

Tree species and size drive water consumption of beech/spruce forests - a simulation study highlighting growth under water limitation

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Abstract

Aims By using a growth model, a simulation study was done to detect differing transpiration sums of an evergreen and a deciduous tree species within a mixed stand. The dependence of summer drought and transpiration on tree size and species, and the relationship of water use efficiency and tree growth was analyzed.

Methods The process-based growth model BALANCE was used to simulate the water balance and the growth of individual trees for the isohydric species *Picea abies* and the anisohydric species *Fagus sylvatica* within a mixed forest stand.

Results The individual tree based model was able to realistically simulate the water balances at tree and stand level. Actual evapotranspiration and soil water content differed in species and was size-dependent. Spruce was more affected by drought than beech. Drought stress increased with tree size, an effect which was more pronounced for spruce than for beech. Wood

productivity was positively correlated with water-use efficiency being more distinct in beech than spruce.

Conclusions Using individual tree based growth models effects of tree individuals in structured forest stands on water consumption, growth and productivity can be analyzed. The simulation results, i.e. the information of species-specific water consumption, growth rates and dependencies between water consumption and tree growth in stands of Norway spruce and European beech can help to mitigate effects of climate change on forest stand productivity and preserve an appropriate proportion of high quality timber mainly provided by spruce.

Keywords Drought · Transpiration · Soil water content · Mixed forests · Process based growth model · Water balance

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Introduction

During upcoming decades of this century temperature will increase and precipitation patterns will change significantly (Füssel and Jol 2012; IPCC 2007, 2013). Europe will experience more frequent and more severe summer heat waves during the remainder of the twenty-first century than in the past (Fischer and Schär 2010), as both lengths and occurrences of weather extremes such as drought may increase severely (Easterling et al. 2000; Meehl et al. 2000; Jonas et al. 2005). Drought implies both abnormally low plant-available soil moisture and high atmospheric water deficits (Wilhite and Glantz 1985). Precipitation and temperature will most likely

change substantially (e.g. IPCC 2007; UBA 2007; KLIWA 2006) with distinctly differing spatial and temporal variations (KLIWA 2006). Climate change as a global and regional phenomenon (e.g. IPCC 2007; UBA 2007; KLIWA 2006) will markedly differ between both scales by temporal variation in annual precipitation (KLIWA 2006). Long-term effects are likely on forest growth and species composition, and as a result, of site water balances and carbon flux dynamics on forests (e.g. Kirschbaum 2000; Van der Meer et al. 2002; Fuhrer et al. 2006). Ultimately, atmosphere-hydrosphere-biosphere interactions will become perturbed (Rebetez and Dobbertin 2004). Summed up, less is known about the water balance of individual trees, their interactions with neighboring trees, particularly when growing in mixed stands and having different reaction strategies on drought periods, and the impacts on tree and stand growth.

Duration, intensity and timing (e.g. early or late within the growing period) of droughts will drive productivity effects (Rötzer et al. 2012), modified by soil properties (see e.g. Pretzsch et al. 2014a) and feedbacks within the atmosphere-vegetation system, probably altering ecosystem functionality. However, such interactions lack thorough understanding, as studies have mostly focused on ecosystem components (e.g. Bergh et al. 2003; Rötzer et al. 2005; Garcia-Gonzalo et al. 2007a, b; Rötzer et al. 2013a, b).

In Central Europe water plays a key role for the competitive success of trees, both in monospecific and mixed-species forest ecosystems, being accentuated in the case of contrasting life strategies between species (Kuptz et al. 2011). While Norway spruce (*Picea abies*), pursues an isohydric strategy, i.e. trees respond to incipient drought by stomatal closure (Lyr et al. 1992), European beech (*Fagus sylvatica*) follows a contrasting anisohydric strategy, i.e. an ongoing leaf gas exchange and above and belowground growth under drought (Leuschner 2009; Nikolova et al. 2009). The effects of species mixing with isohydric and anisohydric tree species on growth and hydrological functioning has been studied for several ecosystems (e.g. Klein et al. 2013; Meinzer et al. 2014; Garcia-Ferrer et al. 2016; Goisser et al. 2016) and underlines the potential universality of such species mixing for forests and woodlands. In any case, water consumption is closely related to carbon relations (Hartmann 2011; Brodribb 2009). However, the effects of species specific strategies (e.g. stomatal behavior) with regard to water supply and the consequences for tree and stand growth has only marginally been studied.

Further on, the different phenological developments in the course of a year of the evergreen tree species Norway spruce and the deciduous tree species European beech had an influence not only on tree growth (Rötzer et al. 2004; Pretzsch et al. 2014b) but also on the water balance of the trees (e.g. interception or time of transpiration) and the light supply (Rötzer et al. 2010). The access to water can also be restricted by the different rooting systems (Rothe 1997) with spruce having a more shallower rooting system than beech. However, under drought increased root growth can change this pattern (e.g., Cienciala et al. 1994; Leuschner et al. 2001; Frank 2007; Rötzer et al. 2012). Aboveground the contrasting crown structure, leaf biomass, specific leaf area, and albedo of beech and spruce may further change the provision of light and the amount of interception, which in turn affects transpiration and growth processes. All these processes and structures are species specific and differ within a year but also from year to year and particularly during drought periods. Allocation processes of tree individuals (e.g. Landsberg 1986; Niklas 1994) and average stand growth dynamics have largely been analysed (e.g. Oliver and Larson 1996; Pretzsch 2009), although non-linearities originating from complex tree-level interactions impede functional understanding of stand growth. Stand structure both in terms of species mixture and distribution of small vs. big, young vs. old, and suppressed vs. dominant trees within a stand, may change tree interactions types (such as facilitation, competition or compensation) and alter with changing levels of abiotic stress like drought (Bertness and Callaway 1994). Interactions between tree size and resource availability, however, have rarely been examined (Schwinning and Weiner 1998).

For analyzing such interrelationships between tree and stand-related resource fluxes underlying water consumption and productivity, process-based growth models are ideal tools. Such models simulate forest growth in terms of generally accepted eco-physiological principles (e.g. Landsberg and Waring 1997; Friend et al. 1997; Gracia et al. 2002). Some models, e.g. individual tree based models like FOREST v5.1 (Schwalm and Ek 2004), MAESPA (Duursma and Medlyn 2012) or 4C (Lasch et al. 2005), can consider competition and facilitation effects. Given that models further assess the water cycle and its interactions and feedbacks with growth from individual up to stands level, BALANCE is one example of combined assessment (Rötzer et al. 2010; Pretzsch et al. 2015). Such kind of modeling renders non-linear emergences in

stand-level performance functionally traceable to tree-level interactions in response to carbon and water fluxes (Grimm 1999).

This study was based on simulations by the growth model BALANCE for analyzing and scaling annual courses of transpiration and water balances of individual trees from different species to stand and long-term levels. Water balance of trees and stands can further be linked with carbon and nutrient cycles. Such simulation studies are an alternative to empirical studies if logistically too demanding or complex. This can be the case, if for example competitive interactions and stand growth analysis are to be interpreted in dependence on water relations.

The present simulation study was performed at the site Kranzberger Forst where the precipitation exclusion experiment, KROOF (Pretzsch et al. 2014a) had started in 2013. The aim was to interpret intra- and inter-specific competition of tree individuals for water. This way, growth and water balance measurements that are performed at the site Kranzberger Forst since 1998 and that are intensified since 2013 form an outstanding base for model development, validation and simulation studies. By using the process-based model BALANCE the following research questions were addressed:

Is the model BALANCE able to realistically simulate the water balance of individual spruce and beech trees?

How does transpiration differ between the isohydric evergreen tree species and the anisohydric deciduous tree species within a mixed spruce beech stand?

How does the water balance of spruce and beech trees vary inter-annually under extreme summer drought?

Is summer drought stress and summer transpiration of beech and spruce trees dependent on tree size?

Is the water use efficiency linked with tree growth of beech and spruce trees?

Material and methods

Site and stand description

The Kranzberger Forst site is located at 11°39'42"E, 48°25'12"N, in the southern part of Bavaria, approximately 35 km northeast of Munich. At an elevation of

490 m a.s.l., this site has an average annual precipitation of 750–800 mm yr⁻¹ and of 460–500 mm during the growing season (May–September), whereas the average air temperature is at 7.8 °C on an annual and 13.8 °C during the growing season (1971–2000). For the simulations daily meteorological data (air temperature, humidity, wind speed, radiation, and precipitation) from 1998 to 2013 as drivers for growth and base for the water balance were available from the nearby climate station “Freising” (distance: 1.5 km) which is part of the European Level 2 programme (LWF 2015).

