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Tree growth reactions on drought in mixed versus pure forests of Norway spruce and European beech

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Contents

Summary

Climate change is expected to cause changes in temperature and precipitation and alter the duration and frequencies of drought events and heatwaves. This thesis is a contribution to resolve effects of climate change on water relations and growth of Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) in intra- and interspecific neighborhoods. While forest management strategies have focused mainly on monospecific rather than on mixed stands over the past 200 years, mixed species stands have received more attention in the last decades for the sustainable handling of forest resources.

For a determination of drought stress reactions in intra- and interspecific neighborhoods, the effects of site conditions along a precipitation gradient from the dry northwest to the humid southeast of Bavaria were considered. At each of the four sites, stand triplets exist with spruce and beech in a monospecific and mixed neighborhood. The resistance and resilience of growth and $\Delta^{13}C$ in response to the drought event of 2003 were measured by means of increment cores. During the dry year 2003, the $\Delta^{13}C$ of mixed spruce trees revealed a higher resilience to drought stress on dry sites. However, beech trees showed an increasing resistance and resilience of growth and $\Delta^{13}C$ from dry to moist sites. The mixture of beech with spruce led to an increasing resistance and resilience for $\Delta^{13}C$ of beech trees with increasing site moisture. On dry sites, the mixture did not show a positive effect for beech trees.

The effect of extreme drought was determined within a rainfall exclusion experiment in Kranzberg forest by roofing and thus induced extreme dry conditions. The Kranzberg forest is positioned in the middle range of the rainfall availability (814 mm a^{-1}) within the gradient. The dry and hot year 2015 supported the drought stress analysis and was compared with the wet year 2014. Species-specific and mixture-specific differences of the experimental trees were determined within an analysis of stem radius growth and the tree water status via high temporal resolution dendrometer measurements. Measurements of stem radius variations provide information about the tree water status by daily swelling and shrinking of the tree stem. When xylem water potential is reduced and leaf transpiration exceeds root water uptake, the stem begins to shrink. Conversely, the stem begins to expand in the evening and the following morning, when water uptake is greater than the water loss through transpiration.

At first the relationship of leaf water potentials and stem radius variations were proven with a detected coherence with the diameter in breast height (BH), 50 % tree height (H50) and the

coarse roots. Furthermore, the allometry of growth and stored water in the living tissue of the stem between the upper (H50) and lower stem (BH) and coarse roots were investigated to show how drought influence the allometry of increment and stored water along the stem. Overall, we have detected that at the beginning of the growing period the upper stem growth is preferred, but during the course of the year, the growth of lower stem becomes more priority. Under drought, the growth was shifted more to the roots than in BH and more to H50 than in BH. The tree water deficit (TWD) shifted under drought more to BH compared to the roots and more to H50 compared to BH.

For the consideration of diurnal changes in the tree water status, daily amplitudes (difference between daily shrinking and swelling) were generated. Spruce and beech trees have different water management strategies and different phloem thicknesses. Spruce trees have approximately 50% higher daily stem radius variations in the growing period than beech trees. The daily stem radius amplitudes were greater on the rainfall exclusion plots than on the control plots because of a higher use of water from the storage tissue (phloem). Spruce trees in intraspecific neighborhoods at the rainfall exclusion plots were an exception with decreasing amplitude and with increasing drought stress in the summer months of 2015. At a soil volumetric water content of 0.21 $m^3\ m^{-3}$, the amplitude of spruces in intraspecific neighborhoods began to shrink due to exhaust soil water reserves. In contrast, beech trees could be supported in intraspecific neighborhoods under extreme drought due to a higher soil water content. These findings match well with the results along the precipitation gradient. Beech trees in mixture had the lowest resistance on dry sites. Consequently, stem radius variations give insights into a tree's water supply, which could help to understand changes in tree growth. In combination with analyses of increment cores, it could support adapted forest management strategies under a changing climate.

Zusammenfassung

Im Zusammenhang mit dem Klimawandel wird eine Temperatur- und Niederschlagsänderungen mit einhergehenden längeren Dauer und Häufigkeit von Dürreereignissen und Hitzewellen erwartet. Diese Arbeit ist ein Beitrag zur Ermittlung der Auswirkungen des Klimawandels auf die Wasserversorgung und das Wachstum von Fichte (*Picea abies* [L.] Karst) und Buche (*Fagus sylvatica* [L.]) in intra- und interspezifischen Nachbarschaft. Aufgrund von wirtschaftlichen Überlegungen und geschichtlichen Rahmenbedingungen wurden in den letzten 200 Jahren die Wälder in Deutschland vornehmlich als Reinbestände bewirtschaftet. Mit zunehmenden Anforderungen an den Wald durch die Gesellschaft nach Multifunktionalität und nachhaltiger Bewirtschaftung trat die Etablierung von Mischbeständen in den letzten Jahrzehnten immer stärker in den Fokus.

Zur Bestimmung von Trockenstressreaktionen wurden die Auswirkungen von Standortbedingungen entlang eines Niederschlagsgradienten vom trockenen Nordwesten bis zum feuchten Südosten Bayerns betrachtet. Der Einfluss von intra- und interspezifischer Konkurrenz unter Trockenheit konnte mithilfe von Triplets an jedem der vier Standorte miteingeschlossen werden. Anhand von Jahrring-Bohrungen wurde die Resistenz und Resilienz des Wachstums und $\Delta^{13}C$ in dem extremen Trockenjahr 2003 bestimmt. Ein positiver Mischungseffekt machte sich bei der Fichte durch eine verbesserte Resilienz auf den trockenen Standorten bemerkbar. Die Buchen zeigten eine verbesserte Resistenz bezogen auf das Wachstum und $\Delta^{13}C$ von trockenen zu feuchten Standorten, wobei die Mischung von Buche mit Fichte mit zunehmender Standortfeuchtigkeit ebenfalls zu einer zunehmenden Resistenz und Resilienz für $\Delta^{13}C$ führte. Auf dem trockenen Standort konnte kein positiver Effekt der Mischung für die Buche festgestellt werden.

Die Wirkung extremer Trockenheit wurde im Kranzberger Forst innerhalb eines Niederschlagausschlussexperiments untersucht. Der Kranzberger Forst ist gut wasserversorgt und ordnet sich somit im mittleren Bereich des Standortsgradienten ein. Dabei wurde die extreme Trockenheit durch überdachte Flächen induziert. Das trockene und warme Jahr 2015 unterstützte die Trockenstressanalyse und wurde mit dem feuchteren Jahr 2014 verglichen. Messungen anhand elektronischer Dendrometer ermöglichten eine Beobachtung von artspezifischen und mischungsspezifischen Unterschieden. Die hochaufgelösten generierten Daten von Stammradiusschwankungen zeigten neben dem Wachstumstrend auch den Wasserstatus der Bäume. Der Wasserstatus ist durch tägliches Anschwellen und Schrumpfen des Stammes sichtbar. Wenn das Wasserpotential im Xylem reduziert wird und die Transpiration die Wasseraufnahme über

die Wurzel übersteigt, beginnt der Stamm zu schrumpfen. Umgekehrt führt die höhere Wasseraufnahme über die Wurzeln und reduzierter Transpiration abends bis in die folgenden Morgenstunden zu einem anschwellen des Stamms.

Zunächst wurde der Zusammenhang von Blattwasserpotentialen und Stammradiusschwankungen in Brusthöhe (DBH), in 50% Baumhöhe (H50) und an der Hauptwurzel nachgewiesen. Des Weiteren wurde die Allometry des Zuwachses und des gespeicherten Wassers im lebenden Gewebe des Stamms zwischen dem oberen (H50) und unterem Stamm (BH) und an den Wurzeln analysiert, um darzustellen wie die Trockenheit die Allometry entlang des Stammes beeinflusst. Im Allgemeinen konnten wir nachweisen, dass zu Beginn der Wachstumsperiode das Wachstum am oberen Stamm begünstigt ist und im Laufe der Wachstumsperiode das Wachstum des unteren Stamms eine höhere Priorität hat. Bei Trockenheit verschob sich das Wachstum mehr zu den Wurzeln verglichen mit BH und mehr zu H50 verglichen mit BH. Das Baumwasserdefizit (TWD) verschob sich bei Trockenheit mehr zu BH als zu den Wurzeln und mehr zu H50 verglichen mit BH.

Für die Beobachtung von täglichen Änderungen im Wasserhaushalt der Baumarten wurden die Stammradiusamplituden (Differenz zwischen täglichen schrumpfen und schwellen) täglich über ein Jahr betrachtet und abgebildet. Die Ergebnisse zeigten artspezifische Strategien zur Bewältigung von Trockenstress. Fichtenbäume besitzen ein dickeres Phloem und zeigten ca. 50% höhere tägliche Stammradiusschwankungen in der Wachstumsperiode als Buchen. Im Allgemeinen zeigten die Stammtagesamplituden auf den überdachten Flächen eine stärkere Schrumpfung, als auf den Kontrollplots aufgrund eines höheren Wasserverbrauchs aus dem Speichergewebe (Phloem). Die Fichten in intraspezifischer Nachbarschaft der überdachten Flächen stellten in den Sommermonaten 2015 eine Ausnahme dar, mit abnehmenden Amplituden bei zunehmendem Trockenstress. Ab einem Bodenwassergehalt von 0,21 m^3 m^{-3} begann die Amplitude der Fichten in intraspezifischer Nachbarschaft zu schrumpfen. Durch die starke Trockenheit konnte das Speichergewebe im Stamm über Nacht nicht wieder gefüllt werden. Im Gegensatz dazu profitieren Buchen bei extremer Trockenheit von einer intraspezifischen Nachbarschaft durch einen höheren Bodenwassergehalt. Diese Ergebnisse sind Vergleichbar mit den Untersuchungen entlang des Niederschlagsgradienten. Die Buche zeigte in der Mischung mit der Fichte eine geringere Resistenz auf trockenen Standorten.

Folglich geben Stammradiusschwankungen Einblicke in die Wasserversorgung eines Baumes, was dazu beitragen kann, Veränderungen im Baumwachstum zu verstehen. In Kombination mit

Analysen von Zuwachsbohrungen könnten angepasste Waldbewirtschaftungsstrategien in einem sich verändernden Klima unterstützt werden.

Summary Articles

This cumulative dissertation is based on investigations that were published and submitted in the following research articles:

Article I

Schäfer, Cynthia; Grams, Thorsten; Rötzer, Thomas; Feldermann, Aline; Pretzsch, Hans (2017): Drought Stress Reaction of Growth and $\Delta^{13}C$ in Tree Rings of European Beech and Norway Spruce in Monospecific Versus Mixed Stands Along a Precipitation Gradient. In: Forests 8 (6), S. 177. DOI: 10.3390/f8060177.

Abstract:

Tree rings include retrospective information about the relationship between climate and growth, making it possible to predict growth reaction under changing climate. Previous studies examined species-specific reactions under different environmental conditions from the perspective of tree ring growth and ^{13}C discrimination ($\Delta^{13}C$). This approach is extended to monospecific versus mixed stands in the present paper. We investigated the resistance and resilience of Norway spruce (Picea abies [L.] Karst) and European beech (Fagus sylvatica [L.]) in response to the drought event in 2003. The study was carried out along a precipitation gradient in southern Germany. Responses of basal area increment (BAI) and $\Delta^{13}C$ were correlated with a Climate-Vegetation-Productivity-Index (CVPI). The species showed different strategies for coping with drought stress. During the summer drought of 2003, the BAI of spruces reveal a lower resistance to drought on dry sites than those of beech. For beech, we found an increasing resistance in BAI and $\Delta^{13}C$ from dry to moist sites. In mixture with spruce, beech had higher resistance and resilience for $\Delta^{13}C$ with increasing site moisture. The combination of $\Delta^{13}C$ and tree ring growth proxies improves our knowledge of species-specific and mixture-specific reactions to drought for sites with different moisture conditions.

Author Contributions: Thomas Rötzer, Thorsten Grams and Hans Pretzsch initiated the project. Cynthia Schäfer and Aline Feldermann performed the experiments and analyzed the data. Cynthia Schäfer wrote the manuscript. Thorsten Grams, Thomas Rötzer and Hans Pretzsch revised the manuscript.

Article II

Schäfer, Cynthia; Goisser, Michael; Rötzer, Thomas; Thurm, Eric Andreas; Biber, Peter; Kallenbach, Christian; Pretzsch, Hans (major revisions): High resolution dendrometer data to detect resource allocation in mixed stands under heavy drought. In: Canadian Journal of Forest Research.

Abstract:

Although several studies suggest that tree species in mixture resist drought events better than in pure stands, but little is known about the resource allocation of these trees. With dendrometer data at the upper and lower stem and coarse roots, we calculated the tree water deficit (TWD) and growth (ZGmax) to show how mixture and drought influenced resource allocation. The analyses were made in a mature temperate forest of Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) while half of the plots were under extreme drought by automatic closing roof systems within the stand. At the beginning of the growing period, the upper stem growth is preferred, but during the course of the year, the growth of lower stem becomes more priority. Growth allometry in mixture is comparable to trees under drought. However, the spruce in interspecific neighborhood exhibited the same TWD allometry like spruces with good water supply. Interspecific beeches showed no benefit compared to intraspecific beeches which can be seen for TWD as well as growth allometry. Mixture seems to benefit the water supply of spruce trees, which should increase the stability of spruces in time of climatic warming.

Author contributions: Hans Pretzsch and Thomas Rötzer conceived and designed the experiment. Cynthia Schäfer, Michael Goisser and Christian Kallenbach performed the experiments. Cynthia Schäfer analyzed the data. Eric Andreas Thurm and Peter Biber contributed the analysis. Cynthia Schäfer wrote the manuscript. Michael Goisser, Thomas Rötzer and Hans Pretzsch revised the manuscript.

Canadian Journal of Forest Research: under review (major revisions). 5-Year IF: 2.038 (2017).

Article III

Schäfer, Cynthia; Thurm, Eric Andreas; Rötzer, Thomas; Kallenbach, Christian; Pretzsch, Hans (2018): Daily stem water deficit of Norway spruce and European beech in intra- and interspecific neighborhood under heavy drought. In: Scandinavian Journal of Forest Research 125(1): 1–15. DOI: 10.1080/02827581.2018.1444198.

Abstract:

High-resolution measurements of stem radius variations provide information about the tree water status with changing climate conditions by swelling and shrinking due to the reduction of xylem water potential and to the exceedance of leaf transpiration over root water uptake. The aim of this study was to analyze daily stem radius variations of Norway spruce and European beech in intra- and interspecific neighborhood. The experimental plots are part of a rainfall exclusion experiment. These variations are species-specific, i.e. spruces have a higher phloem thickness and higher amplitudes during a day than beeches. The amplitudes were significantly higher at the rainfall exclusion plots, but the amplitudes of spruces decreased above 27°C with increasing drought due to reduced transpiration rates and exhausted soil water reserves. The shrinking amplitude was observed for spruces in intraspecific neighborhood from a soil volumetric water content of 0.21 m^3 m^{-3}. In interspecific neighborhood, a shrinking amplitude for spruces could not be observed and revealed a lesser tree water deficit than in intraspecific neighborhood. Beeches showed minor differences with a higher tree water deficit in interspecific neighborhood. Consequently, stem radius variations give insights into a tree's water supply, which could help to understand changes in tree growth.

Author Contributions: Hans Pretzsch and Thomas Rötzer conceived and designed the experiment. Cynthia Schäfer performed the experiments and analyzed the data. Eric Andreas Thurm contributed the analysis and revised the manuscript. Cynthia Schäfer wrote the manuscript. Christian Kallenbach contributed the soil moisture and VPD data. Thomas Rötzer, Christian Kallenbach and Hans Pretzsch revised the manuscript.

Overview of Co-Authored Articles

Nickel, Uwe T.; Weikl, Fabian; Kerner, René; Schäfer, Cynthia; Kallenbach, Christian; Munch, Jean C.; Pritsch, Karin (2017): Quantitative losses vs. qualitative stability of ectomycorrhizal community responses to 3 years of experimental summer drought in a beech-spruce forest. In: Global Change Biology 24 (2), S. 560-576. DOI: 10.1111/gcb.13957. IF: 8.444 (2015).

Rötzer, Thomas; Biber, Peter; Moser, Astrid; Schäfer, Cynthia; Pretzsch, Hans (2017): Stem and root diameter growth of European beech and Norway spruce under extreme drought. In: Forest Ecology and Management (406), S. 184–195. DOI: 10.1016/j.foreco.2017.09.070. 5-Year IF: 3.524 (2017).

Thesis

I. Introduction

Species Mixture

Conforming to the requirements of sustainability has been one of the major objectives of forest management strategies in Central Europe over the last decades. Hans Carl von Carlowitz first mentioned the term “sustainability” in Germany in 1713 in connection with a responsible handling of forest resources. One possibility for handling forest resources sustainably is the plantation strategy of monospecific or mixed forest stands. Historically, forest management and anthropogenic land use often resulted in a homogenous forest structure with monospecific stands due to for example agricultural land use with degraded soil, which permitted the cultivation of only a few species. Further reasons for monospecific plantations were timber production for commodity products or, especially in Central Europe, reforestation conducted after the war with seeds from a restricted number of species (Pretzsch et al. 2017).

Whether monospecific or mixed forest stands are preferable is now the subject of much scientific discussion. Earlier critics such as the silviculturist Karl Gayer (Gayer 1886) pointed out the drawbacks of monospecific stands and the advantages of mixed stands on environmental risks, economy and management. More recently, Ammer et al. (2008) described the arguments for the introduction of the deciduous tree species European beech (*Fagus sylvatica* [L.]) in a monospecific plantation of the coniferous tree species Norway spruce (*Picea abies* [L.] Karst), which is the most widespread tree species in Central Europe. Generalizations are difficult, but they concluded that beech trees improve soil properties, biodiversity and productivity in spruce forests in many cases. In addition, the introduction of a broadleaved species is recommended because of the high vulnerability of spruce trees to climate change (Ammer et al. 2008; Zang et al. 2012). Especially under a changing climate, facilitation or competitive reduction in mixed forest stands can increase tree resistance and resilience (Pretzsch et al. 2013). Facilitation occurs when one of the mixed species is positively influenced by another species in terms of growth or survival. The theory of hydraulic lift constitutes a facilitated effect through hydraulic redistribution of water through the deep-rooting beech, which can be used by the shallow-rooting spruce (Caldwell et al. 1998; Siqueira et al. 2008). A further facilitation effect is the atmospheric nitrogen fixation by one species to benefit another species with nitrogen (Forrester and Pretzsch 2015). In the case of competitive reduction, the interspecific concurrence is less evident than the intraspecific concurrence, e.g. due to the differentiation in resource use (Vandermeer 1989). An example of competitive reduction is the plantation of a short shade-tolerant species with a tall light-demanding species. The light-demanding species can use the more available light compared to the intraspecific situation and the shorter shade-tolerant species can use the light that is transmitted through the canopy of the light-demanding species (Bauhus et al. 2004).

Alongside different rooting systems and nitrogen fixation, the crown structure of mixed species can lead to complementary effects by mixing broadleaved and evergreen tree species. The much denser canopy filling in mixed stands of broadleaved beech and evergreen spruce can increase interception of light and precipitation, stand density, productivity and growth resilience to disturbances (Pretzsch 2014). Fig. 1 highlights the effect of two mixed species with different crown structures in a feedback-loop diagram. The structure of the crowns is determined for the feedback between habitat structure, environment and growth. The bold arrows in Fig. 1 reveal the slow but continual feedback between structure, environment and growth with a morphological acclimatization of the mixed species as a result. The crown morphology and canopy structure are both pivotal drivers and a result of stand dynamics (Pretzsch 2014). Site conditions also play a key role in the consideration of mixing effects under different environmental conditions. The stress-gradient hypothesis from Callaway and Walker (1997) predicts that facilitation of mixture dominates on poor sites rather than rich sites. The stress-gradient hypothesis was extended in Maestre et al. (2009) by considering the life history of the interacting species (tolerance to stress vs. competitive ability) and whether the factor of stress is a resource or not. Also Malkinson and Tielbörger (2010) emphasized that the fitness of the individuals, as the product of facilitation and competition, plays an important role. Pretzsch et al. (2010) concluded in a study through Central Europe that the growth of spruce trees is facilitated in mixture with beech on nutrient-poor sites, while the growth of beech in mixture with spruce has a benefit on good sites. In addition to soil characteristics, ecological gradients from dry to moist sites can reveal the effect of drought stress in mixture on sites with similar nutrient availability.

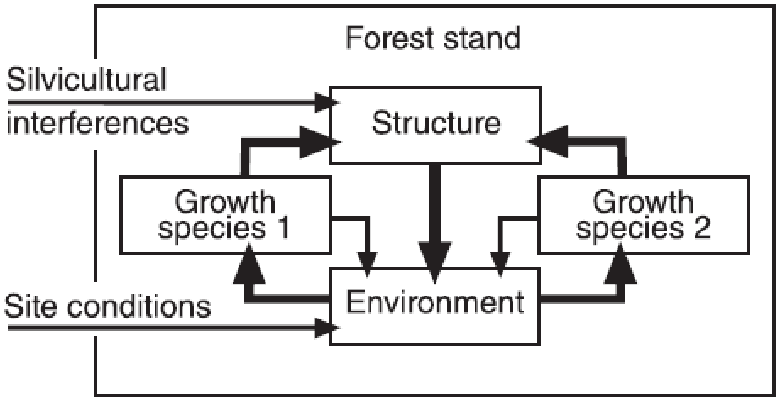

Fig 1 The feedback loop between stand structure, environment and tree growth of a stand with two species by Pretzsch (2014). The loops between structure, environment, growth and structure (bold arrows) are slow, compared with the inner loops environment, growth and environment as a faster feedback loop.

Resource availability and the climate vary from site to site and affect stand dynamics and species interactions. The determination of climate, site quality and other site characteristics is crucial to determine mixing effects within the gradients (Forrester 2014). Based on the high complexity of mixed species under different site conditions and climate conditions, general interpretations are difficult. To examine mixing effects within a gradient, the detection of temporal and spatial changes of site quality is important. Furthermore, the effects of over- and underyielding of mixed versus monospecies stands require replicated experiments at different sites and over years for general conclusions (Forrester and Pretzsch 2015).

Drought Stress Reactions

Increasing drought stress under a changing climate is a hard challenge for forest ecosystems. Rising greenhouse gas emissions are considered the major impact on recent changes in global mean temperatures and changes in the hydrological cycle (IPCC 2007). Alongside rising temperatures, future climate change will cause an increase in the frequency, duration and severity of drought events (IPCC 2013; Meehl and Tebaldi 2004). Drought events alter forest ecosystems, forest structures and the biogeography in many parts of the continents and can result in tree decline and mortality. Wang et al. (2012) illustrated the impact of tree mortality on the earth system in a loop diagram (Fig. 2). Changes in forest structure due to changing climate would alter for example carbon, energy and water fluxes between the atmosphere and ecosystems and change the land surface albedo. This, in turn, leads to negative consequences for the climate, but also to positive feedbacks due to for example higher productivity through higher CO_2 concentrations or longer-lasting growing seasons (Lindner et al. 2010). Negative consequences are drought events as one result of a changing climate. Reduced soil water availability leads to restrictions of transpiration and CO_2 fluxes in the entire tree, which is essential for tree growth and vitality. The transpiration process during the day produces a water gradient throughout the tree and favors the transport of water from the soil through the roots due to negative water potentials. Low soil water content can induce a more negative water potential and lead ultimately to limiting water fluxes, stomata closure and reduced CO_2 assimilation (Baumgarten et al. 2014; Bréda et al. 2006; Whitehead 1998). Further, water and CO_2 fluxes through the leaf are controlled by the stomatal behavior, which is controlled by leaf temperature, vapor pressure deficit (VPD), intercellular CO_2 concentration via photosynthesis, leaf water potential and irradiance (Cowan 1978; Hall et al. 1976; Tuzet et al. 2003). Therefore, the effect of drought stress on a given species depends on annual and seasonal weather conditions and on whether the current species can adapt to new conditions. Resistance or tolerance to drought stress is driven by either or both structural and physiological adjustments of the species.

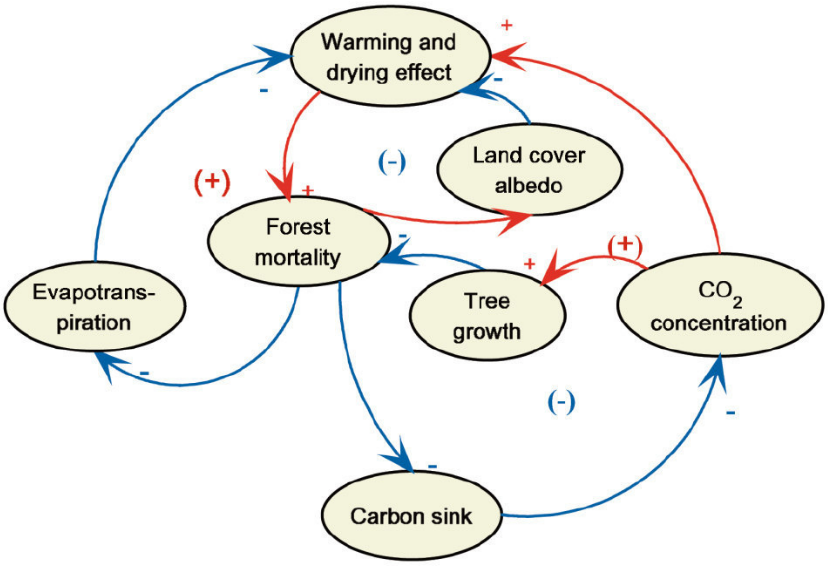

Fig 2 Loop diagram of drought-induced forest mortality and its effects on ecosystems and the climate system in energy, carbon and water cycles by Wang et al. (2012). (+) describes positive feedbacks and (-) negative feedbacks. Blue arrows with (-) and red arrows with (+) represent an effect-and-cause relationship in which the two variables change in the same and opposite directions.

A model of stomatal conductance, photosynthesis and transpiration of plants at different stages of soil drying is illustrated in Tuzet et al. (2003). The diurnal cycles of climate data such as air temperature (T_a), dew point temperature (T_r), wind speed (U) and global (R_g) and atmospheric longwave radiation (R_a) are shown in Fig. 3. The data represent an idealized day of typical clear summer conditions in temperate agricultural regions. T_a and T_r reveal a peak after noon with approximately 2 h shift from the global longwave radiation which has its maximum at midday and symmetrically declines around the midday maximum. R_a is constant through the day and the wind speed increases in the morning hours, remains constant throughout the day and decreases in the evening hours.

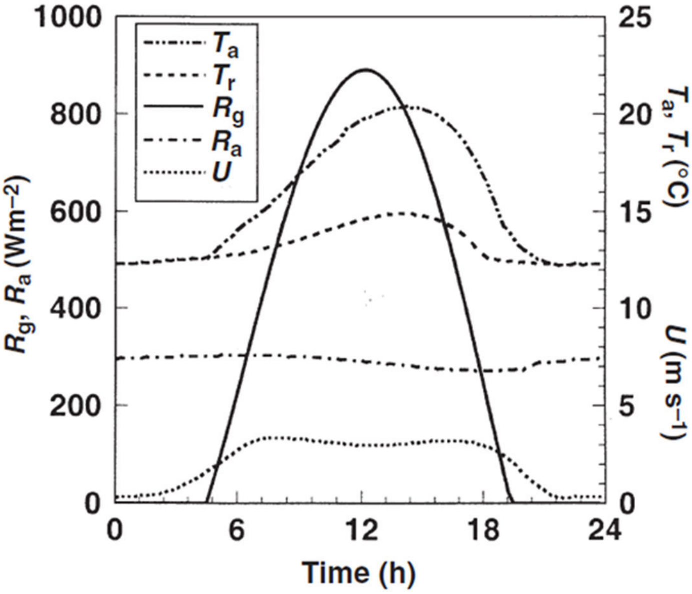

Fig 3 Diurnal cycle of air temperature (T_a), dew point temperature (T_r), wind speed (U), global (R_g) and atmospheric longwave radiation (R_a) at 3 m above the ground by Tuzet et al. (2003).

Compared to the diurnal weather conditions, in Fig. 4 stomatal conductance (g_{CO2}), latent heat flux (LE), assimilation rate (A) and the ratio of the intercellular and extracellular CO_2 concentration (c_i/c_a) is displayed throughout a day at different drying cycles (1, 10, 13, 16 days) (Tuzet et al. 2003). When soil water is non-limiting, all variables show a smooth and symmetrical variation around noon and follow the course of temperature and humidity deficit with a little or no asymmetry in the mid-afternoon. With increasing drought stress, the course of g_{CO2}, A and LE reveal an increasingly asymmetrical course with higher values in the morning than in the afternoon. The asymmetry is caused by the lower leaf water potentials in the afternoon than in the morning hours and resulting from a higher atmospheric demand and the declined soil moisture and reduced matric potentials. The variation in A is less pronounced than in g_{CO2} due to the increasing CO_2 concentration difference (c_i/c_a) under increasing drought and damping the variation in A. For the (c_i/c_a), effects of soil drying are also observable. With a moist soil, (c_i/c_a) reveal a small amplitude but with increasing drought the amplitude increases (Tuzet et al. 2003).

However, stomatal behavior and water potential is species-dependent. The determined species in this study, spruce and beech, reveal different strategies to cope with drought stress. Spruces are found to follow a more isohydric strategy and to reduce the stomatal conductance at an early stage of drought stress. Beech trees, on the other hand, follow a more anisohydric strategy and indicate a later stomatal closure when water is limited (Klein 2014; Lyr et al. 1992). Furthermore, it is well known that spruce is a boreal, mountainous tree species, which is well adapted to low temperatures. It is expected that rising temperatures and increasing frequency and duration of drought periods will increase the vulnerability of spruce (Lindner et al. 2010; Pretzsch et al. 2013; Zang et al. 2012). Besides that, beech trees are known as a more drought-resistant species compared to spruce trees (Ammer et al. 2008; Pretzsch et al. 2013) and are less affected by climate change than spruce (Kölling et al. 2007; Lexera et al. 2002).

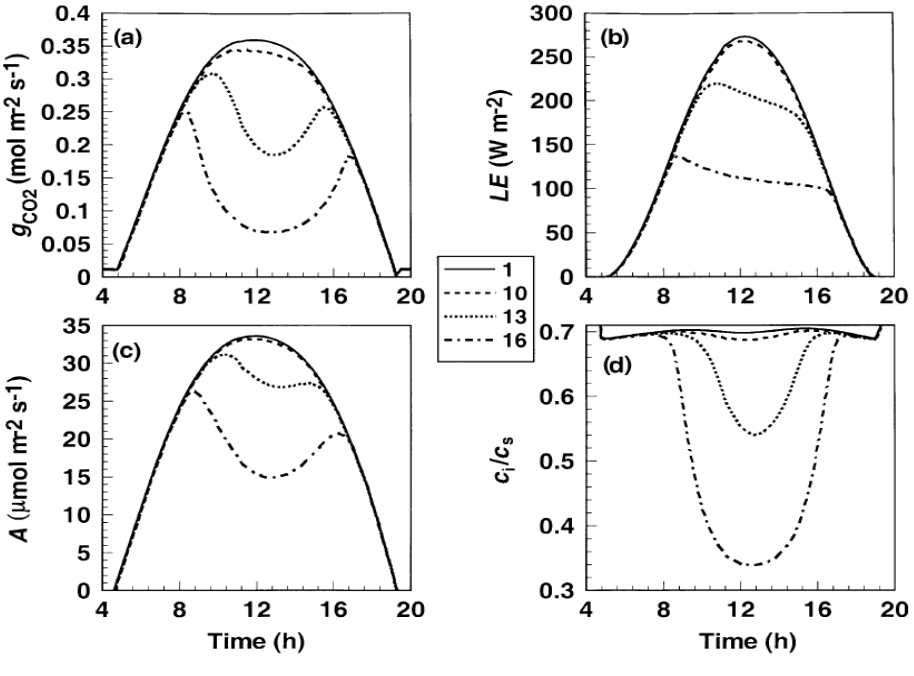

Fig 4 Daily variations of (a) CO_2 stomatal conductance, (b) latent heat flux, (c) assimilation rate and (d) the ratio of the intercellular and extracellular CO_2 concentration at 1, 10, 13 and 16 days of the drying cycle (by Tuzet et al. (2003)).

Drought Stress Reactions at a High Temporal Resolution

To understand the physiological mechanism driving radial stem growth, studies of the major fluxes and pools of water inside a stem of a tree are helpful. Electronic dendrometers meet these conditions through high-resolution measurements from minutes to hours with observed variations of the tree stem linked to a combination of growth and water transport within the tree. These stem variations are a combined result of mainly four co-acting mechanisms (De Swaef et al. 2015):

(i) reversible shrinking and expansion of dead conducting xylem elements due to increase and relaxing of internal tensions

(ii) reversible shrinkage and expansion of the elastic, living phloem tissue

(iii) irreversible stem growth

(iv) thermal shrinking and expansion

The course of stem radius variations represents the sum of all external and internal conditions that control tree water relations (Zweifel and Häsler 2001). The anatomy of the stem of dicots is illustrated in Fig. 5 with the elements of the wood and the living phloem tissue from inside to outside of the stem. The rigid xylem tissue contributes little to the reversible stem radius variations (< 10%, Irvine and Grace (1997)). Shrinking and swelling of the stem is mostly restricted to the extensible tissue outside of the cambium (De Schepper and Steppe 2010; Zweifel et al. 2000). The daily amount of water withdrawn from storage tissue to daily transpiration range from 5-22% (Goldstein et al. 1998; Köcher et al. 2013; Steppe and Lemeur 2004). Zweifel et al. (2001) showed for Norway spruce that water in the needles and internal stored water contributed ~10% to the daily transpiration on sunny days and ~65% on cloudy days and at the time of maximum transpiration the internal stored water contributed up to 75% to daily transpiration. Dendrometer measurements are a versatile tool and can further be used as a drought stress indicator, as represented in different reviews, such as Ortuño et al. (2010), and increase the understanding of soil-plant-atmosphere coupling. Most studies have focused on isolating stem growth to explore the influence of different environmental conditions (Deslauriers et al.

2003; King et al. 2013; Zweifel et al. 2005). Consequently, investigations focusing on the tree water status due to shrinking and swelling could improve knowledge about tree water relations.

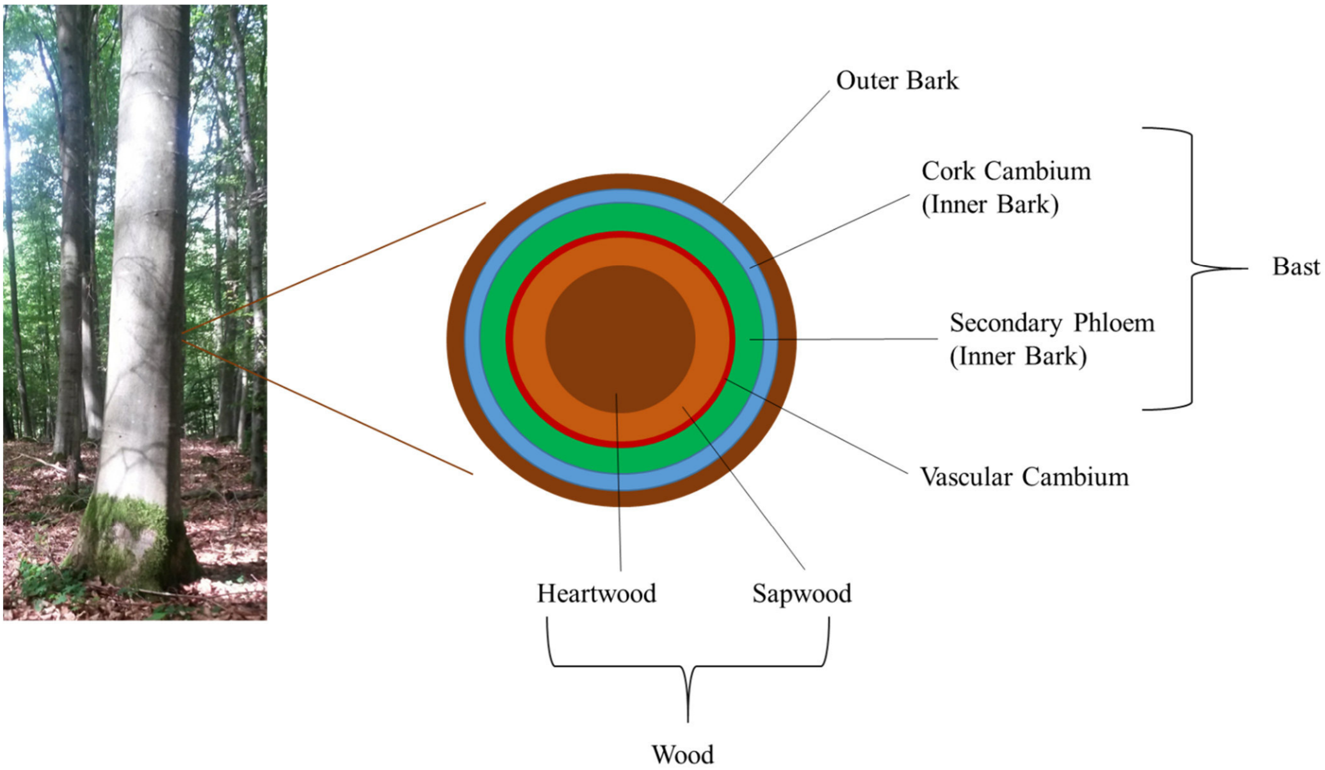

Fig 5 Schematic representation of the stem anatomy. The vascular cambium is the source of secondary xylem growth inwards towards the pith (wood) and secondary phloem growth outwards to the bark (bast).

Mechanistic plant model and supporting observations indicate that water flows from the living phloem cells to the rigid xylem conduits when xylem water potential decreases when transpiration exceeds root water uptake (Sevanto et al. 2011; Steppe et al. 2012). Consequently, cell turgor in the dividing cambium and expanding cells follows the course of stem water potentials and shows the same decreasing trend as water potentials in contraction (Steppe et al. 2015). From the afternoon under rising water potentials, cell turgor, cell expansion (growth) resumes. The water flow from xylem conduits into the living cells of the phloem. Furthermore, growth is influenced by the turgor pressure (wall-yielding threshold value is estimated at 0.9 MPa for woody tissue (Genard 2001)) in the living phloem cells, below which the cell cannot expand further (Steppe et al. 2015). Because of the highest turgor values after sunset, stem growth is assumed during nighttime (Steppe et al. 2015).

In Fig. 6, the daily course of stem radius variations is illustrated. In general, the stem contracts during the day due to transpiration around noon and expands during the nighttime and on rainy days when water reserves are gradually replenished. The characteristics of the diurnal cycle of shrinking and expansion reveal a sinusoid waveform; the differences between the maximum in stem radius (Rmax) and minimum (Rmin) represent the daily amplitude.

