to water loss to avoid hydraulic failure.

However, the XWF simulations showed a distinct reduction of the potential transpiration due to stomatal closure during the whole growing season and all years examined (Fig. 5). In fact, the stomatal response in absence of a strong soil drought ($REW > 0.4$) is supposed to be a necessary leaf physiological response to avoid xylem dysfunction under the high evaporative demand and with regard to the maximal hydraulic conductance of the individual trees. Cruiziat et al. (2002) showed a 90 % stomata closure in European beech at a xylem water potential of -2.0 MPa . Thus, we assume that stomatal conductance is minimal prior to reaching the specific hydraulic threshold and the occurrence of embolism. Indeed, Lemoine et al. (2002) observed an early and sufficiently fast stomatal response of European beech to water stress protecting the xylem from dysfunction. In the XWF model, however, g_s is controlled by the water potential gradient within the tree and, thus, depends on both the environmental conditions and the hydraulic properties of the tree. Hence, the parameterization of the hydraulic architecture of the trees, for example the porosity of the xylem tissue, influences the occurrence of critical water deficits within the whole tree water relations and in turn the response of g_s .

Several mechanisms control g_s (see for review Damour et al. 2010) and complex feedback loops with environmental drivers and tree-specific properties are involved (McDowell et al. 2008, 2011). Furthermore, metabolic regulation of stomatal aperture is difficult to estimate (e.g., Buckley et al. 2003; Buckley and Mott 2013) but certainly plays a role to optimize plant gas exchange, i.e., the loss of water to gain carbon (Chaves et al. 2003). Hence, the mechanistic determination of the variability in water and carbon balances and underlying processes is complex, and thus we summarize the main uncertainties and assumptions of the applied XWF model in the following two paragraphs.

Evidence of the mechanistic linkage between stomatal conductance and the leaf water potential was obtained by hydrodynamic modeling as shown, e.g., by Bittner et al. (2012a), Bohrer et al. (2005) and Sperry et al. (2002). Therefore, the XWF model follows a hydraulic approach determining the leaf water status in dependence of the evaporative demand of the atmosphere, the soil water availability and of the hydraulic properties of the individual tree. This approach benefits from the simulation of the stomatal response towards drought under consideration of the whole tree hydraulic conductance and a species-specific hydraulic threshold of the water-conducting (xylem) tissue (Johnson et al. 2011). Due to the complexity of the tree architecture (see for review Cruiziat et al. 2002), however,

the structural and morphological features determined by TLS, root distribution modeling and beech-specific parameterization of the wood properties (“XWF modeling” in “Materials and methods”), cannot account for the full heterogeneity of the hydraulic architecture. For example, xylem characteristics are assumed to be homogeneous within aboveground and belowground parts of the tree, which is not exactly the case (Früh and Kurth 1999). Other uncertainties concerning the fully representation of the hydraulic framework within the soil–plant–Atmosphere continuum might be added. In particular, the soil–root interface, representing the main hydraulic resistance within the hydraulic pathway of trees (Bréda et al. 1995; Kolb and Sperry 1999) is subject to typical uncertainties inherent in the representation of the rooting system and the soil water balance. For example, the soil water availability at our study site is prone to high vertical and horizontal variability (Holst et al. 2010).

The evaluation of the XWF model for 12 trees conducted at the same study site for the year 2007 (Hentschel et al. 2013), however, showed good agreement with sap flow density measurements. In average, the authors obtained a normalized root mean square error of 15 %. The parameterization of the XWF model for beech trees was obtained from literature sources (see also Table 3 in the appendix) and TLS imaging (Fig. 1) and has been applied without any fitting procedures. Hence, we suggest a reliable representation of the stomatal control by f_s (Eq. 3) also for other years. The stomatal conductance has been derived from simulated transpiration of the individual trees and VPD (“Stomatal conductance”) and might be biased when VPD was below 0.6 kPa (Ewers and Oren 2000). To obtain an adequate temporal resolution of g_s , however, a VPD down to 0.1 kPa has been considered for g_s calculations as suggested by Phillips and Oren (1998). Furthermore, we assumed a homogenous distribution of the climatic driving forces within the crown space and have not accounted for vertical pattern of VPD within the canopy (e.g., Schäfer et al. 2000). In addition, the vertical variations in leaf structural, chemical and photosynthetic characteristics associated with vertical variation in light availability (e.g., Ellsworth and Reich 1993) could not be considered in the simulation of whole canopy carbon assimilation and stomatal conductance. The beech-specific parameterization of the photosynthesis model (Farquhar et al. 1980) (“Photosynthesis”), e.g., the maximum photosynthetic capacity, was kept constant within the beech stand; however, variability of such parameters between individual beech trees was observed by others (e.g., Epron et al. 1995; Wullschlegel 1993). Furthermore, the differentiation between sun- and shade-leaves as suggested by Thornley (2002) has not been considered since no information about particular leaf distributions was available.