The mixed stand Kranzberger Forst comprises groups of European beech trees (*Fagus sylvatica* [L.]) surrounded by Norway spruce trees (*Picea abies* [L.] Karst), which is typical for Central European mixed forest stands. At the initial measurements in 1997 the tree ages were determined as 46 ± 2 years for spruce, and 66 ± 4 years for beech. To initialise the model information about size (*dbh* and height) and position of each tree is needed. For the simulation study we used a section with 5000 m² of the entire stand, i.e. 260 trees of the Kranzberger Forst, measured in autumn 1997 (Fig. 1). To avoid border effects 40 surrounding trees of the study plot were simulated but excluded from the subsequent analyses. Based on measurements of the individual trees in autumn 1997 and using the climate data set the tree growth simulations could be performed for the period 1998–2013.

The size of the analysed study plot comprises 2815 m², the stand characteristics are listed in Table 1. The initial stand characteristics of the analysed section match well to the recordings done in 1999 for the entire Kranzberger Forst resulting in 803 trees per ha, a basal area of 44.9 m² ha⁻¹ and a standing volume of 554 m³ ha⁻¹ (Schütze et al. 2005). Consequently, the section of the entire stand chosen for the simulation study appropriately represents the Kranzberger Forst. The stand is comprised of large groups of beech surrounded by spruce trees. The long-term over-yielding at the stand level is 18% for the age series ‘FRE813’ in which the Kranzberger Forst is included (Pretzsch et al. 2010). However, within this study we concentrate on species specific differences in the growth behaviour and the water balance by analysing individual trees.

The soil of the site is a luvisol originating from loess over Tertiary sediments, which provides high water and nutrient supply to a depth of 100 cm. To simulate the water balance of individual trees within Kranzberger Forst the total depth of the soil layer was assumed to

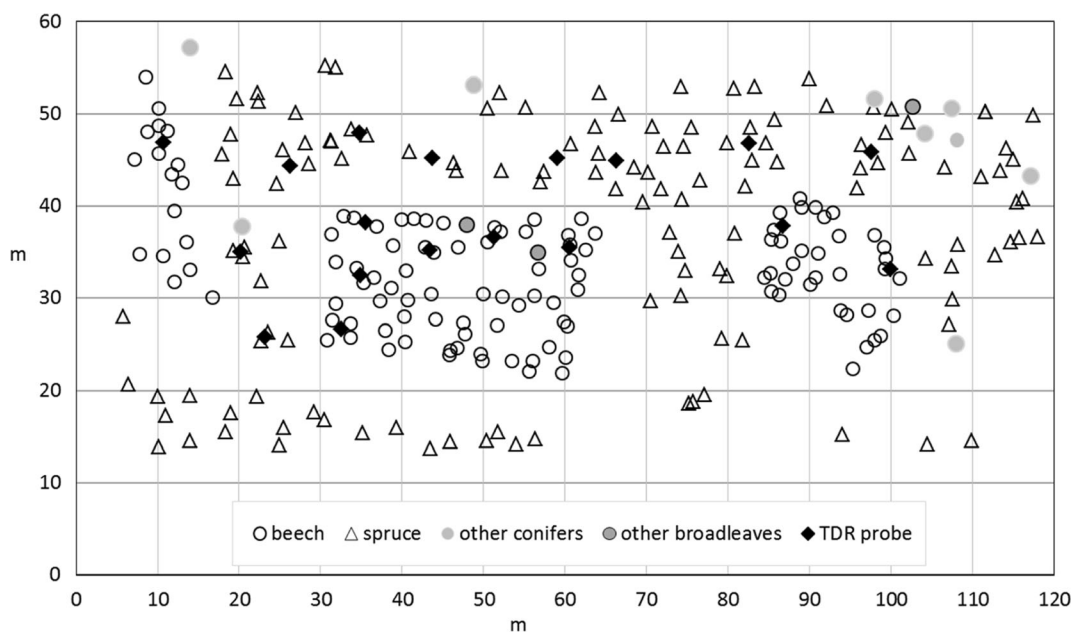


Fig. 1 Site map with tree species distribution (including border trees) and positions of TDR-probes

be 100 cm. Because more than 90% of the roots of the beech and spruce trees were found between 0 and 50 cm (Häberle et al. 2012), we concentrate our analysis to the upper layers. All soil information was taken from Schuhbäck (2004; Table 2).

Measurement of soil water content

Within the KROOF-project (Pretzsch et al. 2014a) which started in 2013 soil water content *swc* is measured. We used measured *swc* of the first year 2013 for a validation of simulated soil water content values. Time-Domain-Reflectometry probes (TDR 100, Campbell Scientific, Inc., Logan, Utah, USA) were used for the measurement of the soil water content. At 18 points of the study site TDR-probes were installed (Fig. 1). At 9 points the probes are surrounded by beech trees, while the other 9 probes are only surrounded by spruce trees. The closest trees were then assigned to the probes (see supplement STab. 1). Probes are installed in two depths representing the volumetric soil water content for the soil layers of 0–10 cm and 10–30 cm.

Volumetric soil water content was measured up to 29 times per year in 2013. This way, between 247 and 253 comparisons per tree species and per layer could be made resulting in 241 and 240 values for the total layer from 0 to 30 cm (see supplement STab. 2).

The size (i.e. the diameter at breast height *dbh*) of the assigned trees varied from 18.8 cm to 39.5 cm for the selected beeches, and from 15.1 cm to 49.6 cm for the selected spruces (data from 1997). Consequently, the simulated soil water content could be validated for differently sized trees of the two tree species.

General description of the growth model BALANCE

The tree growth model BALANCE is an example of a complex forest growth model (Pretzsch et al. 2015) and simulates growth responses at tree level, assessing influences of competition, stand structure, species mixture, and management impacts (as e.g. thinning), as development of a tree individual can be characterized as the reaction on individual environmental conditions and changes during tree and stand development. A detailed description of the model with validation results can be found at <http://waldwachstum.wzw.tum.de/index.php?id=balance&L=1> or in Grote and Pretzsch (2002) and Rötzer et al. (2010, 2012).

The dendrometrical variables tree height, height to crown base, diameter at breast height, and crown radii determine the initial biomass of a tree. The interaction of the multiple physiological processes which depend on the physical and chemical micro-environment results in an increase of biomass which might change the spatial

Table 1 Stand characteristics of the initial stand in autumn 1997

species	N [ha ⁻¹]	dq [cm]	hq [m]	B [m ² ha ⁻¹]	V [m ³ ha ⁻¹]
beech	397	24.1	24.5	18.0	211
spruce	383	29.4	25.6	26.0	351
total	780			44.0	562

N number of trees per hectare, *dq* quadratic mean diameter, *hq* height of the dq-tree, *B* basal area, *V* standing volume

structure of the stand. Hereby, asymmetric crown shapes generate spatially explicit representations of the environment. These calculations are done for all crown and root layers, which are spatially subdivided into segments, and can be up-scaled to tree and stand level (Fig. 2). Thus, biomass increase is estimated for each segment of each layer depending on the carbon and nitrogen uptake, its energy supply and resource availability.

The carbon, water and nutrient flows of the tree individuals form the fundamental processes for the growth simulations. They are parameterized for the tree species European beech (*Fagus sylvatica* [L.]), Sessile oak (*Quercus petraea* L.), Common oak (*Quercus robur* L.), Norway spruce (*Picea abies* [L.] Karst), Scots pine (*Pinus sylvestris* L.), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Table 3 gives the parameters of the tree species European beech and Norway spruce.

On the base of temperature, radiation, precipitation, humidity and wind velocity micro-climate and water balance are calculated daily for each layer and segment. Using the aggregated driving variables the physiological processes such as assimilation, respiration, nutrient uptake, growth, senescence and allocation are simulated in 10-day time steps. Dimensional tree growth is calculated once a year based on the tree's annual biomass increase in woody tissue. This way, tree growth can be modeled depending on weather conditions, CO₂-concentration, soil conditions, competition between individuals, and

stress factors as for example drought and nutrition deficiency (Fig. 2).

BALANCE uses different approaches for the simulation of the growth and resource availability of each individual tree. Photosynthesis is calculated according to Haxeltine and Prentice (1996) and linked with the water balance by stomatal regulation. Gross primary production is a function of leaf area, photosynthetically active radiation (PAR), temperature, CO₂-concentration, water supply as well as nitrogen supply. Total respiration is consisting of maintenance losses and growth respiration. In BALANCE the unfolding of new leaves of a tree species is simulated on the base of an air temperature sum model. In other words the date of foliage emergence is reached when the summed up daily temperature values exceed a species-specific threshold temperature sum (Rötzer et al. 2004). Foliage senescence is estimated in the same way by using a respiration sum model, however based on the potential respiration capacity of the foliage and the actual respiration rates (Rötzer et al. 2010).

To allocate the gained carbon and nitrogen into roots, branches, foliage and stem, functional balance (Mäkela 1990) and pipe model principles (Shinozaki et al. 1964) are applied, i.e., all tissues are mechanistically linked to each other. As a fraction of the living woody tissue a share of the gained carbon is stored as non-structural carbon (=NSC) for respiration and defense aspects. On base of the biomass accumulation during the year dimensional tree growth is calculated for that year. The development of the crown is favored in the direction of best assimilation conditions during the previous year, because crown volume increment is governed by the necessary amount of twigs and transport branches as well as by the amount of coarse roots within root segments.