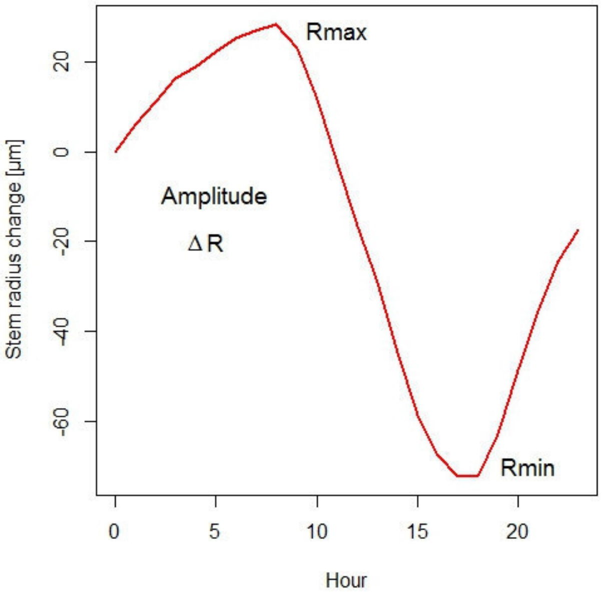

Fig 6 Daily course of stem radius variations with the daily maximum in stem radius (Rmax) and minimum (Rmin). The differences between Rmax and Rmin represent the amplitude.

Different models illustrate the mechanisms underlying stem radius variations (De Schepper and Steppe 2010; Genard 2001; Steppe et al. 2006; Zweifel et al. 2001) as a helpful variant to understand complex and interlinked relationships between the plant tissues. The model of Steppe et al. (2006) (Fig. 7) divided the plant into vertical and radial components in which water flows, driven by the water potential gradient. The crown and stem contain a xylem (X) and a storage pool (S). Incoming and outgoing flows indicate water aggregation or depletion in each compartment, which results in stem diameter change.

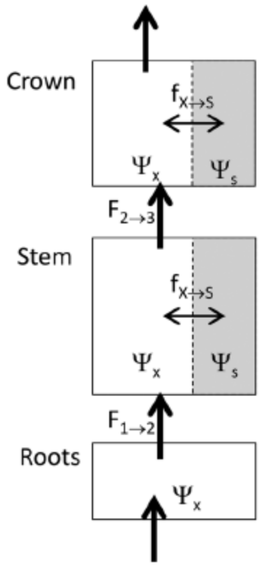

Fig 7 Model of stem radius variations by considering the stem divided in vertical (F) and radial (f) water flow, which is driven by water potential gradients (Ψ). The stem is radially divided into xylem tissue (X) and storage tissue (S) (Steppe et al. 2006).

Research Questions of the Thesis

The focus of this thesis is placed on how growth and water relations in monospecific and mixed stands modify the impact of changing climate. For this consideration, the following research questions are addressed:

(1) How do the growth and $\Delta^{13}C$ of spruce and beech differ in relation to sites with different moistures and species neighborhoods as a result of the drought year of 2003?

(2) Is there a connection between the tree water status and tree water deficit (TWD)? Is the reaction of growth and the respective TWD the same at the three different positions H50, BH and root (root-stem allometry)?

(3) How do spruce and beech differ in relation to changes in tree water status under extreme drought conditions at a high temporal scale and in intra- and interspecific neighborhoods?

II. Hypotheses of the Scientific Articles and Results

Alongside species-specific reactions, resilience and resistance to varying climate conditions depending on tree species mixture (Pretzsch et al. 2013; Pretzsch et al. 2017) and site conditions (Pretzsch and Dieler 2011), the prediction and understanding of responses to drought stress of forest ecosystems are of high relevance. The aim of this thesis was to analyze spatial and temporal reactions of two tree species in intra- and interspecific environments to heavy drought stress. The determination on different sites allows the observation on a spatial resolution, while the observation of stem radius variations offers the opportunity to consider tree reactions on drought stress at a high temporal resolution. Drought events affect physiological processes in trees such as photosynthesis, transpiration and carbon allocation, which can lead to altered tree water relations and reduced growth rates. Hence, the determination of growth reactions under drought stress was supported by the analysis of the discrimination against ^{13}C ($\Delta^{13}C$). On this account, the following research hypothesis was investigated:

(I.I.) Resistance and resilience of tree ring growth and $\Delta^{13}C$ decreased from moist to dry sites along a precipitation gradient in the drought year 2003, in which spruce trees react more sensitively than beech trees.

In the drought year 2003, the study revealed that tree ring growth of spruce trees was reduced at dry sites. In contrast, $\Delta^{13}C$ of spruce trees showed a higher resistance in dry sites. Beech trees showed a greater resistance of tree growth and $\Delta^{13}C$ at moist sites. The resilience of beech trees was higher in moist sites.

(I.II.) Under dry conditions, the growth of beech benefits from the mixture with spruce due to increased water availability.

Results reveal that resistance and resilience of beech trees profit from mixture in moist sites with an increasing trend from dry to moist sites. Only for $\Delta^{13}C$ were significant differences found.

(II.I.) There is a relationship between stem radius variations and the leaf water potential for beech and spruce at the different measured tree compartments.

We found for spruce and beech significant relationships between the tree water deficit (TWD_{min} and TWD_{max}) and leaf water potentials (midday and predawn) for all tree compartments (50 % tree height (H50), breast height (BH), root).

(II.II.) The relationship of growth response to the respective TWD is the same at the three different positions H50, BH and root.

The analysis showed that the stem radius growth corresponds with the TWD in all tree heights, except the allometry of beech in 50 % tree height (H50) and breast height (BH).

(II.III.) Interspecific neighborhood with beech trees facilitates spruce trees under drought stress. Spruce trees could profit from species mixing. For beech trees, we found a benefit in intraspecific environments.

(III.I.) Norway spruce reveal a more sensitive reaction to dry conditions than European beech trees through more distinct modifications in the stem radius amplitudes.

Spruce trees showed a higher stem water change than beech trees and decreased amplitude under extreme drought stress during the summer months of 2015 due to a lack of soil water.

(III.II.) An interspecific neighborhood has a facilitated effect on Norway spruce and reduces the use of water reserves in the living tissues of the stem, especially under drought conditions due to higher soil water storage in interspecific neighborhoods compared to intraspecific neighborhoods.

Results reveal that spruce trees have a lower tree water deficit and accordingly lower amplitude in interspecific neighborhoods through higher water availability in interspecific neighborhoods. On a daily scale, spruces in intraspecific neighborhoods use more water from the storage tissue under drought for transpiration because of lacking soil water stocks.

III. Material and Methods

Gradient Study

Tree growth depends for example on the availability of resources and the resource use efficiency. These factors are variable with species, species interactions and site quality. Therefore, investigations were carried out at all these levels (Fig. 8). Species-specific and mixture-specific reactions were observed via triplets on each site. A triplet is an examination in monospecific plots of a given species and in a mixed plot of both species. For the two investigated tree species, two monospecific and one mixed plot exist (triplet). The site, structure and age should be similar within the triplet. With a homogenous structure, a comparison of monospecific and mixed species is possible. Monospecific plots comprise approximately 30 trees of the species, whereas mixed plots have 60 to 100 trees. The triplets are in close proximity to each other and have not recently been thinned. Site-specific differences were carried out along a precipitation gradient from the northwest to southeast of Bavaria (from Arnstein, Parsberg (Kelheim), Wasserburg to Traunstein, Fig. 9), with the locations becoming more humid towards the southeast.

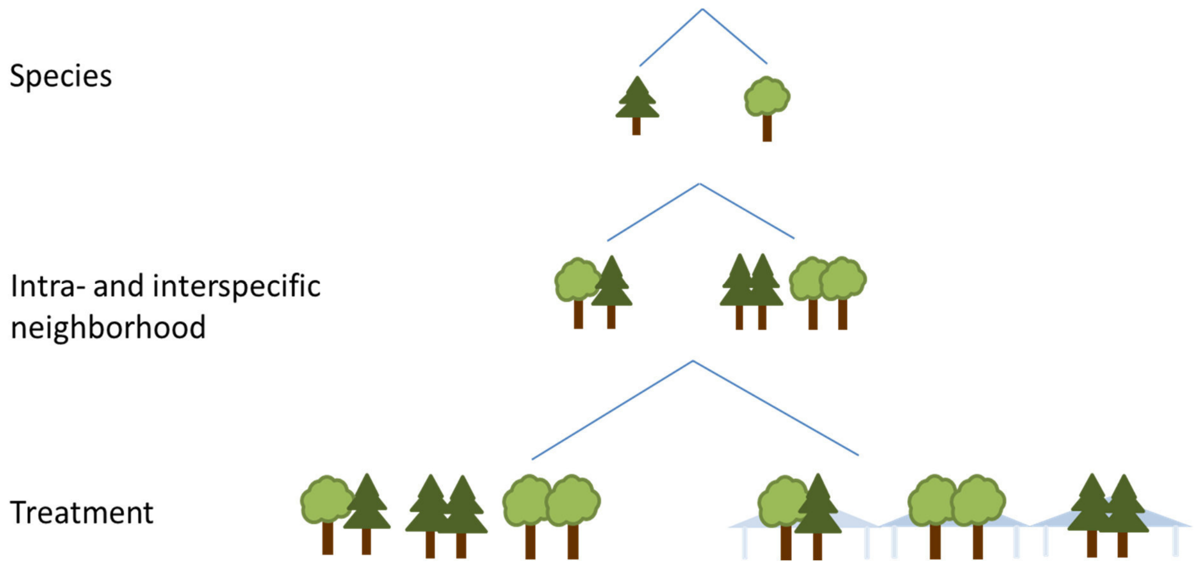

Fig 8 Levels of investigation in the present study. Species-specific, mixture-specific and drought-related (drought treatment vs. control) investigations were carried out.

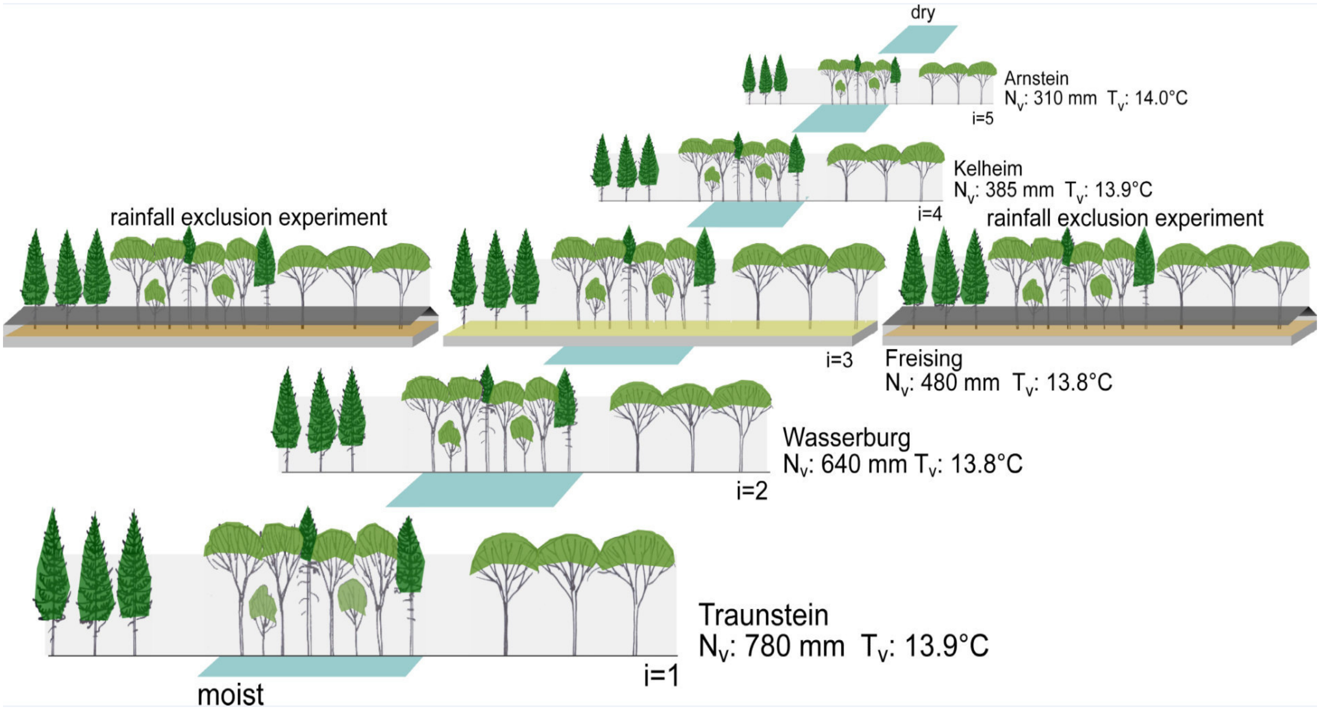

Fig 9 Precipitation gradient from northwest to southeast of Bavaria (Arnstein, Kelheim, Freising, Wasserburg and Traunstein). The sites become more humid from the north to the south of the gradient. All sites consist of a triplet with monospecific and mixed stands of beech and spruce. The site in Kranzberg forest (Freising) involves a drought treatment experiment through roof constructions and resulting rainfall exclusion (by Pretzsch et al. (2014)).

The precipitation in the growing season (N_v) (April–September) ranged from 310 mm in Arnstein to 780 mm in Traunstein (Bavarian State Research Center for Agriculture 2016). The sites represent a precipitation gradient from the upper colline to sub-mountainous altitudes. Altitudes range from 330 m in the northwest to 600 m in the southeast of Bavaria. Mean annual temperature for the period 1980–2010 ranged between 8.5 and 9.5°C. In the year 2003 an extreme climate anomaly occurred in Europe with high temperatures, particularly in August, and long-lasting drought events.

Tab 1 Geography and the annual and growing season (April to September) temperature (T_a, T_v) and precipitation (N_a, N_v) of the sites along the precipitation gradient (data: Bavarian State Research Center for Agriculture (2016)).

Site	**Latitude (°)**	**Longitude (°)**	**Elevation above sea level (m)**	**Geological substrate**	T_a **(°C)**	N_a **(mm)**	T_v **(°C)**	N_v **(mm)**
Arnstein	49.903	9.977	330	valley sediments	9.5	654	14.0	310
Kelheim	48.936	11.822	550	Loess over detoriated limestone	8.5	713	13.9	385
Freising	48.419	11.661	490	Loess over tertiary sediments	7.7	814	13.8	480
Wasserburg	48.142	12.073	620	moraines from Würm glaciation	8.8	858	13.8	640
Traunstein	47.939	12.672	600	moraines from Würm glaciation	9.1	962	13.9	780

Tree Measurements

From each experimental tree, diameter in breast height (DBH), tree height, crown position, crown radii, Kraft class (1-5), coordinates and altitudes were recorded (Tab. 2). Kraft classes of 1-3 are dominant trees in the tree stand and from 4-5 are suppressed trees. Kraft classes reflect the social position of a tree in a stand and through this, its growth potential (Assmann 1961). The crown radii were measured in eight directions (S, SW, SO, W, O, N, NE, NW). Furthermore, increment cores in DBH (north and east direction) were sampled from the sample trees and permanent tree girth tapes were fixed to every tree for the monthly reading.

Tab 2 Stand characteristics of the monospecific and mixed stands along the precipitation gradient from the NE to the SW of Bavaria.

Site	Species	Mixture	Age (yrs)	N (n/ha)	HO (m)	DO (cm)	HG (m)	DG (cm)	GV (m^2 ha^{-1})	VV (m^3 ha^{-1})
Arnstein	spruce	mono	70	484	32.7	41.6	30.4	33.5	42.6	624
	beech	mono	85	1018	26.9	38.4	22.7	21.7	37.5	453
	beech	mixture	77	514	27.3	37.3	23.9	22.1	19.8	249
	spruce	mixture	77	269	31.2	45.0	27.7	31.1	20.4	276
	total	mixture		783					40.2	525
Parsberg	spruce	mono	60	889	30.5	45.5	26.9	28.7	57.6	756
	beech	mono	95	470	32.7	39.6	30.5	30.7	34.8	558
	beech	mixture	90	136	36.3	53.3	33.9	42.2	19.0	298
	spruce	mixture	90	214	32.8	47.3	30.4	33.8	19.3	316
	total	mixture		350					38.3	613
Wasserburg	spruce	mono	50	733	25.1	38.4	22.8	27.9	44.7	498
	beech	mono	55	595	24.4	36.6	22.5	24.7	28.4	328
	beech	mixture	60	208	28.6	40.7	25.4	28.3	13.1	162
	spruce	mixture	60	433	24.6	34.5	22.2	22.3	16.9	192
	total	mixture		641					30.0	354
Traunstein	spruce	mono	50	523	28.6	41.4	26.9	33.0	44.7	579
	beech	mono	65	375	26.5	42.3	24.9	30.8	28.0	367
	beech	mixture	67	143	30.2	41.0	29.1	34.0	13.0	197
	spruce	mixture	67	294	33.8	46.8	31.3	36.0	29.9	445
	total	mixture		437					42.9	643

Tree age in years (age); tree number per ha (N); average height of 100 dominant trees [m] (HO); average diameter of 100 dominant trees [cm] (DO); height of mean basal area tree [m] (HG); diameter of mean basal area tree [cm] (DG); basal area [m^2 ha^{-1}] (GV); volume [m^3] (VV)

Tree Ring Sampling

Along the ecological gradient, 30 trees in the monospecific stands and 60 to 100 trees in the mixed stands were cored. In addition, seven increment cores were used for the isotope analysis of each species in the mixed and monospecific stands, which has been shown to be a satisfactory number of replicates for a representative study of isotopes (Leavitt and Long 1984; McCarroll and Loader 2004; Treydte et al. 2001). To compare carbon isotopes in tree rings and the basal area increment (BAI), we used the same sample trees. The trees were cored in north and east direction to the pith (56 cores for the isotope analysis and about 240 trees for the increment analysis per site) at breast height (1.30 m) and arithmetic means of the two cores of each tree were built. The trees were chosen based on vitality, similar stem diameter and height. Only dominant trees in relation to surrounding trees were selected for the analysis.

Tree Ring Measurements

The sampled increment cores were measured with a digital positiometer (Biritz GmbH, Gerasdorf, Austria) with an accuracy of 0.01 mm. For cross-dating and synchronization of the tree chronologies, the software platform TSAP-Win (Rinntech, Heidelberg, Germany) was used. The basal area increment (BAI) was calculated for a better representation of tree growth (Biondi and Qeadan 2008). A double detrending procedure was applied for the standardization of BAI time series (Holmes et al. 1986) and a Hugershoff function (Hugershoff 1936) was used for eliminating age trend and other background noise. With this method, high-frequency climate signals were preserved. Because of the residual growth trends of trees (e.g. thinning) a second detrending procedure was applied, a cubic spline (Holmes et al. 1986). Cubic splines can fit and remove ring width trends that are not linear or do not have a monotonic course. The cubic spline and its wavelength were fixed to 15 years with a frequency response of 0.5 (Thurm et al. 2016a). The BAI and $\Delta^{13}C$ (^{13}C discrimination) is used as an indicator for stress response, because of its sensitivity to stress events through growth decline and changing $^{13}C/^{12}C$ ratio. For the consideration of resistance (RT) and resilience (RS) of basal area increment in view of drought stress, the indices by Lloret et al. (2011) were applied. These indices were also applied to $\Delta^{13}C$. For the consideration of drought stress on growth and $\Delta^{13}C$ in tree rings along the precipitation gradient, the drought year 2003 was chosen and the indices were calculated on the basis of annual mean values of the BAI and the $\Delta^{13}C$. For the calculation, three years before (2000-2002) and after (2004-2006) the drought year 2003 were used for the description of the pre-drought and post-drought situation. The resistance describes the decrease in the year of drought stress compared to the previous years with the formula:

$$RT = \frac{drought}{pre - drought}$$

When RT = 1, a complete resistance is reached. The resilience describes the capacity to reach the level before the drought year with the formula:

$$RS = \frac{post - drought}{pre - drought}$$

When RS ≥ 1 a full recovery or overcompensation is reached.

Climate Data

The Climate-Vegetation-Productivity Index (CVPI) by Paterson (1956) was calculated for the determination of climatic site conditions (data: Bavarian State Research Center for Agriculture (2016)). The CVPI has the form: CVPI = $(T_v \times P \times G \times E)/(T_a \times 12 \times 100)$ and estimates the potential productivity of a forest area based on climatic variables (Benavides et al. 2009; Pretzsch and Rötzer 2016; Vanclay 1994). Here, T_v gives the mean temperature of the warmest month (°C), and T_a is the mean annual range of the temperature between the coldest and warmest month (°C). P is the mean annual precipitation (mm), G is the length of the growing season in months (April to September), and E is an evapotranspiration reducer (based on latitude and giving generalized total annual radiation received as a percentage of that at the equator). For the sites of the precipitation gradient, the values ranged between 280 at dry sites to 412 at moist sites, where a high index value indicates a high productivity under moist conditions.

Kranzberg Forest

Study Site

The study site Kranzberg forest is located in the southern part of Bavaria (approximately 35 km northeast of Munich, 11°39’42’’E, 48°25’12’’N) within the medium range of the precipitation gradient (Fig. 9). The site has a size of 0.5 ha, at an altitude of 490 m. The trees grow on a luvisol that originated from loess over Tertiary sediments with a high nutrient and water supply. The plant available water ranges between 17% and 28%, depending on soil depth (Göttlein et al. 2012). Annual mean precipitation (1971-2000) was 750-800 mm and 460-500 mm during the growing season. Annual mean temperature is around 7.8°C, in the growing season 13.8°C (Hera et al. 2011). The site comprises spruce and beech trees in an intra- and interspecific environment with ages of 66±2 for spruce trees and 86±4 for beech trees (in the year 2017). Overall, 12 plots comprise the site, separated as six control (Fig. 10, C 1-6) and six drought treatment plots (Fig. 10, T 1-6) with a roof construction under the crown of the trees. Each plot carries four measurement trees – two spruces and two beeches – in each intra- and interspecific environment. Mean diameter at breast height is around 34.3 cm for spruce trees and 28.9 cm for beech trees at a mean stand height of 29.0 m for spruce trees and 26.0 m for beech trees (Tab. 3). The plot sizes range between 110 and 200 m² and all plots were trenched with a heavy-duty plastic trap to about 1 m depth to avoid external effects and lateral water flow (Pretzsch et al. 2016). The roof constructions at 3 m above the drought treatment plots only close automatically during rainfall through a precipitation sensor, to exclude unintended micro-meteorological effects (Pretzsch et al. 2014). The annual drying cycles on the drought treatment plots ran from May to December in 2014 and March to November in 2015.

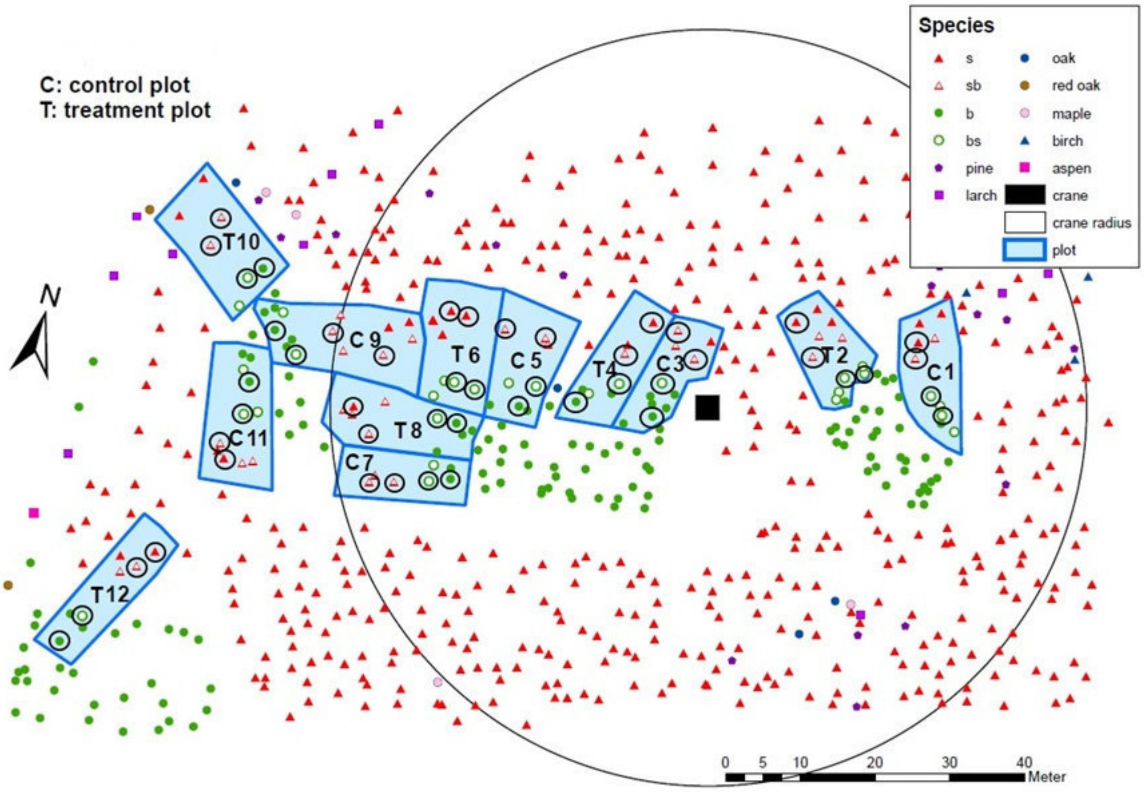

Fig 10 Map of the control (C) and drought treatment (T) plots within Kranzberg forest (Pretzsch et al. 2014).

Tab 3 Characteristics of the investigated stand where the treatment and control plots are located. (N: number of trees per ha; n- number of trees with dendrometers; BA: basal area per ha; V: total stem volume per ha; hq: mean height; dq: quadratic mean diameter at 1.3 m breast height).

	Area [m²]	N	n	BA [m²]	V [m³]	hq [m]	dq [cm]
Treatment							
Spruce		301	12	29,7	422	29,3	34,8
Beech		352	12	22,9	309	26,1	29,1
Total	145	653	24	52,6	730		
Control							
Spruce		310	12	28,8	400	28,7	33,8
Beech		356	12	22,6	305	26	28,7
Total	144	666	24	51,4	705		

Stem Radius Variations

Stem radius variations were measured with automatic radius dendrometers of the DR type (Ecomatik, Dachau, Germany) at breast height (BH, 1.3 m) and 50 % tree height (H50). The dendrometers in BH were only fixed in a northeast direction to avoid environmental influences. The aluminum frames of the dendrometers were fixed with two screws and the daily variations of the bark were measured through a linear transducer which was directly in contact with the tree stem (Fig. 11). The temperature sensitivity of the sensor is < 0.1 µm/K (Ecomatik, Dachau, Germany) and was not further corrected. Measurements were done every 10 minutes. Overall, measurements of 24 European beech and 24 Norway spruce trees were analyzed in 2014 and 2015. From spruce trees, the outermost tissue of the bark was removed to reduce hygroscopic swelling and shrinking of the outer bark.

For the measurements on roots of the 48 sampling trees, circumference dendrometer of the DC2 type were selected and fixed on a main root of every experimental tree. The tension was applied in the radial direction. Variation in root size were measured throughout the changing pressure of the wire cable on the tree. Slide rings reduce the friction between the wire cable and the tree bark. Dendrometers were installed, wherever applicable, in NW-direction, to avoid environmental influences. Variations of radial growth were determined in 10 min intervals. Both, the irreversible tree growth and the reversible swelling and shrinking of stem and root can be record.

Fig 11 Automatic radius dendrometer of the DR type (Ecomatik, Dachau, Germany) in breast height and of the DC2 type on the main root of a experimental tree.

To separate the irreversible growth trend (ZGmax) from reversible shrinking and swelling, we used the method of Zweifel et al. (2016). This method results in growth curves with a stepwise shape. The growth increases when the current maximum of the stem radius is exceeded (Fig. 12 a, blue line). To calculate the tree water deficit (TWD) due to swelling and shrinking of the stem, differences of the fully hydrated stem (ZGmax, blue line) and shrinking were established (Fig. 12 b). Negative values in the tree water deficit reveal a shrinking phase of the stem. Hourly means were established and set to zero every day for a comparison of daily amplitudes (Δ R) (Fig. 12 c). Data are illustrated based on the day of the year (DOY).

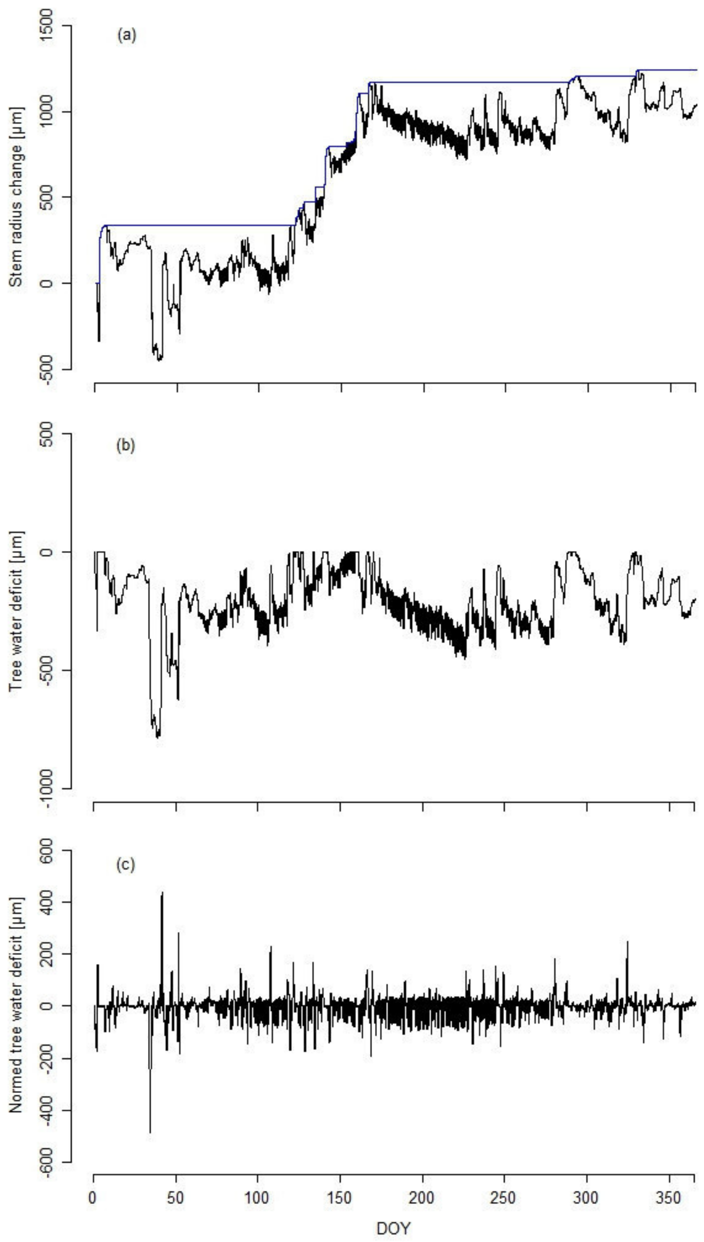

Fig 12 Illustration of the calculated tree water deficit of a spruce tree. Reversible stem radius variations were separated from the irreversible stem radius. The growth trend is shown in (a) as a blue line. The reversible swelling and shrinking were subtracted from the growth trend (ZGmax) (b) and is called tree water deficit. The tree water deficit was set to zero every day for a daily comparison (c).

Relationship of TWD and Leaf Water Potentials

Furthermore, the relationship between tree water deficit and leaf water potentials was tested.

Midday (Ψ_m) and predawn (Ψ_p) leaf water potential was measured several times during the vegetation periods (April – October) in 2014 and 2015 (measured by the working group eco-physiology of plants). In the early morning between 2 a.m. and 3:30 a.m. MEZ predawn measurements were done. South-exposed twigs from the sun crown in 25-30 m height and of about 10-20 cm length were chosen. The twigs were enclosed in humid plastic bags to prevent water loss. The leafs were immediately measured with a pressure chamber (Model 3000 Pressure Extractor, Soil Moisture Equipment Corp., Santa Barbara, CA, USA). The relationship of midday leaf water potential and daily maximum tree water deficit (TWDmin, maximum shrinkage) of all tree heights (BH, H50, root) were tested and in addition the relationship of predawn water potentials and minimum tree water deficit (TWDmax, maximum expansion). The differences of the daily TWDmax and TWDmin of leaf water potentials or tree water deficits reveal the daily amplitude.

Allometry of Stem and Root Growth and TWD

To show how growth allometry or the TWDmin react under drought, we examined both ZGmax (stem or root growth) and TWDmin at a measurement position above (H50 – BH) to the measurement position below (BH - Root). The results show values above zero for an increasing growth or TWD in the upper tree compartment or a value below zero for an increasing growth or TWD in the lower tree compartment such as the roots compared to the BH. The differences between the tree compartments were used instead of the ratio because of the low TWDmin or ZGmax values that can lead to meaningless outliers in the analysis. The difference value of the upper and lower tree compartment serves as independent variable. Further, the TWDmin and ZGmax increase over the growing season. At the end of the growing season, the difference between the upper and lower tree compartment can be higher than at the beginning.

Meteorological Data

The data for temperature and relative humidity were measured in ten-minute intervals on the forest site. At a height of 27 m, the temperature was monitored with a temperature sensor (RTF-2, UMS) and stored in a data logger (Logger Campbell CR100, Multiplexer AM16/32). The temperature measurements were protected against irradiation with a ventilated radiation shield.

The rainfall data was used from the nearby weather station (Bavarian State Institute of Forestry 2015) at Kranzberg forest (2 km from the study site).

Statistics

The study at hand mainly applied linear mixed effect models to describe statistical differences in data. For the consideration of linear mixed effects, a “lmer” model was applied (lme4 R package (Bates et al. 2015) and lmerTest package (Kuznetsova et al. 2015)). Linear mixed effect models have the form:

$$y_{ijk} = a_1 x_{1ijk} + a_2 x_{2ijk} + a_3 x_{3ijk} \dots a_n x_{nijk} + b_{i1} z_{1ij} + b_{i2} z_{2ij} \dots b_{in} z_{nij} + \varepsilon_{ijk}$$

where y_{ijk} describes the outcome variable, a_1 through a_n stand for the fixed effects coefficients and x_1 through x_n represent the fixed effect variables, random effect coefficients b_{i1} through b_{in} with the random effect variables z_{1ij} through z_{nijk}. ε_{ijk} represents the independent and identically distributed random error.

To show how mixture and drought treatment influence the growth allometry or TWDmin pattern of the upper and lower compartments (*Diff*) also linear mixed models where applied. Mixture (Mix) or drought treatment ($Treat$) were included as fixed effects in this models:

$$Diff_{ijkt} = \beta_0 + \beta_1 \cdot lowComp_{ijkt} + \beta_2 \cdot Mix + \beta_3 \cdot lowComp_{ijkt} \cdot Mix + b_i + b_j + \varepsilon_{ijkt}$$

$$Diff_{ijkt} = \beta_0 + \beta_1 \cdot lowComp_{ijkt} + \beta_2 \cdot Treat + \beta_3 \cdot lowComp_{ijkt} \cdot Treat + b_i + b_j + \varepsilon_{ijkt}$$

The significances of the fixed effects where tested by an F test with Satterthwaite’s approximation ((Kuznetsova et al. 2015), R-package *lmerTest*). To consider the great amount of measurements points, we also calculate the conditional coefficient of determination (R^2) for the mixed-effect models with the command *r.squaredGLMM* from the *MuMln* package. Additionally, the quality of the models where checked by the root square mean error (RMSE)

Furthermore, a generalized additive mixed model ‘GAMM’ (R package mgcv (Wood 2006)) was applied for the description of statistical differences of non-linear data as daily stem radius variations with a sine wave form. The GAMM displays estimated cubic smoothing spline fits of the daily variations with confidence intervals (95%). All analysis was performed with the R version 3.2.3.

IV. Main Findings

Drought Stress Reactions along the Precipitation Gradient

For the analysis of drought stress reactions in the year 2003, resistance (RT) and resilience (RS) of the reference period 2000 to 2006 were calculated. The influence of the climate has been taken into account by the Climate Vegetation Productivity Index (CVPI).

Differences in stand composition were only found at the $\Delta^{13}C$ analysis. Beech trees revealed a higher resistance and resilience in mixture with spruce on moist sites under drought, whereas on dry sites beech trees in intraspecific environments showed significantly higher resistance and resilience ($\Delta^{13}C$) (Fig. 13 and Tab. 4). In contrast, $\Delta^{13}C$ of spruce trees indicated a higher resilience at dry sites in mixture with beech trees and a lower resilience in mixture at moist sites. The mixture-specific resilience of spruces along the gradient showed a weak relationship ($p < 0.1$), but a significantly higher intercept ($p < 0.001$) for $\Delta^{13}C$ of spruce trees in mixture was found.

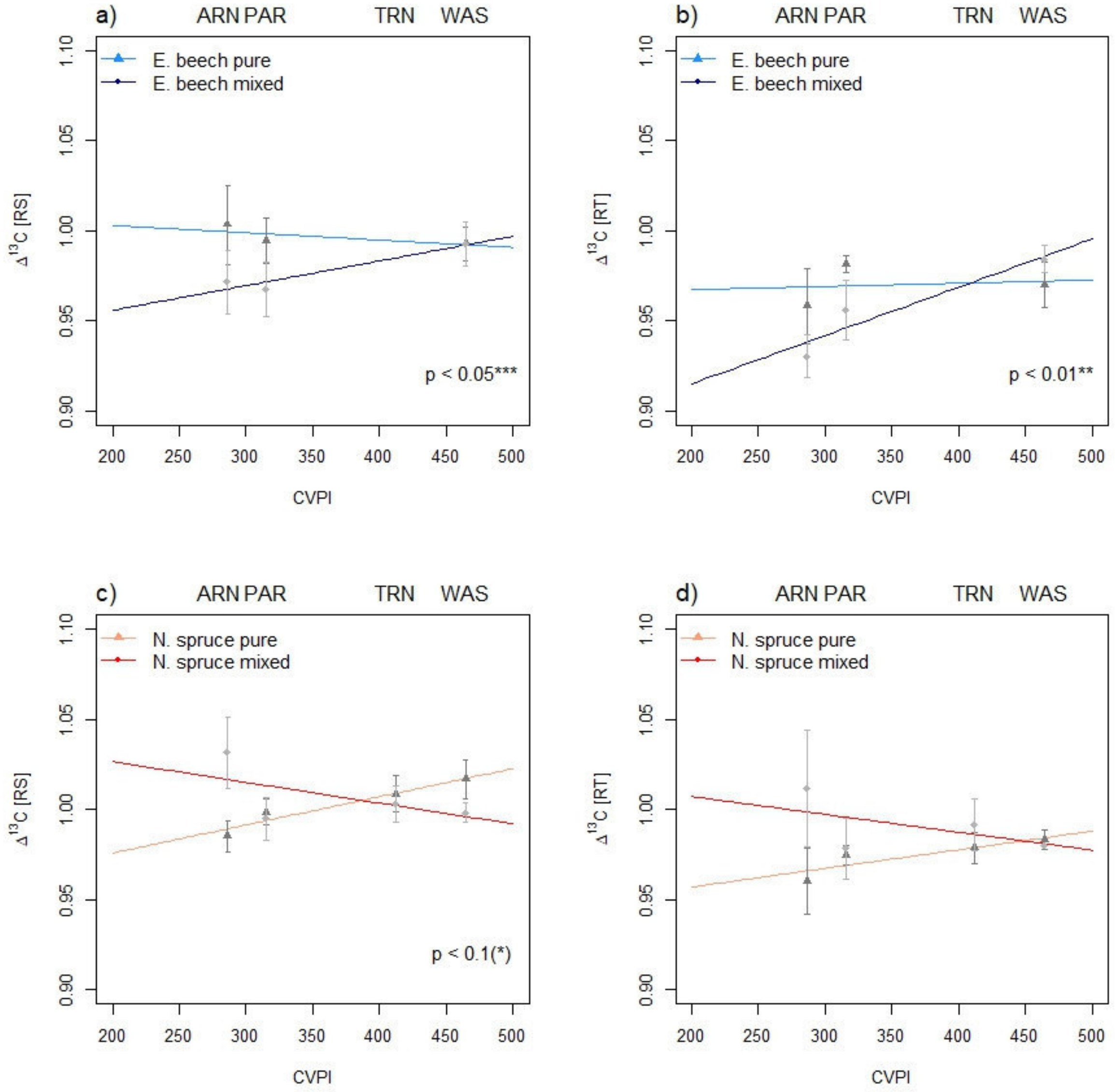

Fig 13 Linear mixed effect model of species and sites relative to the drought period in 2003 for the resilience (a, c) and resistance (b, d) of beech and spruce trees of $\Delta^{13}C$ in monospecific or mixed environments along the gradient represented by the Paterson index (CVPI). The higher the CVPI, the higher the site moisture. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '(*)' 0.1.