Despite the many uncertainties of eco-physiological modeling mentioned in the last two paragraphs, the XWF simulations, however, show a plausible range of A_{XWF} and g_s for beech trees corresponding to other studies at diurnal, daily, or seasonal scales (e.g., Epron et al. 1995; Keel et al. 2006; Keitel et al. 2003; Urban et al. 2014). Furthermore, we observed a plausible physiological response towards prevailing environmental conditions. In fact, the XWF simulations revealed a strong coupling of the water relations within the soil–leaf continuum, most obvious in 2003 when REW dropped below 0.4. Indeed, stomatal aperture is strongly coupled with soil water availability (Sperry 2000). As a consequence, the model predicts a reduced CO_2 assimilation rate with decreasing g_s . A corresponding translation into growth, however, would suggest a distinct decrease of DBH_i in 2003, which was not observed (see Poschenrieder et al. 2013; van der Maaten et al. 2013).

In contrast, Lebourgeois et al. (2005) found in a dendroclimatological study of 15 European beech stands across different French bioclimatic regions that soil water deficit at the particular sites were most predictive for the annual diameter growth and showed agreement with other investigations of beech forests in Central Europe. While XWF simulations indicated a distinctly decreased gas exchange at leaf level, the annual diameter growth was not significantly affected by the drought of 2003, which might be explained by storage/remobilization processes and the seasonal timing of drought (see “Growth response”). From the hydrodynamic modelling results, however, we can accept our second hypothesis of a distinctly reduced H_2O and CO_2 exchange in 2003 due to an effective stomatal regulation of beech trees (b).

Physiological response

To characterize the tree physiological response towards drought, we compared the results of growth assessment, the tree ring isotope analysis and the XWF modeling. As an integrative record of the carbon–water balance, we focused on the intrinsic water use efficiency and related our findings to the predicament of the loss of water to gain carbon.

According to the carbon isotope signature, no significant differences in $IWUE_{iso}$ occurred between the years (2002–2007). However, the mean $IWUE_{iso}$ of the drier SW slope was about 14 % higher than at the NE slope, thus, confirming a physiological acclimation of the beech trees to drier site conditions by increasing $IWUE$. In fact, various authors observed an increased $IWUE_{iso}$ of trees under conditions of high temperature and high water vapor pressure deficits of the air (Battipaglia et al. 2014; Härdtle et al. 2013; Voltas et al. 2013). The ability to increase the $IWUE$ is indeed a competitive advantage for plants under water-limiting conditions (Richards et al. 2002). This may

match to the earlier increase of DBH_i after the drought at the SW-exposed slope compared to the NE-exposed slope showing decreased DBH_i until 2007 (Fig. 3).

However, since water limitation generally evokes a reduction of g_s leading to lowered leaf internal CO_2 concentration and, in turn, increased $\delta^{13}C$ (Farquhar et al. 1989), we expected a significant increase of $IWUE_{iso}$ in 2003. That has not been observed neither at the SW- nor the NE-exposed study site. As discussed above (“Growth response”), the seasonal timing of drought and the incorporation of stored carbohydrates into the tree ring archive might have masked the isotopic imprint. Furthermore, Granier et al. (2007) observed a simultaneous decrease in daily evapotranspiration and gross primary production, indicating rather constant $IWUE$.

Nevertheless, Damour et al. (2010) stressed that under conditions of drought, a shift in the A -to- g_s ratio is most likely to occur. In fact, by expressing g_s as a function of water relations, the hydraulic model simulates a shift towards increasing $IWUE_g$ and $IWUE_w$ under conditions of limited water availability (2003 and 2006; Fig. 6). This is consistent with existing theory and findings of a meta-analysis of 50 plant species exposed to mild water stress (Manzoni et al. 2011). We observe a strong coupling of the leaf physiological response (g_s and $IWUE_{XWF}$ in Fig. 5) with the soil water supply at intra-seasonal scale (REW in Fig. 2). The increase of the $IWUE$ obtained by XWF modeling and induced by a reduction of g_s , however, is not reflected by $IWUE_{iso}$. Since the decrease in g_s during drought is suggested to be a necessary response to avoid xylem dysfunctioning (“XWF modeling” in “Discussion”) the increase in $IWUE$ may be added to the explanation of the maintenance of growth in 2003 as discussed in “Growth response” in “Discussion”. In fact, the mean A_{XWF} in 2003 is still higher compared to the years 2002, 2004 and 2005.