Negative net assimilation rates mean that the crown segment is dead. A tree is assumed dead if no segments contain living biomass. This tree will then be removed from the simulation.

Table 2 Soil characteristics for the site Kranzberger Forst

layer [cm]	field capacity [vol%]	wilting point [vol%]
0–5	40.0	11.0
5–30	35.0	8.0
30–85	35.0	10.0
85–100	35.0	23.0

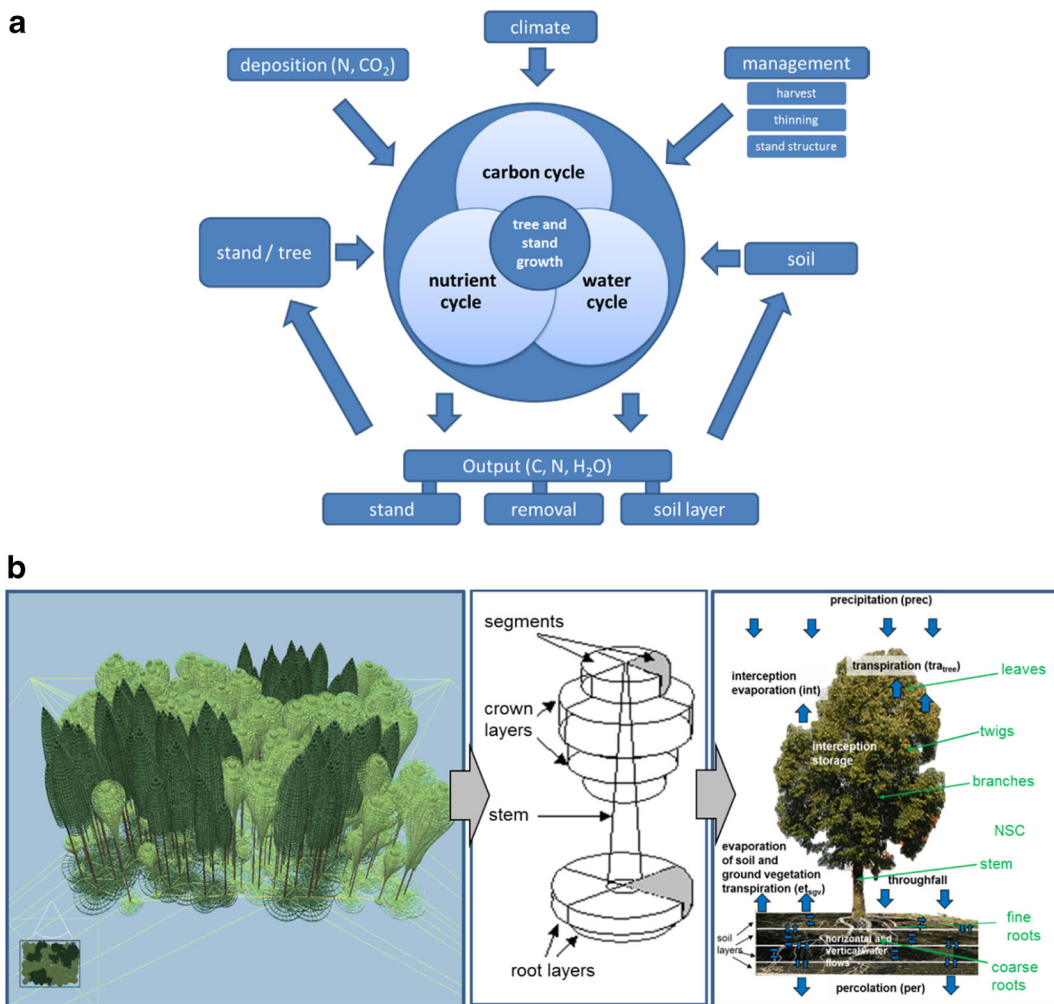


Fig. 2 The process based growth model BALANCE: **a** Scheme of the model: The linked cycles represent the cause and effect relationships; tree and stand growth is simulated based on environmental conditions and competition of neighboring trees which can

be changed by management measures; **b** Spatial representation and components as well as water balance of an individual tree for the simulation

Description of the water balance module of the BALANCE model

By using the model BALANCE the individual water balance of a tree can be simulated for each day considering the soil conditions in the different layers under a tree (Fig. 2).

For each layer field capacity and wilting point must be known. Vertical water flows are considered by a multi-layer bucket soil water model, while horizontal water can flow between the rooted and non-rooted fractions of each layer. Providing the water within the rooted fraction for a tree's transpiration demand the water balance

of a tree individual can be described as:

$$\Delta swc = prec - et_a - per \tag{1}$$

- swc soil water content in mm
- Δswc change in *swc* in mm
- prec precipitation in mm
- et_a actual evapotranspiration in mm
- per percolation in mm.

Hereby actual evapotranspiration et_a can be defined as

$$et_a = tra_{tree} + et_{sgv} + int \tag{2}$$

Table 3 Species specific parameters used in the growth model BALANCE for Norway spruce and European beech

Parameter	Unit	Norway spruce	European beech
water balance module			
Albedo	-	0.08	0.15
Maximum conductance for water	mm s ⁻¹	1.40	2.20
Relative amount of water at which water deficiency starts wdr	-	0.60	0.43
Specific foliage interception capacity	mm m ⁻² leaf surface	0.35	0.26
growth module			
Maximum leaf area density per leaf volume	m ² m ⁻³	7.20	4.65
Factor of development for the change of the specific leaf area		0.12	0.20
Maximum specific leaf area	m ² kg ⁻¹	7.10	30.00
Minimum specific leaf area	m ² kg ⁻¹	2.40	11.00
Branch biomass (without transport) per sapwood area	kg cm ⁻²	0.02	0.03
Foliage biomass per sapwood area (green area)	kg cm ⁻²	0.07	0.10
Average branching angle (between tree top and branch base)	-	80	35
Branch diameter change with length	cm m ⁻¹	0.00	0.20
Specific fine root surface	m ² kg ⁻¹	20	35
Proportion of dead fine roots per year	-	0.40	0.30
Maximum C-amount reserved per structure tissue	kgC kg ⁻¹	0.20	0.25
Maximum ratio between height and diameter increment	-	467	430
Reduction factor for photosynthesis	-	0.70	0.50
Wood (space) density for branches	kgDW m ⁻³	585	620
Wood (space) density for root	kgDW m ⁻³	451	580
Wood (space) density for stem	kgDW m ⁻³	377	554
phenology module			
Constant of the equation temp.-sum equation		19.6	20.8
Beginning the addition of the temperature	doy	60	0
Factor of the equation temp.-sum equation	-	0.02	0.02
Number of effective needle years	-	6	1
Maximum longevity of foliage	days	1996	160
Factor for potential respiration sum for foliage senescence	-	0.40	0.60
nutrient module			
Minimum nitrogen concentration for photosynthesis	%N	0.70	1.02
Optimal nitrogen concentration for photosynthesis	%N	1.40	2.50
Optimal nitrogen concentration in the fine roots	%N	1.63	1.50
Optimal nitrogen concentration in the reproduction	%N	1.00	1.00
Optimum nitrogen concentration in the sapwood	%N	0.10	0.10
Specific uptake rate of NH ₄ nitrogen	gN (kgDW) ⁻¹	5.80	2.20
Specific uptake rate of NO ₃ nitrogen	gN (kgDW) ⁻¹	1.40	0.70
C-loss (kg) per N (g), per kgDW and Kelvin in foliage	kgC (gN) ⁻¹ (kgDW) ⁻¹ K ⁻¹	0.10	0.10
C-loss (kg) per N (g), per kgDW and Kelvin in the fine roots	kgC (gN) ⁻¹ (kgDW) ⁻¹ K ⁻¹	0.20	0.20
C-loss (kg) per N (g), per kgDW and Kelvin in the sapwood	kgC (gN) ⁻¹ (kgDW) ⁻¹ K ⁻¹	0.10	0.10

tra_{tree} transpiration of the tree in mm
 et_{sgv} evapotranspiration of the soil and the ground
 vegetation in mm

int interception evaporation of the tree in mm
 If the soil water content of a layer is higher than the
 swc of a neighboring layer vertical water flows occur. In

the same way horizontal water flows take place between the rooted and non-rooted soil layer fractions. Percolation per of an individual tree is equivalent to the percolation from the deepest soil layer. It arises if swc is above field capacity. In this case the soil water content of the layer is reduced to field capacity. This way, precipitation, interception, actual evapotranspiration, and percolation determine the daily change of the soil water content under a tree (Eqs. 1 and 2).