Tab 4 Estimates of the linear mixed effect model of spruce and beech in monospecific and mixed stands along the precipitation gradient (CVPI) (spruce n = 45; beech n =41). Standard deviation is represented in brackets. Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘(*)’ 0.1.

	Dependent Variable:			
	Spruce		**Beech**	
	RS	RT	RS	RT
	$\Delta^{13}C$	$\Delta^{13}C$	$\Delta^{13}C$	$\Delta^{13}C$
Intercept	1.050 ***	1.027***	0.928 ***	0.861 *
	(−0.033)	(-0.032)	(−0.022)	(−0.041)
CVPI	−0.0001	-0.0001	0.0001 *	0.0003
	(−0.0001)	(-0.0001)	(−0.0001)	(−0.0001)
Mixture (Pure)	−0.105 (*)	-0.091	0.083 *	0.102 ***
	(−0.047)	-0.047	(−0.031)	(−0.027)
CVPI Mixture (Pure)	0.0003 (*)	0.0002	−0.0002 *	−0.0003 **
	(−0.0001)	-0.0001	(−0.0001)	(−0.0001)

Kranzberg Forest – Tree Water Relations under Extreme Drought Conditions

The stem radius variations (BH) in 2014 and 2015 are shown in Fig. 14 for different species, neighborhoods and the drought treatment. Annual diameter increments were significantly higher for spruce trees in 2014 at the control plots. In the year 2015, no significant differences between species were found. In the comparison of control and drought treatment plots, differences were smaller for beech trees compared to spruce trees. At the drought treatment plots, spruce trees grew significantly less than beech trees in the drought year 2015 (Rötzer et al. 2017).

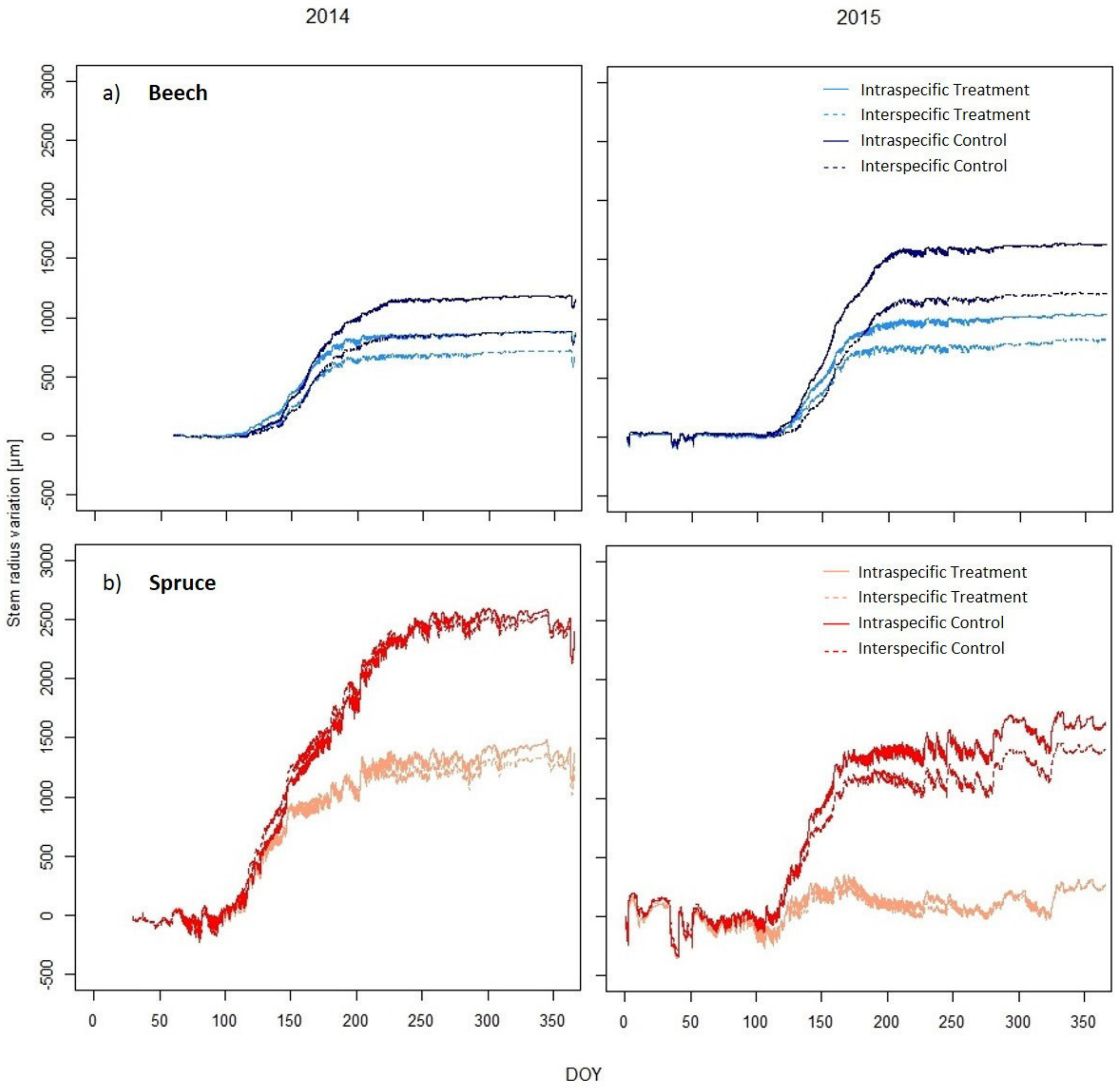

Fig 14 Mean stem radius variations (BH) of beech (a, blue color) and spruce trees (b, red color) of the years 2014 and 2015 in intra- and interspecific (bold and dashed line) neighborhoods of drought treatment (light color) and control (dark color) plots.

Connection between Tree Water Deficit and Leaf Water Potentials in Different Tree Compartments

For the determination of differences in tree water relations in intra- and interspecific neighborhoods, the overall relationship of the TWD and leaf water potentials at all measured tree compartements (H50, BH, root) was tested. For the comparison we used the minimum and maximum of the TWD (TWD_{min}, TWD_{max}) and the water potential at midday (Ψ_m) and predawn (Ψ_p)) respectively. A significant relationship of the TWD and leaf water potentials could be detected for all tree compartments (Fig. 4 and Tab. 2 in Schäfer et al. (major revision)). This suggests that the TWD is a good predictor of the water status for both tree species.

In the upper part of the stem, stem radius fluctuations were higher than in BH and roots. The roots had similar stem radius fluctuations as the stem in BH. On a temporal scale, the fluctuations showed a little time lag between the tree compartments. This was not statistical examined.

Stem and Root Growth Allometry and TWD

The tree appears to invest growth in the upper stem (H50) at the beginning of the growing season and then more in the BH (Fig. 15 a-d, $p < 0.001$ Table 5 a-d). In addition, at dry conditions the increment of the upper stem increased. In contrast, the increment of the BH increased with good water supply.

Spruces of the control plots had a higher stem radius increment in BH than in H50. The drought treatment shifted the curve more to H50 (Fig. 15 a). Intraspecific spruces had higher increment in BH over H50 in comparison of interspecific spruces (Fig. 15 b). The beeches of the drought treatment and interspecific neighborhood revealed a lesser diameter growth in BH than the beeches of the control plots or intraspecific neighborhood (Fig. 15 c-d, $p < 0.001$, Table 5 c-d).

Spruces had a higher TWDmin in H50 than in BH and the drought treatment trees shifted the slope of TWDmin more to H50 compared to the control trees (Fig. 15 e, $p < 0.001$ Table 5 e). Spruce trees in interspecific neighborhood showed the same reaction pattern as spruce trees of the control plots, with a lesser TWDmin in H50 in interspecific neighborhood (Fig. 15 f, $p < 0.001$ Table 5 f). Beech trees revealed a higher stem shrinkage in BH than in H50 and a higher shrinkage of control trees in BH than in H50 (Fig. 15 g, $p < 0.01$ Table 5 g). Beech trees in interspecific neighborhood showed a lesser shrinkage in BH similar to the drought treatment (Fig. 15 h, $p < 0.001$ Table 5 h).

Overall, spruce and beech trees revealed a higher stem increment in BH than in the roots. Spruce trees of the drought treatment (Fig.16 a, $p < 0.001$ Table 6 a), revealed a lesser stem increment in BH than the control and spruces in interspecific neighborhood also had a lesser stem increment in BH (Fig. 16 b, $p < 0.05$ Table 6 b). Beeches of the control plots revealed also a higher stem increment in BH than beeches of the drought treatment (Fig. 16 c, $p < 0.001$ Table 6 c). Furthermore, beech trees in intraspecific neighborhood showed a higher increment in BH compared to the interspecific beeches (similar to beeches of the control plots) (Fig. 16 d, $p < 0.001$ Table 6 d).

The TWDmin of spruces was higher in the roots than in BH. Spruce trees revealed for the roots a higher TWDmin at the control plots than at the drought treatment plots (Fig. 16 e, $p < 0.001$ Table 6 e). Spruces of interspecific neighborhood (Fig. 16 f, $p < 0.001$ Table 6 f) revealed also a higher TWDmin than intraspecific spruces in the roots like spruces of the control plots. For beech trees, the TWDmin was higher in the roots compared to BH, comparable with the spruce trees, but with no significant differences between drought treatment and control plots (Fig. 16 g, n.s. Table 6 g). Beeches in intraspecific neighborhood revealed a lesser shrinkage of the roots compared to the beech trees in interspecific neighborhood (Fig. 16 h, $p < 0.001$ Table 6 h).

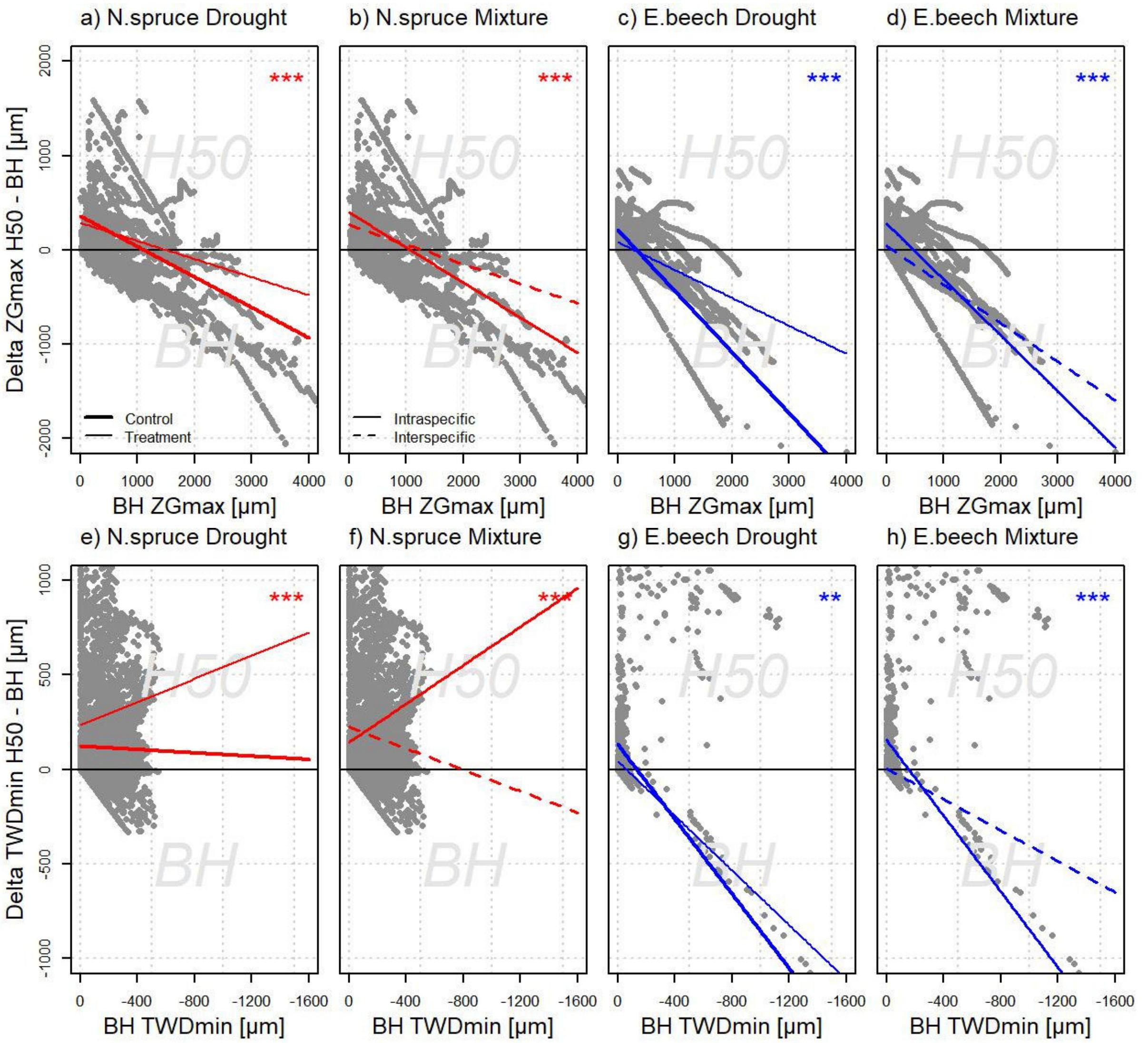

Fig 15 Relationship of growth (ZGmax, above) and the tree water deficit (TWDmin) (below) represented by the difference of the measurements in 50% tree height (H50) and breast height (BH) in dependency of the breast height measurement. Values below the zero line mean a growth allocation or water relocation into the lower stem compartment at breast height. For the TWDmin the negative values represent a lower tree water deficit at breast height. Linear mixed models depict how strong the allometry is influenced by drought treatment (thick line – control, thin line - treatment) or mixture (intraspecific competition – straight line, interspecific competition – dashed line). The respective models are shown in Table 3. Significance levels: ***, $p < 0.001$; **, 0.01; *, 0.05; (*), 0.1.

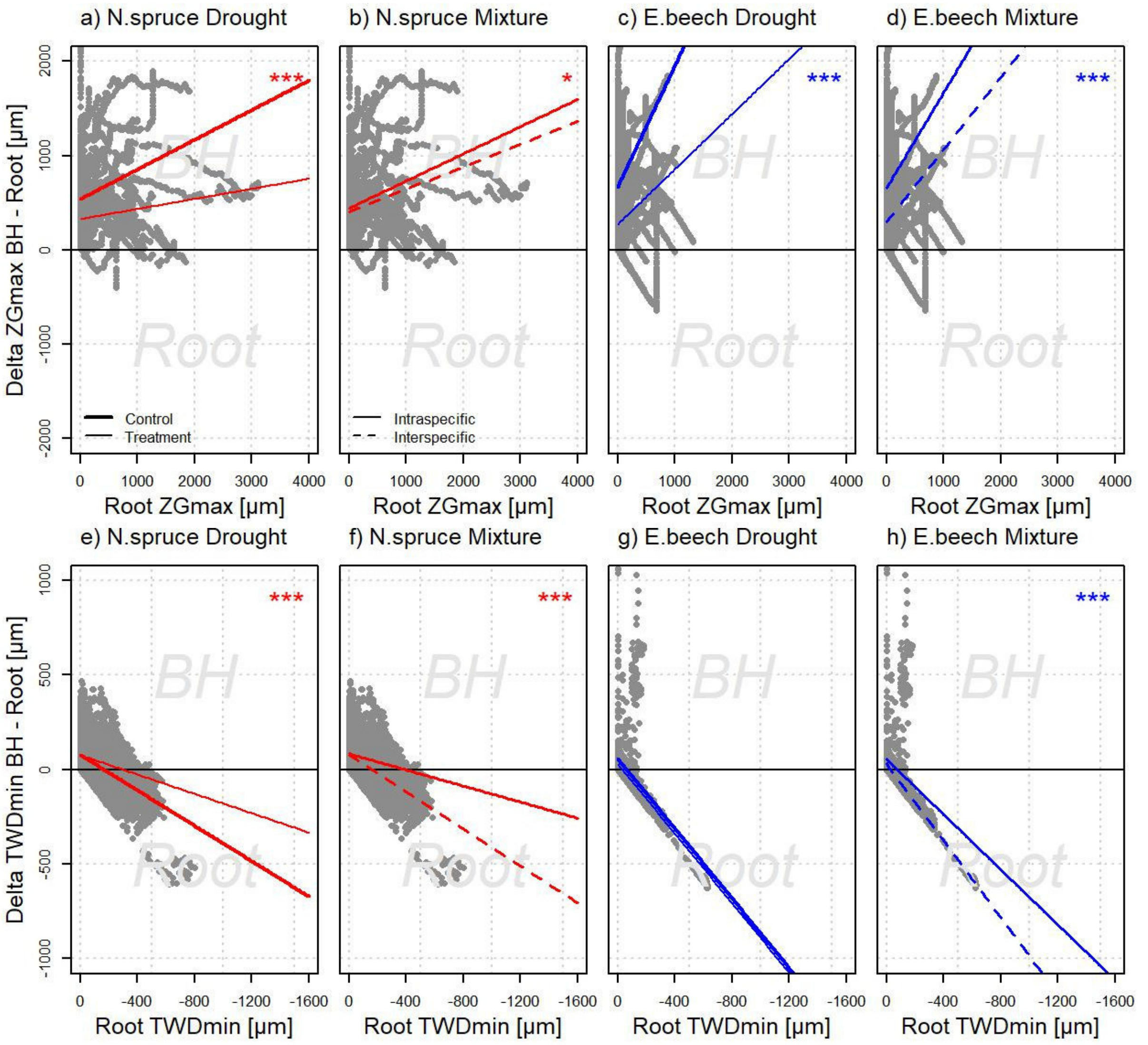

Fig 16 Relationship of growth (ZGmax, above) and the tree water deficit (TWDmin) (below) represented by the difference of the measurements in breast height (BH) and at the roots in dependency of the root measurements. Values below the zero line mean a growth allocation or water relocation into the roots. For the TWDmin the negative values represent a lower tree water deficit in the roots. Linear mixed models depict how strong the allometry is influenced by drought treatment (thick line – control, thin line - treatment) or mixture (intraspecific competition – straight line, interspecific competition – dashed line). The respective models are shown in Table 4. Significance levels: ***, p < 0.001; **, 0.01; *, 0.05; (*), 0.1.

Tab 5 Parameter estimates and statistics for the diameter growth (ZGmax) and tree water deficit (TWD) of the 50% tree height (H50) and stem at breast height (BH) allometry in dependence on drought (treat) and species mixing (mixture). The dependent variables are in the columns. Rows show the output of the model with the fixed variables (N: number of measurements). Significance levels: ***, p < 0.001; **, 0.01; *, 0.05; (*), 0.1.

Position	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH
ZGmax/TWD	ZGmax				TWD			
	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
Art	N.spruce	N.spruce	E.beech	E.beech	N.spruce	N.spruce	E.beech	E.beech
Factor	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture
Intercept	358.825 **	266.228 **	214.488	43.009	121.517	223.763 *	132.545	4.516
BH	-0.323 ***	-0.208 ***	-0.648 ***	-0.409 ***	-0.044	-0.283 ***	-0.988 ***	-0.409 ***
Treat	-71.721		-131.272		112.579		-89.295	
Treat*BH	0.131 ***		0.352 ***		0.351 ***		0.265 **	
Mixture		132.963		240.248		-81.43		151.639
Mixture*BH		-0.164 ***		-0.185 ***		0.793 ***		-0.594 ***
R²	0.78	0.78	0.94	0.93	0.61	0.62	0.84	0.84
N	8107	8107	6330	6330	8107	8107	6330	6330

Tab 6 Parameter estimates and statistics for the diameter growth (ZGmax) and tree water deficit (TWD) of the stem at breast height (BH) and root allometry in dependence on drought (treat) and species mixing (mixture). The dependent variables are in the columns. Rows show the output of the model with the fixed variables (N: number of measurements). Significance levels: ***, p < 0.001; **, 0.01; *, 0.05; (*), 0.1.

Position	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root
ZGmax/TWD	ZGmax				TWD			
	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
Art	N.spruce	N.spruce	E.beech	E.beech	N.spruce	N.spruce	E.beech	E.beech
Factor	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture
Intercept	540.56 **	403.758 **	670.177 *	296.51	77.256 **	77.76 ***	58.306 (*)	29.673
Root	-0.343 ***	-0.38 ***	0.142 ***	-0.117 ***	-0.734 ***	-0.745 ***	-0.962 ***	-1.008 ***
Treat	-213.283		-397.388		-1.879		-30.161	
Treat*Root	-0.104 ***		-0.35 ***		0.106 ***		0.002	
Mixture		38.568		360.569		5.108		24.555
Mixture*Root		0.024 *		0.124 ***		0.139 ***		0.143 ***
R²	0.76	0.77	0.85	0.85	0.90	0.90	0.94	0.94
N	8290	8290	8306	8306	8290	8290	8306	8306

Tree Water Deficit on an Annual and Daily Scale

The year 2015 was a very dry year with high temperatures compared to the years 2014 and 2016 (Fig. 17). In the summer months of 2015, the maximum daily temperatures reached 35.8°C and the mean daily temperature was 26°C. The soil volumetric water content (SVWC) of the year 2015 (Fig. 18) shows a clearly lower SVWC in the summer months than in 2014 and 2016. The years 2014 and 2016 had more humid summer months without any long drought periods.

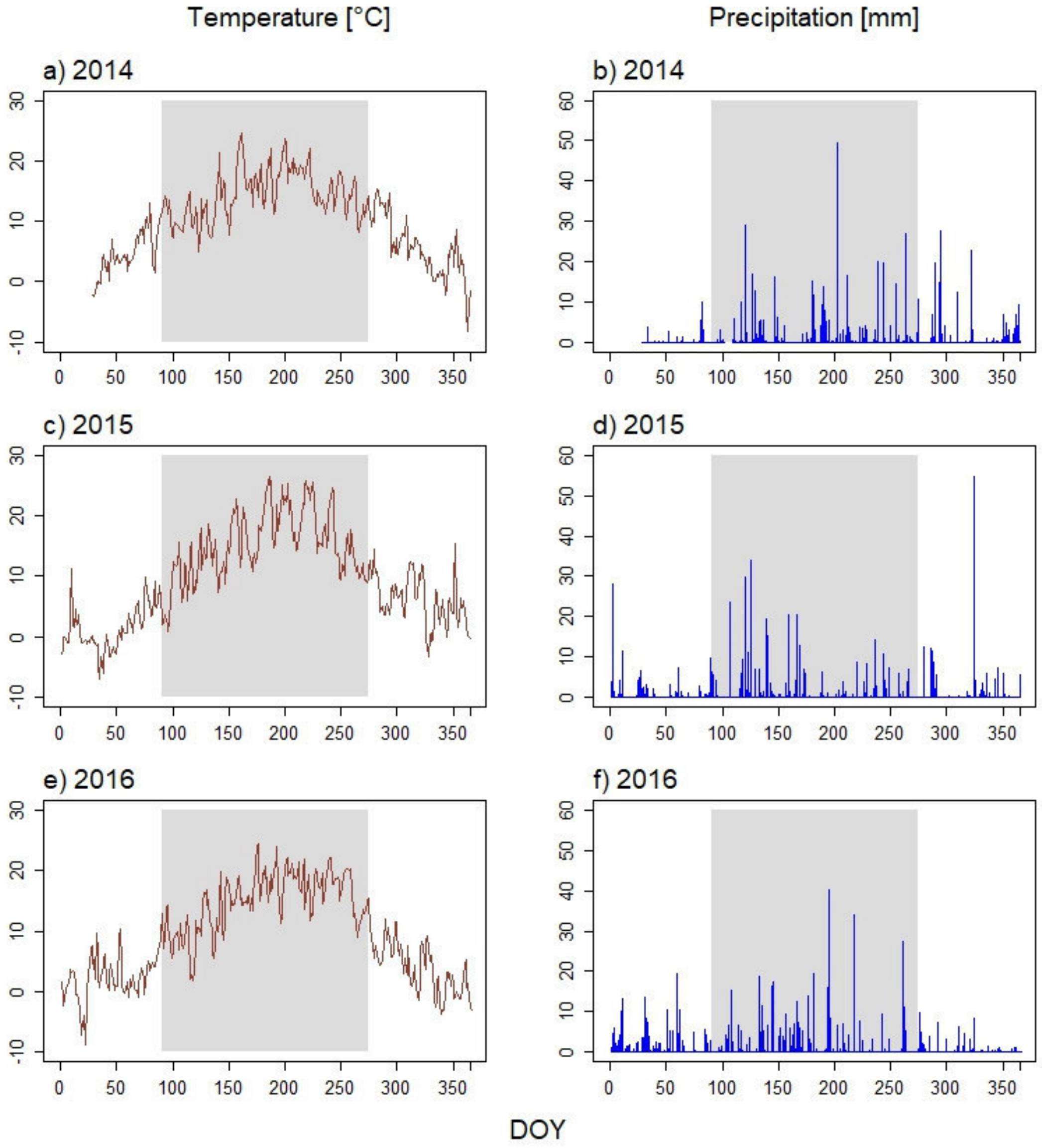

Fig 17 Daily mean temperature (a, c, e) and precipitation sums (b, d, f) of the years 2014 (above), 2015 (middle) and 2016 (below). Months of the growing season (April – September) are shaded in grey.

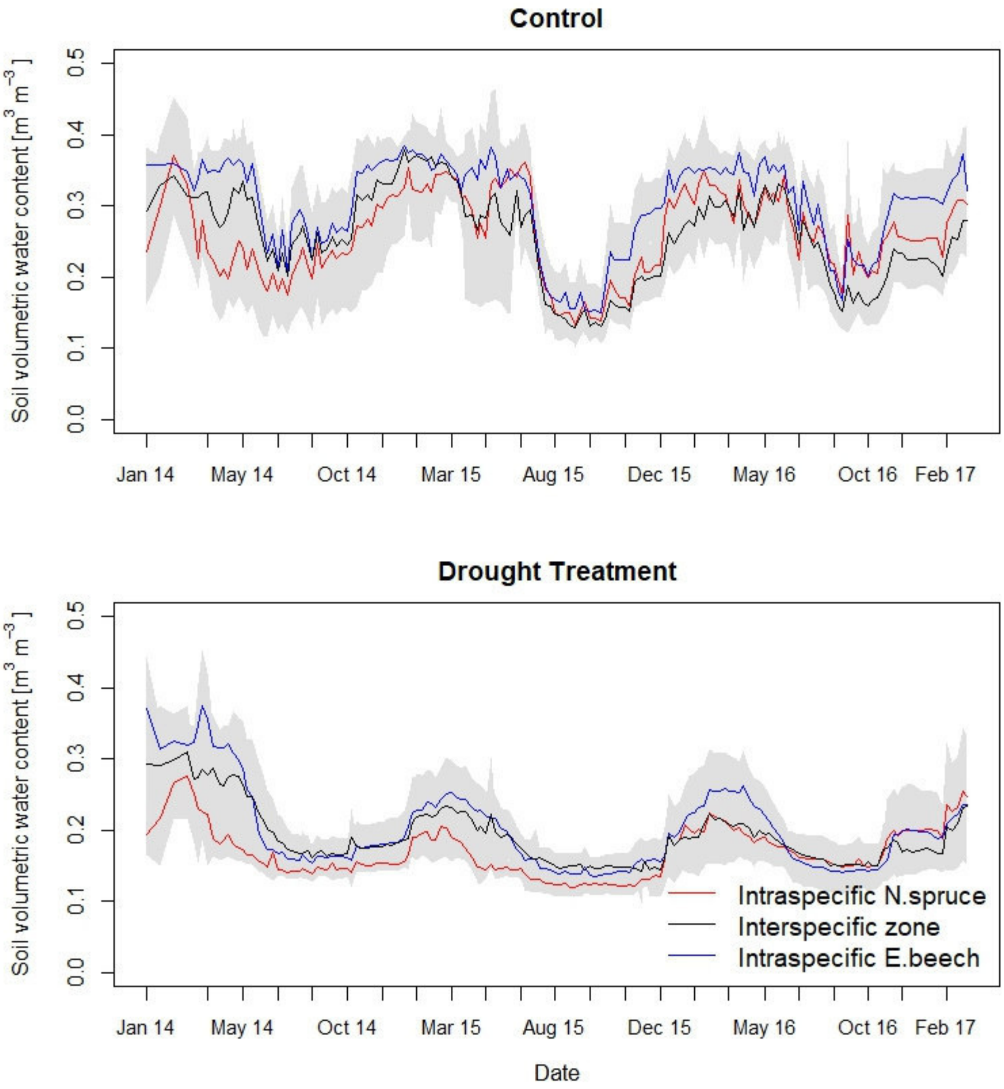

Fig 18 Soil volumetric water content of the years 2014 to 2017 at the control and drought treatment plots for spruces in an intraspecific neighborhood (red line), beeches in an intraspecific neighborhood (blue line) and the interspecific zone (black line).

In the present work, the mean daily amplitudes (BH) of every month are displayed for beech trees (Fig. 19, a-c) and spruce trees (Fig. 20, a-c) in intra- and interspecific environments at the control and drought treatment plots. The results of Schäfer et al. (2018) were extended with the observations of the year 2016. For beech trees, significant differences between control and drought treatment plots are visible in the summer months, except the very dry months of 2015, where amplitudes of the control and drought treatment were similar due to the dry conditions on the treatment as well as control plots. Differences in intra- and interspecific neighborhoods are only visible after three years of the drying experiment. Beech trees had significantly higher daily amplitudes in the interspecific environment than in the intraspecific in the year 2016. More water from the storage tissue was used for transpiration in the interspecific neighborhood and the daily tree water deficit increased.

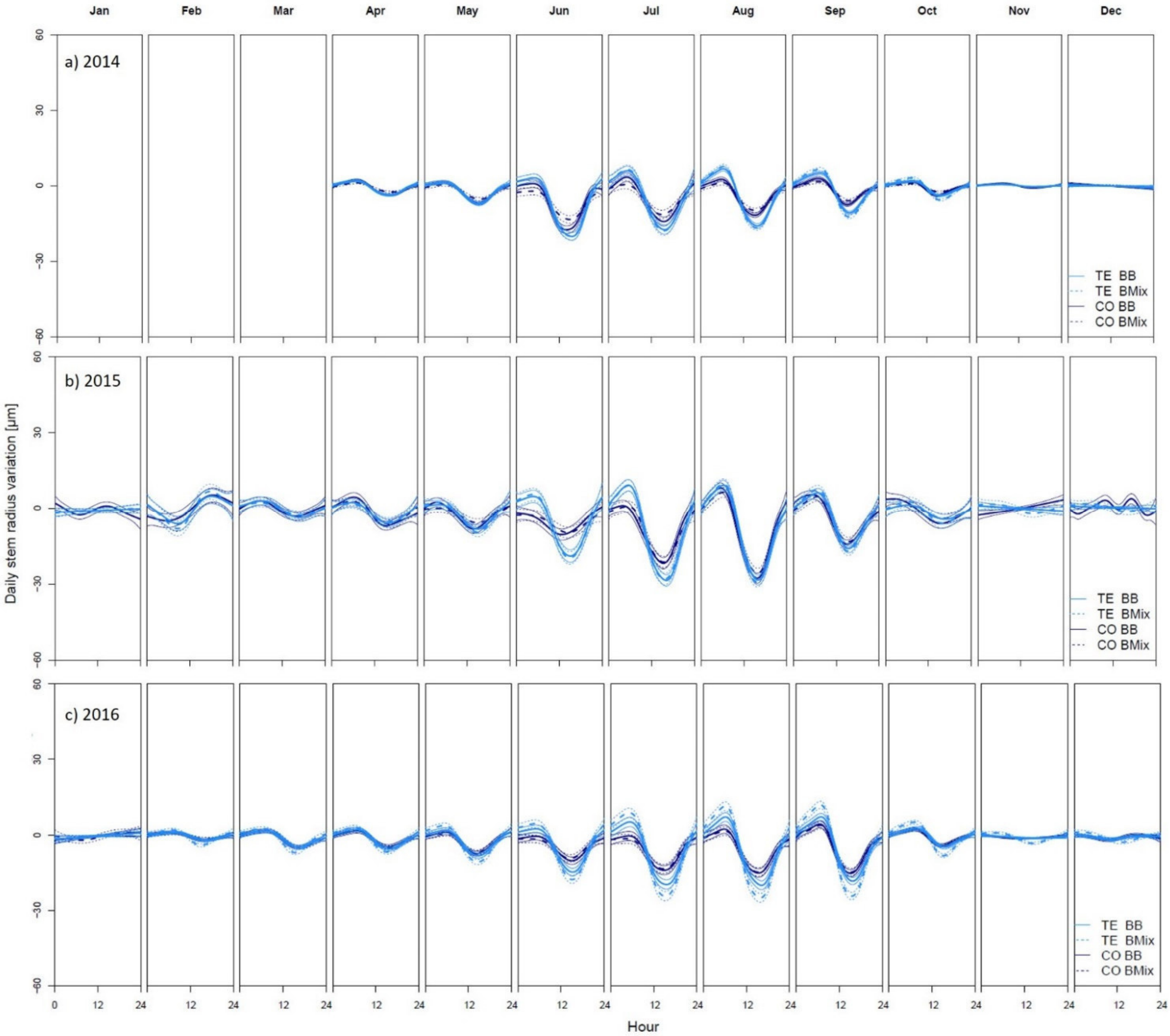

Fig 19 Generalized additive mixed model (GAMM) of daily stem radius variations (amplitude in breast height (BH)) of beech trees for each month and the years 2014 (a), 2015 (b) and 2016 (c) separated by control (CO, dark color) and drought treatment (TE, light color) in intraspecific (BB, solid line) and interspecific (BMix, dashed line) neighborhoods. Lines are cubic smoothing spline fits (bold line) and surrounding lines are 95% confidence intervals (thin lines).

In contrast, spruce trees showed no significant differences in control and drought treatment plots in the first year of soil drying, but in the second year, the differences were more pronounced and acute than for beech trees. The amplitudes of spruces at the drought treatment were higher than of the control plots, but at a high stage of drought from July 2015, the amplitudes of the drought treatment shrank due to not fully replenished living tissues overnight, as mentioned above. The year 2016 was a more humid year similar to 2014 and the drought treatment showed higher amplitudes than the control plots in the spring and summer months.

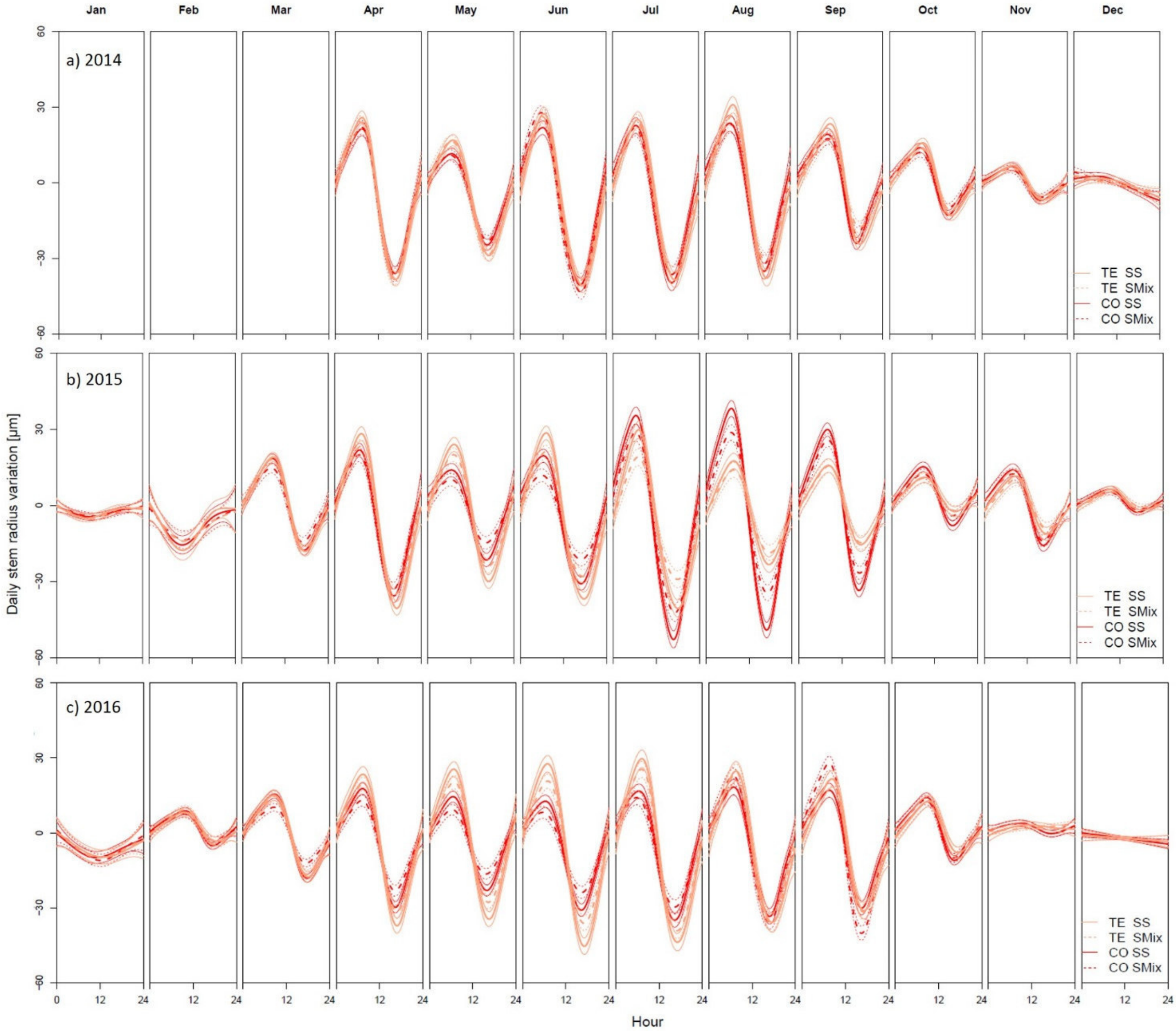

Fig 20 Generalized additive mixed model (GAMM) of daily stem radius variations (amplitude in breast height (BH)) of spruce trees for each month and the years 2014 (a), 2015 (b) and 2016 (c) separated by control (CO, dark color) and drought treatment (TE, light color) in intraspecific (SS, solid line) and interspecific (SMix, dashed line) neighborhoods. Lines are cubic smoothing spline fits (bold line) and surrounding lines are 95% confidence intervals (thin lines).