On the other hand, Grassi and Magnani (2005) showed that with increasing drought intensities, the contribution of non-stomatal limitation on light-saturated net photosynthesis increased and nearly equaled stomatal limitation. In agreement to these results, Epron et al. (1995) showed that CO_2 internal resistances in beech can limit A by approximately 30 %—the same order of magnitude as stomata resistance. Indeed, evidence was found that the mesophyll conductance represents the main component of non-stomatal limitation of A (Grassi and Magnani 2005) and that the balance between mesophyll and stomatal conductance is reflected in changes in leaf level intrinsic water use efficiency (Flexas et al. 2013). Furthermore, the mesophyll conductance is highly variable within the species (e.g., height, age) in response to environmental conditions and changes even faster than stomatal conductance (Flexas et al. 2008; Han 2011; Douthe et al. 2012; Hommel et al.

2014). Indeed, Aranda et al. (2012) observed a decrease in both, stomatal and mesophyll conductance of beech seedlings faced to mild drought stress. Hence, we cannot exclude an overestimation of A_{XWF} in our study because of neglecting non-stomatal limitations.

However, in particular in the mid- and late season of 2003, we observed very dry environmental conditions and the simulated decrease in g_s can be seen as most likely (“XWF modeling” in “Discussion”). Thus, a physiological acclimation towards the observed drought conditions by an increased $IWUE$ is suggested as most plausible. Furthermore, we suggest that the seasonal timing of the drought events and the usage of storage compounds have diminished both, the growth response (DBH_i , “Growth response” in “Discussion”) and the isotopic signal in the tree ring archive ($\delta^{13}C$, “Tree ring stable isotope” in “Discussion”). Therefore, we might accept our third hypothesis of increasing $IWUE$ under drought (c) even so the tree ring isotope proxies did not record such a physiological response towards the drought of 2003.

Conclusion

Although European beech can be seen as a highly drought-sensitive tree species (Gessler et al. 2004a), the leaf physiological control and changes in root water uptake during water loss needs to be taken into consideration and might display an adaptive strength towards drier future climates. We demonstrate that the beech trees in Tuttingen maintained growth in 2003 which can be partly explained by the occurrence of rather moderate drought stress at the study site (“Growth response” in “Discussion”). However, the hydrodynamic modeling approach also suggests an adjustment of the intrinsic water use efficiency during the drought events, thus, improving the ratio of carbon gain towards water loss (“XWF modeling” in “Discussion”).

Stomatal regulation together with adjustment of internal conductance is able to avoid harmful water tension within the xylem. However, a reduced gas exchange was neither reflected by a significant reduction in DBH_i (Fig. 3) nor by a significant increase in $IWUE_{iso}$ (Fig. 6). In fact, despite a significant decrease in g_s in 2003, the mean seasonal A_{XWF} was higher compared to the previous and the following year (Fig. 5). Thus, we suggest that the seasonal timing of the drought in 2003, the leaf physiological adjustment and, furthermore, the usage of storage carbohydrates mitigated the growth response of the beech trees examined. The seasonal timing of the drought and the remobilization processes, in particular, may furthermore explain the lack of an imprint of the physiological response into the isotopic tree ring archive (“Tree ring stable isotope” in “Discussion”). Nevertheless, it is likely that the beech trees have

operated at the hydraulic limits of the water-conducting xylem tissue and that the impacts of a prolonged drought in subsequent years would have affected the growth considerably.

The study highlights the importance of acclimation to drought stress in beech trees and points out several uncertainties of its determination. To better identify the respective processes, a combination of ecological and physiological approaches including continuous tree growth assessments, gas exchange, and isotopic measurements in several parts of the plant are required. Due to the rapid reaction of stomatal and non-stomatal limitation of gas exchange (Flexas et al. 2008), measurements in high temporal resolution would be desirable. Furthermore, mechanistic modeling and estimation of beech vulnerability to drought would benefit from a tighter coupling between biochemical and hydraulic approaches as well as a better resolution of physiological and anatomical crown properties. For representing growth response, we particularly emphasize the consideration of dynamic carbon storages in the plant allocation scheme.

Author contribution statement AG, RG and EP designed the general framework of the study. The hydrodynamic modeling

approach was developed, tested and applied by RHe, CB and EP. The terrestrial laser scanning used for parameterization of the hydrodynamic model was conducted by RHe. Tree cores were taken by RHo and WP. The tree ring dating, cellulose extraction and stable isotope measurement were performed by RHo. The stable isotope analysis and the determination of the intrinsic water use efficiency have been conducted by RHo and AG. The measurements of tree ring width and the growth analysis were performed by WP and RG. The climate data and soil water measurements were provided by JH. All authors are experts in the field of forest drought response and contributed to the discussion. As part of their PhD projects, RHe and RHo contributed equally to this study and were responsible for the overall storyline, structure and analysis. All authors contributed to the writing of the manuscript.

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Appendix

See Table 3.