Using the Penman-Monteith approach (e.g. Allen et al. 1998; DVWK 1996) potential evapotranspiration et_p of a tree can be calculated based on air temperature, radiation, air humidity and wind speed:

$$et_p = 1/L^* \left[\left(s^* r_{net} + \delta_{air}^* c_p^* vpd / r_a \right) / \left(s + p^* \left(1 + r_c / r_a \right) \right) \right] \quad (3)$$

L	specific vaporization heat of water in $W m^{-2}$
s	slope of the saturation curve for vapour pressure deficit in $hPa K^{-1}$
r_{net}	net radiation in $W m^{-2}$
δ_{air}	air density = $1.202 kg m^{-3}$ [20 °C]
c_p	heat capacity of the air = $1005 J kg^{-1} K^{-1}$
vpd	vapour pressure deficit in hPa
r_a	boundary layer resistance in $m s^{-1}$
r_c	canopy resistance in $m s^{-1}$
p	psychrometer constant = $0.662 hPa K^{-1}$

Daily net radiation r_{net} of Eq. 3 can be derived by

$$r_{net} = (1-\alpha)^* r_{short} - r_{long} \quad (4)$$

α	albedo
r_{short}	short wave radiation balance in $W m^{-2}$
r_{long}	long wave radiation balance in $W m^{-2}$

Canopy resistance r_c needed for Eq. 3 can be estimated on the base of leaf area index and of the species-specific maximum conductivity for water while the boundary layer resistance r_a is a function of stand height and wind speed.

By using et_p and the maximum water uptake derived from the water content within the soil volume that contains fine roots, the actual evapotranspiration et_a of a tree or of the ground cover can be calculated. Hereby, et_p is shortened if the demand for water by the tree is higher than the maximum water uptake. The reduction of the potential evapotranspiration is calculated based of the soil water content, the physical soil characteristics

and by a species specific factor:

$$et_a = \min \left[1, (swc - swc_{wp}) / (wd_r^* (swc_{fc} - swc_{wp})) \right]^* et_p \quad (5)$$

swc_{fc}	soil water content at field capacity in mm
swc_{wp}	soil water content at wilting point in mm
wd_r	species specific relative amount of water at which water deficiency starts

Consequently, the ratio $et_a:et_p$ is closely related to the relationship between water supply and water demand. The increase of this relationship above a threshold defined by the species-specific water deficiency coefficient determines drought stress for photosynthesis.

On the base of the leaf area index, the species-specific parameter interception capacity and the degree to which the interception storage is filled, interception *int* can be estimated. It evaporates potentially according to the Penman-Monteith equation for wet surfaces and is calculated for each tree's crown covered area, which is estimated dynamically based on crown extensions. Throughfall in remaining gaps between the trees is equal to precipitation. Because water can be exchanged between rooted and un-rooted soil layers, the soil water content of the rooted fraction within the same layer is refilled by throughfall precipitation in gaps between trees. A newly implemented hysteresis effect considers soil remoistening depending on the previous drying out of the soil. Stem flow as well as the water exchange between the different trees is not yet realized. A snow module considers snowfall and melting of snow by using the degree day factor approach by Baumgartner and Liebscher (1990) in which the daily amount of melting water is estimated.

While a tree's transpiration sum is the amount of water that is lost into the atmosphere by the individual tree, evapotranspiration et_a includes additionally evaporation of the soil, transpiration of the ground vegetation and interception evaporation of the tree (Fig. 2). The total water consumption of a tree in m^3 per tree is calculated from the sum of evapotranspiration multiplied by the stand area of the tree.

Within this simulation study, the entire mixed forest stand (260 tree individuals, Fig. 1) was simulated for the period 1998–2013. To uncover specific characteristics of the tree species growth and water balance parameters were calculated for each individual tree based on the tree's surface area, which in turn depends on the crown

radii measured for 8 cardinal points. Thus, means and standard errors of the stem diameter increment could be calculated for the two species as well as for different tree size classes. Water balance parameters were based on square meter tree surface area, i.e. values such as transpiration or interception represent the average amount of a tree individual ($L/m^2 = mm$). This way, means and standard errors could be derived for the two tree species as well as for tree size classes.

Results

Model validation

Growth of beech and spruce trees

A prerequisite for a plausible simulation of the water balance of beech and spruce trees is to realistically simulate tree and stand growth. Fig. 3 denotes both measured and simulated diameter development of the beech and the spruce trees starting in 1997 throughout 2013. Over the entire 17-year period measured and

modeled annual mean diameters agree with each other both for the spruce and the beech trees.

Soil water content under spruce and beech trees

The model validation of the water balance was done for the *swc* in the different soil layers at 18 positions within forest stand (see supplement STab. 2), for the course of the *swc* over the year (Fig. 4) and for the all single *swc* values separately for the two layers and the two species (see supplement –SFig. 1).

The mean absolute error *mae* of the simulated and measured volumetric soil water content in the upper layer ranged from 1.9 to 8.8 vol% and from 1.9 to 7.7 vol% for beech and spruce, respectively. With values from 2.8 to 5.0 vol% for beech and from 2.5 to 6.4 vol% for spruce the range for the lower layer (10–30 cm) was smaller compared to the upper layer. For the entire layer from 0 to 30 cm *mae* for beech varied between 1.8 and 5.8 vol% and for spruce between 2.0 and 5.7 vol%. With the exception of sample No. 9 the coefficient of correlation was always higher or equal than 0.8 for the beech samples, while it ranged between 0.5 and 0.93 for the spruce samples.

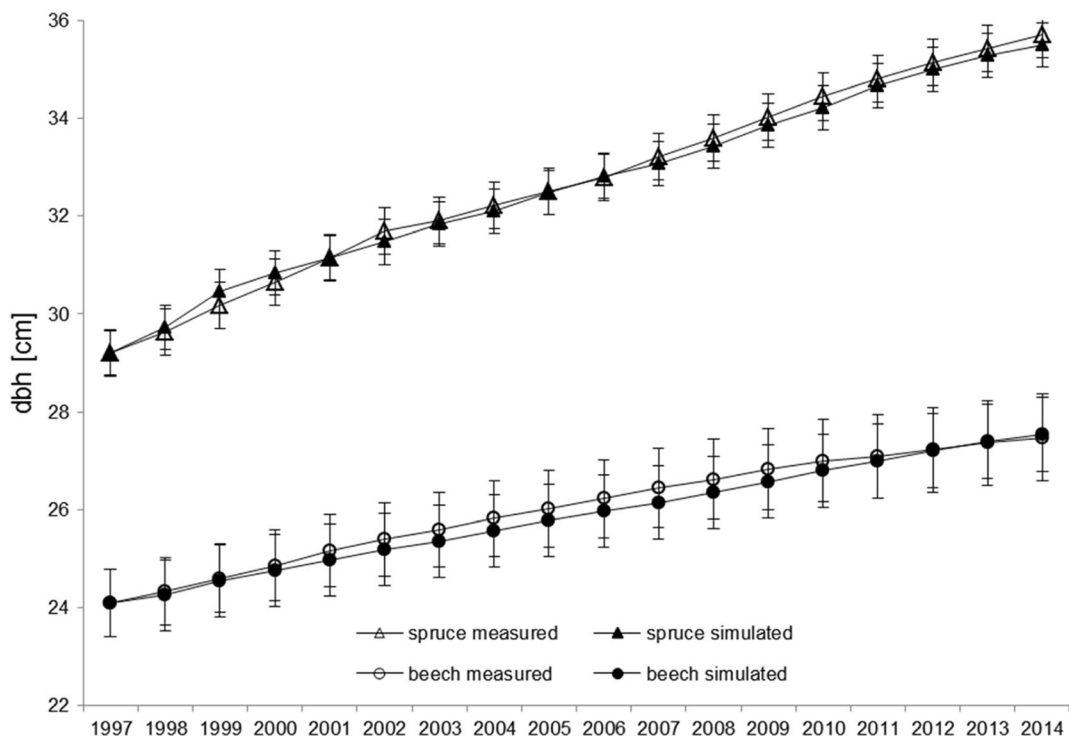


Fig. 3 Simulated and measured dbh values (mean \pm standard error) of beech and spruce at the site ‘Kranzberger Forst’ for the years 1997 to 2013