The coherences of the inner-annual tree water deficit (TWD) and the tree water deficit at a daily scale (daily amplitudes) are illustrated in Fig. 21. Significant differences of spruces were found in the year 2015 with a higher TWD for trees in intraspecific neighborhoods at all stages of drought stress. The trees used more stem water at different stages of drought (dry control plots in 2015 vs. drought treatment plots). Compared with the daily amplitudes of the year 2015 in the months June and July, the higher amplitudes of intraspecific spruces are also visible (Fig. 21, right side).

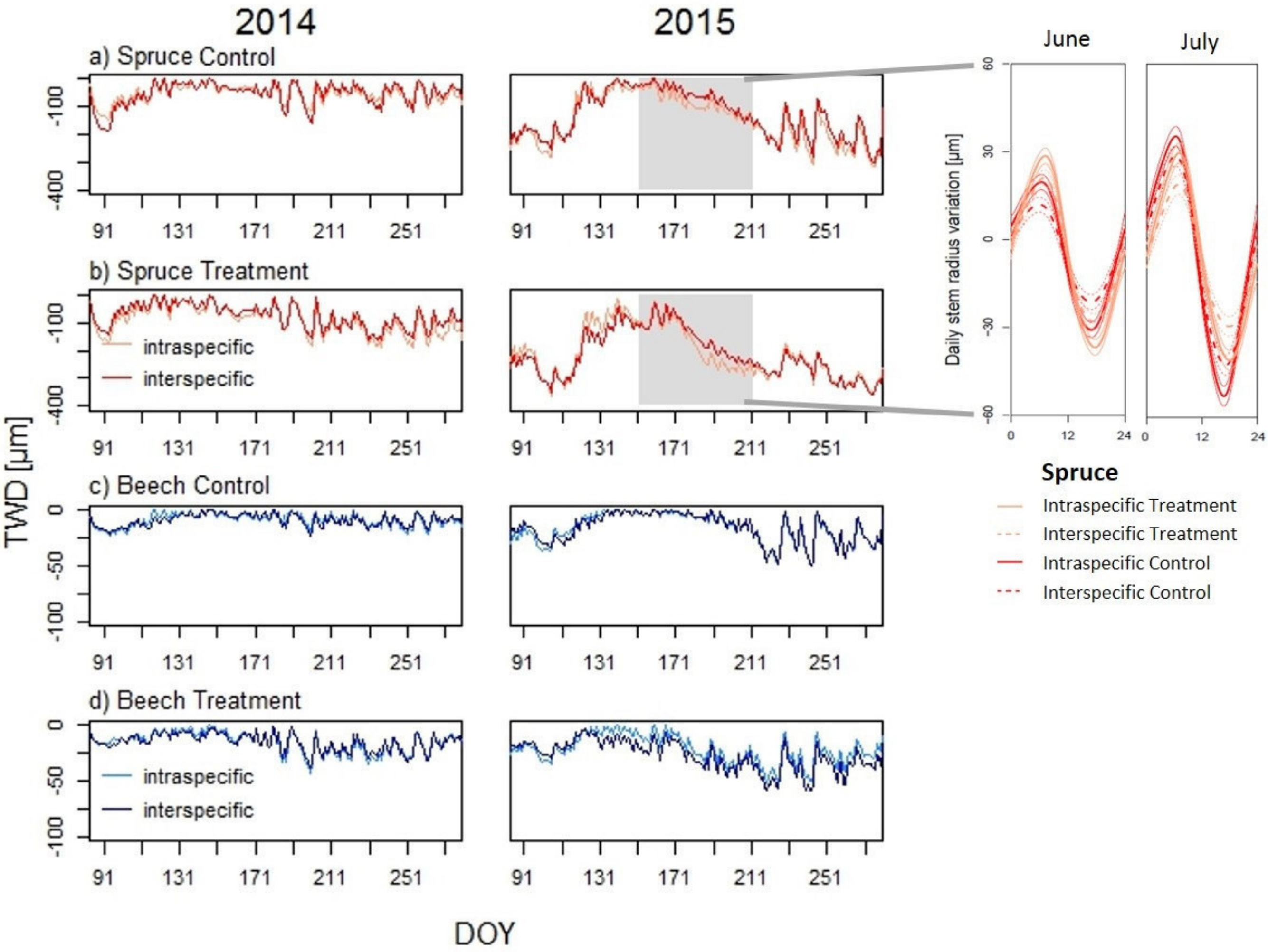

Fig 21 TWD (breast height) in 2014 (left) and 2015 (right) for spruces in intra- and interspecific environments at the control (a) and drought treatment (b) plots and for beech in intra- and interspecific environments at the control (c) and drought treatment (d) plots. For the comparison of the TWD and the daily amplitude in the hot and dry summer of 2015, the mean daily amplitudes of June and July are illustrated on the right side of the figure. The grey shaded areas of the TWD of spruce trees show the timespan of June to July. The amplitudes of spruces are shown for the intra- (solid lines) and interspecific (dashed lines) neighborhood and for the drought treatment (light color) and control (dark color) plots.

Influence of Climate

The dependencies of daily amplitudes on maximum temperature and soil water content (SVWC) of both species are shown in Fig. 22. The daily amplitude increases with rising temperatures and decreasing SVWC (Tab. 7 and 8). The only exception were spruce trees in the intraspecific neighborhood with the shrinking amplitude with decreasing SVWC from 0.21 $m^3 m^{-3}$. On rainy days and with a high soil moisture, the amplitude is also smaller and the storage tissue of the stem is fully replenished of water from the soil.

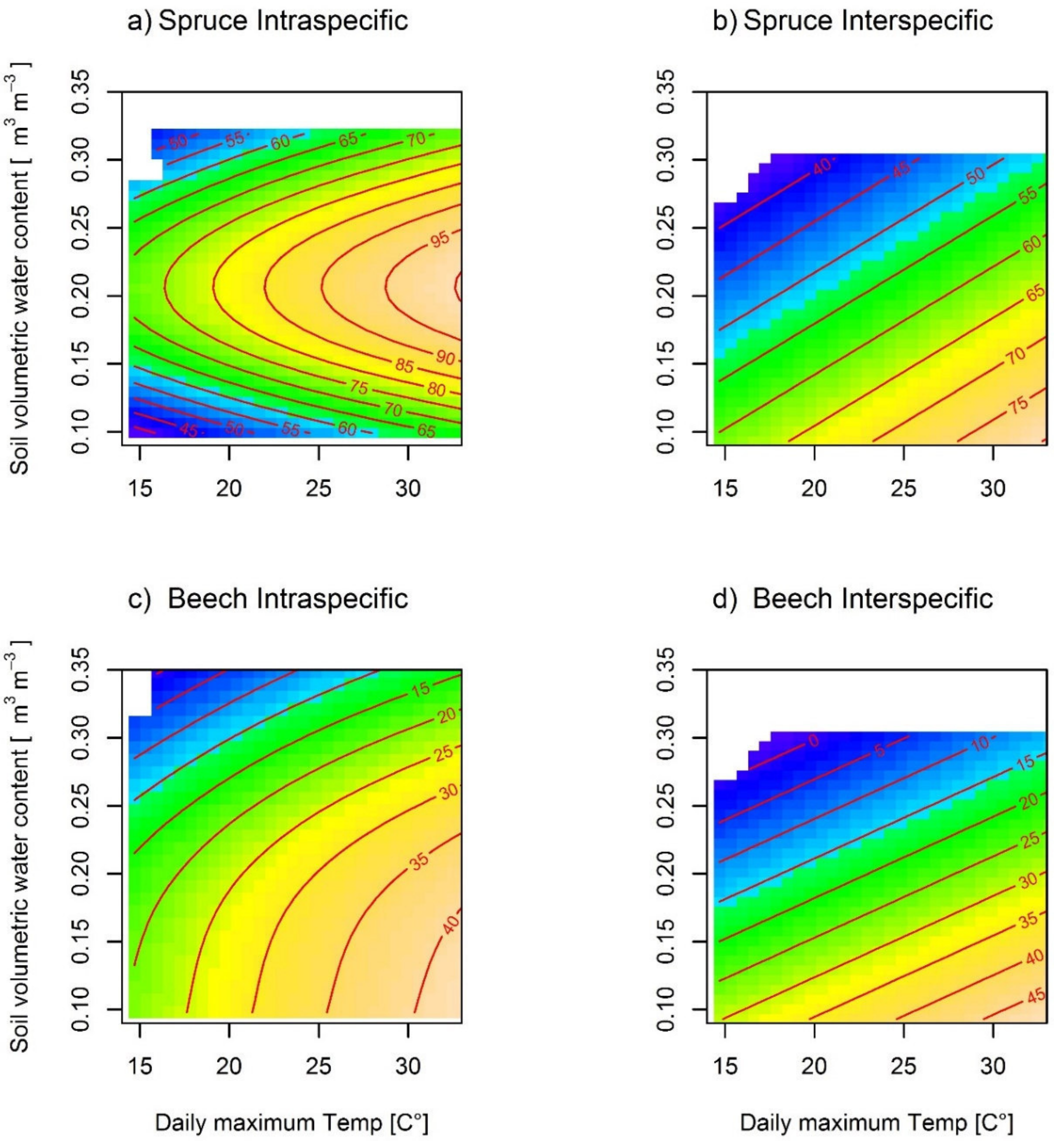

Fig 22 Daily stem radius amplitudes of spruce (a-b) and beech (c-d) trees at the drought treatment and control plots in intra- and interspecific neighborhoods dependent on soil volumetric water content (SVWC) and temperature in the summer months of 2015.

Tab 7 Mean daily Amplitude (ΔR) of spruce and beech trees in June to September 2015 with monthly mean maximum temperature, mean VPD and mean soil volumetric water content (SVWC) at the control and drought treatment plots.

Month	Spruce ΔR [µm]	Beech ΔR [µm]	Spruce ΔR [µm]	Beech ΔR [µm]	Max Temp [°C]	VPD [kPa]	SVWC [$m^3 m^{-3}$]	SVWC [$m^3 m^{-3}$]
	Treatment	Treatment	Control	Control			Treatment	Control
Jun	65.5±28.0	26.0±18.2	48.4±32.0	24.4±35.0	22.6±4.9	0.7±0.4	0.17±0.03	0.3±0.06
July	61.2±23.1	39.0±17.5	82.9±41.7	32.7±28.0	27.8±4.7	1.2±0.4	0.15±0.02	0.2±0.05
Aug	52.8±16.9	39.6±18.3	86.0±41.8	40.7±38.1	28±5.6	1.2±0.6	0.14±0.02	0.15±0.03
Sep	43.1±22.1	26.6±14.5	75.0±37.1	26.8±35.5	18.6±4.6	0.5±0.2	0.14±0.02	0.15±0.03

Tab 8 Estimates of the linear mixed effect model for the daily amplitude in relation to precipitation at the control plots (CO) in 2015 and 2014 (left site) and soil volumetric water content (SVWC) of all plots for 2015 and 2014 (right site). Standard deviations are in brackets. Significance codes: ‘***’: $p < 0.001$; ‘**’: $p < 0.01$; ‘*’: $p < 0.05$; ‘.’: $p < 0.1$.

	Dependent variable:			
	Amplitude			
	2015	2014	2015	2014
Intercept	43.38**	34.50***	33.03***	46.51***
	(10.83)	*(4.80)*	*(6.8)*	*(4.4)*
Precipitiation	0.05	-0.29***		
	(0.11)	*(0.07)*		
SVWC			44.72**	*-50.25****
			(15.5)	*(11.8)*
Observations	8299	6805	2208	1935

V. Discussion

The present thesis highlights drought stress reactions of spruce and beech in intra- and interspecific neighborhoods at different spatial and temporal resolutions. Mixtures of tree species are of great interest due to the possibility to stabilize ecosystem functions or services especially under drought stress. Traditionally, drought stress reactions were observed via increment cores and altered growth patterns over years and decades under different site conditions and for a variety of species. An additional and more novel method is to investigate the growth patterns and tree water relations via electronic dendrometers with the opportunity to determine drought stress reactions at a high temporal resolution. This method reveals short- and long-term reactions on a species-specific and mixture-specific level.

Drought Stress Reactions along the Precipitation Gradient

Along the precipitation gradient, species- and mixture-specific drought stress reactions were observed via tree ring analyses (Schäfer et al. 2017). In this study, tree ring growth and the ^{13}C discrimination under different moisture conditions three years before and after the drought year 2003 were investigated. The $\Delta^{13}C$ of beech trees was higher than that of spruce trees, which suggests a higher internal CO_2 concentration (c_i) of beech trees. The higher c_i results from a higher stomatal conductance (Leavitt 2010; Levesque et al. 2013). Especially under drought stress, the stomatal control of transpiration is crucial for plant survival and tree ring growth. Klein (2014) described the different water management strategies of various tree species on the basis of stomatal conductance and leaf water potentials and detected a higher stomatal conductance and lower leaf water potential for beech trees than for spruce trees under drought. These specific characteristics of beech trees are related for example to the deeper rooting system of beech trees and the possibility to reach additional water reserves in deeper soil layers (Bolte and Villanueva 2006). They keep on transpiring and growing during drought events until water reserves are depleted. Thus, they have a lesser or no reduction in growth (Rötzer et al. 2017), but risk morphological changes and the loss of leafs or fine roots (Meier and Leuschner 2008). On the other hand, spruces reduce the stomatal conductance and thus growth and water consumption in an early stage of drought stress. This water management strategy can prevent against impairment, especially during drought events. The different water management strategies to cope with drought stress are visible along the precipitation gradient. The resistance of spruce trees related to the BAI and $\Delta^{13}C$ was lower than that of beech trees on dry sites. For beech trees, the resistance of BAI and $\Delta^{13}C$ and resilience of $\Delta^{13}C$ increased with increasing soil moisture. Zeide (1985) and Pretzsch et al. (2013) concluded that at sites with a high water supply, beech trees avoid a strong reduction in growth while a drought event happened. This trait arises with increasing moisture and nutrient supply.

Mixture-specific differences under drought stress along stress gradients are described in various studies (Dieler and Pretzsch 2013; Meier and Leuschner 2008; Pretzsch et al. 2010; Thurm and Pretzsch 2016). A well-known conceptual model to describe facilitation and competition along ecological gradients is the stress-gradient hypothesis from Callaway and Walker (1997). The stress-gradient hypothesis predicts that facilitation of mixture dominates on poor sites rather than rich sites. In this study, the stress-gradient hypothesis could not be fully confirmed. Differences in stand composition were only found in the $\Delta^{13}C$ analysis. Beech trees revealed a higher resistance and resilience in mixture with spruce on moist sites under drought, whereas on dry sites beech trees in intraspecific environments showed significantly higher resistance and resilience ($\Delta^{13}C$) (Fig. 13 and Tab. 4). In contrast, $\Delta^{13}C$ of spruce trees indicated a higher resilience at dry sites in mixture with beech trees and a lower resilience in mixture at moist sites. The mixture-specific resilience of spruces along the gradient showed a weak relationship ($p < 0.1$), but a significantly higher intercept ($p < 0.001$) for $\Delta^{13}C$ of spruce trees in mixture was found.

That beech trees profit from mixture of spruces more on moist sites than on dry sites could be explained by the low self-tolerances of beech trees on fertile sites (Pretzsch et al. 2010; Zeide 1985). On stands with high competitive intraspecific beech trees, e.g. moist and fertile sites, a mono-layered structure dominates and admixtures open and change the canopy space with light gaps for understory trees (Otto 1994). On dry sites, the competition of beech in monocultures (e.g. self-thinning dynamics) is less, with more heterogeneous structures (Pretzsch 2009). In contrast, spruce trees could profit from admixture with beech trees on dry sites, because of the abundant nutrient input from beech litter and the improved decomposition and turnover and accordingly improved water storage. For a general conclusion, more measurements could be done due to the complex mix of environmental factors that affect tree ring growth and $\Delta^{13}C$. Despite this, the improved water relations for spruce trees in mixture and for beech trees in intraspecific neighborhoods under dry conditions and extreme drought could also be observed at the experimental site Kranzberg forest using electronic dendrometers.

Kranzberg Forest – Tree Water Relations under Extreme Drought Conditions

Besides the drought stress consideration on a spatial resolution along the gradient, drought stress investigations were carried out at the Kranzberg forest experimental plots at a high temporal resolution with electronic dendrometers. Electronic point or band dendrometers have been used since the 1970s (Dobbs and Scott 1971; Klepper et al. 1971; Kozlowski 1972) with the focus on the close link between variations in stem diameter and plant water status. These studies led to further investigations with the focus on drought stress reactions (Brinkmann et al. 2016; Deslauriers et al. 2007; Vieira et al. 2013; Zweifel et al. 2005) and plant-based irrigation scheduling (Goldhamer and Fereres 2001; Ortuño et al. 2006; Ortuño et al. 2010). In context with this thesis, the drought stress related investigations were extended with stem radius variations in a drought-exposed environment and examined the effect of extreme drought on the growth, inner-annual tree water deficit and diurnal stem radius cycles (amplitudes) in intra- and interspecific neighborhoods.

In addition to this study, growth-induced measurements of these experimental setups were also investigated in Rötzer et al. (2017) for the years 2014 and 2015. The stem radius variations in 2014 and 2015 are shown in Fig. 14 for different species, neighborhoods and the drought treatment. Annual diameter increments were significantly higher for spruce trees in 2014 at the control plots. In the year 2015, no significant differences between species were found. In the comparison of control and drought treatment plots, differences were smaller for beech trees compared to spruce trees. At the drought treatment plots, spruce trees grew significantly less than beech trees in the drought year 2015. The higher growth reduction of spruce trees compared to beech trees under drought was also observed in the studies of Pretzsch et al. (2013) and Pretzsch (2005) in the drought years 1976 and 2003. On this basis, spruce trees, as a more isohydric species, showed typical response in growth with a quick stomatal response and a maintained minimum leaf water potential under drought conditions (Goisser et al. 2016). Carbon uptake and thus stem growth declined significantly under the drought conditions of 2015. In contrast, beech trees as an anisohydric species close their stomata slowly under drought events and maintain the process of photosynthesis. On the other hand beech trees have the risk of hydraulic failure and cavitation (McDowell et al. 2008). This fact can also be seen for the beech trees in 2015 with a higher increment than in 2014 despite the drought. The stem radius growth differences between inter- and intraspecific neighborhoods were small and not significant (Rötzer et al. 2017).

The species-specific differences were also visible in the ectomycorrhizal (ECM) fungal community composition and functions and is described for the experimental trees in Kranzberg forest in Nickel et al. (2017). The contrasting physiological strategies to cope with drought stress were reflected through the differences in diversity of EMC fungal communities from the beech and spruce zones. Beech trees indicated a decline in ECM fungal diversity after the first year of drought treatment in 2014 and then maintained a slightly lower level than on the control plots. In contrast, ECM fungal diversity of spruces did not reveal a change in the first drought year, but declined dramatically after the second year (2015). Tree mixing had an overall positive effect on the ECM fungal community diversity of both tree species after the third year (2016) of drought treatment. In both species, ectomycorrhizae with long rhizomorphs increased under drought, which indicates long-distance water transport (Nickel et al. 2017).

Link between Tree Water Deficit and Leaf Water Potential in different tree compartments

For the determination of differences in tree water relations in intra- and interspecific neighborhoods, the overall relationship of the TWD and leaf water potentials was tested. For the comparison we used the minimum and maximum of the TWD (TWD_{min}, TWD_{max}) and the water potential at midday (Ψ_m) and predawn (Ψ_p)) respectively. A significant positive relationship of the TWD and leaf water potentials could be detected for all measured tree compartments (H50, BH, root) (Schäfer et al. major revision). This suggests that the TWD is a good predictor of the water status for both tree species and is very useful for drought stress considerations. Also the daily amplitude of TWD and Ψ are a useful tool to detect missing soil water stocks.

This relationship was also found for example in Cohen et al. (2001), Goldhamer and Fereres (2001), Drew et al. (2011), Ehrenberger et al. (2012) and Brinkmann et al. (2016) along different species and reveal the connection with the transpiration amount, which is influenced by the species-specific stomatal morphology, stomatal activity and root characteristics (Buckley 2005; De Schepper and Steppe 2010; Whitehead 1998). The stomatal behavior and thus tree water status are highly dependent on the VPD (Ehrenberger et al. 2012; Köcher et al. 2012).

The data showed a diffusion within the species despite the significant relationship of TWD and leaf water potentials, which could be explained through the tree individual, e.g. with different diameters and tree ages. The different individual trees with varying phloem thicknesses should be taken into account for the consideration of the tree water status predicated on dendrometer-based data. Moreover, the method of Zweifel et al. (2016) supposes no growth during the stem contraction phase, an assumption which could lead to a bias of 1-5% of the total annual growth (1% in beech trees and 5% in spruce trees) (Zweifel et al. 2016).

From the tree height H50 to the root, differences in heights of the TWD could be found. The TWD was higher in H50 than in BH and the roots. An explanation of this higher water use of the stem storage tissues near the crown could be the near position to the crown and thus the transpiration. Zweifel and Häsler (2001) determined temporal and spatial patterns of stem radius variations of Norway spruces and they found similar but not identical stem radius fluctuations at different tree heights (6, 10, 14, 18 m aboveground and on roots). Furthermore, they found a time lag between the different tree heights and the highest TWD in the upper stem part within the crown, similar to the present study. Hinckley et al. (1978) illustrated that the water storages near the crown can be reached faster than water storages from the soil. The water movement of the storage tissue in the bark is therefore higher in the vicinity of the crown than in the roots. Investigations of the time lag between the different tree compartments were not carried out and could be an option for further studies.

Stem and Root Growth Allometry and TWD

The considerations of stem radius variations in different tree heights allowed analyses of the growth allometry and differences of the TWD along the stem and under drought. It could be found that more radial growth was invested in the upper stem (H50) at the beginning of the growing season. In the further course of the year, more growth was invested in the lower stem (BH). The seasonal distribution of the growth hormone auxin might be an explanation of this growth pattern. The hormone auxin will produced in spring in the apical meristem and then transported down to the stem of the tree and the growth increases in the lower stem (Kozlowski 1962; Speer 2013). Also under drought, stem radius growth was favored in the upper stem than in the lower stem part. Mette et al. (2015) and Sterba (1981) stated out that tree ring growth of the lower stem decreased in comparison to the upper stem under drought conditions. A further explanation for an early height growth is the competition for light resources.

Drought stress shifted stem radius growth more to the roots, this is in accordance of the optimal partitioning theory of McCarthy and Enquist (2007). The optimal partitioning theory illustrated that the limiting of a resource leads to a promotion of growth of the plant organ that receives this resource, as the roots. The results of the present study support this theory and is consistent with other studies (McConnaughay and Coleman 1999; Nikolova et al. 2011; Thurm et al. 2016b). The TWDmin endorsed this results with a higher TWDmin in the roots and thus missing soil water stocks. The tree water deficit was less pronounced for beech trees than for spruce trees. It also showed the higher resistance of beech trees to drought (Ammer et al. 2008; Brinkmann et al. 2016). The TWD was higher in the tree compartment, when the growth was reduced. Thus the pattern of growth match well with the pattern of TWD at the three different tree positions.

At the consideration of intra- and interspecific neighborhoods, no clear results could be found. The BH-root analysis of interspecific spruces showed a higher stem radius growth in the roots than intraspecific spruce trees under drought. In contrast, the TWDmin was lesser in interspecific neighborhood under drought, therefore spruce trees could be facilitated in interspecific neighborhood in terms of TWD under drought, but not for stem radius growth. On the contrary beech trees profit more from an intraspecific neighborhood. Pretzsch et al. (2010) also described that intraspecific beeches profit most at dry conditions. Overall, the tree is influenced by several environmental conditions alongside TWDmin and this could cause this growth pattern in intra- and interspecific neighborhoods.

Tree Water Deficit on an Annual and Daily Scale

The greater decrease in the TWD for spruces under dry conditions is also observable on a daily scale when considering the mean monthly daily amplitudes of the shrinking and swelling stem in the years 2014 and 2015. In article III (Schäfer et al. 2018), the daily amplitudes of beech and spruce trees at the drought treatment and control plots are illustrated via a GAMM. Drought treatment plots revealed a higher amplitude for spruce and beech trees, except spruces under extreme drought conditions and exhaust soil water reserves. The amplitude began to shrink with missing water from the soil and reduced stomatal conductance. At the drought treatment plots, more water reserves were used from the living tissues of the stem. Thus, trees at the drought treatment plots reveal a higher daily tree water deficit. Water flows from the living cells to the xylem conduits when the xylem water potential is reduced and leaf transpiration exceeds root water uptake (Sevanto et al. 2011; Steppe et al. 2012). The cell turgor follows the same reduced trend as stem water potential and the stem shrinks (Steppe et al. 2015). However, in very dry periods, soil and stem water potentials are lower and water storage pools in the stem are not fully replenished overnight. This leads to a more pronounced stem shrinkage during the day and lower amplitudes (Steppe et al. 2015). The amplitudes of spruce trees in the summer months of 2015 showed this pattern with shrinking amplitudes from July to September at the drought treatment plots. The year 2015 was a very dry year with high temperatures compared to the years 2014 and 2016 (Fig. 15). In the summer months of 2015, the maximum daily temperatures reached 35.8°C and the mean daily temperature was 26°C. The soil volumetric water content (SVWC) of the year 2015 (Fig. 16) shows a clearly lower soil water content in the summer months than in 2014 and 2016. The years 2014 and 2016 had more humid summer months without any long drought periods.

In the present work, the mean daily amplitudes of every month are displayed for beech trees (Fig. 17, a-c) and spruce trees (Fig. 18, a-c) in intra- and interspecific environments at the control and drought treatment plots. The results of Schäfer et al. (2018) were extended with the observations of the year 2016. For beech trees, significant differences between control and drought treatment plots are visible in the summer months, except the very dry months of 2015, where amplitudes of the control and drought treatment were similar due to the dry conditions on the treatment as well as control plots. Differences in intra- and interspecific neighborhoods are only visible after three years of the drying experiment. Beech trees had significantly higher daily amplitudes in the interspecific environment than in the intraspecific in the year 2016. More water from the storage tissue was used for transpiration in the interspecific neighborhood and the daily tree water deficit increased. Zeide (1985) described positive effects of mixed beech trees with other species due to competitive reduction through the low self-tolerance of beech compared with other species. In contrast, Pretzsch (2009) detected lower intraspecific competition and self-thinning dynamics under dry and poor conditions through more heterogeneous structures in monospecific stands on dry sites. The competitive release caused by mixture with spruce was therefore lower after three years of such dry conditions.

In contrast, spruce trees showed no significant differences in control and drought treatment plots in the first year of soil drying, but in the second year, the differences were more pronounced and acute than for beech trees. At a high stage of drought in the year 2015, the amplitudes of the drought treatment shrank due to not fully replenished living tissues overnight, as mentioned above. The year 2016 was a more humid year similar to 2014 and the drought treatment showed higher amplitudes than the control plots in the spring and summer months.

King et al. (2013) found similar results for the species spruce (*Picea abies*) and larch (*Larix decidua*) in the Central Swiss Alps along a gradient. Amplitudes were one ninth smaller on rainy days and approximately 40% larger when the daily temperatures were between 15 and 20°C. Furthermore, King et al. (2013) assumed that the daily amplitudes of spruce trees began to shrink with increasing drought. Spruces maintained similar amplitudes up to 5-6 days following the last rain event before a 40% decrease of amplitudes after 9-10 days.

Beech trees revealed a more constant amplitude at different stages of drought, but with a higher amplitude at the drought treatment plots. Van der Maaten et al. (2013) determined daily stem radius variations of beech trees located at opposing north-east and south-west exposed slopes of a valley in Germany and found a high synchronicity in the daily weather response, despite large differences in site conditions. Therefore, beech trees revealed a high flexibility under different environmental conditions compared to spruce trees.

These results are comparable with the ECM fungal community diversity in Kranzberg forest (Nickel et al. 2017), where beech exhibit a faster and spruce a later but stronger decline. The daily amplitudes of beech showed significant differences of control and drought treatment in the first year with a higher tree water deficit under the drought treatment, whereas spruce trees showed significant differences as recently as in the second year of drought treatment with a higher tree water deficit and a shrinking amplitude under the drought treatment.

Goisser et al. (2016) also found that spruces operate at higher intrinsic water-use efficiencies (WUEi) than beech within the experimental setup of Kranzberg forest. However, in midsummer 2013 a drought-related reduction of stomata conductance resulted in decreased WUEi of spruces. This stomata closure under high insolation increases temperature (Lin et al. 2012), photo-oxidative stress (Foyer et al. 1994) and photoinhibition (Sage and Kubien 2007) and reduces WUEi of photosynthesis under drought, which explained the high susceptibility of spruces under dry conditions.

The coherences of the inner-annual tree water deficit (TWD) and the tree water deficit at a daily scale (daily amplitudes) are illustrated in Fig. 19. Significant differences of spruces were found in the year 2015 with a higher TWD for trees in intraspecific neighborhoods at all stages of drought stress. The trees used more stem water at different stages of drought (dry control plots in 2015 vs. drought treatment plots). Such response reveals a benefit of spruce trees in interspecific environments. Compared with the daily amplitudes of the year 2015 in the months June and July, the higher amplitudes of intraspecific spruces are also visible (Fig. 19, right side). At the drought treatment plots, the tree water deficit of spruces increased with high aridity and the daily amplitudes began to shrink. The different structural advantages such as different root systems and crown architectures of mixed isohydric spruce with anisohydric beech support the soil water availability and increasing light availability (Dieler and Pretzsch 2013; Matyssek et al. 2012; Pretzsch et al. 2012). The soil water content was improved for spruces in mixture (Fig. 16) during the summer drought of 2015 (e.g. by hydraulic lift). In addition, the different crown structures of spruce and beech could also be a benefit of mixture due to a higher water use efficiency at the leaf scale as a result of an increasing photosynthetic capacity of the canopy (Forrester et al. 2010).

Influence of Climate

The influence of meteorological drivers on the TWD as atmospheric vapor pressure deficit (VPD), temperature, precipitation and the soil volumetric water content (SVWC) was tested. The daily TWD of both species are strongly dependent on VPD, temperature, precipitation and the soil moisture (Paper III, Schäfer et al. (2018), table A1 and A2). Different studies of stem radius variations dependent on climate variables have found similar results (Brinkmann et al. 2016; King et al. 2013; Köcher et al. 2012; Ortuño et al. 2006; Van der Maaten et al. 2013; Zweifel et al. 2005). Dependent on the season, the amplitude increases with increasing temperature and VPD because of the increasing transpiration processes (Jarvis and McNaughton 1986). King et al. (2013) also found the highest amplitudes in the summer months with the highest temperatures and greater amounts of sunshine. The increased transpiration leads to a higher water requirement and due to time lags with the root system, the higher demand was met with water from the storage tissue in the stem. At a high level of drought stress and an absence of water in the storage tissue, the stomata close for avoidance of drought-induced hydraulic failure, leading to carbon starvation (McDowell et al. 2008; Zweifel and Häsler 2001). This pattern could be observed for spruces under the drought treatment from June to September 2015. The daily amplitude decreased because of exhaust soil water reserves. This can be connected with the results of the increment in 2015. Spruce trees had a significantly lower increment in 2015 than in 2014 at the drought treatment as well as at the control plots.

The dependencies of daily amplitudes on maximum temperature and soil water content of both species are shown in Fig. 20. The daily amplitude increases with rising temperatures and decreasing soil water content. The only exception were spruce trees in the intraspecific neighborhood with the detected shrinking amplitude with decreasing soil water content from

0.21 m^3 m^{-3}. On rainy days and with a high soil moisture, the amplitude is also smaller and the storage tissue of the stem is fully replenished of water from the soil. Daily stem water status is thus highly temperature and moisture dependent and can have an influence on the annual increment.

VI. Conclusions and Prospects

Conclusions for Forest Science

Studies of forests under climatic warming have shown both positive and negative effects on forests. Positive effects might be e.g. higher growth rates from increasing CO_2 in the atmosphere, longer growing seasons and increased water use efficiency. In contrast, increasing temperatures and long-lasting drought events might lead to higher stress and reduced growth, increasing susceptibility to insects and pathogens and thus tree mortality. Uncertainties remain in modeling, how these and other relevant factors will influence the risk of future tree vigor and mortality.

Tree physiology is complex in its response to climate change and is species-, species-mixture- and site-specific. Emergence of different species combinations represents an early selection mechanism of evolution. Their results are in line with the so-called hologenome theory. This evolutionary theory assumes that natural selection is influenced by changes in the hologenome. Anthropogenic interventions have changed the natural occurrence of species combinations and increasing drought could be critical. Thus, consideration on different spatial and temporal resolutions of the different species mixtures is crucial to maintain the forest ecosystems and services under a changing climate. This thesis is a contribution to determining the reaction of mixed spruce and beech trees, as the most common in Central Europe, to dry conditions and extreme drought.

Results revealed species-specific water management strategies, with spruce as a more isohydric and beech as a more anisohydric tree species. Spruce trees reacted more sensitively to continuing drought than beech trees. Beech trees continued their functions despite the harsh conditions. Due to the different water management strategies and tree morphologies of a conifer and deciduous tree species, spruce and beech are presented as a complementary species combination. This thesis highlights a suggested mixture of spruce with beech under dry conditions and rising temperatures due to a facilitated water status of spruce trees, whereas for beech no benefit could be found. The stabilizing effect of mixed spruce with beech seems to be an advantage on sites that will no longer be suitable in the future for a monospecific environment.

The effect of different site conditions was considered along a precipitation gradient. A well-known conceptual model to describe facilitation and competition along gradients with varying moisture conditions is the stress gradient hypothesis. In this study mixtures of beech with spruce were not more productive on dry sites than in monospecific stands, how it is predicted from the stress-gradient-hypothesis. This could be explained through the dependency on covariates such as limiting resources, species characteristics and environmental factors. All these factors should be including at the future selection of stress gradients.

Drought stress reactions are difficult to detect in increment cores due to the high dependency on the timing of drought events and can often only be observed in the following year. Besides, there are various factors which influence tree growth (e.g. nutrient availability and the duration of the growing season). Measurements via electronic dendrometers allowed drought stress considerations on a high temporal resolution and reveal short-term reactions on drought with the method of TWD. The TWD seems to be a good indicator for drought stress reaction, due to their relationship with leaf water potentials. Furthermore, measurements of the tree water status via dendrometers are easy to record compared to expensive and circuitous stem or leaf water potential measurements.

The TWD refined the effect of tree mixture, which were not or less visible in the growth reaction. Based on our investigation, we recommended to combine TWD with measurement of weather conditions or soil water content. This is necessary to interpret the pattern in TWD. With both parameter, it is possible to describe a decreasing TWD as a shift of the individual tree to a critical water stress level.

Conclusion for Forest Practice

Spruce is the major timber tree species in Central and Northern Europe. Due to its good growth performance, it was often cultivated in large-scale pure stands, as well as far beyond its ecological niche. The investigated precipitation gradient covers a very wide climatic area. It extends from the higher elevations (Traunstein), where spruce with beech trees naturally occur, to the lower and drier areas (Würzburg), where spruce trees not would naturally occur. However, the growth reduction in mixture with beech was lesser on dry sites than on moist sites. This adaptability clarifies, that choosing the accurate mixture is important for spruce trees.

The main reason for the mortality of spruce trees is the damage caused by the bark beetle. This is a challenge particularly on dry sites and will probably increase in future due to the prolonged vegetation periods. Thus, the choice of a mixed stock with increasing dryness is an advantage to build a buffer against drought stress for the future.

Based on the roofing experiment in the Kranzberg Forest, we revealed that the direct neighborhood of spruce with beech has a positive effect on the water supply of spruce trees. In order to obtain the mixing effect, it is necessary to aim a possible intensive mixture in old stocks by the forestry. The beech responded less or not to drought stress.

In order to preserve the climate resistance of pure spruce stands, the reduction of the stand density would be another possibility. This alternative is also used by some forest companies. The establishment of mixed stands is seen as a better option as it preserves stand performance and reducing drought risk and calamity risk.

Perspective

The present thesis provides new knowledge of drought stress reactions of trees along a stress gradient and under heavy drought at the rainfall exclusion experiment, but more knowledge is needed for a general conclusion. In the next paragraphs, several suggestions for future research will be presented.

The investigations of TWD and zero growth with the electronic dendrometers gives new insights in tree water management strategies under drought on a very high timely resolution which cannot found with standard yield growth measurements. The results of the dendrometer measurements showed that the installation of dendrometers is also meaningful on other relevant mixtures. Especially mixtures which are good examined with classical yield measurement methods should stay in focus like Norway spruce and European beech, Scots pine and European beech, Douglas-fir and beech or sessile oak and beech. This would enable a better comparison of long-term mixing effects which were detected by classical yield measurement methods and the short-term responses of the trees measured by dendrometers.

Interesting insights about the resource allocation of trees under drought within the growing period were found in the present study. These dendrometer measurements at different tree compartments should be extended for other species. Very little is known about this relationship. The investigations should be examined first without the factor mixture for a common statement. The stand density should be also considered due to its influence on the height and stem and root diameter growth. In addition, it is important to measure species with a high amount of experimental trees. The use of fix measurement heights (1.3 m, 3 m, 6 m, etc.) and the installation of dendrometers at several coarse roots of a tree should also improve the results.

Several findings of this thesis could only be determined due to the unique experimental setup of the roof experiment. The rainfall exclusion construction was a very expensive setup. Nevertheless, the results revealed that it is crucial to analyze climatic warming effects under controlled conditions. These controllable moisture conditions allow the modeling and prediction of various climatic conditions that could be caused by climate change. The climatic conditions at every extreme drought year were different. For example, the two extreme drought years 2003 and 2015 differ in the temperature course at the growing period, and also the growing conditions one year before and after an extreme event mainly influence the resilience potential of the trees. This could be proved at the gradient study in the present thesis. Every extreme event is unique and also the intensity varies above spatial gradients. In this context, considerations could also be given to the resilience of the trees after the extreme drought experiment and should be repeated at different sites and for trees with different age and proveniences. Also the inclusion of an irrigated plot next to the control and drought treatment plot could be considered for a gradient from dry to moist conditions. This could help to find suitable tree species mixtures to revive tree vitality and to reduce tree mortality and high management costs.