Table 3 Summary of parameters applied in the hydrodynamic XWF simulation of carbon gain and water loss of individual beech trees

	Unit	Value	References
Parameters of the hydrodynamic model			
CPA_f , crown overlapping	%	32	Hentschel et al. (2013)**
$k_{max,root}$, max. root hydraulic conductivity	$mm\ s^{-1}$	0.13	Bittner et al. (2012a, b)*
$k_{max,branch}$, max. branch hydraulic conductivity	$mm\ s^{-1}$	0.017	Bittner et al. (2012a, b)*
k_{fs} , soil/root hydraulic conductivity	$m\ MPa^{-1}\ s^{-1}$	4.70E-08	Korn (2004)*
E , specific elastic modulus	mm	3.50E + 06	Oertli (1993)*
LAI, leaf area index	$m^2\ m^{-2}$	5.12	Gessler et al. (2004a, b)**
RAI, root area index	$m^2\ m^{-2}$	11	Leuschner et al. (2004)*
Parameters of stomata model			
St_b , parameter of stomatal response	mm	2.29E + 05	Köcher et al. (2009)
St_c , parameter of stomatal response	–	3.5	Köcher et al. (2009)
Parameters of the xylem water retention curve			
α , xylem air entry value	mm	–3.16E + 05	Oertli (1993)*
ε , xylem porosity	$mm^3\ mm^{-3}$	0.52	Gebauer et al. (2008)*
λ , Borriks and Corey parameter	–	0.86	Oertli (1993)
Parameters of the vertical root distribution			
β , Gale and Grigal parameter	–	0.94	Gale and Grigal (1987)
Parameters of the photosynthesis model			
Ea_J , activation energy for J_{max}	$J\ mol^{-1}$	65300	Dreyer et al. (2001)*
Ea_c , activation energy for K_c	$J\ mol^{-1}$	59430	Tuzet et al. (2003)
Ea_o , activation energy for K_o	$J\ mol^{-1}$	36000	Tuzet et al. (2003)
Ea_{Rd} , activation energy for Rd	$J\ mol^{-1}$	62500	Falge et al. (1996)
Ea_v , activation energy for V_{max}	$J\ mol^{-1}$	75400	Dreyer et al. (2001)
Ed_j , deactivation energy for J_{max}	$J\ mol^{-1}$	129000	Dreyer et al. (2001)*

Table 3 continued

	Unit	Value	References
E_{dV} , deactivation energy for V_{\max}	J mol ⁻¹	175000	Dreyer et al. (2001)*
f_{Rd} , scaling constant of Rd	–	25	Falge et al. (1996)
J_{\max} , potential rate of whole-chain electron at T_{ref}	μmol m ⁻² s ⁻¹	46	Epron et al. (1995)*
K_c , Michaelis coefficient for CO ₂	mol mol ⁻¹	460	Farquhar et al. (1980)
K_o , Michaelis coefficient for O ₂	mol mol ⁻¹	330	Farquhar et al. (1980)
o_i , intercellular oxygen concentration	mol mol ⁻¹	210	Tuzet et al. (2003)
S_J , entropy term for J_{\max}	J mol ⁻¹ K ⁻¹	420	Dreyer et al. (2001)*
S_V , entropy term for V_{\max}	J mol ⁻¹ K ⁻¹	559	Dreyer et al. (2001)
T_{ref} , reference temperature	K	298.2	Epron et al. (1995)
V_{\max} , max photosynthetic capacity at T_{ref}	μmol m ⁻² s ⁻¹	109	Epron et al. (1995)*
α , quantum yield of electron transport	–	0.2	Tuzet et al. (2003)
γ_0 , parameter CO ₂ compensation point	mol mol ⁻¹	2.80E – 07	Tuzet et al. (2003)
γ_1 , parameter CO ₂ compensation point	–	5.09E – 02	Tuzet et al. (2003)
γ_2 , parameter CO ₂ compensation point	–	1.00E – 03	Tuzet et al. (2003)
θ_e , parameter of electron transport function	–	0.9	Tuzet et al. (2003)
Parameters of the soil water retention curve			
K_S , saturated soil hydraulic conductivity	mm day ⁻¹	148	Hentschel et al. (2013)**
α , van Genuchten parameter	cm ⁻¹	0.02	Hentschel et al. (2013)**
n , van Genuchten parameter	–	2.5	Hentschel et al. (2013)**
θ_r , residual soil water content	%	11	Hentschel et al. (2013)**
θ_s , saturated soil water content	%	61	Hentschel et al. (2013)**

The table is organized in parameter sets for hydrodynamic modeling, photosynthesis modeling and soil water balance modeling. The asterisks at the right border of the table indicate beech-specific parameters, whereas double asterisk indicate site-specific parameters

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