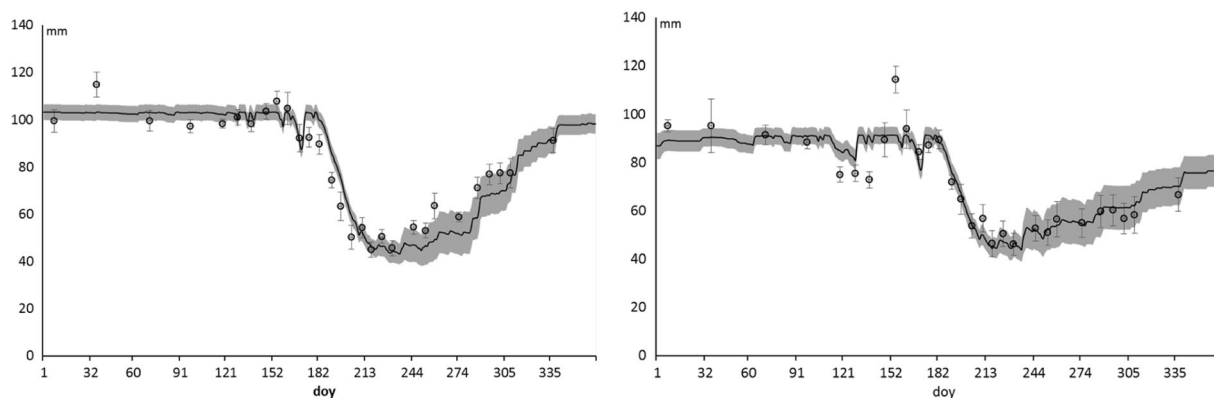


Fig. 4 Soil water content (mean \pm standard error) of the layer 0–30 cm under beech (left) and spruce trees (right) in the year 2013 at the site ‘Kranzberger Forst’, measured values (dots) compared with simulation data (solid line with grey areas)

In addition to the above shown spatial analysis of the soil water content the temporal development of the soil water content under spruce and beech trees within a year is important. In Fig. 4 simulated daily soil water content values of the year 2013 under beech and spruce trees are compared to corresponding measurements. Hereby, the values of each date were averaged over all 9 samples.

With the exception of some single measurements the annual course of the simulated soil water content in the upper layer from 0 to 30 cm agreed well with measurements, both for beech and spruce. The two species show characteristic developments over time which corresponded well with the model simulation results (see supplement SFig. 1). With coefficients of determination between 0.61 and 0.71 the simulation results correspond to measurements.

In a further analysis we quantified the depleted water *dWater* from two soil layers under spruce and beech trees starting at the beginning of 2013 throughout the end of August 2013 (Table 4). Average differences between the measured and simulated depleted water (0–30 cm) were 4 mm in beech and 1 mm in spruce.

The entire simulated water uptake from the soil (0–70 cm depth) from the 1st of January until the end of August was 141 mm for the beech trees, but 107 mm for the spruce trees. The simulated transpiration during July and August 2013 of beech was higher than of spruce (i.e. 199 mm versus 181 mm, respectively).

Water balance of beech and spruce trees in a mixed forest stand

The average annual courses (1998–2013) of the soil water content distinctly differed between beech and spruce (Fig. 5). Under spruce trees, field capacity was not reached during winter months as contrasting with beech. From mid-May through the end of July *swc* under both species approached each other, although on average levels were lower under spruce than under beech.

Such outcome resulted from the actual evapotranspiration. Averaged over the entire period transpiration of spruce started earlier and finished later compared to beech. E_{t_a} was higher in spruce before May (average

Table 4 Mean and standard error se of the depleted water (*dWater*) from the soil from the 1st of January to the end of August 2013 under beech and spruce trees at the site ‘Kranzberger Forst’ based on measured and simulated data

species	layer [cm]	n	dWater simulated [mm]		dWater measured [mm]	
			mean	se	mean	se
beech	0–30	9	41	2	46	2
	0–70	9	100	4	-	-
spruce	0–30	9	29	2	28	3
	0–70	9	78	3	-	-

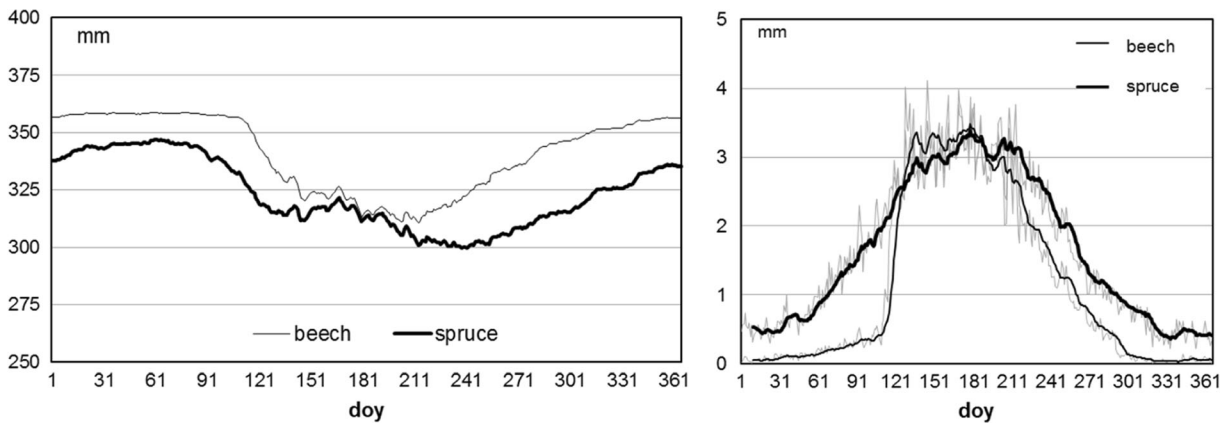


Fig. 5 Daily sums and 10-day moving averages of the soil water content (*left*) and actual evapotranspiration et_a (*right*) of beech and spruce averaged over the period 1998–2013 at the site ‘Kranzberger Forst’

bud break of beech is at doy 112 = April, 2nd) and during fall and winter. From the end of May to mid-July, however, et_a of beech exceeded the values of spruce.

For spruce the simulated annual average transpiration sum was 403 mm while the interception sum was 167 mm (see supplement –SFig. 2). Levels were close to the sums of the validation year 2013 with 396 mm for the transpiration and 148 mm for the interception. Precipitation of the year 2013 was 807 mm, i.e., slightly lower compared to the long-term mean (841 mm). For beech transpiration in 2013 (343 mm) surpassed the long-term average (324 mm), whereas interception was low with 54 mm and 62 mm for both the year 2013 and the long-term mean (see supplement –SFig. 2). Minimum annual transpiration sums were simulated for 2001 with 263 mm in beech and 322 mm in spruce. Interception was lowest in 2003 with 47 mm for beech and 131 mm for spruce.

Water balance of beech and spruce trees in the drought year 2003

During exceptionally hot and dry 2003 annual transpiration amounted to 379 mm in beech and 465 mm in spruce trees probably supported by the high soil water capacity of the site. The actual evapotranspiration sums of 2003 for spruce and beech trees were higher than the long-term means from the beginning of March (doy 60) until the mid (spruce) or the end (beech) of August (doy 228 and doy 243; Fig. 6a). Particularly high values can be found for May and June. Consequently, the annual et_a sums of spruce (638 mm) and beech (474 mm) for the

year 2003 surpassed the averages of the entire simulated period with 604 mm and 421 mm, respectively.

Total different courses can be seen for the reference year 2013, where in the first half of the year et_a was clearly below the mean of the simulated period (1998–2013) and below the 2003 values, and where the highest values were achieved in July/August (Fig. 6a).

At the beginning of 2003, field capacity was reached (Fig. 6b). Because of high evapotranspiration rates soil water content declined sharply. The low levels at the end of July and in August indicate strong drought stress, being more pronounced in spruce than in beech. By the end of the year soil water content remained very low.

Effects of tree size on the summer transpiration of beech and spruce

During June through August growth and transpiration reached maxima (Figs. 5, and 6). Tree size effects on et_a of these months were compared for drought year 2003 and the reference year 2013 by relating summer et_a (=month June to August) of beech and spruce trees to stem diameter classes (width 5 cm, Fig. 7).

Increases of the summer et_a with size class were found for beech trees (exception: size class 35–40 cm in 2013), with consistently lower evapotranspiration sums in 2003. However, the difference gradually declined from diameter class 15–20 cm with 66 mm to –2 mm for diameter class 35–40 cm. In spruce summer evapotranspiration was slightly decreased in 2003, with 255 mm for size class 20–25 cm and 221 mm for size class >40 cm. In 2013, spruce trees of all diameter classes >30 cm had similar summer et_a values between