VII. References

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Article I

forests

Article

Drought Stress Reaction of Growth and $\Delta^{13}C$ in Tree Rings of European Beech and Norway Spruce in Monospecific Versus Mixed Stands Along a Precipitation Gradient

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Abstract: Tree rings include retrospective information about the relationship between climate and growth, making it possible to predict growth reaction under changing climate. Previous studies examined species-specific reactions under different environmental conditions from the perspective of tree ring growth and ^{13}C discrimination ($\Delta^{13}C$). This approach is extended to monospecific versus mixed stands in the present paper. We investigated the resistance and resilience of Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) in response to the drought event in 2003. The study was carried out along a precipitation gradient in southern Germany. Responses of basal area increment (BAI) and $\Delta^{13}C$ were correlated with a Climate-Vegetation-Productivity-Index (CVPI). The species showed different strategies for coping with drought stress. During the summer drought of 2003, the BAI of spruces reveal a lower resistance to drought on dry sites than those of beech. For beech, we found an increasing resistance in BAI and $\Delta^{13}C$ from dry to moist sites. In mixture with spruce, beech had higher resistance and resilience for $\Delta^{13}C$ with increasing site moisture. The combination of $\Delta^{13}C$ and tree ring growth proxies improves our knowledge of species-specific and mixture-specific reactions to drought for sites with different moisture conditions.

Keywords: mixed forest; resistance; carbon isotope; climate change; resilience; tree rings

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1. Introduction

Forests provide fundamental ecosystem services and play a key role in the global carbon and hydrological cycle. For the maintenance of ecosystem services under a changing climate, ecosystems with high resilience and resistance are of great importance. Resilience and resistance depend on the ability of the species to maintain fundamental ecosystem processes under disturbances such as drought events. For the extreme drought event in 2003 in Europe, Cias et al. [1] described the consequences for forest ecosystems with up to 30% reduction in gross primary productivity caused by rainfall deficits and extreme summer heat.

Drought episodes affect physiological processes in trees such as photosynthesis, transpiration, and carbon allocation, which can lead to reduced growth rates and a higher tree susceptibility. The consideration of different tree species is thus crucial due to differences in physiological and anatomical adjustments to cope with drought events. Therefore, it is important to predict responses of forest tree species to changing environmental conditions in order to understand if silvicultural conversion (e.g., mixtures) are meaningful [2]. Two important indices for depicting the effect of climate change are $\delta^{13}C$ in tree rings and the radial stem growth of trees [3–5]. Discrimination against ^{13}C ($\Delta^{13}C$) can be used as an indicator for changes in stomatal conductance and photosynthetic rates and thus reflect changes in soil water content and evaporative demand of trees, even though coupling between leaf physiological processes and incorporated stem cellulose may be dampened [6]. During drought stress, the transpiration rate is reduced by stomatal conductance [7]. In parallel, reduced stomatal aperture reduces the internal CO_2 concentration (C_i) and thus photosynthetic discrimination against $^{13}CO_2$ at the leaf level. Hence $\Delta^{13}C$ in tree rings decreases [8]. Another indicator of environmental changes is the reduction in radial growth due to limited water availability. In each particular year, newly formed wood cells reflect the environmental conditions for tree growth. Andreu et al. [9] examined tree-ring widths and $\delta^{13}C$ chronologies from an Iberian pine forest and concluded that $\delta^{13}C$ reveals drought stress signals more precisely than radial stem growth. However, the relationship between tree rings and $\Delta^{13}C$ does not only represent physical archives but also biological processes such as the competition for water and light. Studies by Thurm et al. [10], Pretzsch et al. [11], and Lebourgeois et al. [12] provide evidence based on radial stem growth that species mixture may reduce the climate sensitivity of the species. It is generally accepted that mixed forest stands can improve soil properties [13,14], biodiversity [15,16], and productivity [17,18] at stand level. Complementary resource use allows significant positive effects on yield in mixed compared to monospecific stands [19,20]. Certainly, stands with species mixture are not always more productive than stands with monocultures, as facilitation effects among species are dependent on site conditions, age of the stands, and mixing structure [17,21,22].

The relationship between tree ring growth and $\Delta^{13}C$ under contrasting levels of competition (e.g., intra- and interspecific competition) has rarely been explored [5,23]. Tree ring growth and carbon isotopes can provide information about competition-induced changes in the water balance of the tree species explored. The aim of this study is to interpret the response of spruce and beech to the drought in 2003 in terms of tree ring growth and $\Delta^{13}C$. In this regard, spruces are found to follow a more isohydric strategy and to reduce the stomatal conductance at an early stage of drought stress. Beech trees, on the other hand, follow a more anisohydric strategy and indicate a later stomatal closure when water is limited [24,25].

Furthermore, the focus is placed on how growth in monospecific or mixed stands along a precipitation gradient modifies the impact of changing climate. We applied the indices developed by Lloret et al. [26] to determine resistance and resilience of beech and spruce trees. The following hypotheses are addressed: (1) During the summer drought of 2003, resistance and resilience of tree ring growth and $\Delta^{13}C$ decreased from moist to dry sites along the gradient, in which isohydric spruce trees reacted more sensitively than anisohydric beech trees; (2) Under dry conditions, the growth of beech benefits from mixture with spruce due to increased water availability.

2. Materials and Methods

2.1. Experimental Sites

Four locations in southern Germany were selected to cover a precipitation gradient. The gradient has a northwest–southeast (Arnstein, Parsberg, Wasserburg, Traunstein) extent, with the locations becoming more humid towards the southeast. The precipitation in the growing season (P_{gr}) (April–September) ranged from 320 mm in Arnstein to 850 mm in Traunstein (Table 1; data: Bavarian State Research Center for Agriculture (LfL) [27]). The sites represent a precipitation gradient from the upper colline to sub-mountainous altitudes. The altitudes range from 330 m in the northwest and 600 m in the southeast of Bavaria. Mean annual temperature for the period 1980–2010 ranged between 8.5 to 9.5 °C, with slightly higher temperatures in the southeast. In the year 2003, an extreme climate anomaly occurred in Europe with high temperatures, particularly in August, and long-lasting drought events. At the investigation plots, the total precipitation in this year was the equivalent of 10 months below the annual average. To calculate resistance and resilience in the drought year 2003, we used values from the years 2000 to 2006, that is three years prior to and post drought.

Table 1. Geography and the annual and growing season (April to September) temperature (T_a, T_{gr}) and precipitation (P_a, P_{gr}) of the sites along the precipitation gradient. CVPI means Climate-Vegetation-Productivity-Index (CVPI) based on the period 1980–2010.

Site	**Latitude (°)**	**Longitude (°)**	**Elevation above the Sea Level (m)**	**Geological Substrate**	T_a **(°C)**	P_a **(mm)**	T_{gr} **(°C)**	P_{gr} **(mm)**	**CVPI**
Arnstein	49.903	9.977	330	limestone (mid Triassic)	9.5	654	13.6	320	280
Parsberg	48.936	11.822	550	limestone (Jurassic)	8.5	713	13.5	400	315
Wasserburg	48.142	12.073	620	moraines from Würm glaciation	8.8	858	13.5	650	464
Traunstein	47.939	12.672	600	moraines from Würm glaciation	9.1	962	13.3	850	412

Table 2 gives an overview of the characteristics of the plots. The comparison of mixed versus monospecific plots is enabled by triplets, represented by two monospecific plots and one mixed plot of European beech (*Fagus sylvatica* [L.]) and Norway spruce (*Picea abies* [L.] Karst). Consequently, 12 plots are included in this study. Monospecific plots comprise approximately 30 trees of the species, whereas mixed plots have 60 to 100 trees, respectively. The triplets are in close proximity to each other and have not recently been thinned.

Table 2. Stand characteristics of the monospecific and mixed stands along the precipitation gradient from the northwest to the southeast of Bavaria.

Site	**Species**	**Mixture**	**Age (years)**	**N (n/ha)**	**HO (m)**	**DO (cm)**	**HG (m)**	**DG (cm)**	**GV ($m^2 \cdot ha^{-1}$)**	**VV ($m^3 \cdot ha^{-1}$)**
Arnstein	spruce	mono	70	484	32.7	41.6	30.4	33.5	42.6	624
	beech	mono	85	1018	26.9	38.4	22.7	21.7	37.5	453
	beech	mixture	77	514	27.3	37.3	23.9	22.1	19.8	249
	spruce	mixture	77	269	31.2	45.0	27.7	31.1	20.4	276
	total	mixture		783					40.2	525
Parsberg	spruce	mono	60	889	30.5	45.5	26.9	28.7	57.6	756
	beech	mono	95	470	32.7	39.6	30.5	30.7	34.8	558
	beech	mixture	90	136	36.3	53.3	33.9	42.2	19.0	298
	spruce	mixture	90	214	32.8	47.3	30.4	33.8	19.3	316
	total	mixture		350					38.3	613
Wasserburg	spruce	mono	50	733	25.1	38.4	22.8	27.9	44.7	498
	beech	mono	55	595	24.4	36.6	22.5	24.7	28.4	328
	beech	mixture	60	208	28.6	40.7	25.4	28.3	13.1	162
	spruce	mixture	60	433	24.6	34.5	22.2	22.3	16.9	192
	total	mixture		641					30.0	354
Traunstein	spruce	mono	50	523	28.6	41.4	26.9	33.0	44.7	579
	beech	mono	65	375	26.5	42.3	24.9	30.8	28.0	367
	beech	mixture	67	143	30.2	41.0	29.1	34.0	13.0	197
	spruce	mixture	67	294	33.8	46.8	31.3	36.0	29.9	445
	total	mixture		437					42.9	643

Age, tree age in years; N, tree number per ha; HO, average height of 100 dominant trees (m); DO, average diameter of 100 dominant trees (cm); HG, height of mean basal area tree (m); DG, diameter of mean basal area tree (cm); GV, basal area ($m^2 \cdot ha^{-1}$); VV, volume (m^3).

The sites were selected on the basis of similar soil characteristics, stand density, and comparable stand age. Soil types of the sites are cambisol, with the exception of Arnstein which has a luvisol soil. In September 2014, in order to determine the characteristics of the soils, four soil cores were taken at each plot and divided into five fractions (organic layer, 0–10 cm, 10–40 cm, 40–80 cm, 80–150 cm) to estimate the plant available soil water at field capacity and the cation exchange capacity (CEC) (Table 3). The CEC was high to very high at Arnstein, Parsberg, and Traunstein and between medium and high at Wasserburg compared to national standards [28]. The two calcareous sites Arnstein and Parsberg compensate for their low soil depth through higher nutrient concentrations. The water storage capacity reflects the gradient and increases from dry to moist sites.

Table 3. Soil characteristics (availability of water and nutrients (cation exchange capacity, CEC)) in the monospecific and mixed stands [29].

Site	Species	Mixture	Exposition	Cation Exchange Capacity (CEC) (kmol·ha^{-1})	Plant Available Soil Water (L·m^{-2})
Arnstein	spruce	mono	south	1072	83
	beech	mono	plain	2931	89
	spruce/beech	mixture	plain	1552	79
Parsberg	spruce	mono	northwest	2060	67
	beech	mono	northwest	1813	67
	spruce/beech	mixture	northwest	2477	80
Wasserburg	spruce	mono	south	920	217
	beech	mono	south	685	215
	spruce/beech	mixture	south	921	250
Traunstein	spruce	mono	west	1604	204
	beech	mono	west	2215	198
	spruce/beech	mixture	north	1975	209

2.2. Sampling Procedure

In order to determine tree growth, a total of 112 trees were sampled, i.e., 28 trees per site. For the analysis of Δ^{13}C, seven trees of each species in the mixed and monospecific stands were used. The number of sampled trees has been shown to be a satisfactory number of replicates for a representative study of isotopes [3,30,31]. For tree ring width measurements, 30 trees at the monospecific stands and 60 to 100 trees, respectively, at the mixed stands were cored. To compare carbon isotope in tree rings and the basal area increment (BAI), we used the same tree individuals. All sample trees were cored in east and north direction to the pith (overall 56 increment cores per site) at 1.30 m stem height, using 5-mm increment borers. The arithmetic means of the annual ring widths from north and east sides are used for the analysis. Dominant trees were selected according to vitality, i.e., stem diameter and height in relation to surrounding trees. The monospecific plot of beech in Traunstein was excluded from the analysis because no suitable stand trees with the same light conditions were found at this site. However, it is still used to illustrate BAI.

2.3. Tree Ring Measurements

Ring widths were measured with digital positiometer (Biritz GmbH, Gerasdorf, Austria) with an accuracy of 0.01 mm. Cross-dating and synchronization of the tree chronologies were carried out with the help of the software platform TSAP-Win (Rinntech, Heidelberg, Germany). The basal area increment (BAI) was used instead of radial increment for detrending and statistics because it better represents tree growth [32]. For the standardization of BAI time series, a double detrending procedure was applied [33]. Using a Hugershoff function [34], age trend and other background noise were eliminated, while still preserving high frequency climate signals in tree ring series. As a second detrending procedure, a cubic spline was used because of the residual growth trends of trees, for instance, thinning [33]. Cubic spline can fit and remove ring width trends that are not linear or do not have a monotonical course. The cubic spline and its wavelength were fixed to 15 years with a frequency response of 0.5 [10].

2.4. Carbon Isotope Analysis

To determine the Δ^{13}C for the reference period of 2000 to 2006, the cores of the sample trees were mechanically fixed on a wooden holder and prepared with a WSL-core-microtome (WSL, Birmensdorf, Switzerland). Individual tree rings of both cores (east and north direction) were ripped with a scalpel under a binocular. The years 2000 to 2002, representing the initial period, were pooled. After drying in the dry oven at a temperature of 60 °C, the tree ring samples (mass > 50 mg) were cut into small pieces and processed into a fine powder in sample tubes using a ball mill (Mixer Mill MM2, Retsch, Haan, Germany). Sample mass was always above 50 mg; thus, contamination from sample tube material appeared negligible [35]. Subsequently, aliquots of 2 mg were weighed into tin capsules. For carbon isotope measurements, the samples were combusted to CO_2 using a Euro EA 3000 Elemental Analyzer (Eurovector S.p.A, Milan, Italy). The measurements of the isotope ratio $^{13}C/^{12}C$ were carried out using an Isoprime 100 isotope ratio mass spectrometer (GV Instruments Ltd., Manchester, UK).

To calculate $\Delta^{13}C$, the long-term changes in the atmospheric $^{13}CO_2$ signal were corrected for: $\Delta^{13}C = (\delta^{13}C_{atmosphere} - \delta^{13}C_{plant})/(1 - \delta^{13}C_{plant}/1000)$ [3]. The Belemnite of PEE-Dee-formation from North-Carolina, USA was used as the standard: $\delta^{13}C$ (‰) = $((R_{sample}/R_{standard}) - 1) \cdot 1000$, with $R = {}^{13}C/{}^{12}C$. The isotopic fractionation enrichment of ^{13}C relative to ^{12}C isotope is described through the simplified equation of Farquhar et al. [36]: $\Delta^{13}C = a + (b - a)\ (c_i/c_a)$. The c_i/c_a indicates the leaf internal to atmospheric CO_2 concentration. The constant a gives the kinetic fractionation of $^{13}CO_2$ during diffusion (4.4‰). The constant b describes the discrimination by CO_2-fixation of the carboxylating enzymes (29‰). Both stomatal conductance and photosynthesis rate determine c_i and thus discrimination of ^{13}C during photosynthesis [8].

2.5. Climatic Site Conditions

To determine the influence of climatic site conditions on $\Delta^{13}C$ and BAI, we calculated the Climate-Vegetation-Productivity-Index (CVPI) defined by Paterson [37] (data: Bavarian State Research Center for Agriculture (LfL) [27]). The CVPI is a climatic index of forest growth. The index has been developed for areas at a global scale, but it can also be very useful for comparing zones located in the same region [38–40]. The CVPI estimates the potential productivity of a forest area based on climatic variables: $CVPI = (T_v \times P \times G \times E)/(T_a \times 12 \times 100)$. Hereby, T_v gives the mean temperature of the warmest month (°C), and T_a is the mean annual range of the temperature between the coldest and warmest month (°C). P is the mean annual precipitation (mm), G is the length of the growing season in months (in the study region from April to September), and E is an evapotranspiration reducer (based on latitude and giving generalized total annual radiation received as a percentage of that at the equator). A high index value indicates high productivity under moister conditions. For our sites, the values ranged from 280 at dry sites to 412 at moist sites (Table 1).

2.6. Data Analysis and Statistics

To compare the trees in view of basal area increment and carbon isotope signatures under drought stress, indices for resistance (RT) and resilience (RS) by Lloret et al. [26] were applied. The indices were calculated on the basis of annual mean values of the BAI and the $\Delta^{13}C$. Our study focused on the drought event of 2003. We used three years before and after the drought year to describe the post-drought and pre-drought situation of BAI and $\Delta^{13}C$. Resistance describes the decline in the year of drought stress compared to the previous year (RT = drought/pre-drought). RT = 1 stands for a complete resistance. Resilience describes the capacity to reach the level present before the drought event (RS = post-drought/pre-drought). RS $\geq$ 1 represents a full recovery or overcompensation.

A linear mixed effect model "*lmer*" (lme4 R package [41] and lmerTest package [42]) was applied. All analyses were performed with the R version 3.2.3 (R Core Team, 2015). We used a linear mixed effect model to verify if RT and RS of tree growth and $\Delta^{13}C$ values depend on the variables site, species, and mixture. To take into account the nesting in the data, plot and site are included as random effects in the models. Species, CVPI, or mixture were used as fixed effects. The fixed effects, species and mixture, were coded as binary variables. Linear mixed effect models have the form:

$$y_{ijk} = a_1 x_{1ijk} + a_2 x_{2ijk} + a_3 x_{3ijk} \ldots\ a_n x_{nijk} + b_{i1} z_{1ij} + b_{i2} z_{2ij} \ldots\ b_{in} z_{nij} + \varepsilon_{ijk}$$

where y_{ijk} describes the outcome variable (in our case RT or RS), a_1 through a_n stand for the fixed effects coefficients and x_1 through x_n represent the fixed effect variables, random effect coefficients b_{i1} through b_{in} with the random effect variables z_{1ij} through z_{nijk}. ε_{ijk} represents the independent and identically distributed random error. The indices I, j, and k stand for site, plot, and tree. To fit the relationship of BAI and Δ^{13}C for RT and RS, we logarithmized RT and RS in the model. The significances of the coefficients were calculated with an F-test with Satterthwaite's approximation [42] from the R-package lmerTest.

Differences amongst the least square means (population means) and confidence intervals for the fixed effect part mixture (monospecific/mixed) for both species of the linear mixed effect model (R package lmerTest [42]) were calculated. This allows a comparison of the performance of both species in different mixtures.

3. Results

3.1. Ring Width Variations and Tree Ring Δ^{13}C Signatures

In monospecific stands, the mean basal area increment (2000–2006) of spruce reached 21 ± 13 cm^2, whereas for beech it was 16 ± 12 cm^2. In mixture, the BAI for spruce was 20 ± 14 cm^2, whereas for beech it reached 17 ± 12 cm^2. The mean Δ^{13}C of spruce in monospecific stands was 17.4 ± 0.2‰ and in mixture, it was 16.9 ± 0.6‰. In general, beech generated higher Δ^{13}C values with 17.8 ± 0.6‰ in monospecific and 18.2 ± 0.7‰ in mixed stands.

Along the gradient, both mean Δ^{13}C and BAI from the period 2000 to 2006 increased from dry to moist sites, in particular for beech Δ^{13}C (Figure 1). The BAI values of beech trees in Parsberg (PAR) and Wasserburg (WAS) were similar. The BAI of spruce at the moist site Traunstein was an exception, with a decreasing value. In terms of the Δ^{13}C of spruce trees, only the difference between Arnstein and Parsberg was significant. The BAI of spruce trees were higher than those of beech trees, whereas beech trees showed a higher discrimination in comparison with spruce trees.

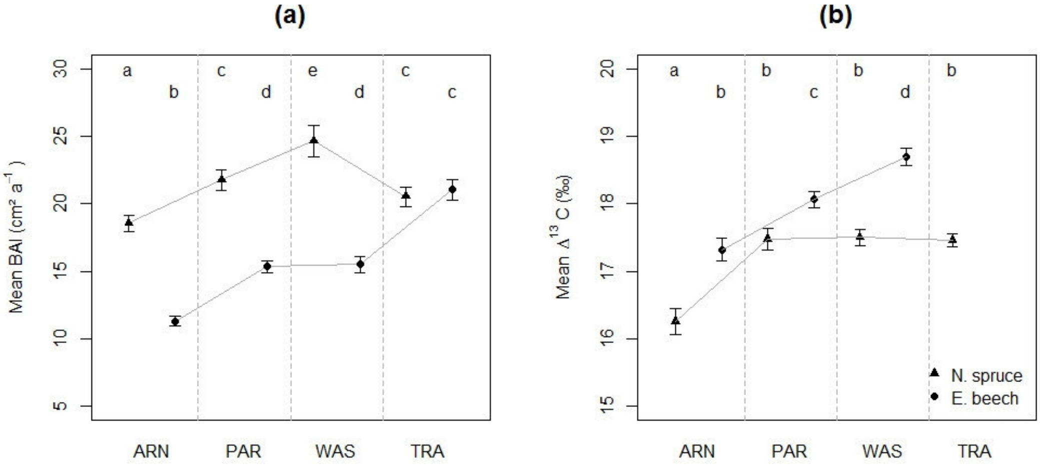

Figure 1. Mean basal area increment (**a**) and Δ^{13}C signatures (**b**) of spruce trees (triangles) and beech trees (circles) from the dry site Arnstein to the moist site Traunstein. The means of the years 2000 to 2006 were used. Significances are represented by the letters a to e, calculated with an ANOVA and Tukey HSD (honest significant difference) test for E. beech (European beech) and N. spruce (Norway spruce). The letters represent the significances for spruce trees (above) and for beech trees (below) ($p < 0.05$). The same letters indicate no significant differences.

The mean basal area increment index (BAII) in Figure 2 shows the detrended data over the reference period (2000–2006). The figure gives an overview of the data of BAII and Δ^{13}C in the period before and after the drought year 2003. The decreased BAII and Δ^{13}C in the year 2003 can be seen in most cases. The drop in 2003 is calculated and evaluated through the results for resistance (RT). For Δ^{13}C, beech trees of the mixed stands reveal a higher discrimination compared to the same species in a monospecific environment. In contrast, spruce trees had a higher discrimination in a monospecific environment.

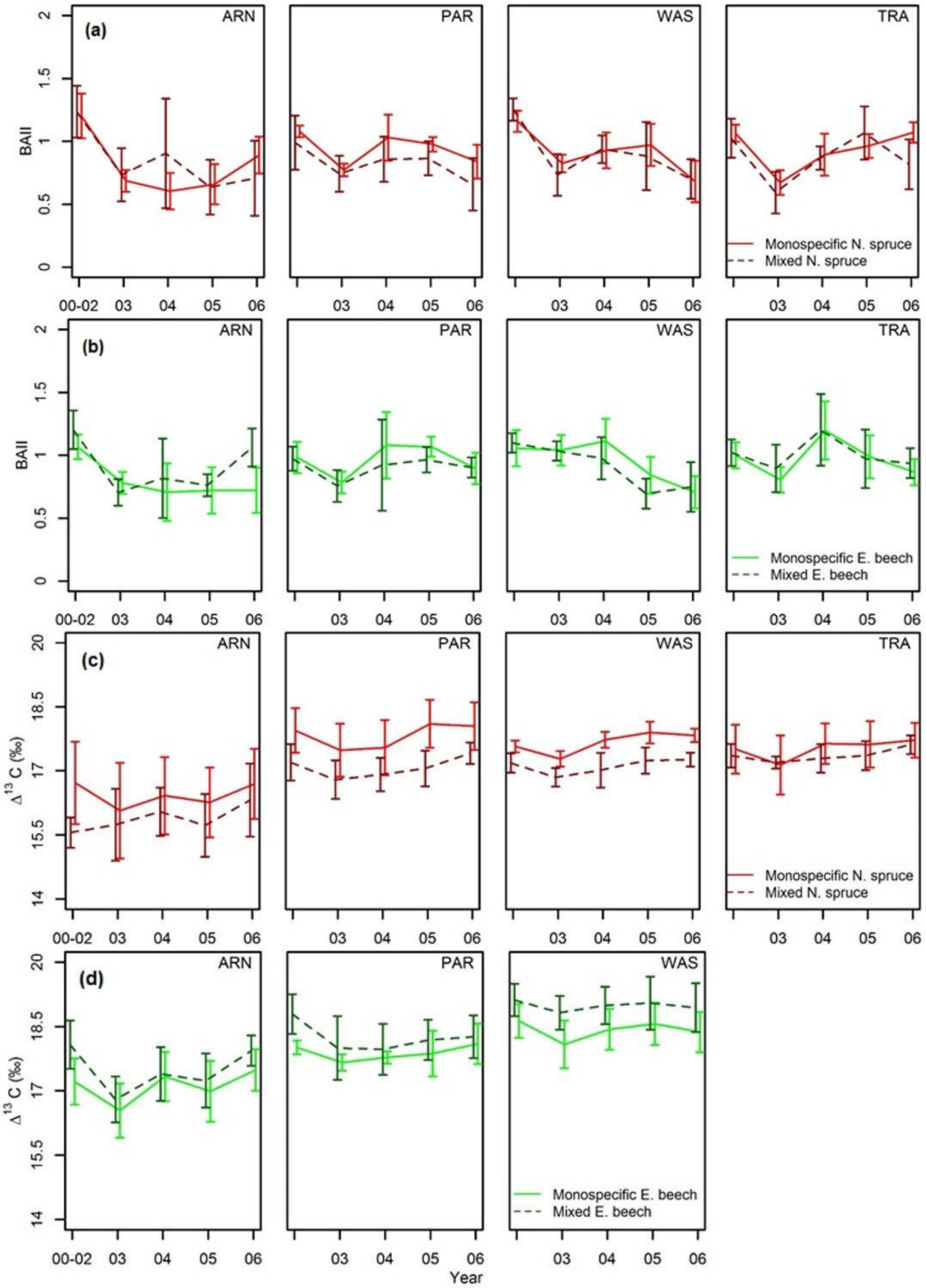

Figure 2. Standardized mean basal area increment (BAII) (**a**,**b**) and mean Δ^{13}C (**c**,**d**) (for the period 2000 to 2006) of spruce and beech in monospecific and mixed neighborhood at the sites Arnstein (ARN), Parsberg (PAR), Wasserburg (WAS), and Traunstein (TRA) with confidence intervals (CI, 95%).

3.2. Species-Specific Differences in Resistance and Resilience

Resistance (RT) and resilience (RS) of the reference period (2000 to 2006) were calculated to analyze the drought stress reaction in the year 2003. The relationship between the RT and RS of Δ^{13}C and BAI in 2003 was chosen to determine whether these two proxies react in the same way under drought conditions (Figure 3, Table 4 Model description (1) and (2)). Resistance indices demonstrated different reactions between the two species. A significant oppositional trend in the relationship between the RT of Δ^{13}C and BAI ($p < 0.01$) for spruce and beech can be seen for the drought year 2003. Because of an absence of linearity, we logarithmized RT and RS in the model. The RT of spruce trees reveals a significant negative relationship between Δ^{13}C and BAI (Table 3). In contrast, beech trees were positively correlated to a significant degree. For both species, the resilience indices of Δ^{13}C and BAI indicated no significant correlation.

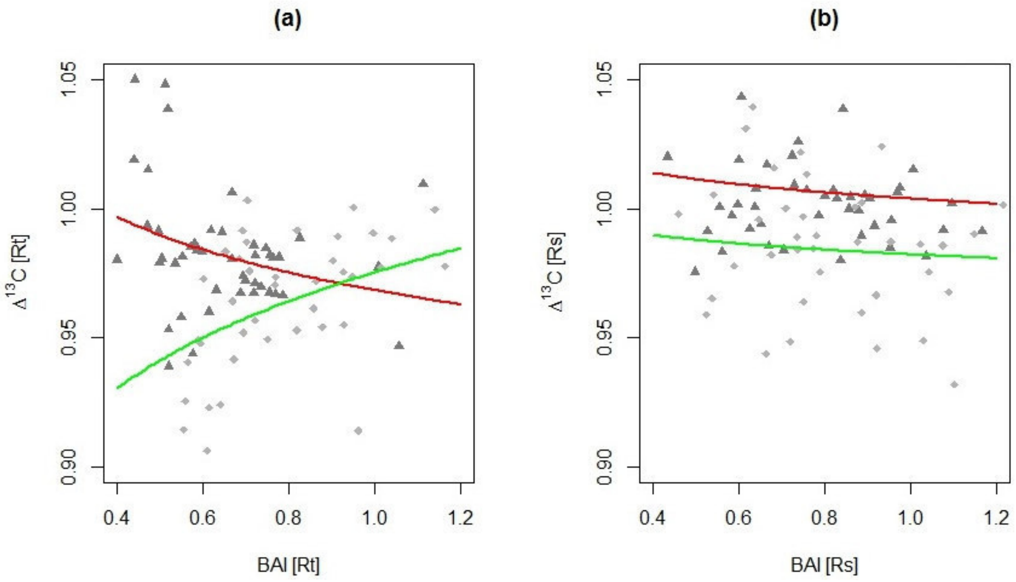

Figure 3. Relationship between the resistance (**a**) and resilience (**b**) of the Δ^{13}C and BAI of spruce and beech trees in the drought year 2003 (lmer with logarithmic transformation of resistance (RT) and resilience (RS) in the model). Differences are significant between the species for the RT ($p < 0.01$ **). Light grey circles represent the values of resistance or resilience in 2003 of beech trees, dark grey triangles represent those of spruce trees.

3.3. Differences in Resistance and Resilience of Monospecific vs. Mixed Stands

To compare species and species mixing (i.e., monospecific vs. mixed stands, group comparison), the means of RT and RS were used. The difference between the means of beech and spruce reveals which species or species mixing had a higher RT or RS (Table 5, differences). The BAI of beech indicates that it has significantly higher RT (difference 0.15) and RS (difference 0.11) than spruce. Values of Δ^{13}C present the opposite trend with spruce having a significantly higher RT (difference 0.02) and RS (difference 0.02) than beech. Regarding mixture, significant differences were found in Δ^{13}C for a higher RT of spruce trees in mixed than in monospecific stands. Beech trees in a monospecific neighborhood also reveal a significantly higher RS (0.02) than in mixed stands.

3.4. Relationship with Climate Variables

To analyze the influence of the climate on RT and RS, the relationships based on the Climate-Vegetation-Productivity-Index (CVPI) were tested (Figure 4, Table 4 model description (3–6)). Spruce and beech trees show significantly different courses along the gradient for BAI and Δ^{13}C RT, with a significantly greater difference on moist sites for RT BAI ($p < 0.001$). The RT of spruce trees'

$\Delta^{13}C$ indicates a significantly greater difference for the species at dry sites and a decrease from dry to moist sites. The resistance of BAI spruce is significantly less than that of beech trees along the gradient. Beech trees indicate a significantly increasing relationship between RT and RS (except BAI RS) with increasing CVPI from dry to moist sites (BAI and $\Delta^{13}C$).

Table 4. Estimates of the linear mixed effect models of resistance and resilience for BAI, $\Delta^{13}C$, and CVPI for beech and spruce trees (n = 86; standard deviations in brackets). Empty cells are not included in the model. Model description (1) and (2) describe results of the relationship between RT and RS of BAI and $\Delta^{13}C$ in Figure 3, (3–6) describe the linear mixed effect models of Figure 4. Signif. codes: '***', 0.001; '**', 0.01; '*', 0.05; '(*)', 0.1.

	Dependent Variables:					
	(1) Log(RT) $\Delta^{13}C$	**(2) Log(RS) $\Delta^{13}C$**	**(3) RT BAI**	**(4) RS BAI**	**(5) RT $\Delta^{13}C$**	**(6) RS $\Delta^{13}C$**
Intercept	−0.02 *** −0.005	−0.018 ** −0.005	0.249 −0.198	0.812 −0.482	0.884 *** −0.029	0.939 *** −0.028
Log(RT) (BAI)	0.052 ** −0.015					
Log(RS) (BAI)		−0.008 −0.013				
CVPI			0.002 (*) −0.001	0.0002 −0.001	0.0002 * −0.0001	0.0001 −0.0001
Species (N. spruce)	−0.007 −0.009	0.022 ** −0.007	0.488 ** −0.17	−0.168 −0.211	0.131 *** −0.029	0.091 *** −0.026
Log(RS):Species (N. spruce)		−0.003 −0.017				
Log(RT):Species (N. spruce)	−0.083 *** −0.022					
CVPI:Species (N. spruce)			−0.002 *** −0.0005	0.0002 −0.001	0.0003 *** −0.0001	−0.0002 * −0.0001

Table 5. Means of RT and RS, differences between means, and significance levels (linear mixed effect model) of $\Delta^{13}C$ and BAI. Species and mixture situation are independent variables. Significance levels: '***', $p < 0.001$; '**', 0.01; '*', 0.05; '(*)', 0.1.

Group Comparison		**Type**	**Variable**	**Group Comparison (Means)**		**Difference**	***p* Value**
1	**2**			**1**	**2**		
E. beech–	N. spruce	BAI	RT	0.80	0.65	0.15	0.00 ***
E. beech Mixed–	E. beech Pure	BAI	RT	0.76	0.84	−0.09	0.09 (*)
N. spruce Mixed–	N. spruce Pure	BAI	RT	0.64	0.67	−0.03	0.60
E. beech–	N. spruce	BAI	RS	0.89	0.78	0.11	0.02 *
E. beech Mixed–	E. beech Pure	BAI	RS	0.86	0.91	−0.05	0.38
N. spruce Mixed–	N. spruce Pure	BAI	RS	0.77	0.79	−0.02	0.74
E. beech–	N. spruce	$\Delta^{13}C$	RT	0.96	0.98	−0.02	0.00 ***
E. beech Mixed–	E. beech Pure	$\Delta^{13}C$	RT	0.96	0.97	−0.01	0.07 (*)
N. spruce Mixed–	N. spruce Pure	$\Delta^{13}C$	RT	0.99	0.97	0.02	0.03 *
E. beech–	N. spruce	$\Delta^{13}C$	RS	0.98	1.00	−0.02	0.00 **
E. beech Mixed–	E. beech Pure	$\Delta^{13}C$	RS	0.98	1.00	−0.02	0.03 *
N. spruce Mixed–	N. spruce Pure	$\Delta^{13}C$	RS	1.01	1.00	0.01	0.49

In general, spruce and beech trees in monospecific stands did not significantly differ from mixed ones in terms of resistance and resilience along the gradient. Significant differences were only found for $\Delta^{13}C$ of beech ($p < 0.01$) (Figures A1 and A2, and Table A1, Appendix A). The RT and RS of beech in mixture were significantly higher on the moist sites for $\Delta^{13}C$ (RT $p < 0.01$, RS $p < 0.05$).

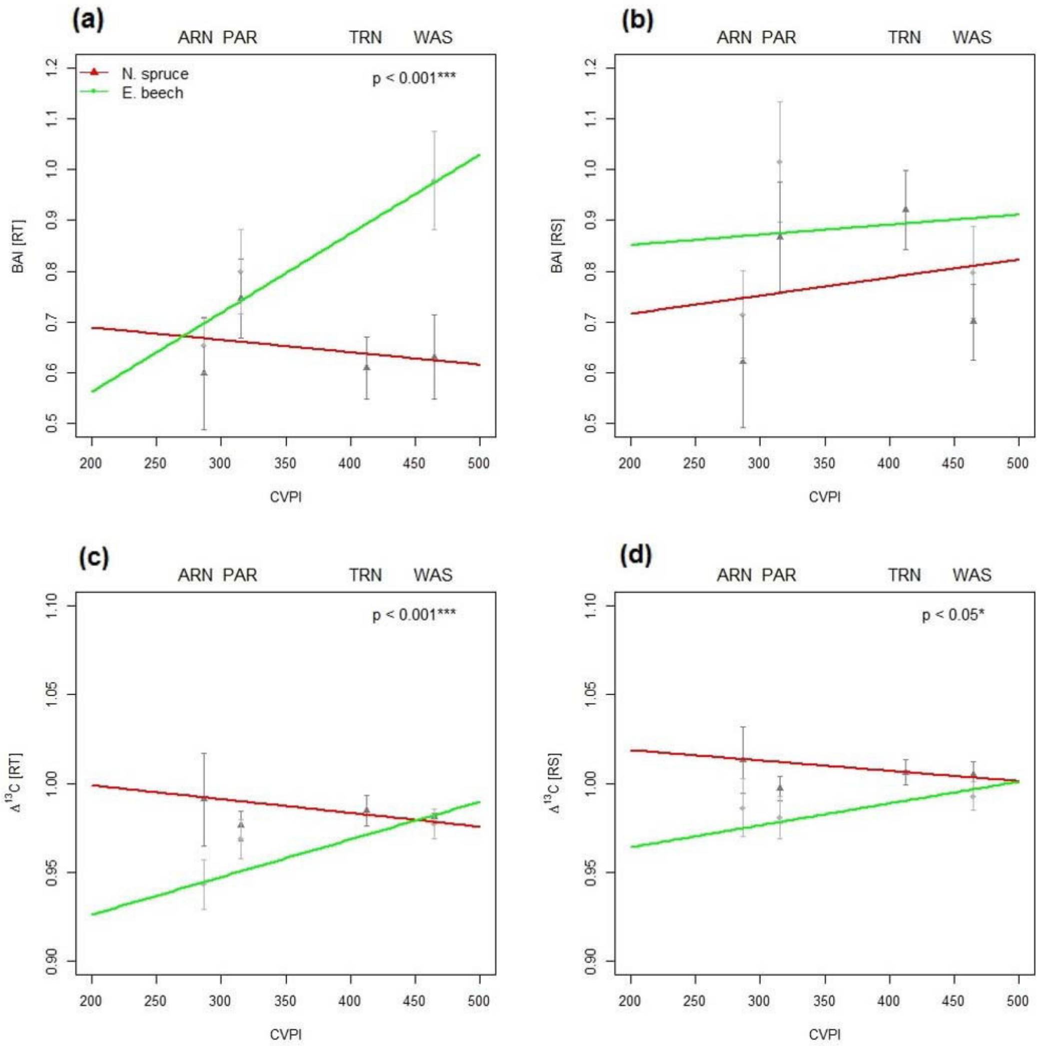

Figure 4. Linear mixed effect model of species and sites relative to the drought period 2003 for the BAI (**a**,**b**) and $\Delta^{13}C$ (**c**,**d**) of beech (green line) and spruce (red line), represented by the CVPI, with means of RT and RS and confidence intervals (CI, 95%). The differences between species along the gradient are significant for BAI RT ($p < 0.001$ ***), $\Delta^{13}C$ RT ($p < 0.001$ ***), and $\Delta^{13}C$ RS ($p < 0.05$ *).

4. Discussion

This study focused on the drought stress reaction in terms of resistance and resilience of spruce and beech trees based on the following hypotheses: (1) During the summer drought of 2003, resistance and resilience of tree ring growth and $\Delta^{13}C$ decreased from moist to dry sites along the gradient, in which isohydric spruce trees reacted more sensitively than anisohydric beech trees; (2) Under dry conditions, the growth of beech benefits from mixture with spruce due to increased water availability.

4.1. Species-Specific Differences of BAI and $\Delta^{13}C$ Signatures in Tree Rings

In view of the present results, the dendrochemical isotope analysis revealed a clearer signal in drought response among site and stand composition than the dendrochronological tree ring analysis. Likewise, Hartl-Meier et al. [4], Mölder et al. [5], Andreu et al. [9], and Saurer et al. [43] found a strong sensitivity of the C isotopic signatures to climate variables such as precipitation for different species. Tree ring width variations may reflect more local factors i.e., site conditions [9]. The ratio of leaf intercellular and ambient CO_2 concentration and, further, the photosynthetic fractionation of carbon isotopes, generally allow the characterization of environmental effects with the use of $\Delta^{13}C$ of newly assimilated organic matter [44]. However, tree ring growth and Δ^{13}C in tree rings relationships are not always straightforward, since several factors may concurrently influence isotope fractionation i.e., species-specific differences [3,6].

The Δ^{13}C of deciduous beech trees was higher than that of evergreen spruce trees. The higher Δ^{13}C of beech reflects a higher c_i, resulting from a higher stomatal conductance and/or a lower photosynthetic rate and hence different intrinsic water use efficiencies (iWUE = net photosynthesis/stomatal conductance) [45–47]. The stomatal control of transpiration is crucial for plant survival and growth performance, especially under drought stress. Klein [25] described contrasting water management strategies (anisohydric or isohydric) of tree species on the basis of the stomatal conductance and the leaf water potential. Following a more anisohydric strategy, beech trees have higher stomatal conductance under drought and lower leaf water potentials than spruce. Moreover, beech's greater capacity for higher soil water exploration is related to its deeper root system compared with spruce. As a consequence, spruce as an isohydric species was more susceptible to drought than beech [11,48] due to the lower stomatal conductance at an early stage of soil drought.

Species-specific differences were observable when comparing the resistance and resilience of BAI and Δ^{13}C. The Δ^{13}C of spruces revealed a high drought resistance, while the resistance of tree ring growth is low. On the other hand, the resistance of BAI and Δ^{13}C of beech trees showed a positive correlation. One possible explanation for this pattern is that evergreen and deciduous species have different seasonal carbon storage amounts and remobilization patterns of starch and sugars and a subsequent isotopic coupling among tree rings and leaves [49]. Thus, for evergreen species, a stronger coupling between isotope composition of new assimilates and tree rings is assumed [6,50]. Klein et al. [51] and Barbour et al. [52] showed a rapid response in Δ^{13}C with changing environmental conditions. Photosynthates of the evergreen species are transferred directly to the tree ring with limited involvement of C stores. In addition, spruce trees begin growing earlier than beech trees in the study region and could involve more Δ^{13}C in tree rings at the beginning of the growth period.

Along the gradient, we suggest that on moist sites during the drought event of 2003, new assimilates of beech trees were transferred more to the stem, whereas under drought at the dry sites, allocation of photoassimilates to the stem ceased. Hommel et al. [53] and Zang et al. [54] indicated that beech trees allocate photoassimilates to a greater extent belowground under moderate drought, compared to situations where water supply is unlimited. That beech trees benefit on moist sites also concurs with the findings in the data for tree ring growth. The higher the water supply, the greater the capacity demonstrated by beech to avoid a strong reduction in the growth level when the drought event happened [11,55]. For BAI, spruce trees had a lesser resistance on dry sites than beech trees. In contrast, the Δ^{13}C of spruce trees showed greater resistance on dry sites during the drought year compared to beech. The ability of tree species to cope with a decrease in the water availability at xeric and mesic sites in Central Europe for δ^{13}C was determined in a study by Levesque et al. [46]. Trees at the xeric site were particularly sensitive to soil water recharge in the preceding autumn and early spring. At mesic sites, trees were more vulnerable to water deficits of shorter duration than at the xeric site. The assumptions of the first hypothesis can be confirmed for the BAI of spruces, but must be rejected for Δ^{13}C of spruce trees. With respect to BAI, spruce trees have a lower resistance at the dry site, whereas beech trees reveal a greater resistance at the moist site.

4.2. Species Interaction in Monospecific Versus Mixed Stands

The influence of the mixture structure of spruce and beech stands has been analyzed in many studies [12,23,56–58] but no common statement could be found in these. Species mixture could lead to positive effects as well as to negative consequences for tree ring growth. For instance, the shading effects of beech or its deep-rooting system and the consequent restriction of water and nutrient supply could have negative effects on spruce [17,59]. Positive effects of beech on spruce might include hydraulic lift by the roots. At night, when transpiration is low and tree water potential high, roots receive water from deeper soil layers. If the water potential is lower in the upper soil layer compared to deeper soil layers, as in drought situations, water emerges from these layers to the surface layer. This water can be used from the beech tree itself, but also from the surrounding trees [60–62]. This could provide an explanation for the higher resistance of spruce trees in mixture with regard to $\Delta^{13}C$.

Positive effects of spruce trees on beech trees could include competitive reduction through the low self-tolerance of beech compared with other species [55] or the capability of beech trees to occupy the crown space of spruce with relatively low biomass investment [63,64] which results in positive growth reactions compared to beech in monospecific stands. Additionally, Metz et al. [23], Bolte et al. [65], and Mölder et al. [5] reveal that growing in a neighborhood with other species has a positive effect on beech. This positive effect is detected in this study which shows that beech grown in a neighborhood with spruce has significantly higher resistance and resilience ($\Delta^{13}C$) on moist sites. Thus, the second hypothesis is confirmed for $\Delta^{13}C$ of beech trees in mixture at moist sites, but not dry sites. Therefore, $\Delta^{13}C$ also indicates higher sensitivity to neighborhood effects in addition to environmental factors, as mentioned above.

The stress-gradient hypothesis from Callaway et al. [66] predicts that facilitation of mixture dominates on poor sites rather than rich sites, which is also reflected by the precipitation gradient in the present study. Maestre et al. [67] extended the stress-gradient hypothesis by considering the life history of the interacting species (tolerance to stress vs. competitive ability) and whether the factor of stress is a resource or not. Malkinson et al. [68] emphasized that the physiological response is not linear with respect to environmental changes along stress gradients and that the fitness of the individuals, as the product of facilitation and competition, plays an important role. These findings support the results of the present paper, that it is not possible to explain the stress reaction pattern of mixtures exclusively on the basis of the level of resource stress of the examined species. Therefore, we were not able to confirm the stress-gradient hypothesis. Beech trees indicated a higher resistance on moist sites in mixture than on poor sites, in accordance with the findings of Pretzsch et al. [69], where beech trees were shown to profit most from a mixture on fertile sites. On dry sites, monospecific beech was facilitated. Tree ring growth and ^{13}C discrimination are affected by a complex mix of environmental factors and a greater number of samples are necessary to make a general statement. Moreover, drought may uncouple tree ring growth from photosynthesis, which leads to weak relationships between secondary growth and $\Delta^{13}C$ [70]. Further studies in other mixed forests are needed to further clarify the effect of mixture on species with different adaption strategies.

5. Conclusions

Our findings indicate that drought stress reaction patterns of $\Delta^{13}C$ and BAI provide short- or long-term responses to climate variability. Along a precipitation gradient, the more isohydric spruce revealed a lower resistance in BAI under harsh environmental conditions (i.e., low soil moisture). Anisohydric beech trees had an increasing resistance for BAI and $\Delta^{13}C$ with increasing soil moisture. Furthermore, the discrimination of carbon and stem growth is strongly affected by climate conditions, whereas the $\Delta^{13}C$ helped to inform the analysis of drought stress reaction. During drought events, beech trees are facilitated in mixture with spruce with a higher resistance on moist sites. On dry sites, monospecific beech trees are favored. The more sensitive reaction of $\Delta^{13}C$ in tree rings to climate indicates that $\Delta^{13}C$ is a beneficial indicator of climate change in combination with tree ring growth.

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Author Contributions: Thomas Rötzer, Thorsten E. E. Grams, and Hans Pretzsch initiated the project; Cynthia Schäfer and Aline Feldermann performed the experiments and analyzed the data; Cynthia Schäfer wrote the manuscript; and Thorsten Grams, Thomas Rötzer, and Hans Pretzsch revised the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Estimates of the linear mixed effect model of spruce and beech in monospecific and mixed stands along the precipitation gradient (CVPI) (spruce *n* = 45; beech *n* =41). Standard deviation is represented in brackets. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '(*)' 0.1.

	Dependent Variable:							
	N. Spruce				**E. Beech**			
	RT BAI	**RT $\Delta^{13}C$**	**RS BAI**	**RS $\Delta^{13}C$**	**RT BAI**	**RT $\Delta^{13}C$**	**RS BAI**	**RS $\Delta^{13}C$**
Intercept	0.871 *	1.027 ***	0.672	1.050 ***	0.157	0.861 *	1.033	0.928 ***
	−0.252	−0.032	−0.453	−0.033	−0.213	−0.041	−0.608	−0.022
CVPI	−0.001	−0.0001	0.0003	−0.0001	0.002 ***	0.0003	−0.001	0.0001 *
	−0.001	−0.0001	−0.001	−0.0001	−0.001	−0.0001	−0.002	−0.0001
Mixture (Pure)	−0.342	−0.091	−0.062	−0.105 (*)	0.173	0.102 ***	−0.263	0.083 *
	−0.245	−0.047	−0.309	−0.047	−0.229	−0.027	−0.288	−0.031
CVPI·Mixture (Pure)	0.001	0.0002	0.0002	0.0003 (*)	−0.0002	−0.0003 **	0.001	−0.0002 *
	−0.001	−0.0001	−0.001	−0.0001	−0.001	−0.0001	−0.001	−0.0001

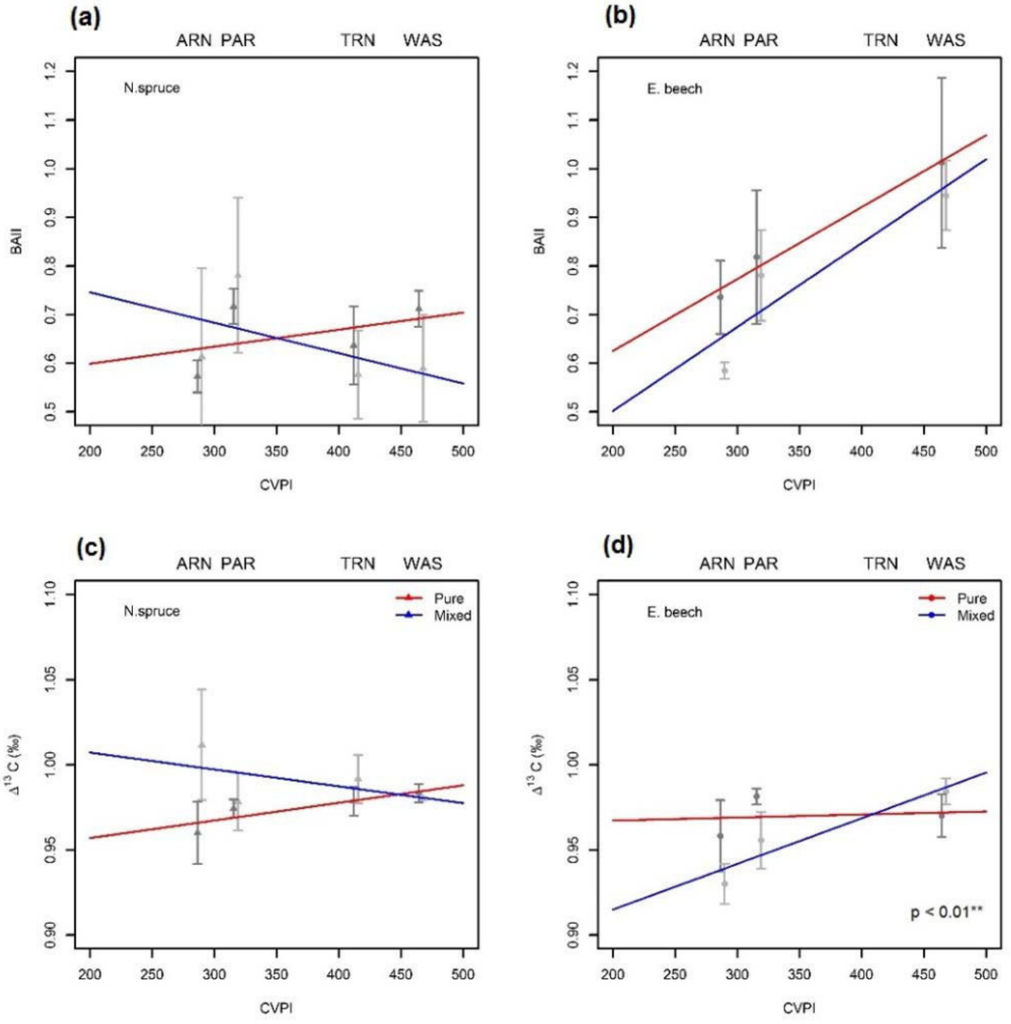

Figure A1. Linear mixed effect model of species and sites relative to the drought period in 2003 for the resistance of spruce and beech of BAII (**a**,**b**) and $\Delta^{13}C$ (**c**,**d**) in monospecific or mixed environments along the gradient represented by Paterson-index (CVPI).

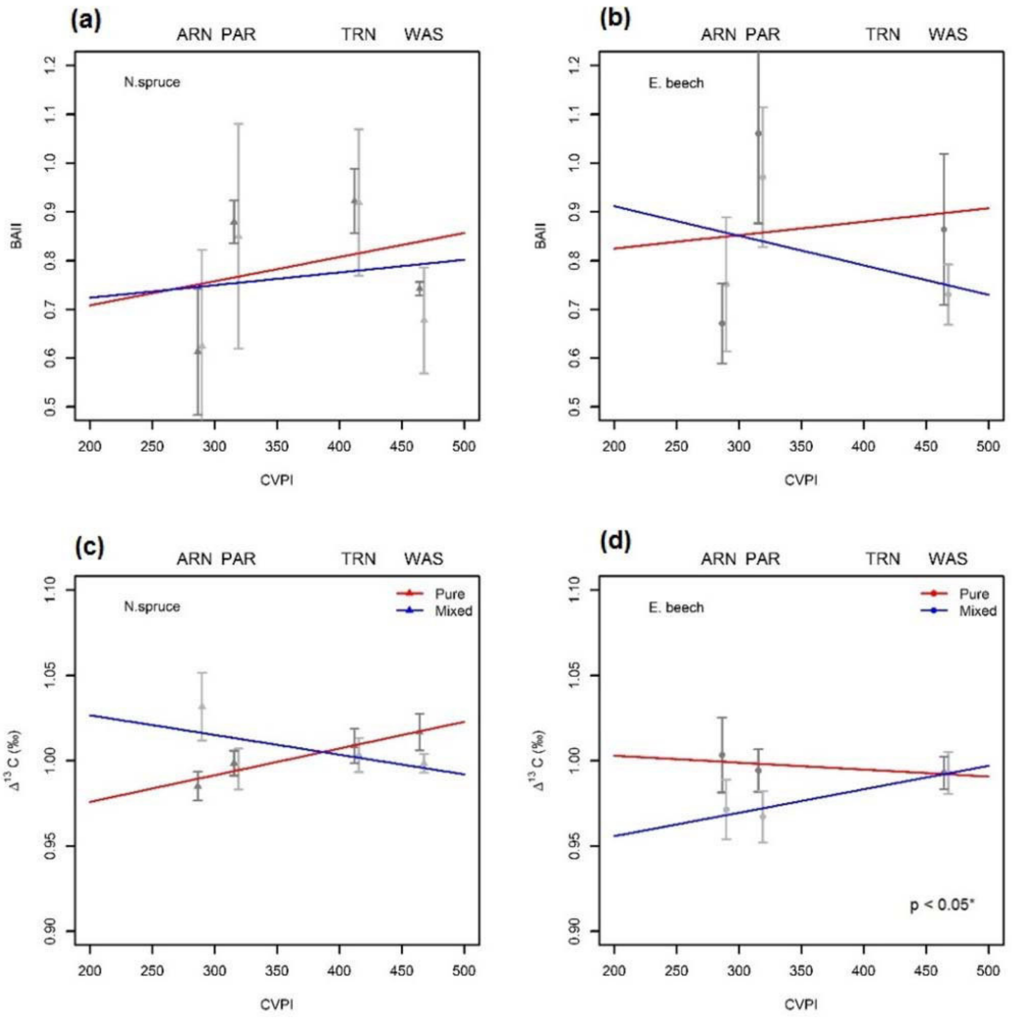

Figure A2. Linear mixed effect model of species and sites relative to the drought period in 2003 for the resilience of spruce and beech of BAII (**a**,**b**) and $\Delta^{13}C$ (**c**,**d**) in monospecific or mixed environments along the gradient represented by Paterson-index (CVPI).

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Article II

High resolution dendrometer data to detect resource allocation in mixed stands under heavy drought

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Abstract

Although several studies suggest that tree species in mixture resist drought events better than in pure stands, little is known about how these trees allocate resources.

With dendrometer data at the upper and lower stem and coarse roots, we calculated the tree water deficit (TWD) and growth (ZGmax) to show how mixture and drought influenced resource allocation. The analyses were made in a mature temperate forest of Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*). Half of the plots were placed under conditions of extreme drought through automatic closing roof systems within the stand.

Whereas at the beginning of the growing period, trees prioritized growth of the upper stem, during the course of the year the growth of lower stem became a greater priority. Growth allometry in mixture was comparable to trees under drought conditions. However, the spruce in interspecific neighborhood exhibited the same TWD allometry as spruces with good water supply. Interspecific beeches showed no benefit compared to intraspecific beeches, which can be seen for TWD as well as growth allometry.

Mixture seems to benefit the water supply of spruce trees, which should increase the stability of this species in a time of climatic warming.

Keywords: tree water status, tree water deficit (TWD), rainfall exclusion, Picea abies, Fagus sylvatica, root-shoot allometry.

Introduction

Climate models have predicted (Meehl and Tebaldi 2004; IPCC 2013) an increased number of drought events of longer duration and stronger intensity that are likely to alter the growth and stability of forests (Fuhrer et al. 2006; Allen et al. 2010; Rötzer et al. 2013). Ciais et al. (2005) give evidence that precipitation deficits and extreme summer heat are capable of causing a Europe-wide reduction of ecosystem primary productivity. Drought stress will affect trees directly and indirectly through their increasing susceptibility (Dukes et al. 2009). Furthermore, changing resource availability leads to shifts in resource allocation within trees (Dieler and Pretzsch 2013). As predicted by functional equilibrium models (Thornley 1972; Chapin 1980) and proven by extensive studies (Poorter et al. 2012), plants allocate additional biomass to those organs that acquire the most limiting resources. Consequently, plants allocate more biomass to the roots in cases where below-ground resources, such as water and nutrients, are limiting. When light or CO_2 are limiting factors, the plants allocate more biomass above ground. Drought susceptible tree species can therefore respond to extreme drought with reduced stem growth and increased root growth (Rötzer et al. 2009; Poorter et al. 2012).

Drought stress reactions can be determined, inter alia, via the leaf water potential (tree water status). The coordination of stomatal and hydraulic regulations allows for an adjustment of the tree water use. Various environmental influences (e.g. temperature, vapor pressure deficit) control these mechanisms and thus the tree’s water use. Continuous high-resolution measurements of stem radius variations provide the opportunity to gain deeper insights into dynamics of tree water relations and growth patterns in mature forests. Stem radius variations are increasingly used in plant physiology to analyze stem growth and the tree water status (Zweifel et al. 2001; Steppe et al. 2006; Brinkmann et al. 2016; Dietrich et al. 2018) and have been analyzed for different tree species (Zweifel et al. 2000; Ortuño et al. 2006; Brinkmann et al. 2016). Furthermore, stem radius variations offer the opportunity to assess tree water status without a canopy crane or other circuitous methods for taking leaf water potential measurements in the tree crown. As such, they offer huge potential for ecological research under a changing climate.

Diurnal stem radius variations were measured by electronic, high-resolution point or band dendrometers (Zweifel et al. 2005; Ortuño et al. 2010). The drought-induced changes can be recognized through modified characteristics of the bark tissue (decreasing cell turgor, which results in stem shrinking) and changes in radial growth (Daudet et al. 2005; Vieira et al. 2013). When transpiration exceeds the water uptake from the soil, the tree relocates water storages – mainly located in the living cells within the cortex – to maintain the transpiration process. Thus on a diurnal scale, shrinking and swelling of the stem is the result of alternating depletion and replenishment of the involved tissues. This process is driven by the transpiratory demand during daytime and overnight refilling of the living cells of the phloem tissue with water from the soil (Klepper et al. 1971; Kozlowski 1976; Zweifel et al. 2006). There are many ecophysiology models describing the dynamic radial and vertical water flow between the tree tissues (Steppe et al. 2006; De Schepper and Steppe 2010; De Swaef et al. 2015; Steppe et al. 2015). Zweifel et al. (2000) investigated stem radius changes and their relation to stored water in stems with truncated stem segments of living Norway spruces and were able to attribute the stem contraction to the living tissue outside of the cambium. Shrinking and swelling of the stem can hence be used as indicator for the whole tree water status (Irvine and Grace 1997; Zweifel et al. 2000; De Swaef et al. 2015) and can be measured for any tree organ and any species.

In addition to site and climatic conditions, the mixture of species also has a significant impact on the water supply and growth of a tree. Species mixture can improve forest ecosystem functions under changing climate through complementary interactions between a pair of species (Pretzsch 2005; Forrester 2014). Complementary effects depend on the type of species and the changing resource availability (Rötzer 2013; Forrester 2014; Pretzsch et al. 2017). The most widespread mixed forest stands in Central Europe consist of Norway spruce (*Picea abies* [L.]

Karst) and European beech (*Fagus sylvatica* [L.]). Mixtures of these tree species are analyzed in many studies (Wiedemann 1942; Pretzsch et al. 2010; Pretzsch et al. 2014; Metz et al. 2016). Evergreen spruce is considered to be particularly sensitive to drought stress (Zang et al. 2012; Pretzsch et al. 2013) with a drought sensitive stomata closure (Klein 2014) and correspondingly impeded photosynthesis. Deciduous beech is known to be more drought resistant as compared to spruce (Ammer et al. 2008; Pretzsch et al. 2013; Schäfer et al. 2017). The mixture of these two tree species can have several advantages for both tree species. For example, Bolte and Villanueva (2006) detected a deeper rooting system of beech in mixture with spruce compared to monocultures and consequently an enhanced water and nutrient availability for beech trees. The improved soil water storage due to the reduced interception of beech in mixture with spruce (Schume et al. 2004; Cremer and Prietzel 2017; Rötzer et al. 2017) can also have a positive effect on the water availability and change the entire stand water balance (Pretzsch et al. 2012).

In the present study, we determined the diameter growth (ZGmax) and tree water status (tree water deficit, TWD; as described by Zweifel et al. (2016)) at three tree compartments: the upper stem (50% tree height – H50, at approximately 15 m tree height), the lower stem (breast height (1.3 m), BH) and at the coarse roots (roots). The TWD as the measurement unit for the tree water status was analyzed in relation to the leaf water. Subsequently, TWDs at H50, BH and the roots were employed to analyze species-specific differences between beech and spruce in terms of drought-related changes in root-stem allometry.

The aim of the study was to show how the growth allometry and the tree water deficit is allocated across the different tree compartments under drought and in intra- and interspecific neighborhoods. Therefore, we used a rainfall exclusion experimental setup to provide drought stressed mature trees in the treatment plots and unstressed trees in the control plots. Naturally occurring drought was experimentally enhanced by means of stand scale rainfall exclusion, the

Kranzberg **ROOF** Experiment (**KROOF**). We demonstrated how the allometry pattern of control and treatment trees or trees in intra- and interspecific neighborhoods look.

We hypothesized that: (1) there is a relationship between stem radius variations and the leaf water potential for beech and spruce at the different measured tree compartments; (2) the relationship between growth response and the respective TWD is the same at the three different positions H50, BH and root; and (3) interspecific neighborhood with beech trees facilitates spruce trees under drought stress.

Materials and Methods

Site description

The study is located in southern Germany (longitude: 11°39'42"E, latitude: 48°25'12"N, altitude 490 m.a.s.l), near Freising (Kranzberg forest) and approximately 35 km northeast of Munich. The soil of the Kranzberg forest is a luvisol developed from loess over Tertiary sediments with high nutrient and water availability. The forest stand comprises European beech (*Fagus sylvatica* [L.]) and Norway spruce (*Picea abies* [L.] Karst). The age of trees varies between 64±2 years for spruce and 84±4 years for beech (in 2015). In 2010, twelve plots were established with a total area of 1730 m² with 63 beech trees (mean height 26.1 m, mean diameter 28.9 cm at breast height) and 53 spruce trees (mean height 29 m, mean diameter 34.3 cm at breast height) (Table 1). On each plot, four trees were selected as measured trees (48 trees in total) (Table S4). Each of the 12 plots contained zones of spruce or beech trees in intraspecific neighborhood and zones of spruce or beech trees in interspecific neighborhood.

For the throughfall exclusion experiment (TE), six roof constructions were built below the crown of the trees at a height of about 3 m. The other six plots acted as control plots (CO). In spring 2010, the plots were trenched with a heavy-duty plastic trap to a depth of about 1 m to avoid external effects on and water intake in the experimental plots (Pretzsch et al. 2016). The roofs close only during rainfall through a set of precipitation sensors, to avoid unintended micro-meteorological and physiological effects (Pretzsch et al. 2014). The drying cycles with closing roofs lasted from May to December 2014 and from March to November 2015. The annual precipitation average for the Kranzberg forest ranges between 750 and 800 mm for the entire year and between 460 to 500 mm yr^{-1} in the growing season (mid-April to the end of October) (1971–2000) (Hera et al. 2011). The annual average temperature is 7.8 °C and the average temperature for the growing season is 13.8 °C (detailed description in Pretzsch et al. (2012)).

Table 1 Characteristics of the investigated stand where the treatment and control plots are located. (N: number of trees per ha; n: number of trees with dendrometers; BA: basal area per ha; V: total stem volume per ha; hq: mean height; dq: quadratic mean diameter at 1.3 m breast height).

	Area [m^2]	N	n	BA [m^2]	V [m^3]	hq [m]	dq [cm]
Treatment							
Spruce		301	12	29,7	422	29,3	34,8
Beech		352	12	22,9	309	26,1	29,1
Total	145	653	24	52,6	730		
Control							
Spruce		310	12	28,8	400	28,7	33,8
Beech		356	12	22,6	305	26	28,7
Total	144	666	24	51,4	705		

Water potential (Ψ leaf)

Leaf water potentials at predawn (LWPpre) and midday (LWPmid) were measured several times during the vegetation periods (April–October) in 2014 and 2015. Leaf water potential measurements were conducted in time windows from 2:00 h to 3:30 h CET for LWPpre and 13:00 to 15:00 h CET for LWPmid. The same experimental trees were used as for the dendrometer measurements that could be conducted with the canopy crane (n=31). At a height of 25–30m, south-exposed twigs of about 10–20 cm in length were taken from the sun crown (access through canopy crane) and were enclosed in humid plastic bags to prevent water loss. The leaves were immediately measured with a pressure chamber (Model 3000 Pressure Extractor, Soil moisture Equipment Corp., Santa Barbara, CA, USA).

Stem radius variations (growth and tree water deficit)

On each of the 48 trees selected for measurement, three automatic dendrometers of two types (Ecomatik, Dachau, Germany) were installed. The DR-type dendrometer was installed at breast height (1.3 m, BH) and 50% tree height (H50). For measurements of the roots, circumference dendrometers of the DC2 type were used and fixed on one main root per measured tree. Slide rings reduced the friction between the wire cable and the tree bark. All dendrometers were fixed in a northeast direction to avoid environmental influences. From the spruce trees, the outermost tissues of the bark were removed to minimize hygroscopic effects of the outer bark. The frames of the dendrometers were fixed with stainless steel screws on the tree stem, with the linear transducer in direct contact with the stem/root surface. Measurements were recorded every 10 minutes. All measurement errors and proven outliers in the raw data where eliminated prior to further processing. Hourly means of the raw 10-minute measurements of stem radius variations were analyzed during the growing season (mid-April to the end of October).

To describe how drought affects the tree organs, we use the tree water deficit (TWD), defined by Zweifel et al. (2016). First, the “pure” growth (further defined as zero growth, ZGmax) was extracted from the stem or root dendrometer measurements to determine the TWD (water signal). For separation, we used the zero growth concept of Zweifel et al. (2016), which results in growth curves with a stepwise shape (Fig.1). When the current maximum of the stem radius is exceeded, the increment increases. For our investigations, we used the maximum ZG value per day (ZGmax).

The TWD was calculated as the difference between the growth-induced expansion of the stem and the daily shrinking and swelling. The negative values of the TWD revealed increasing shrinking of the stem radius. We proved the relationship between the stem water signals and the leaf water potentials at midday and predawn. We found the best match for the relationship between LWPpre and TWD minimum (TWDmin, maximum daily shrinkage) during drought conditions (Supplementary Material, Table S2) and used the LWPpre for further analysis of the relationship between TWDmin and LWPpre.

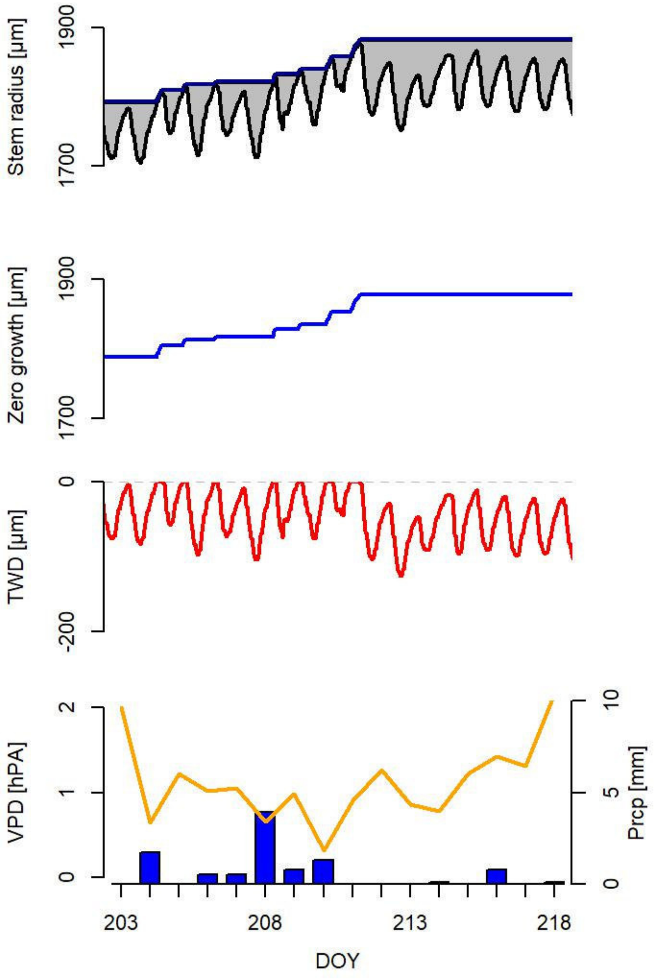

Fig. 1 Exemplary illustration of the course of the stem radius variation and the two applied indices, zero growth (ZGmax) and tree water deficit (TWD), for a period of 16 days in the growing season 2015 of an example spruce tree. The climatic graph of vapor pressure deficit (VPD) and daily precipitation sum (Prcp) illustrated how the deficit of water led to a stagnation of the zero growth and a decrease in the tree water deficit during the last five days of the example period.

Climatic data

The weather data were collected from two sources. Temperature data and relative humidity were measured at 10 min intervals in the forest stand and monitored with a temperature sensor (RFT-2, UMS) at a height of 27 m and stored in a datalogger (Logger Campbell CR100, Multiplexer AM16/32). The sensor was protected against direct irradiation with a ventilated radiation shield. The vapor pressure deficit (VPD) was calculated with these data. Precipitation data were available from the nearby weather station, about 2 km from the study site in Kranzberg forest (Bavarian State Institute of Forestry 2015).

Statistical analysis

Our experimental setup consisted of measurement time series per tree. The individual trees were grouped by different control and treatment plots. Consequently, the analysis was based on nested data. To consider this nesting, we applied linear mixed effect models (*lmer*) from the package *lme4* (Bates et al. 2015). The random effects are the individual tree, with the index i, the plot with the index j and the year abbreviated with the index k. t represents the measurement at which we used the daily maximum value for zero growth (ZGmax) and the daily minimum value for the tree water deficit (TWDmin). ε always represents the residual error of the respective models.

To answer the question of whether the TWDmin at the various tree compartments is able to reflect drought stress, we examined the relationship between the TWDmin and LWPpre at the three different measurement positions. We pooled both years (2014 and 2015) into the same dataset for the analysis.

We applied linear mixed models in a logarithmic form (eq. 1):

$$\ln(TWD\mathrm{min})_{ijkt} = \beta_0 + \beta_1 \cdot \ln(LWPpre_{ijt}) + b_i + b_j + b_k + \varepsilon_{ijkt} \qquad \text{(eq. 1)}$$

The applied logarithm led to a significantly better fitting of the data and considered the non-linear course of the analyzed relationship. The logarithm of the negative TWDmin values was enabled through a transformation by multiplying by -1. For the depiction, we adapted only the y-axis to negative values. All models where fitted species-specific for a straightforward interpretation.

To show how growth allocation or the TWDmin react between the three tree compartments under drought conditions, we examined the difference ($Diff$) of ZGmax and TWDmin at a measurement position above to the measurement position below (H50 - BH and BH - Root). A value above zero would mean that the upper tree compartment has a high growth, a value below zero would indicate that the lower tree compartment profits. We chose to use the difference instead of the ratio because, when using the ratio, meaningful but very low TWDmin or ZGmax values in one compartment can lead to immoderate and meaningless outliers in the analysis.

The resulting difference value of the upper and lower measurements serves as the independent variable. Because TWDmin and especially the ZGmax increase over the growing season, the difference between upper and lower compartments ($lowComp$) can be higher at the end of the growing period than at the beginning. Therefore, we always related the difference to the respective measurement of the lower compartment.

To show how mixture and drought treatment influence the growth allometry or TWDmin pattern of the upper and lower compartments, linear mixed models where applied. Mixture (Mix) or treatment ($Treat$) were included as fixed effects in these models (eq. 2 and eq. 3):

$$Diff_{ijkt} = \beta_0 + \beta_1 \cdot lowComp_{ijt} + \beta_2 \cdot Mix + \beta_3 \cdot lowComp_{ijt} \cdot Mix + b_i + b_j + b_k + \varepsilon_{ijkt}$$

(eq. 2)

$$Diff_{ijkt} = \beta_0 + \beta_1 \cdot lowComp_{ijt} + \beta_2 \cdot Treat + \beta_3 \cdot lowComp_{ijt} \cdot Treat + b_i + b_j + b_k + \varepsilon_{ijkt}$$

(eq. 3)

The significances of the fixed effects of the linear mixed models were tested by an F test with Satterthwaite's approximation ((Kuznetsova et al. 2015), R-package *lmerTest*). To consider the large number of measurements points, we also calculated the conditional coefficient of determination (R^2) for the mixed-effect models with the command *r.squaredGLMM* from the *MuMln* package. Additionally, the quality of the models were checked using the root mean square error (RMSE). All analyses were performed with the R version 3.2.3 (R Core Team 2017).

Results

Temperature and precipitation in 2014 and 2015

There are clear differences in temperature and precipitation between the analyzed years 2014 and 2015 in the growing season (Fig. 2, a–b). The air temperature in 2015 was 1.1 °C above the average from 2001 to 2015 (Bavarian State Institute of Forestry 2016). Compared to the year 2014, the summer months of the year 2015 had a high number of days without rainfall or with low rainfall and simultaneously high temperatures and high vapor pressure deficits (VPD).

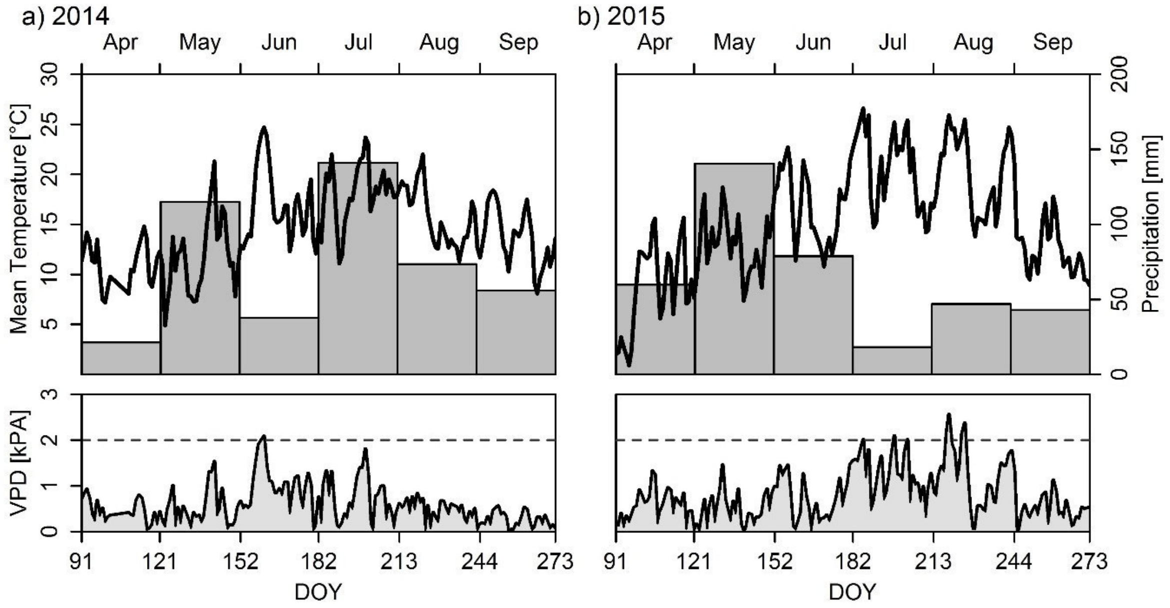

Fig. 2 Monthly precipitation sums and daily mean temperature values (a–b, above) and daily VPD (a–b, below) in the growing season (April–September) of the years 2014 and 2015. The dashed lines exhibit a high VPD of 2 kPa.

Leaf water potentials

Comparing the midday water potentials (LWPmid) for the years 2014 and 2015, the LWPmid were significantly more negative for beech trees than for spruce trees (Supplementary Material, Fig. S2 a–d, $p < 0.001$). We pooled the years 2014 and 2015 and trees in intra- and interspecific neighborhoods to analyze drought stress. There are significant differences between the trees of the control and drought treatment plots (Supplementary Material, Table S1, $p < 0.01$). Predawn water potentials (LWPpre) reveal clearer differences ($p < 0.001$) compared to LWPmid (Supplementary Material, Fig. S3 a–d). The effect of the drought treatment is observable through more negative LWPpre compared to the control plots. No differences were observable between trees in intra- and interspecific neighborhoods.

Zero growth and tree water deficit

To determine growth and TWDmin, we separated the growth from the daily shrinking and swelling. Fig. 3 provides an overview of the data (intra- and interspecific neighborhoods are shown in Fig. S1). Spruce trees had a higher diameter increment compared to beech trees in 2014 at all three measuring positions (H50, BH and roots). The diameter increment of the spruce trees was smaller for the dry year 2015 compared to the year 2014. In beech, by contrast, relevant growth reduction of the drought treated trees was observed in 2015 at H50 and BH, but not at the roots.