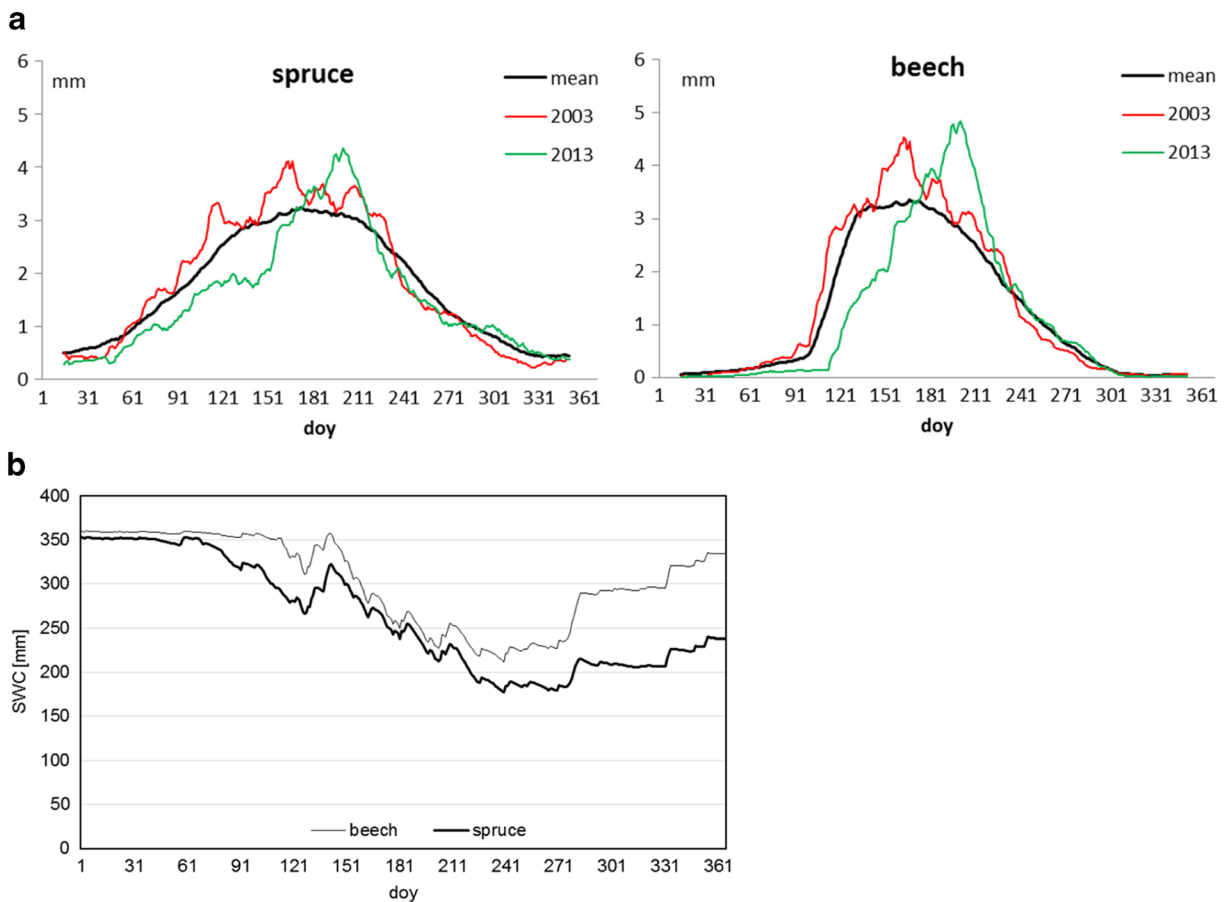


Fig. 6 Water balance in dry years at the site ‘Kranzberger Forst’: **a** actual evapotranspiration et_a of beech and spruce (30 days running means) averages over the period 1998–2013 and for the years

2003 and 2013; **b** soil water content SWC under beech and spruce for the year 2003

250 and 258 mm, being higher than respective levels in 2003. Small-sized spruce trees had summer transpiration lower than 65 mm, as levels hardly differed between 2003 and 2013. In 2013 spruce tree with diameters above 30 cm revealed similar summer et_a sums between 250 and 258 mm which were higher than the respective values of 2003. Small sized spruce trees displayed very low summer et_a sums ($< 65 \text{ l/m}^2$) with only small differences between 2003 and 2013.

The low soil water content under beech and spruce trees in 2003 reflected strong summer drought. For the quantification of drought, the ratio between actual and potential evapotranspiration was calculated as a tree’s drought index and related to tree size, i.e. diameter, (Fig. 8).

During humid 2013 beech trees revealed high indices mostly above 0.8 independent of tree size, indicating no water limitation in the summer months. Small spruce

trees showed high eta/etp ratios above 0.85, while the ratios of the big spruce trees were slightly lower. All ratios indicated sufficient water for transpiration during the year 2013. 2003 contrasted in beech with indices between 0.70 for big trees and 0.78 for small trees, as in spruce trees a size dependency of the index became apparent ($r = 0.57$). Small trees still show high ratios >0.8 , i.e. no drought stress. For big trees, however, the eta/etp ratio decreased below 0.4 indicating strong water limitation.

Water use efficiency of beech and spruce trees

The sum of actual transpiration and interception of a tree was used for calculating the growth-related water use efficiency WUE_{vol} , defined as wood volume increment versus total water consumption (Fig. 9).

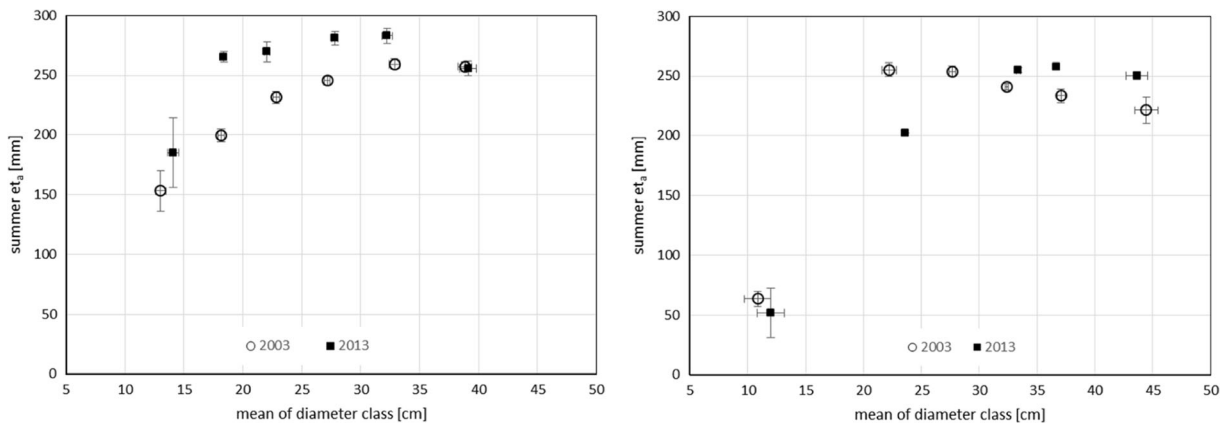


Fig. 7 Summer evapotranspiration sums \pm standard error depending on tree size classes (dbh, average class values is shown) \pm standard error for beech (*left*) and spruce (*right*) of the years 2003 and 2013 at the site ‘Kranzberger Forst’

For both species water use efficiency increased with annual wood volume growth. For all volume increments beech trees denote higher efficiencies than spruce trees.

Discussion

Plausibility of the simulated water balance

Upon agreement between dbh measurements and simulations as well as due to other validation studies done for growth processes by using the model BALANCE (e.g. Rötzer et al. 2005; Rötzer et al. 2013a, b), especially for the Kranzberger Forst (e.g. Grote and Pretzsch 2002; Rötzer et al. 2010) the growth model BALANCE

proved appropriate to simulate tree growth of beech and spruce at Kranzberger Forst.

Most physiological processes within a plant are linked with water (Hartmann 2011). Therefore, precise knowledge about the water availability of a tree or a stand is essential for analyzing the influence of the water balance on a tree’s or a stand’s growth. Because transpiration measurements of individual trees and entire stands are demanding, costly and time consuming, validations of a simulated water balance of an individual tree or an entire stand are often performed by comparing simulated with measured soil water contents. We measured the soil water content under beech and spruce individuals by using 18 TDR-probes and compared recordings with simulation results and found that both absolute levels and time courses were highly correlated.