Comparing the daily TWDmin of the growing season in 2014 and 2015, the effect of the drought year 2015 was observable in the intense shrinking in the summer months (DOY 152–243) (Fig. 3 b, d, f). Furthermore, there was a high shrinkage phase at H50 in 2014 for spruce trees (possibly through an adaptation reaction at the beginning of the drought treatment). The treatment plots indicate a more distinct stem shrinkage compared with the control plots for both years (except for beech trees at H50 and BH in 2015). Species-specific differences can also be seen in the magnitudes of the daily TWD. Spruce trees reveal more distinct stem water changes than beech trees. Overall, the stem shrinkage was highest at H50 compared to BH and the roots.

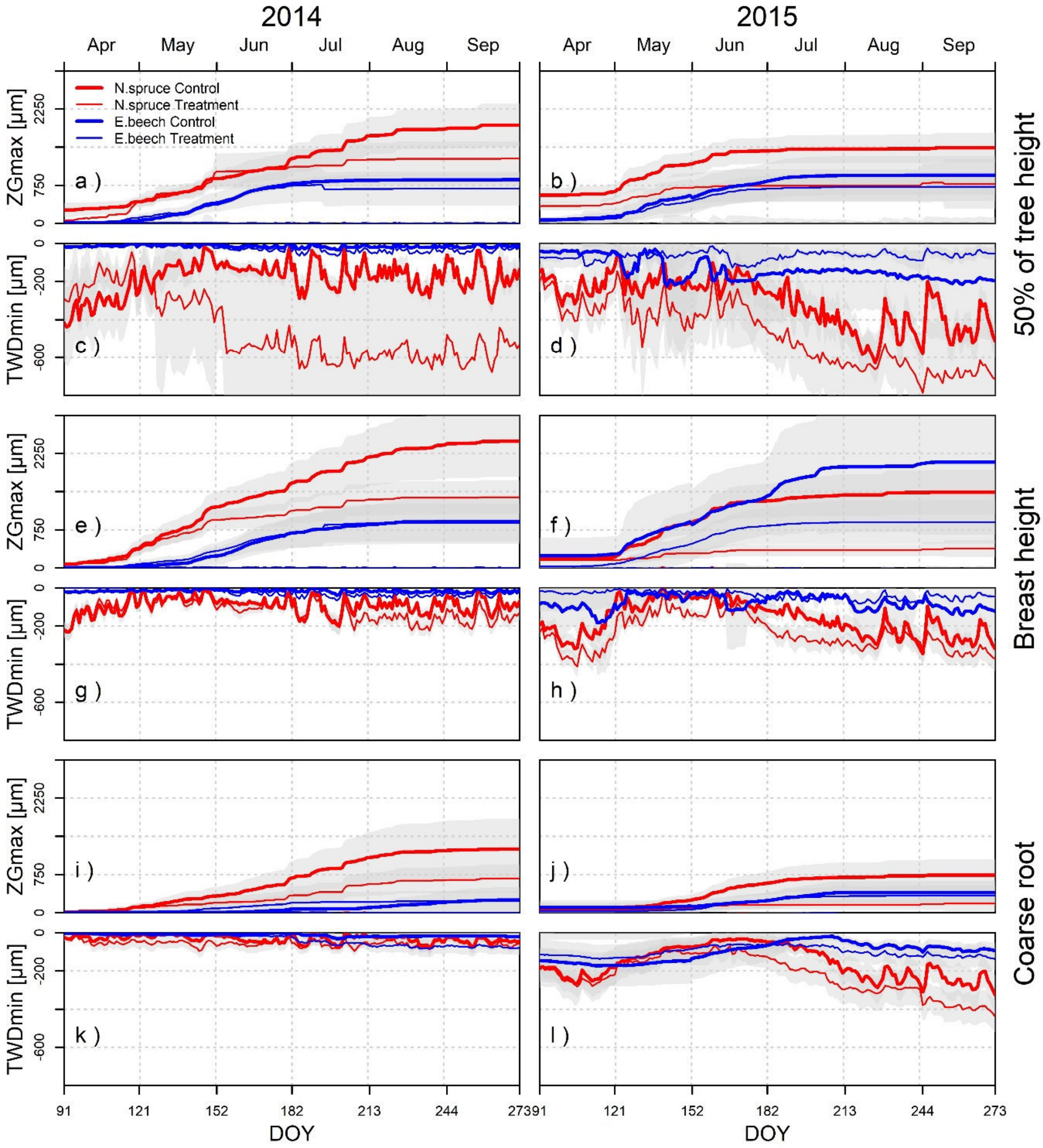

Fig. 3 Mean TWDmin and zero growth (growth without the water signal) for the years 2014 (left) and 2015 (right) for spruce (red) and beech (blue) at the control (thick line) and treatment (thin line) plots at 50% tree height (a–d), breast height (BH, e–h) and of the roots (i–l). Data are shown for the growing season.

Relationship between tree water deficits and water potentials at different tree heights

TWDmin values are more negative when the LWPpre become more negative at the stem (BH, H50) and the roots (Fig. 4 a–c). Spruce trees reveal a higher TWDmin than beech trees at all positions. The r-squared (R²) of the different models ranged between 0.38 and 0.82. The relationship was significant for both species and all positions ($p < 0.001$, Table 2).

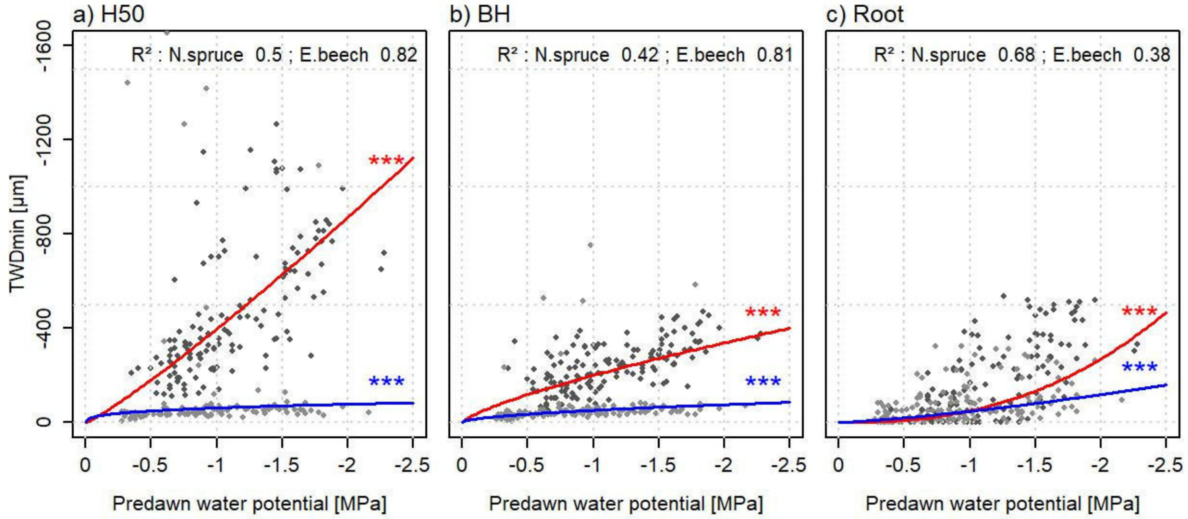

Fig. 4 Relationship between TWDmin and predawn water potential (LWPpre) for spruce (red) and beech (blue) trees for 50% tree height (a), breast height (b) and the roots (c) (*** represents a $p<0.001$; respective models can be found in Table 2).

Table 2 Parameter estimates and statistics for the logarithmized relationship of the tree water deficit minimum (TWDmin) and the predawn water potential (LWPpre) at three different tree heights (50% tree height (H50), breast height (BH) and roots). The dependent variables are in the columns. Rows show the output of the model with the fixed variables (N: number of measurements). Significance levels: ***, $p < 0.001$; **, 0.01; *, 0.05; (*), 0.1.

	log(TWDmin)					
	H50		BH		Root	
Species	N. spruce	E. beech	N. spruce	E. beech	N. spruce	E. beech
Intercept	5.982***	4.117***	5.296***	3.938***	4.58***	4.544***
log(LWPpre)	1.136***	0.333***	0.757***	0.553***	2.466***	1.324***
R²	0.50	0.82	0.42	0.81	0.68	0.38
RMSE	345.65	325.11	81.61	97.79	309.55	161.13
N	134	113	144	140	138	140

Stem and root growth allometry and TWDmin

How the allometry is oriented under control and treatment or inter- or interspecific neighborhoods is illustrated in (Fig. 5–6). On the y-axis, the difference between BH and H50 or BH and the roots is given for the zero growth (panel above) or TWDmin (panel below). On the x-axis, the diameter growth or TWDmin of the respective lower tree compartment is given (BH, Fig. 5 or roots, Fig. 6). The significances of the respective linear mixed effect models are summarized in Tables 3 and 4.

In general, the interaction of treatment or mixture with the lower tree compartment (x-axis) was always significant. However, the corresponding single effects (treatment or mixture), which merely meant a shift of the intercept, were not significant. We left these in the model for completeness based on Zuur et al. (2009). The interpretation of the influence of treatment and mixture always refers to their dependency on the lower tree compartment. We subsequently looked at this interaction or rather the orientation and position of control to treatment curves (or intra- to interspecific curves). We defined the orientation of the two lines to each other as a pattern.

The highly significant models (Tables 3–4) exhibited an apparent deviation in Figures 5 and 6. This impression results from a small number of outliers, which are not agglomerated around the regression lines like most of the measurement points. In addition to the evaluation of the models by the significance, the frequency plots (see Supplementary Material, Fig. S4–S5) and the mean RMSEs of 313.0 (mean of all ZGmax models) and 117.6 (mean of all TWDmin models) confirm the good fitting of the applied modelling approach.

We found that the growth in BH was always higher, except for at the beginning of the growing season where growth in H50 was reinforced. The tree appears to invest in the upper trunk (H50) at the beginning of the growing season and then more in the BH (Fig. 5 a–d, $p < 0.001$ Table 3 a–d). In addition, in dry conditions the increment of the upper stem increased, whereas with good water supply, the increment of the BH increased (Fig. 5 a–d, $p < 0.001$ Table 3 a–d).

In the following, we first describe the whole ZG and TWD allometry of spruce followed by that of beech. Spruces in control plots are able to invest more growth at BH during the growing period than trees from the treatment plot (Fig. 5 a, Table 3 a). The same pattern can be seen for the comparison of inter- to intraspecific neighborhoods where spruce in intraspecific neighborhood is able to invest more at BH (Fig. 5 b, Table 3 b).

Interestingly, the TWDmin allometry between H50 and BH showed the reverse pattern (Fig. 5 e,f). Here, the course of the spruces in interspecific neighborhood was shaped like spruces in control plots, the TWDmin of H50 increased disproportionately with increasing TWDmin of BH. We observed this different pattern of growth and TWD allometry between the tree compartments BH and roots (Fig. 6 a–b, e–f).

Beech did not show this reverse behavior. Here, the growth allometry exhibited that beeches from control plots invest more growth at BH during the growing period (Fig. 5 c), which is similar to beeches from intraspecific neighborhood (Fig. 5d). Also, the TWDmin allometry of control trees is comparable to trees in intraspecific neighborhood (Fig.5 g–h).

Moreover, the relation between BH and root shows that beeches in “unstressed” control plots (Fig. 6 c–d, g–h) showed similar patterns to beeches in intraspecific neighborhood.

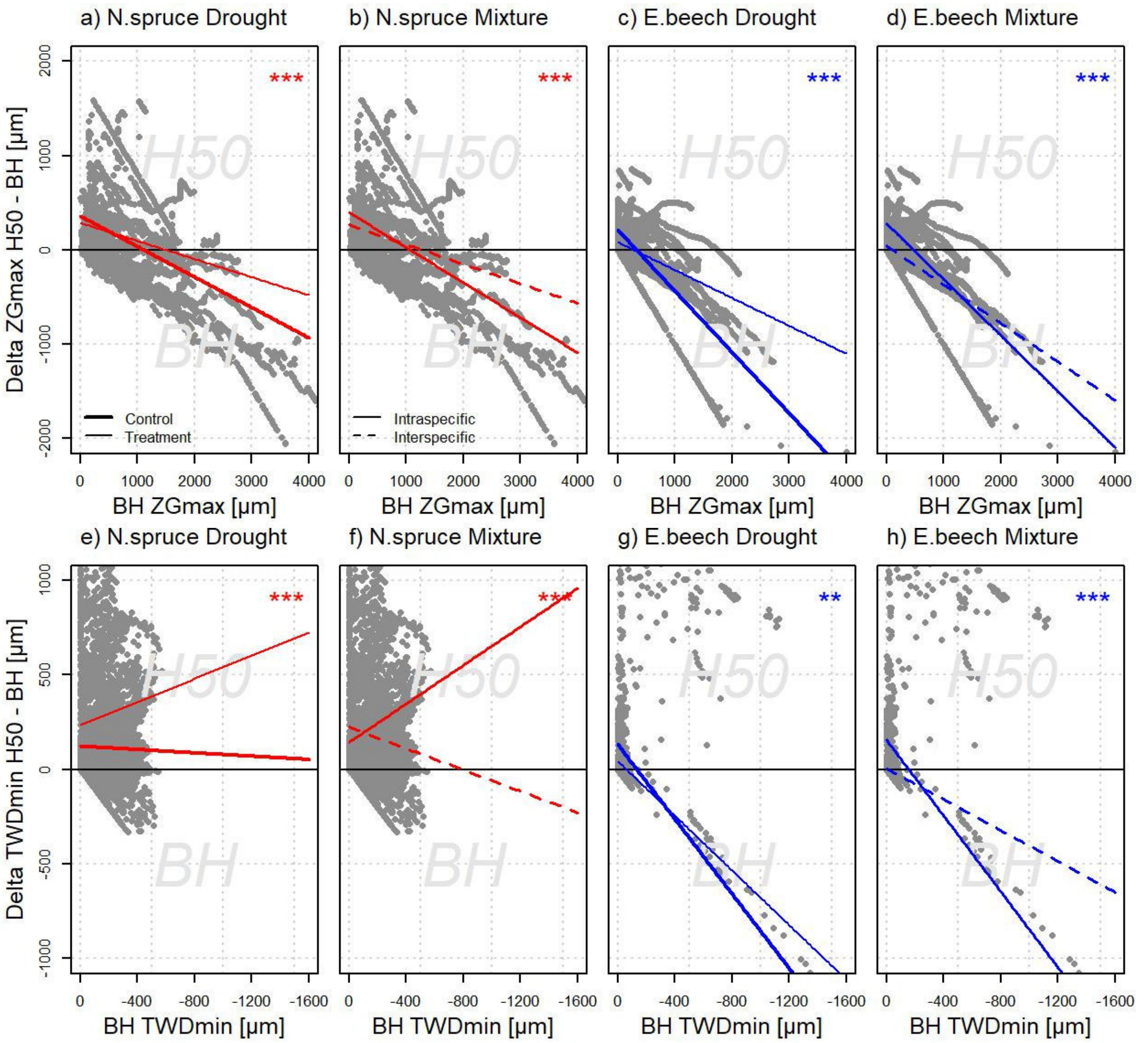

Fig. 5 Relationship of growth (ZGmax, above) and the tree water deficit (TWDmin) (below) represented by the difference of the measurements at 50% tree height (H50) and breast height (BH), dependent on the breast height measurement. Values below the zero line mean a growth allocation or water relocation into the lower stem compartment at breast height. For the TWDmin, the negative values represent a lower tree water deficit at breast height. Linear mixed models depict how strongly the allometry is influenced by drought treatment (thick line – control, thin line – treatment) or mixture (intraspecific neighborhood – straight line, interspecific neighborhood – dashed line). The respective models are shown in Table 3. Significance levels: ***, $p < 0.001$; **, 0.01; *, 0.05; (*), 0.1.

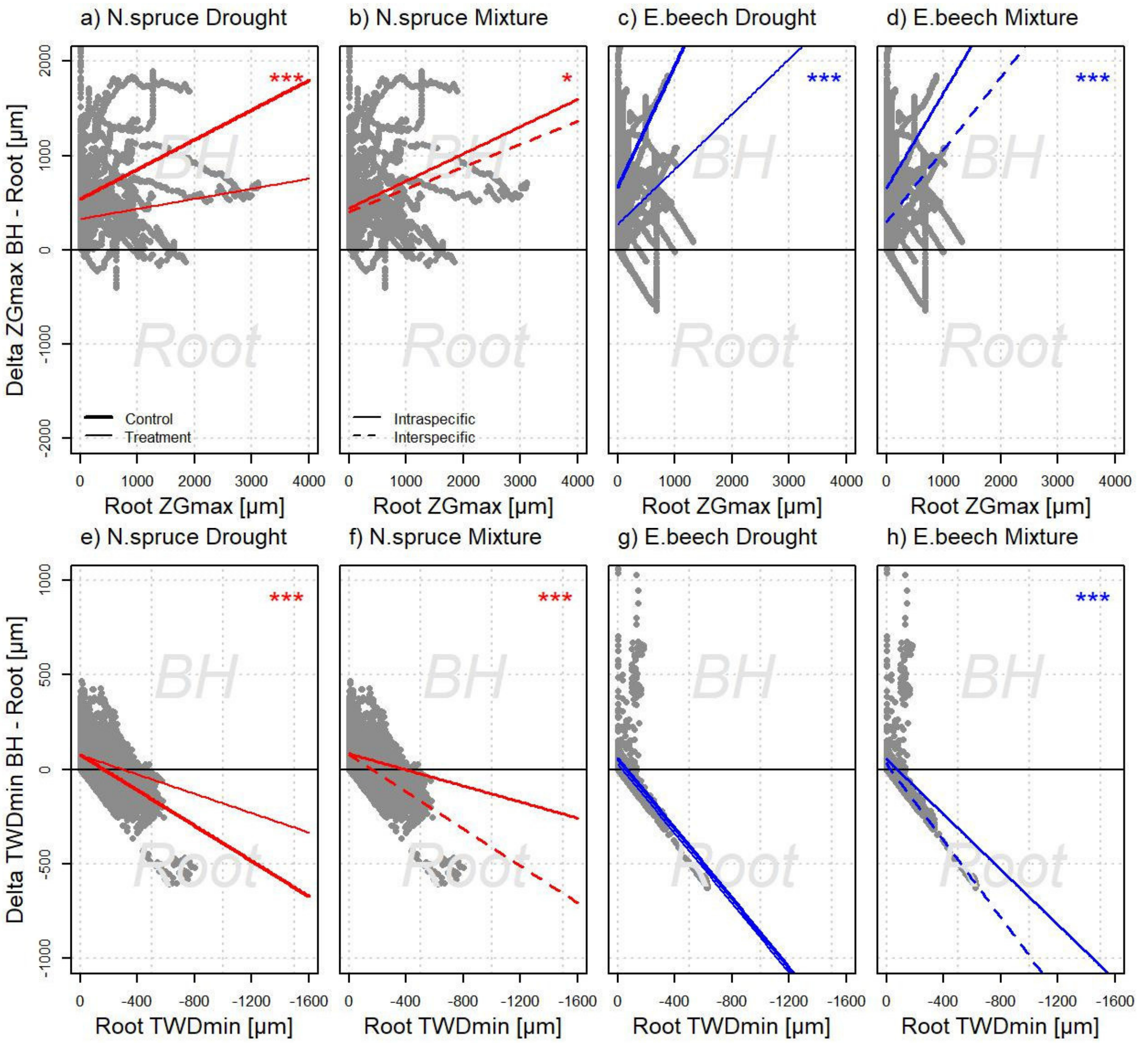

Fig. 6 Relationship of growth (ZGmax, above) and the tree water deficit (TWDmin) (below) represented by the difference of the measurements at breast height (BH) and at the roots, dependent on the root measurements. Values below the zero line mean a growth allocation or water relocation into the roots. For the TWDmin, the negative values represent a lower tree water deficit in the roots. Linear mixed models depict how strongly the allometry is influenced by drought treatment (thick line – control, thin line – treatment) or mixture (intraspecific neighborhood – straight line, interspecific neighborhood – dashed line). The respective models are shown in Table 4. Significance levels: ***, $p < 0.001$; **, 0.01; *, 0.05; (*), 0.1.

Table 3 Parameter estimates and statistics for the diameter growth (ZGmax) and tree water deficit (TWD) of the 50% tree height (H50) and stem at breast height (BH) allometry, dependent on drought (treat) and species mixing (mixture). The dependent variables are in the columns. Rows show the output of the model with the fixed variables (N: number of measurements). Significance levels: ***, $p < 0.001$; **, 0.01; *, 0.05; (*), 0.1.

Position	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH	H50-BH
ZGmax/TWD	ZGmax				TWD			
	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
Art	N.spruce	N.spruce	E.beech	E.beech	N.spruce	N.spruce	E.beech	E.beech
Factor	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture
Intercept	358.825 **	266.228 **	214.488	43.009	121.517	223.763 *	132.545	4.516
BH	-0.323 ***	-0.208 ***	-0.648 ***	-0.409 ***	-0.044	-0.283 ***	-0.988 ***	-0.409 ***
Treat	-71.721		-131.272		112.579		-89.295	
Treat*BH	0.131 ***		0.352 ***		0.351 ***		0.265 **	
Mixture		132.963		240.248		-81.43		151.639
Mixture*BH		-0.164 ***		-0.185 ***		0.793 ***		-0.594 ***
R^2	0.78	0.78	0.94	0.93	0.61	0.62	0.84	0.84
RMSE	243.03	239.60	195.08	212.86	241.81	239.92	112.99	112.77
N	8107	8107	6330	6330	8107	8107	6330	6330

Table 4 Parameter estimates and statistics for the diameter growth (ZGmax) and tree water deficit (TWD) of the stem at breast height (BH) and root allometry, dependent on drought (treat) and species mixing (mixture). The dependent variables are in the columns. Rows show the output of the model with the fixed variables (N: number of measurements). Significance levels: ***, $p < 0.001$; **, 0.01; *, 0.05; (*), 0.1.

Position	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root	BH-Root
ZGmax/TWD	ZGmax				TWD			
	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
Art	N.spruce	N.spruce	E.beech	E.beech	N.spruce	N.spruce	E.beech	E.beech
Factor	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture	Treatment	Mixture
Intercept	540.56 **	403.758 **	670.177 *	296.51	77.256 **	77.76 ***	58.306 (*)	29.673
Root	-0.343 ***	-0.38 ***	0.142 ***	-0.117 ***	-0.734 ***	-0.745 ***	-0.962 ***	-1.008 ***
Treat	-213.283		-397.388		-1.879		-30.161	
Treat*Root	-0.104 ***		-0.35 ***		0.106 ***		0.002	
Mixture		38.568		360.569		5.108		24.555
Mixture*Root		0.024 *		0.124 ***		0.139 ***		0.143 ***
R^2	0.76	0.77	0.85	0.85	0.90	0.90	0.94	0.94
RMSE	349.84	351.21	454.02	458.73	67.20	66.84	50.02	49.52
N	8290	8290	8306	8306	8290	8290	8306	8306

Discussion

Understanding of the connection between soil-root-stem-leaf-atmosphere can help to determine species-specific responses to drought stress. Not only species-specific drought stress reactions are of great interest, but also mixture-specific reactions. The knowledge of species interactions in mixed forest stands has increased in recent years with many investigations about beech and spruce trees (Bolte and Villanueva 2006; Ammer et al. 2008; Pretzsch et al. 2010; 2017). However, most studies have focused on growth-related differences in mixture rather than on changes in tree water status and these were not observed at different tree positions. Further, the differences between stem and root show the shift of growth and tree water under drought conditions for the given species.

Relationship between tree water deficit and leaf water potential

We found a strong relationship between TWDmin and LWP for both species at the three tree positions (H50, BH, roots). This reveals a link between TWDmin and the transpiration amount for all conducted tree compartments. We found the best match for TWDmin and LWPpre, but the relationship between TWDmin and LWPmid was also significant. Early dendrometer studies, such as Cohen et al. (2001), focused on the maximum daily shrinkage and compared the data with the water potential at midday and predawn. The Cohen study shows the link between maximum daily stem shrinkage (MDS) and predawn and midday LWP. The MDS was closely related to the predawn and midday water potential, similar to the present study. A more novel study by Dietrich et al. (2018) showed the relationship between TWD and LWP of different tree species, which included Norway spruce and European beech. It was illustrated that the daily TWD display the tree water status better than the maximum daily shrinkage in which the stem water signal is not separated from the growth signal. Particularly under dry conditions, the TWD was a consistent proxy for the tree water status of tall trees.

The temporal and spatial patterns of stem radius variations of Norway spruces were determined in Zweifel and Häsler (2001). As in the present study, they found similar but not identical dynamics of stem radius fluctuations at different heights (along the stem at 6, 10, 14, 18 m above ground and on roots). There were differences in height of the curves (amplitudes) at different tree heights and there was a time lag between the tree compartments. In the present study, the time offset was not investigated and could be an option for further investigations.

Similar to our study, Zweifel and Häsler (2001) found the greatest fluctuations in the upper stem part, within the crown, due to the proximity to the tree crown and thus transpiration (Tyree and Zimmermann 2011). Hinckley et al. (1978) stated that the water potential increases the water movement within the tree and thus increases the water movement from the internal stored water in the bark. The water storages near the crown can be reached faster than water storages from the soil.

In the present study, the relationship between TWD and LWP could be illustrated at the stem (at H50, BH) and at the roots. This is in line with the first hypothesis.

Root and stem allometry of growth and TWDmin at the different tree compartments

The applied method – the difference between lower and upper tree compartments in relation to the lower tree compartment – led to a visible deviation of the measured TWDmin and ZGmax at the different compartments. We are aware that the results have to interpreted with caution due to included variation. Nevertheless, the applied models considering the offset of the individual trees showed highly significant relationships. Also the R^2 and the RMSE give evidence for a reliable relationship, compared to what could be expected from the visual interpretation of Figures 5 and 6.

We found that the trees invested more in the radial growth of the upper stem (H50) at the beginning of the growing season. Later in the season, growth investment shifts increasingly to the lower stem (BH). An explanation for this might be the theory of the seasonal distribution of the growth hormone auxin. In spring, it is produced in apical meristem and transported down to the stem in the phloem of the tree (Kozlowski 1962; Speer 2013). In this way, the strength of radial growth shifts from the top to stem base.

Additionally, we showed that drought prompts the trees to invest more in growth of the upper than of the lower stem compartments. This could be also explained by the distribution of auxin. Under stressful conditions, its production can fail to initiate growth, especially near the base of the tree (Speer 2013). Tree ring studies on Norway spruce have shown that ring growth of the lower stem decreases in comparison to the upper stem in dry years (Sterba 1981; Mette et al. 2015). However, until now, this pattern had not been measured within a single year.

We also found that TWDmin was higher in the upper stem (H50) than in the lower stem (BH). The dendrometer position at H50 is near the crown and more water reserves could be used for transpiration (Tyree and Zimmermann 2011). This could be related to the higher diameter growth at BH compared to H50 due to the lesser shrinkage at BH. Zweifel et al. (2016) stated that periods of stem shrinkage allow for very little growth. In addition, Van der Maaten-Theunissen and Bouriaud (2012) revealed a reduced growth of Norway spruce at all stem heights during summer drought in southwestern Germany with the greatest reduction in growth at breast height.

For beech trees, the diameter increments were higher at BH. Despite this, the TWDmin was also higher at BH than at H50 in contrast to spruce trees. Overall, the TWD was less pronounced for beech trees than for spruce trees. This could be due to the higher resistance of beech trees to drought (Ammer et al. 2008; Brinkmann et al. 2016). Beech trees have an anisohydric character and continue growing and transpiring under dry conditions in contrast to spruce trees.

Furthermore, spruce and beech trees have different rooting systems (Bolte and Villanueva 2006). Beech trees have a deeper rooting system than spruce trees and can reach water from deeper soil horizons, which may reduce the use of water from the storage tissue. Spruce trees as an isohydric tree species respond with a reduced stomatal conductance under drought stress and thus reduced transpiration, which in turn reduces growth (McDowell et al. 2008; Klein 2014).

Furthermore, spruce and beech trees revealed a higher diameter growth at BH than at the roots and a higher TWDmin at the roots. The roots are affected by drought conditions through the lack of soil water supply and more water from the storage tissue in the roots could be used to maintain the transpiration process. In addition, the growth differences shifted more to the roots for beech and spruce trees with increasing drought, which is in accordance with McCarthy and Enquist (2007) and Ledo et al. (2018). The resource supply of plants is determined by e.g. the shape of the rooting system, the shape of the tree crown, site conditions and neighborhood to other trees (Kelty 2006; Bayer et al. 2013; Metz et al. 2016; Nickel et al. 2017). Depending on the prevailing conditions, biomass is allocated differently in the compartments of the tree (crown, stem and root). The optimal partitioning theory of McCarthy and Enquist (2007) indicates that a limited resource leads to a promotion of growth of the plant organ that receives this resource (roots). Our findings about the allometric relationships for growth – endorsed by the TWDmin results – support optimal partitioning theory and are consistent with the findings of other studies (McConnaughay and Coleman 1999; Nikolova et al. 2011; Thurm et al. 2016).

In contrast, Schall et al. (2012) found a significant increase of the percentage of below-ground compartments for beech seedlings but not for spruce seedlings. When considering the TWDmin of beech trees, no significant differences between control and drought treatment were obvious. Thus, the second hypothesis could be confirmed for spruce trees, but not for beech trees in all cases. Beech trees had a higher TWDmin and a higher diameter growth at BH than at H50.

Differences in intra- and interspecific neighborhoods

Many studies have pointed out that species mixture can have positive effects on the biodiversity (Paillet et al. 2010), productivity (Morin et al. 2011) and soil fertility (Rothe and Binkley 2001) of the whole system and that these effects depend on which species are mixed. Spruce and beech trees have different physiological and morphological traits (Bolte and Villanueva 2006; Pretzsch 2014). Pretzsch (2014) stated that plasticity in crown and root architecture appears to be the key to understanding effects of mixed system productivity.

Our investigations showed differences in inter- and intraspecific neighborhoods under drought conditions when considering TWDmin. Stem radius growth and TWDmin for the H50-BH allometric comparison revealed partly unequal results. For spruce trees, the stem radius growth at BH was higher in intraspecific neighborhood, similar to the control trees. On the contrary, the TWDmin was lesser in interspecific neighborhood at H50, which was similar to the control trees. The BH-root comparison indicated the same results. An explanation for this pattern could be that the growth is influenced by several factors (e.g. soil characteristics, nutrient supply, light) in addition to water availability (Forrester 2014; Pretzsch et al. 2015). The TWDmin reflects the water status of the tree. Therefore, spruces are facilitated in interspecific neighborhood in terms of the tree water status under increasing drought, but not for stem radius growth. Nevertheless, the stem radius growth could be influenced under extreme drought conditions due to the higher TWDmin.

Furthermore, spruce trees had a higher TWDmin compared to beech trees (Schäfer et al. 2018). An explanation could be that the decrease in water potential und drought leads to increased water use from the stem storage tissue toward the xylem. Under dry conditions, spruce trees, with their mainly shallow rooting systems and only few sinker roots, have limited access to deeper soil water resources. Therefore, spruce trees use more water reserves from the storage tissue within one day. In addition, Bolte and Villanueva (2006) found that beech trees in neighborhood with spruce trees rooted in deeper soil horizons than in intraspecific neighborhood. Spruce trees may benefit from this favorable characteristic through the effect of hydraulic lift (Dawson 1993; Caldwell et al. 1998; Siqueira et al. 2008). Hydraulic lift is the passive movement of water from moist to dry soil horizons by plant root systems. Usually at night when transpiration has ceased, water is released from the roots into the upper soil horizon (Caldwell et al. 1998). Beech trees can redistribute water from deeper to shallower soil horizons with their rooting systems. The reallocated water in the dryer soil layers can be used by beech trees as well as by the surrounding spruce trees (Siqueira et al. 2008). This could be an explanation for the lower TWD of spruce trees in interspecific neighborhood compared to spruces in intraspecific neighborhood.

In contrast, beech trees profit more from an intraspecific neighborhood and showed the same pattern under drought stress as the interspecific beeches for the H50-BH comparison, but the effect of drought treatment and control was not significant for the comparison of BH-root. In several studies, positive reactions of mixed beech trees have been detected (Bolte and Villanueva 2006; Mölder et al. 2011; Metz et al. 2016), but we did not found this positive interaction. Comparable with the present study, Pretzsch et al. (2010) described that intraspecific beech trees profit most on dry sites.

Thus, the third hypothesis could be confirmed for the water status of spruce trees, but not for the radius growth.

Conclusion

The present study is one of the first to investigate the growth allometry change of a tree within a single year and at different tree compartments with the help of TWDmin and ZGmax.

We found a relationship between the TWDmin and leaf water potentials at the three investigated tree compartments for spruce and beech. This confirms that dendrometer measurements are a good tool for drought stress analyses at the different tree compartments. The dendrometer measurements are much easier to handle than the water potential measurements and they are able to provide water status information with a timely and high resolution throughout the whole year. However, the relationship between TWDmin and leaf water potentials includes a deviation. Additional measurements, like the phloem thickness, might improve understanding of the relationship of both parameters.

With our allometric investigation of growth and TWDmin in 2014 and 2015, we have shown the growth pattern and compared it with the TWDmin pattern. Nevertheless, several studies have shown that the allometry of a plant changes across the life-course. Therefore, it is important to extend the measurements and to also include a tree's juvenile and senescence stages.

Surprisingly, we found that the allometric pattern of growth for trees in mixture is comparable to that of trees under drought stress. However, TWDmin of spruce trees in mixture showed the same pattern as spruces with a good water supply and a lesser stem shrinkage in mixture with beech trees. In our opinion, an explanation for the allometric growth pattern might be that growth (ZGmax) is influenced by several environmental conditions alongside TWDmin, which reveal the water status of the tree. To answer the question of whether spruce benefited from the mixture with beech under drought conditions, we considered the TWDmin allometric pattern and concluded that the mixture of beech could reduce the drought stress for spruce under future climatic warming.

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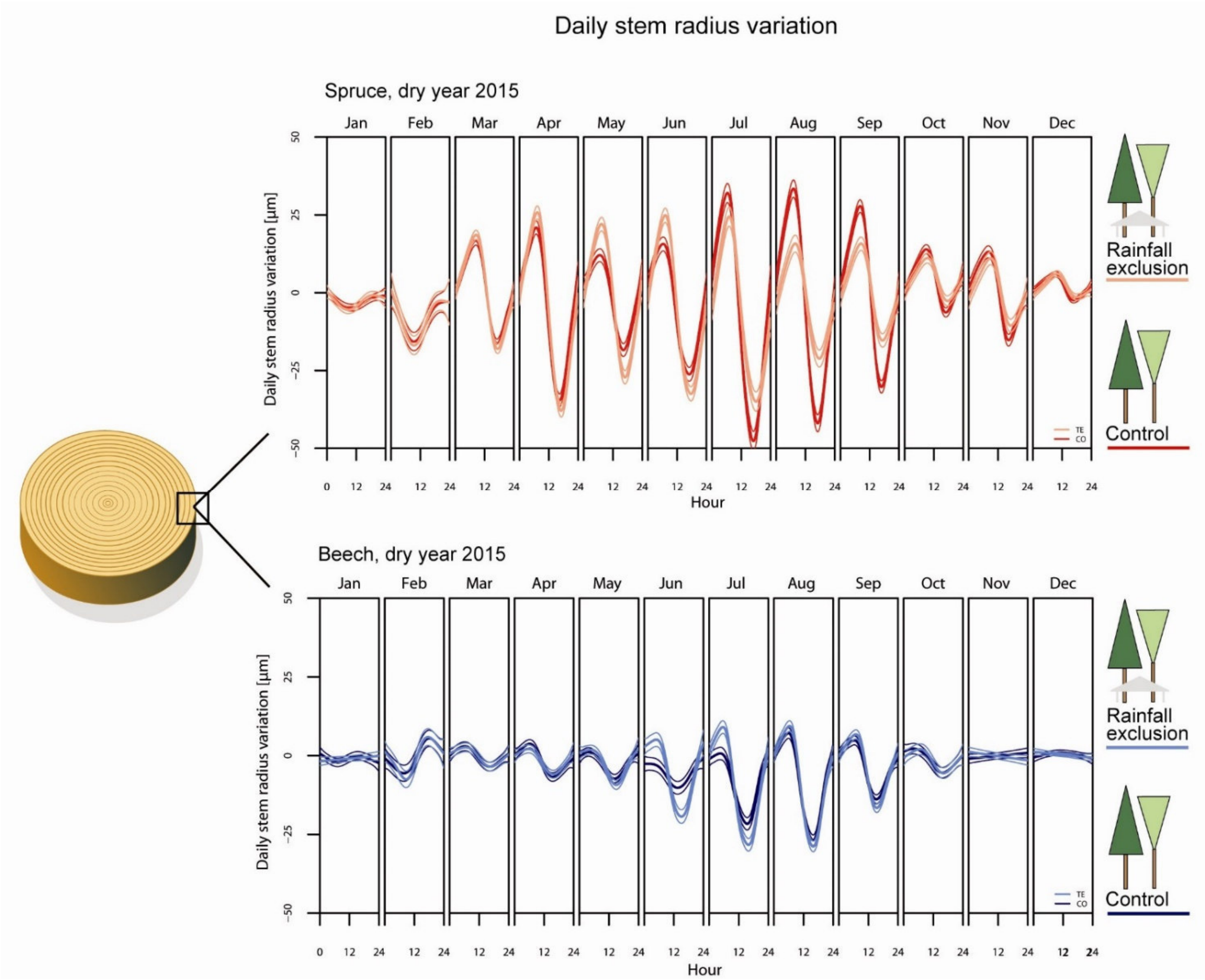
Article III


Daily stem radius variation
Spruce, dry year 2015
Beech, dry year 2015
Jan
Feb
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50
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Rainfall exclusion
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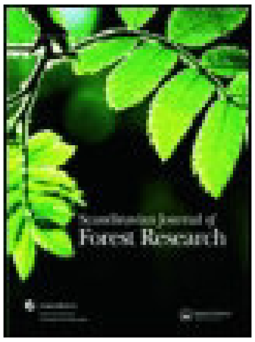

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Daily stem water deficit of Norway spruce and European beech in intra- and interspecific neighborhood under heavy drought

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ABSTRACT

High-resolution measurements of stem radius variations provide information about the tree water status with changing climate conditions by swelling and shrinking due to the reduction of xylem water potential and to the exceedance of leaf transpiration over root water uptake. The aim of this study was to analyze daily stem radius variations of Norway spruce and European beech in intra- and interspecific neighborhood. The experimental plots are part of a rainfall exclusion experiment. These variations are species-specific, i.e. spruces have a higher phloem thickness and higher amplitudes during a day than beeches. The amplitudes were significantly higher at the rainfall exclusion plots, but the amplitudes of spruces decreased above 27°C with increasing drought due to reduced transpiration rates and exhausted soil water reserves. The shrinking amplitude was observed for spruces in intraspecific neighborhood from a soil volumetric water content of 0.21 $m^3 m^{-3}$. In interspecific neighborhood, a shrinking amplitude for spruces could not be observed and revealed a lesser tree water deficit than in intraspecific neighborhood. Beeches showed minor differences with a higher tree water deficit in interspecific neighborhood. Consequently, stem radius variations give insights into a tree's water supply, which could help to understand changes in tree growth.