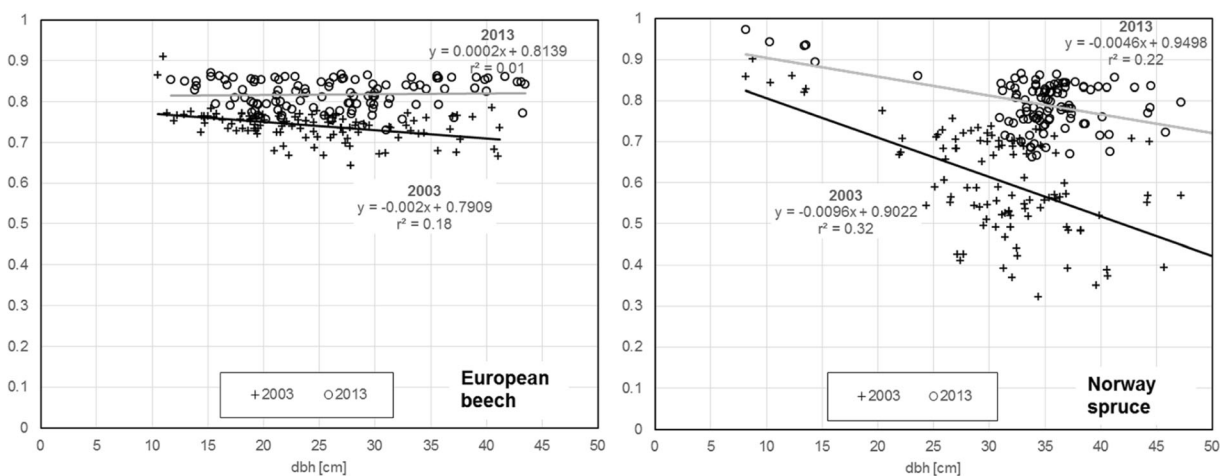
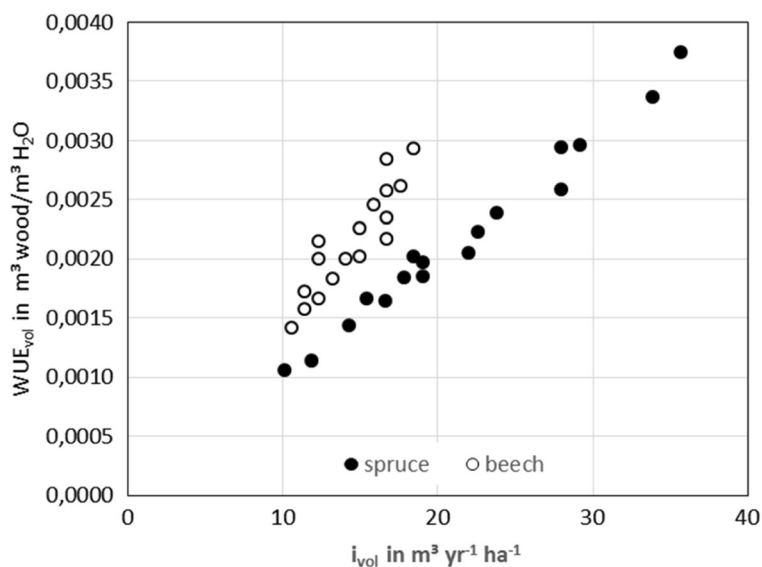


Fig. 8 Drought index ($=e_t/e_p$ of the summer months) depending on tree size (dbh) for beech (*left*) and spruce (*right*) of the years 2003 and 2013 at the site ‘Kranzberger Forst’

Fig. 9 Annual water use efficiency WUE_{vol} depending on the annual wood volume increment i_{vol} for beech and spruce within the period 1998–2013



For the mixed spruce-beech forest at the Kranzberger Forst transpiration sums from literature given by Matyssek et al. (2009) from mid-May through mid-September were 277 mm and 246 mm, respectively for the years 2000 and 2001. These results match with our simulations for these years yielding 245 mm and 240 mm, respectively. According to Matyssek et al. (2009), transpiration in proportion of precipitation was 73% (2000) and 58% (2001) while present simulations yielded 65% (2000) and 60% (2001).

Average annual transpiration sums under Central European conditions for 40 to 50-year-old beech and spruce stands (yield class 2) given by Lyr et al. (1992) with 320–370 mm yr⁻¹ for beech and 390–450 mm yr⁻¹ for spruce match well to the simulated mean transpiration sums of this study with 324 mm yr⁻¹ for beech and 403 mm yr⁻¹ for spruce. The annual transpiration of Central European beech forests estimated based on sap flow measurements by Schipka et al. (2005) varies between 213 mm yr⁻¹ and 421 mm yr⁻¹ and is wider than the spectrum given by Lyr et al. (1992). Our annual sums for beech fit in this range and are close to the reported transpiration sum for a Southern German beech forest (elevation: 495 m, precipitation: 696 mm yr⁻¹) with 323 mm yr⁻¹. Lyr et al. (1992) also cite of Tajchman (1967) who calculated an annual transpiration of 285 mm yr⁻¹ and an annual interception of 142 mm yr⁻¹ for a 70-year-old spruce forest close to Munich. While transpiration is lower than our simulated values the annual interception sum is close to the amount of the simulation with 167 mm. However, comparisons of

transpiration sums of different sites are often very complex due to changed climate and soil conditions and differing stand structures such as by age, stand density or mixing ratio (Schume et al. 2003; Gebauer et al. 2012; Gebhardt et al. 2014). Even so, the presented simulations of the water balance, validations and comparisons to measurements of spruce and beech stands some of which are close to or identical with the study site were successful and convincing.

Using process based growth models such as BALANCE tree and stand growth can be assigned to altered light and/or water supplies, which have been reported for mixed forests (Rötzer 2013; Goisser et al. 2016; Forrester 2015). Physiological growth models are this way able to simulate the effects of structured mixed forest stands on resource allocation such as water (see Pretzsch et al. 2015). A further advantage of such kind of models is that long time series can be computed and annual courses of tree individuals can be simulated. Prognoses of future stand developments under changing environmental conditions can be done (e.g. Lasch-Born et al. 2015; Medlyn et al. 2011; Rötzer et al. 2013a, 2013b). Linkages of the water balance of trees and of the entire stands with the nutrient cycles (nitrogen, phosphorus) are possible (Pretzsch et al. 2015).

Species-specific water consumption in a mixed forest stand

Averaged over the entire period from 1998 to 2013 annual actual evapotranspiration was 421 mm yr⁻¹ for

beech trees and 604 mm yr^{-1} for spruce trees. The higher annual e_t of spruce trees compared to the values of beech trees is due to higher tree and ground vegetation transpiration and higher values of interception. Tree specific structures such as crown architecture and foliage habit, which both can be simulated by the BALANCE model, strongly influence the total sum of evapotranspiration (e.g. Mackay et al. 2003). The two studied species beech and spruce can be characterised as complementary species in terms of crown structure and phenology resulting in clearly different transpiration and interception amounts (Matyssek et al. 2009) as can be seen in the simulation results. However, also stem density within the stand, rooting depth, leaf area index, sapwood area, xylem anatomy, leaf water status and the stomatal regulation are species specific and this way alter transpiration (Gebauer et al. 2012). The individual tree based model BALANCE with a complex tree physiology module is able to consider these factors.

Along with the total amount and intensity of precipitation the interception rate of a forest stand depends to a great extent on tree species, tree size and tree architecture (Menzel 1997). Generally, the rate of interception for deciduous trees is below 25% based on the precipitation while it may sum up to 40% for conifers (Mitscherlich 1998; Oke 1987). Based on an annual precipitation sum of 841 mm we found values of 7% for beech trees and of 20% for spruce trees.

A good indicator for the higher evapotranspiration sum of spruce trees in contrast to beech trees are the on average lower soil water contents (Figs. 4, 5 and 6b) which for spruce were not filled up to field capacity in winter. The reasons for higher evapotranspiration sums of spruce trees compared to the rates of beech trees are manifold. The lower albedo of spruce compared to beech, i.e. the higher energy absorption by spruce trees (expressed through higher potential evapotranspiration rates) might increase the transpiration rate of spruce more than for beech, particularly in times when water supply is not limiting.

Following Gebauer et al. (2012) tree species with differing leaf emergence and senescence patterns in the course of the year will differ significantly in their transpiration rates. In the southern part of Germany deciduous trees such as beech start leaf unfolding in the second half of April and shed their leaves at the end of October (Rötzer and Chmielewski 2001; Rötzer et al. 2004). Consequently, transpiration of these tree species can

take place in a limited time frame of 6–7 months (Fig. 5, Fig. 6). On contrary, transpiration of conifers like spruce is possible throughout the year, even in the winter months if the conditions are favourable. This advantage of the spruce trees compared to the beech trees in autumn, winter and spring cannot be balanced by the higher transpiration rates of the beeches in the summer months. Schume et al. (2003) found that in spring before the leafing of beech soil water content under areas of spruce trees was about 5% lower than under areas dominated by beech trees which is also true for our simulations (Fig. 5, Fig. 6).

We found that the summer transpiration rates for spruce with 181 mm were lower than the rate for beech with 199 mm. This corresponds well with the findings of Schume et al. (2003) that with the beginning of May, i.e. when beeches were fully foliated, beech trees consumed markedly more water than spruce trees. This difference in the summer transpiration may be due to the different strategies of the two species to meet low water availability situations (Lyr et al. 1992). While spruce reacts with an early stomatal closure (isohydric strategy) resulting in lower transpiration values, beech with its anisohydric strategy keeps the stomata open with the consequence of enhanced transpiration rates. Added up for the summer months and averaged over the entire period this behaviour towards summer months revealed higher transpiration sums for beech compared to spruce.

With the end of August radiation sums, temperature and vapor pressure deficits were decreasing in Southern Germany (BayFORKLIM 1996). In addition with an age-related lower activity of beech leaves and possible first frost events which mainly damage beech leaves the changing meteorological conditions cause lower transpiration rates of beech trees compared to spruce trees.

An additional reason for higher transpiration rates of spruce in comparison with beech might be the different rooting patterns of the two species (Polomski and Kuhn 1998). Goisser et al. (2016) found for the Kranzberger Forst that beech trees are likely to produce more roots within deeper soils (28 cm) compared to spruce trees which produce the main part of their roots in the upper soil layer (20 cm). Because of the shallower rooting system of spruce compared to beech, the latter has access to higher amounts of water. Especially in summer when potential evapotranspiration rates are high beech could benefit from the higher amount of available water for transpiration.

Effects of the drought periods

Extreme events such as droughts may increase in the next decades (e.g. Easterling et al. 2000). The exceptional drought in 2003 (Ciais et al. 2005) resulted for the Kranzberger Forst region in an annual precipitation sum of 558 mm denoting a reduction of 34%, and an annual temperature of 8.8 °C, denoting an increase of 0.7 °C, both compared to the mean of the entire period. It is remarkable that et_a of the site for this year both for spruce with 638 mm and beech with 474 mm exceeds the average values with 604 mm and 421 mm, respectively. One part of et_a is the interception which was rather low in 2003 with 47 mm for beech and 131 mm for spruce, probably due to the low daily precipitation sums and its temporal distribution. Therefore, the higher et_a in the year 2003 is caused by higher evapotranspiration rates. Reasons for these higher rates may be the high plant available water storage of the soil at the site Kranzberger Forst with 238 mm for a depth of 100 cm (Table 4) combined with the filled up soil water content at the beginning of the year 2003 under both spruce and beech trees, and the weather conditions in the first half of 2003. With additional 224 mm of precipitation until the end of May 2003, enough water was available for high transpiration rates, which could particularly been used by the evergreen tree species spruce (Fig. 6b).

However, in summer precipitation was shortened by 48% to only 150 mm accompanied by a strong rise of the temperature by 3.5 °C, a higher radiation amount of 14% and lowered air humidity of 8%, all compared to the corresponding means of the simulated period. Additionally, at this time soil water content was at a low level (Fig. 6b). The combination of all these factors resulted in heavy drought stress for the trees. The et_a/et_p ratio of the summer months was clearly lower for the spruce trees than for the beech trees indicating higher drought stress for the spruces (Fig. 8). In a 2 year drought experiment also Göransson et al. (2016) found that beech trees preserve growth and were least affected by the drought compared to two other deciduous tree species.

Effects of tree size on transpiration and summer drought stress of beech and spruce trees

For both species an increasing summer drought stress - expressed by smaller et_a/et_p ratios - with increasing tree size is obvious, which was more pronounced for the spruce trees. We hypothesize that this size effect is based

on the higher water consumption per tree depending on its higher foliage area per surface area. Further on, because of their prominent position big trees receive more radiation and therefore are more stressed by heat while their bigger neighbors often shade smaller trees. As a consequence summer transpiration sums in 2003 of beech trees rose with size up to class 30–35 cm but then remained constant. Spruce trees, on the other hand, revealed a slight decrease in the summer transpiration rates starting from the smaller size class 20–25 cm to trees larger than 40 cm.

The higher drought susceptibility, characterised in this study by the lower et_a/et_p ratios and the stronger slope in 2013 and particularly in 2003, of spruce compared to beech (Fig. 8), has recently been shown by Goisser et al. (2016) but was also described before by Pretzsch et al. (2013) or Zang et al. (2011). The reaction of both species on drought events is also in line with the above mentioned different strategies of the two species. Spruce with its isohydric strategy reduces stomatal conductance and thereby decreases transpiration already at an early drought stage (Lyr et al. 1992), while beech adopts an anisohydric strategy with a less sensitive reaction of stomatal conductance leading to unchanged transpiration rates at the beginning of drought stress (Leuschner 2009).

Transpiration based water use efficiency and its link with the annual wood productivity

The water cycle of a tree is closely linked to its carbon sequestration processes supplying e.g. electrons to the photosynthetic reaction and transports required nutrients from the soil to the plant tissues (Hartmann 2011). Consequently, annual growth and productivity must be influenced by the transpiration and thereby the water use efficiency. We calculated for both species the annual wood volume increment and compared it to the annual WUE_{vol} , i.e. the ratio between wood volume increment and total water consumption. We used the wood volume increment because reduced carbon allocation to stem and wood is one of the most drought sensitive responses at tree level as recommended by Dobbertin (2005). Further on, it is an important parameter for forest ecology and management.

The volumetric water use efficiency of beech is always above the corresponding WUE_{vol} of spruce (Fig. 9), i.e. spruce trees consume more water than beech to produce one m³ of wood. Using the same

growth model, however based on masses Rötzer (2013) calculated the water use efficiency for spruce and beech in mixed stands. The WUE based on mass production was with values between 4.9 g kg^{-1} and 5.2 g kg^{-1} higher for spruce compared to beech which revealed values between 3.3 g kg^{-1} and 3.9 g kg^{-1} . Such values based on biomass production can also be found in literature (Cienciala et al. 1994; Pretzsch 2009) or derived from literature values (e.g. Grünwald and Bernhofer 2007). Pretzsch (2009) further gives water use efficiencies based on mean periodic volume increments for Germany. For spruce with a volume increment of $16.4 \text{ m}^3 \text{ yr}^{-1} \text{ ha}^{-1}$ WUE_{vol} was $0.0057 \text{ m}^3 \text{ wood m}^{-3} \text{ H}_2\text{O}$ and for beech with a volume increment of $11.7 \text{ m}^3 \text{ yr}^{-1} \text{ ha}^{-1}$ WUE_{vol} was $0.0032 \text{ m}^3 \text{ wood m}^{-3} \text{ H}_2\text{O}$. These values are clearly higher than the values found in this study. In contrast to our calculations, Pretzsch (200) used transpiration for the calculation of WUE_{vol} . Consequently, WUE_{vol} for beech and especially for spruce will increase if we exclude interception from our calculations. Both results, i.e. the estimations of Pretzsch (2009) as well as our calculations illustrate, however, that beech is more efficient compared to spruce based on the volume increment. The annual efficiency rises with increasing annual volume growth, indicating that the volumetric efficiency is more depending on the volume increment than on the volume of water consumption. This is particularly true for beech trees and in line with the iso-/aniso-hydric strategy of the two species.

Conclusion

Systematic comparisons of the water consumption in monospecific and mixed forests stands are very rare. Gebauer et al. (2012) found only two publications on hydrological investigations of temperate mixed and monospecific forests (Anders et al. 2006; Schume et al. 2003). On the other hand, over- and underyielding have been uncovered in numerous mixed forest stands in comparison to their corresponding monospecific stands (e.g. Pretzsch et al. 2012; Forrester et al. 2010). Our study arrives at better understanding the species-specific water consumption in stands of Norway spruce and European beech, their growth, and the dependencies between water consumption and growth.

Process based growth models are able to simulate the carbon cycle as well as the water cycle. Using spatially

explicit growth models as for example BALANCE growth and water balance for individual trees of mono-specific and mixed forests can be simulated; an up-scaling from individual tree to stand level is possible.

The simulations for a mixed forest stand delivered realistic results for the water balance of spruce and beech trees which react with different strategies on drought stress. The higher growth resilience in drought periods and overyielding effects can be explained by the contrasting hydrological behaviour of isohydric and aniso-hydric tree species in mixed forest stands independent of climate zone (Klein et al. 2013; Meinzer et al. 2014). This obvious general effect suggests that a mixture of isohydric and aniso-hydric tree species might create sustainable climate change adapted forests. Mixing of spruce and beech trees may lead to altered tree growth and changed water balances, but can enhance stand heterogeneity and survival of the less drought tolerant species. Thus, in general stand productivity will increase as well as diversity (Liang et al. 2016).

Intensified by high interception losses the isohydric strategy of Norway spruce reduced the water use in summer, especially in dry years. Across all years, however this effect was more than compensated by the evergreen phenology of Norway spruce compared to the deciduous phenology of European beech.

Norway spruce showed much higher evapotranspiration amounts than European beech, an earlier stomata closure under intensifying drought, and an overall lower water use efficiency in terms of stem volume production per unit of water. European beech consumed about 30% less water, reduced transpiration much later under drought stress, and was more efficient in water use. Under present climate conditions, Norway spruce is still more productive than European beech, probably due to its evergreen and isohydric character, which means extensive use of water for growth whenever it is available.

The study showed that during drought years, inter-specific interactions between spruce and beech can be neutral or positive, which can stabilize conifer proportions in forests despite trends towards warmer and drier conditions. In this way, a sustainable stock of high quality timber, mainly provided by Norway spruce, can be ensured, even as forests transition to more a more natural forest structure with a high proportion of broad-leaf trees (Pretzsch and Rais 2016).

By simulating inter-annual variation of evapotranspiration and soil water content, including effects of

extreme summer drought, and its dependence on tree size and the hydraulic strategies of different tree species, our study demonstrated how process based models can be used to adapt forest management to changing environmental conditions, specifically in terms of mitigating drought effects.

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