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Introduction

Forests are strongly influenced by the global climate, in particular, due to the concentration of the greenhouse gas CO_2 and the influence on the hydrological cycle, i.e. the water storage and transpiration back to the atmosphere (Hutjes et al. 2003; Gerten et al. 2004; Van der Molen et al. 2011). More intense, frequent and longer lasting heat waves are observed increasingly in parts of Europe (Meehl and Tebaldi 2004; IPCC 2013) and represent a large challenge for temperate forests (Rötzer et al. 2013). Drought reactions of trees are visible, among other physiological behavior, in growth reductions and changes in stem water content (Oberhuber and Gruber 2010; Köcher et al. 2012; Vieira et al. 2013; Oberhuber et al. 2015). Variations in stem radius are the result of the irreversible component "growth" and the reversible component "water loss and refilling of the cells in elastic phloem tissues". The xylem undergoes small fluctuations, but radius variations are mostly restricted to the extensible tissue outside of the cambium (Zweifel et al. 2000; De Schepper and Steppe 2010). Due to transpiration, the stem contracts during the daytime and replenishes over night and at rainy days through water uptake by roots (Dobbs and Scott 1971; Brough et al. 1986; Zweifel and Häsler 2000; Zweifel et al. 2001; Deslauriers et al. 2007; Vieira et al. 2013). Accordingly, the daily stem radius variation can give an overview of the tree water status and can quickly change according to weather conditions (Deslauriers et al. 2003; Zweifel et al. 2005; King et al. 2013). Automatic dendrometers permit the direct assignment of plant responses to environmental influences by recording stem radius at a high temporal resolution.

For adaptive forest management strategies in view of a changing climate, an understanding of the stress physiology for different tree species is crucial. Two widespread tree species in central Europe are Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]). Both species vary in their reaction to drought stress (Pretzsch et al. 2014; Goisser et al. 2016). As a boreal, mountainous tree species, spruce is known as vulnerable against climate change (Ammer et al. 2008; Zang et al. 2012). A rising temperature and drought events will increase the vulnerability of spruce trees (Lindner et al. 2010). In contrast, beech trees are known as a more drought-resistant species compared to spruce (Ammer et al. 2008; Pretzsch et al. 2013). Both tree species have different crown structures (Pretzsch and Schütze 2005; Bayer et al. 2013), stomatal behavior (Lyr et al. 1992; Klein 2014), root systems (Bolte et al. 2003, 2004) and differ in their phenological development (Rötzer et al. 2004) and xylogenesis period (Bouriaud et al. 2005; Martinez Del Castillo et al. 2016). Several mixed stands studies showed that these different tree morphologies can enhance resource use by height (Thurm and Pretzsch 2016) and root stratification (Bolte and Villanueva 2006). Furthermore, mixing of spruce and beech may improve resource availability

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(Rötzer et al. 2013; Forrester 2014), through spatial niche separation above and belowground (Richards et al. 2010) and increase stability and productivity (Kelty et al. 1992; Pretzsch 2005; Forrester 2015; Thurm and Pretzsch 2016). Severe drought can trigger temporary declines in the productivity of the less competitive species (Pretzsch et al. 2013). In this context, the determination of the daily stem radius fluctuations from a conifer and broadleaf species within a rainfall exclusion experiment can improve knowledge about the tree water deficit under longer lasting and extensive drought events and whether an interspecific environment can have a facilitated effect on one or both of the species.

King et al. (2013) studied the daily stem radius variations of larch and spruce trees dependent on climate and along a temperature gradient in the central Swiss Alps. We continued this method with species-specific and mixture-specific daily cycles under extreme conditions. We analyzed the daily stem radius variations of 24 European beech and 24 Norway spruce trees within the intra-annual courses of the years 2014 and 2015 by using point dendrometers.

We separated the growth-induced stem expansion from reversible tree water deficit and analyzed (i) species-specific differences of daily radius changes under no stress and drought stress conditions (control vs. extreme drought induced by the rainfall exclusion experiment), (ii) differences in intra- and interspecific neighborhood of spruce and beech and (iii) the influence of environmental drivers. We hypothesized (1) that Norway spruce reveals a more sensible reaction on dry conditions than European beech trees through more distinct modifications in the stem radius amplitudes and (2) that interspecific neighborhood has a facilitated effect on Norway spruce and reduces the use of water reserves in the living tissues of the stem, especially under drought due to higher soil water storage in interspecific neighborhood compared to intraspecific neighborhood.

Material and methods

Site description and experimental design

The study is located in southern Germany, near Freising at the Kranzberger Forst, about 35 km in the north-east of Munich (longitude: 11°39′42″E, latitude: 48°25′12″N, elevation 490 m .a.s.l). The experiment was established in a managed, mature forest stand of spruce and beech. The mean stand height amounted to 26.1 m for beech and 29.0 m for spruce trees with an average diameter at breast height of 28.9 cm for beech and 34.3 cm for spruce trees. The soil is classified as a luvisol originating from loess over Tertiary sediments with a high nutrient and water availability (Göttlein et al. 2012). The available water for the plant ranges between 17% and 28%, depending on soil depth.

For the period 1971–2000, the annual precipitation averaged of the study site was between 750 and 800 mm yr^{-1} and in the growing season (mid-April to the end of October) between 460 and 500 mm yr^{-1}. The annual average temperature is at 7.8°C and 13.8°C during the growing season (Hera et al. 2011).

The site includes 12 plots with 4 measurement trees (M-tree) per plot. Each plot comprises a spruce M-tree with neighboring spruce trees and a beech M-tree with neighboring beech trees (intraspecific neighborhood), as well as a spruce M-tree with neighboring beech trees and a beech M-tree with neighboring spruce trees (interspecific neighborhood). In total, intensive measurements were done at 48 trees. The age of trees varies between 66 ± 2 years for spruce and 86 ± 4 years for beech (in 2017). For the rainfall exclusion experiment, six roof constructions were built under the crown of the trees at about 3 m height. The other six plots act as control plots. In spring 2010, all plots were trenched with a heavy-duty plastic trap to about 1 m depth, to avoid external effects and lateral water inflow to the experimental plots (Pretzsch et al. 2016). To exclude unintended micro-meteorological and physiological effects, the roofs only close during rainfall with an automatic control through precipitation sensors (Pretzsch et al. 2014). The annual drying cycles with roof closing began in May up to December 2014 and from March to November 2015. Therefore, the effects of rainfall exclusion are visible after this date in spring.

Data collection

Stem radius variations of 24 European beech and 24 Norway spruce trees were monitored since April 2014. The measurement trees were equipped with automatic radius dendrometer of the DR-type (Ecomatik, Dachau, Germany) in breast height (1.3 m) and north-east direction to avoid weather influences. From spruce trees, the outermost tissue of the bark was removed, to reduce hygroscopic swelling and shrinking effect of the outer bark. The aluminum frames of the dendrometers were fixed with screws on the tree stem. A linear variable transducer was directly in contact with the bark. The temperature sensitivity of the sensor was <0.1 µm K^{-1} (Ecomatik, Dachau, Germany) and was not further corrected. For the determination of the daily stem radius cycles, the years 2014 and 2015 were used. Measurements were done every 10 min. The bark thickness was calculated according to Kirschner (1976). The mean bark thickness was 1 ± 0.1 cm for beech and 2 ± 0.15 cm for spruce trees.

The applied weather data were obtained from two sources. The data for temperature and relative humidity were measured in 10 min intervals in the forest stand. Temperature data were monitored with a temperature sensor (RTF-2, UMS) at a height of 27 m and stored in a datalogger (Logger Campbell CR1000, Multiplexer AM16/32). A ventilated radiation shield protected the measurements against direct irradiation. These data were used to calculate the vapor pressure deficit (VPD). Data of precipitation were used from the nearby climate station at Kranzberger Forst, about 2 km from the study site (Bavarian State Institute of Forestry (LWF) 2015). Also, the climatic water balance (CWB) was calculated (CWB = precipitation – potential evapotranspiration) with the data from the weather station.

Soil moisture (i.e. volumetric soil water content, SVWC) was measured via time domain reflectometry (TDR 100, Campbell Scientific, Inc., Logan, Utah, USA). The probe signal measured SVWC at a soil depth of 10–30 cm. At this depth, one TDR probe was installed within each of the three interaction zones of beech and spruce (BB, SS and MIX) on each of the 12 plots. Sensor signals of all probes were assessed weekly throughout the year.

Separating growth signal and tree water deficit

For the analysis of daily stem radius characteristics, hourly averages were calculated. To determine variations in the stem radius due to reversible stem shrinkage, the stem water signal was considered separately from the growth signal. For the separation, we used the zero growth concept according to Zweifel et al. (2016) which results in growth curves with a stepwise shape. The growth increases when the current maximum of the stem radius is exceeded (blue upper line, Figure 1(a)). The tree water deficit was calculated as the difference between the full hydrated stem and the shrinking (Figure 1(b)). Negative values indicate increasing tree water deficit. Daily fluctuations of the stem radius are represented as a sine wave with a morning maximum (between 5:00 h and 6:00 h MEZ) and a minimum in the late afternoon (between 16:00 h and 17:00 h). The differences in the daily maximum and minimum of the sine wave were used to calculate the daily amplitude of the tree water deficit. Data are illustrated based on the day of the year (DOY).

Data analysis

To investigate the influence of temperature, precipitation and the VPD on the tree radius variation, a linear mixed-effect model (R packages lme4, lmerTest) was applied (Bates et al. 2015; Kuznetsova et al. 2015). The climatic variables were used as fixed effects and plot number as well as tree number as random effects. In addition, the generalized additive mixed model (GAMM, R package mgcv) (Wood 2011) was applied for the illustration of the daily radius variation courses of each month related to species, neighborhood effects and rainfall exclusion. The GAMM characterizes the non-linear relationships between the covariates and stem variations with cubic regression smoothing splines. The confidence intervals show significant differences if there is no overlapping between the curves. The analysis was performed with the R version 3.2.3 (R Core Team 2015).

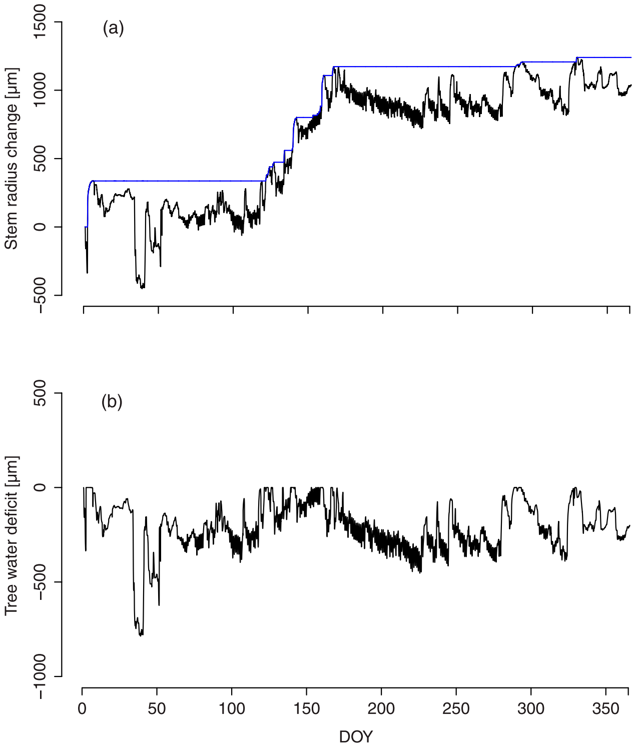

Figure 1. Stepwise illustration of the tree water deficit. The separation of the reversible stem radius changes and the irreversible growth trend line (blue upper line) are shown in (a). The tree water deficit is calculated as the difference between growth trend and the measured stem radius change (b). For the illustration, we chose a spruce tree.

Results

Climate of the years 2014 and 2015

The year 2014 was very warm but rainy (Figure 2(a–d)). Some heavy rain events in the summer months yielded in sums up to 50 mm per day. The highest mean daily temperature was measured in June with 24.7°C. Maximum temperatures were reached in June to August with up to 30°C. Compared to the year 2014, the year 2015 was a very dry year. In July and August, longer periods can be seen without or with very low precipitation. The temperatures reached 35.8°C in August, the mean daily temperature was 26°C. The months June to September showed a huge number of days with a temperature above 31°C.

Soil moisture of the years 2014 and 2015

Figure 3 depicts the SVWC of the years 2014 and 2015 under spruce and beech trees in intra- or interspecific neighborhood. In spring, summer and autumn, spruce trees at the rainfall exclusion plots (TE) had a higher SVWC in interspecific environment compared to trees in intraspecific neighborhood. The SVWC of beech trees was higher in intraspecific neighborhood at the control plots (CO), while no differences can be seen in the summer months at the TE plots. In the winter months, as well as in springtime, beech trees in intraspecific environment had a higher SVWC than in interspecific environment.

Species-specific differences of daily stem radius oscillations

The stem radius variations over the years 2014 and 2015 show the species-specific radius growth and daily shrinking and swelling of the M-trees (Figure 4). Beech trees revealed a significant lesser radial stem growth in 2014 than spruce trees. Spruces on the CO plots revealed a higher increment in 2014 (2.5 ± 1.0 mm yr^{-1}) compared to the trees of the TE plots of the same year (1.5 ± 0.5 mm yr^{-1}). The growth of spruce trees is significantly reduced in the dry year 2015 (1.7 ± 0.6 mm yr^{-1} at the CO, 0.3 ± 0.1 mm yr^{-1} at the TE). In 2014, beech trees showed an increment of 1.2 ± 0.4 mm yr^{-1} at the CO and 0.9 ± 0.3 mm yr^{-1} at the TE plots. In 2015, the growth of beeches at the CO plots increased significantly to 1.6 ± 0.6 mm yr^{-1}. At the TE plots, beech trees revealed also a

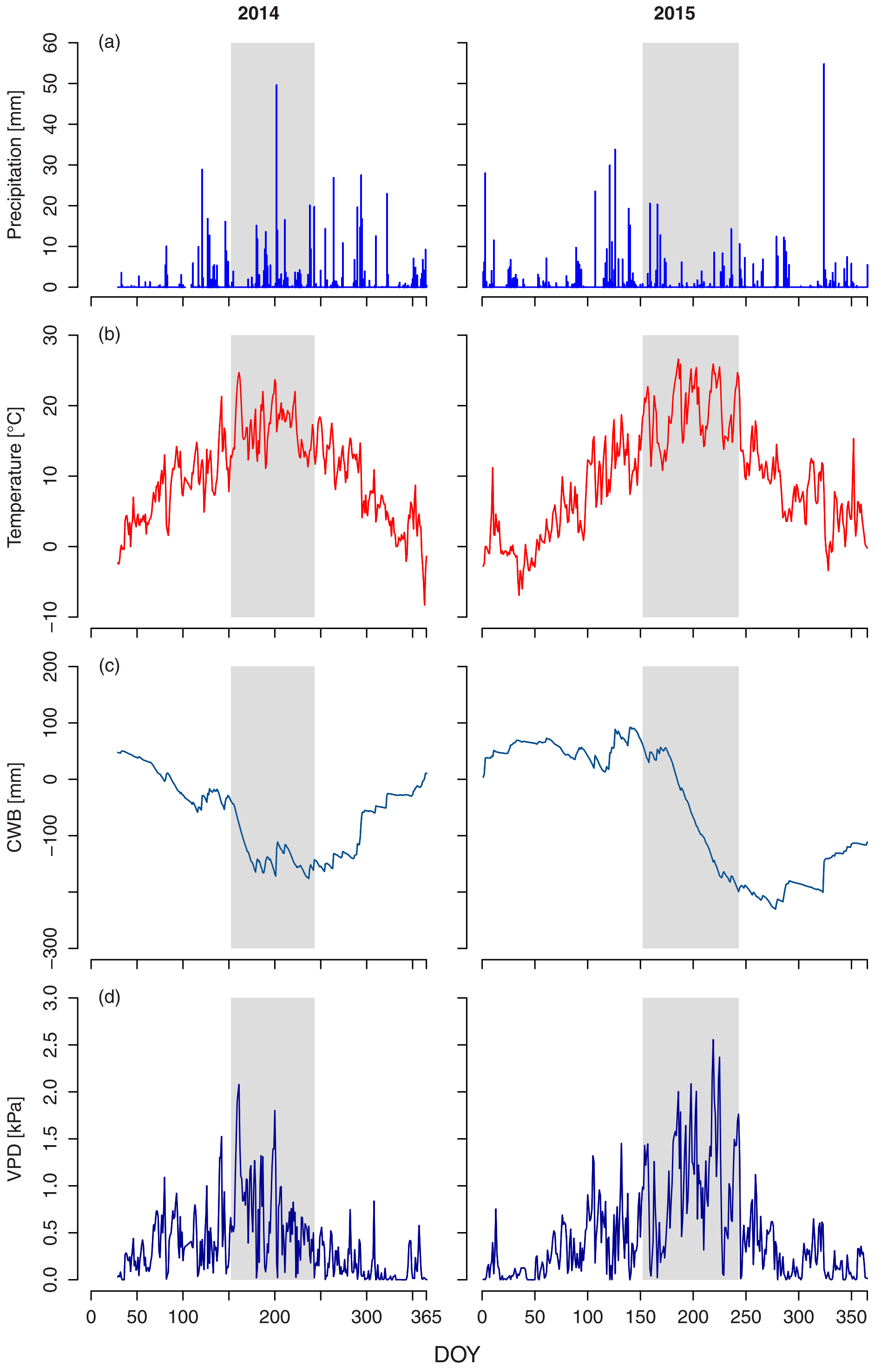

Figure 2. Course of daily precipitation (a), daily mean temperatures (b), daily CWB (c) and mean daily vapor pressure deficit (VPD) (d) in 2014 and 2015, respectively. The summer months (JJA) are shaded in gray.

higher increment in 2015 (1.0 ± 0.4 mm yr^{-1}), but it was not significantly different from the year 2014. Spruce trees had a significantly lower increment in 2015 than beech trees. There are no significant differences between intra- and interspecific neighborhood (Rötzer et al. 2017).

The daily course of the stem radius amplitudes on the base of a GAMM reveal species-specific and climate dependent courses (Figure 5). Spruce trees (Figure 5(b,d)) exhibit more distinct amplitudes than beech trees (Figure 5(a,c)) with greater differences between the morning maximum and late afternoon minimum. The amplitudes vary within the year with observable differences between the months and between the subsequent seasons. The mean amplitude is more pronounced in the summer months (mean 75 ± 37 µm for spruce, 35 ± 25 µm for beech) than in the winter months (mean 53.9 ± 42.1 for spruce, 19.5 ± 43.2 µm for beech). While spruce trees can transpire over the whole year, beech trees show a winter quiescent due to defoliation. At this

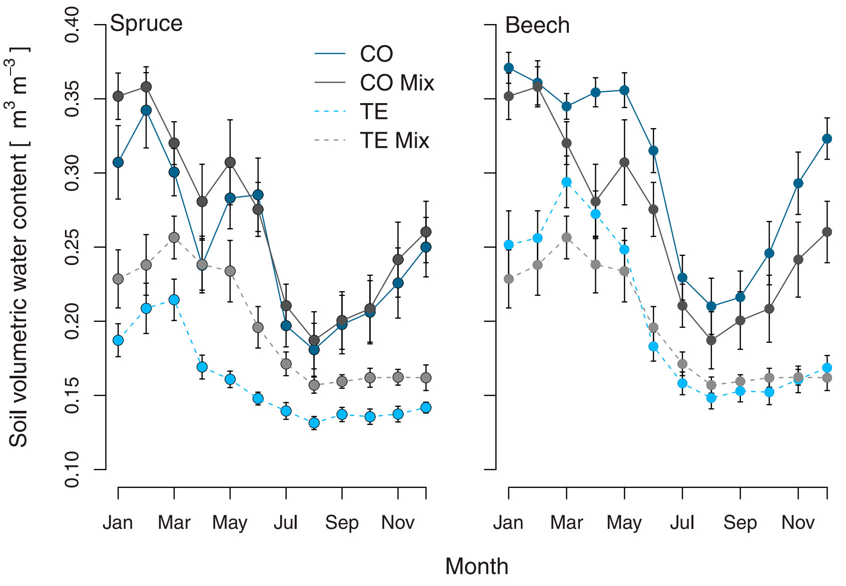

Figure 3. Monthly means of the volumetric soil water content (SVWC) at the control (CO) and rainfall exclusion plots (TE) in intraspecific and interspecific neighborhood (MIX) with confidence intervals (95%): monthly means from January to December averaged over the years 2014 and 2015, assessed weekly at each plot in 10–30 cm soil depth. From May 2014 and March 2015, the roof closed automatically in case of rainfall.

phase, no fluctuations can be seen for beech trees, except freezing events when the air temperature is below −4°C.

Significant differences between the CO and TE are observable for beech trees in the years 2014 and 2015 with no overlapping of the confidence intervals (Figure 5(a,c)). The trees of the TE plots indicate higher amplitudes and, in consequence, higher tree water deficits during the day, particularly in the summer months. Spruces had a significantly higher amplitude under drought and warm conditions, i.e. at the TE plots in May and June 2015 (Figure 5(d)); while in 2014, no significant differences between CO and TE plots could be observed for spruce trees (Figure 5(b)). Overall, the daily amplitude increased with a rise in the temperature, except at heavy drought conditions. In July 2015, the amplitude of spruce trees at the TE plots began to shrink at high temperature values and with increasing drought stress (Table 1). At the TE plots, the amplitude was significantly smaller than at the CO plots (Figure 6). From March to May, when the VPD was low and soil water content high (rainfall exclusion started in April), the slope of the regression line of the daily stem radius changes for both species was similar. In summer, however, when the VPD was high and the soil water content low (particularly at the TE plots), the slope was significantly different for the CO and TE plots (Table 2, summer phase) with a decreasing amplitude at the TE plots.

The influence of the climatic variables, temperature and VPD, on daily stem radius variations is shown in Table A1. For the years 2014 and 2015, both variables are the main driving factors of the daily stem radius fluctuations next to soil moisture and precipitation (Table A2). The influence of all variables was significant.

Inter- and intraspecific neighborhood

For the comparison of intra- and interspecific neighborhood, we also built a GAMM model (Figure 7(a–d)). There were no significant differences between intra- and interspecific neighborhood except for spruce trees in the summer months of 2015 (Figure 7(d)). In June 2015, spruce trees in intraspecific environment had a significantly higher amplitude at both rainfall exclusion and control plots. In August, daily amplitudes of spruce trees were approximately 16% smaller in interspecific neighborhood than in intraspecific neighborhood.

Figure 8 illustrates the relationship between the daily amplitude and daily maximum temperature. Higher temperature values (>25°C) and continuing drought increased the stem radius amplitude of spruce trees at the CO. For spruce at the CO plots, significant differences are obvious between intra- and interspecific neighborhood above a temperature of 27°C. Spruces in intraspecific neighborhood had a higher amplitude with increasing temperature than of spruces in interspecific neighborhood. Due to the extreme summer drought in 2015, the amplitude of spruce trees at the TE plots began to decrease at temperatures above 27°C. There are no differences between intra- and interspecific neighborhood at the TE plots for spruce trees. For beech trees, the stem radius amplitudes were highest at the TE plots in relation to the daily maximum temperature and increase with increasing temperature. Differences of TE and CO plots are visible at a temperature above 15°C.

The daily amplitudes of both species are dependent on the soil moisture next to weather conditions. The daily amplitudes of spruce and beech are presented as contour lines depending on maximum temperatures and soil moisture in intra- and interspecific neighborhood (Figure 9). The relationship of daily amplitudes and maximum temperature and soil moisture revealed significant differences for all cases (spruce and beech in intra- and interspecific neighborhood) (Table A3). At a SVWC of 0.15 $m^3\,m^{-3}$ and a temperature of 30°C, spruce trees had an amplitude of 84 µm in intraspecific neighborhood and 70 µm in interspecific neighborhood. Accordingly, spruce in intraspecific environment had a higher tree

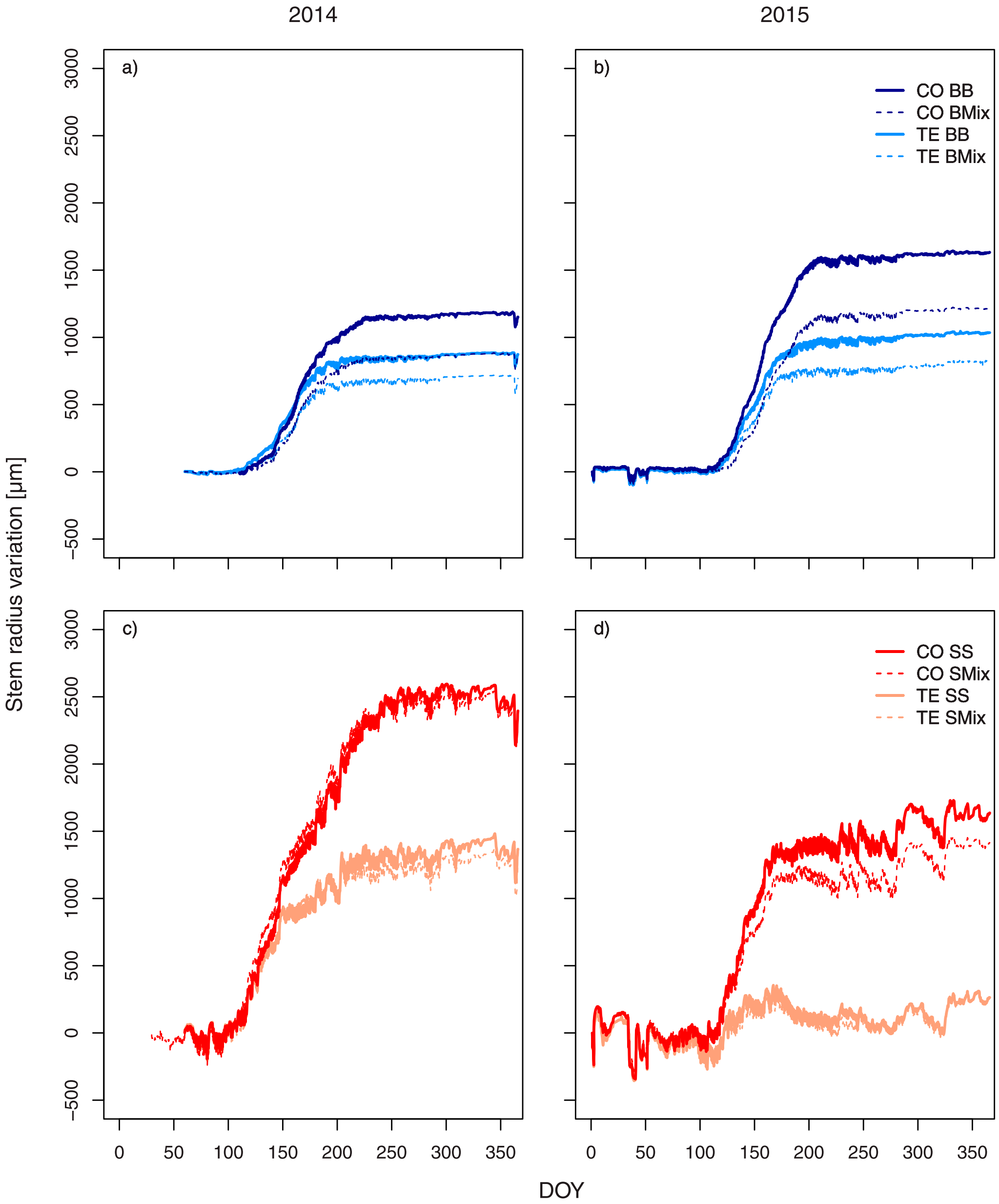

Figure 4. Mean stem radius variations of beech (a–b) and spruce trees (c–d) of 2014 and 2015 in intra- (bold (SS, BB) and interspecific (dashed line (SMix, BMix)) neighborhood of rainfall exclusion (TE, light color) and control plots (CO, dark color).

water deficit and reduced the amplitude due to exhausted soil water reserves. Beech trees showed at the same soil water content and temperature amplitudes of 39 µm in intraspecific neighborhood and 35 µm in interspecific neighborhood. With rising temperatures, the amplitudes increased, except spruces in intraspecific neighborhood. At a decreasing soil moisture, the amplitudes began to shrink from a SVWC under 0.21 $m^3 m^{-3}$.

Discussion

Daily stem radius oscillations under varying soil moisture conditions

Stem radius variations of spruce and beech trees were analyzed in a rainfall exclusion experiment within the scope of intra- and interspecific neighborhood. The daily stem radius variations revealed seasonal temperature and moisture-

Table 1. Mean daily amplitude (ΔR) of spruce and beech trees at the rainfall exclusion and control plots in June–September 2015 with monthly mean maximum temperature, mean VPD and mean SVWC at the control and rainfall exclusion plots.

	Spruce ΔR (µm)	Beech ΔR (µm)	Spruce ΔR (µm)	Beech ΔR (µm)	Max temp (°C)	VPD (kPa)	SVWC	SVWC ($m^3 m^{-3}$)
Month	Treatment	Treatment	Control	Control			Treatment	Control
June	65.5 ± 28.0	26.0 ± 18.2	48.4 ± 32.0	24.4 ± 35.0	22.6 ± 4.9	0.7 ± 0.4	0.17 ± 0.03	0.3 ± 0.06
July	61.2 ± 23.1	39.0 ± 17.5	82.9 ± 41.7	32.7 ± 28.0	27.8 ± 4.7	1.2 ± 0.4	0.15 ± 0.02	0.2 ± 0.05
August	52.8 ± 16.9	39.6 ± 18.3	86.0 ± 41.8	40.7 ± 38.1	28 ± 5.6	1.2 ± 0.6	0.14 ± 0.02	0.15 ± 0.03
September	43.1 ± 22.1	26.6 ± 14.5	75.0 ± 37.1	26.8 ± 35.5	18.6 ± 4.6	0.5 ± 0.2	0.14 ± 0.02	0.15 ± 0.03

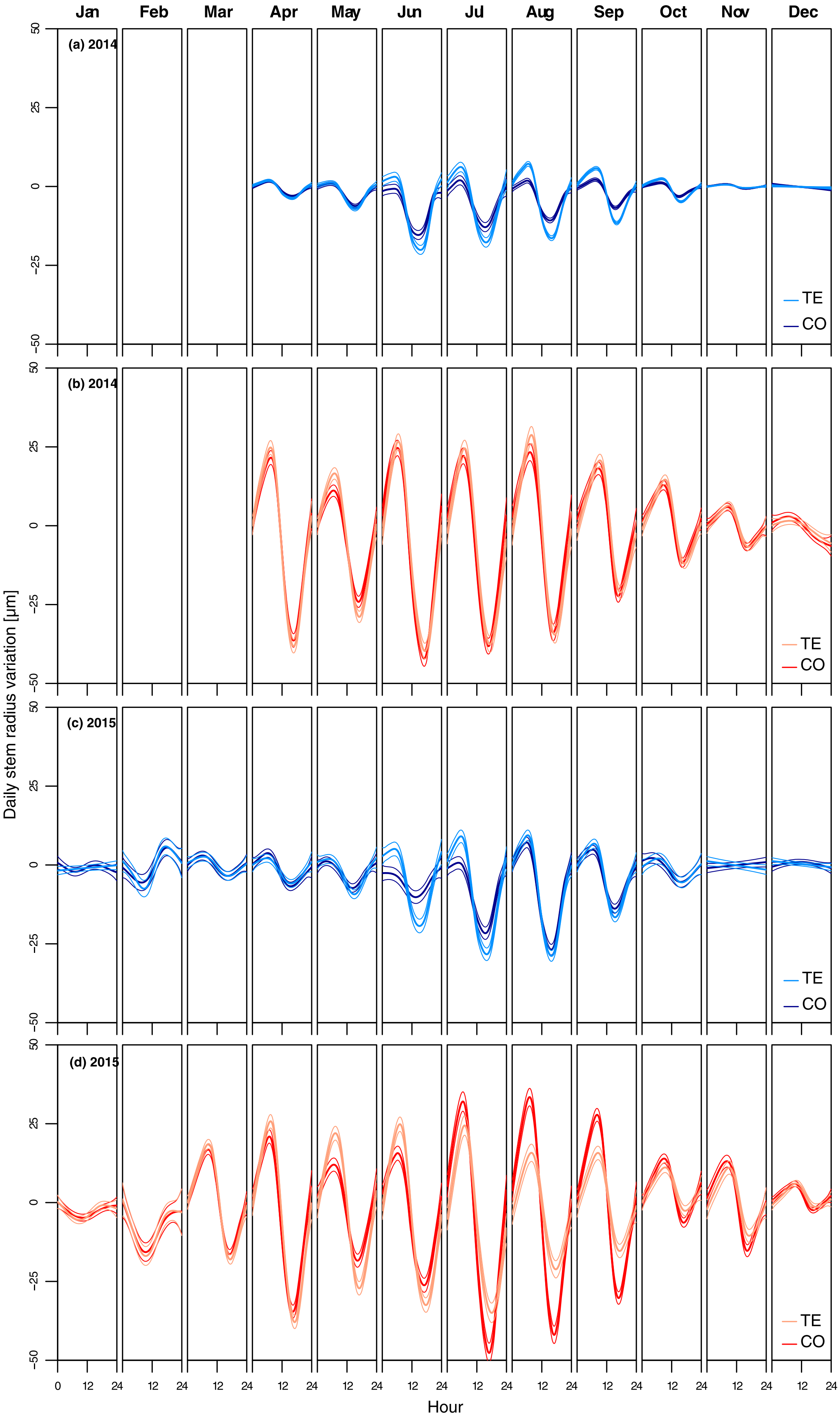

Figure 5. GAMM of daily stem radius variation (amplitude) of each month for the years 2014 (a–b) and 2015 (c–d) of all measurement trees. The fluctuations of spruce (red lines, panel b and d) and beech (blue lines, panel a and c) are separated by control (CO, dark color) and rainfall exclusion (TE, light color) plots. Lines are cubic smoothing spline fits (bold line) and surrounding lines are 95% confidence intervals (thin lines). No overlapping of confidence intervals reveals significant differences.

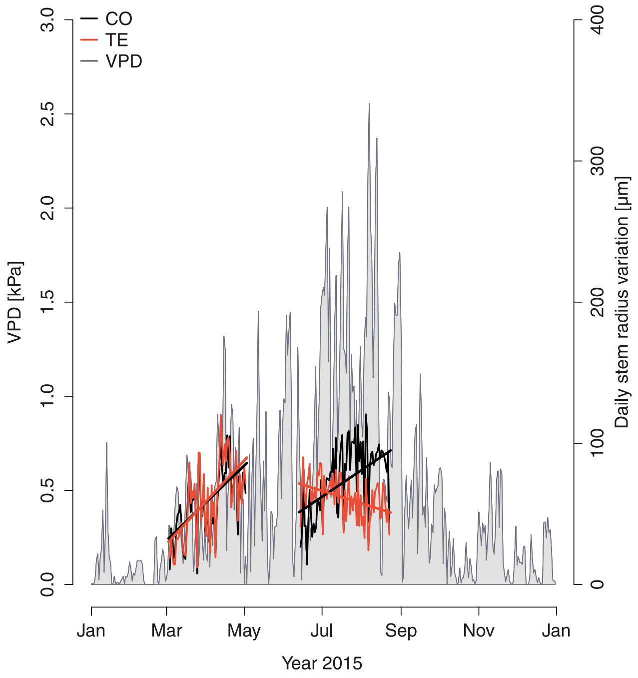

Figure 6. Mean daily VPD (shaded in grey) and daily stem radius change of spruce trees at control (CO, bold black line) and rainfall exclusion (TE, bold red line) plots with a linear mixed-effect model (regression lines). The model is illustrated for the spring (March–May) and summer month (June–August) ($P < .01$) at the year 2015.

dependent courses with differences between intra- and interspecific neighborhood in the summer month, particularly under extreme dry and hot conditions. The daily fluctuations reflect the potential water gradient driven by transpiration and by the roots water uptake. This was observed for the daily stem radius maximum at the morning and a subsequent shrinking until early evening when the transpiration process falls below water absorption by the roots (Landsberg 1986; Herzog et al. 1995; Steppe et al. 2012; De Swaef et al. 2015). The shrinkage is a result of the water flow from the living phloem cells to the xylem, when the xylem water potential is reduced. As a result, cell turgor follows the same trend as the stem water potential. Later in the evening when transpiration ceases, the cell turgor rises because of rising stem water potentials and water flow from the xylem to the living cells in the phloem (Steppe et al. 2015). Thus, the radial variations of tree stems over a day reveal changes in transpiration and soil water content related to the tree water status.

Huge differences of the stem radius amplitudes exist between summer and winter. The highest amplitudes were observed for the summer months with high transpiration rates during the day and subsequent water losses with rising temperature and radiation values (Vieira et al. 2013). As a result of freezing events in winter, changes in the daily stem radius amplitudes of deciduous beech trees were visible even though the trees were not foliated. Below −4°C, water is withdrawn from the bark tissue to the partially frozen wood tissue. In the xylem, the liquid water content can be extremely small at low temperatures. This leads to a more negative water potential and a water movement from the unfrozen bark to the partially frozen woody tissue (Zweifel and Häsler 2000). At temperatures above the freezing point, the water can replenish the phloem cells and the stem expands.

Table 2. Estimates of the linear regression for the stem radius amplitudes of the rainfall exclusion (TE) and control (CO) plots in spring and summer.

	Dependent variable	
	Spring (March–May)	Summer (June–August)
Intercept	−20.88*	−48.72***
	(*7.58*)	(*11.77*)
DOY	0.89***	0.63***
	(*0.06*)	(*0.04*)
TE	−8.49	167.18***
	(*−11.81*)	(*−18.62*)
DOY:TE	0.10	−0.92***
	(*0.09*)	(*0.06*)
Observations	1144	1380

***$p < .001$.
**$p < .01$.
*$p < .05$.
.$p < .1$.

Species-specific differences

Distinct species-specific differences of the daily course of the stem radius amplitudes are observable for evergreen spruces and deciduous beech trees. Spruce trees reveal an approximately 50% higher amplitude than beech trees, indicating a higher water loss and refilling of the living cells. An explanation for these differences is the half times greater phloem thickness of spruces compared to beeches. In consequence, spruces have greater storage tissues and more water could be used for transpiration. A further explanation is regarding the different root systems of the two species. Beech trees have a deeper rooting system than spruce trees (Bolte and Villanueva 2006). This permits beech trees to reach deeper soil horizons whereby the need to use internal stored water is limited.

The diverse stem water status of the two species is also visible when comparing the results of the rainfall exclusion and control plots. Trees at the rainfall exclusion plots, i.e. trees under drought conditions, reveal a higher amplitude and thus a higher water loss of the living cells (higher tree water deficit). The water loss of the trees through transpiration could exceed the water absorption through the roots. Spruce trees at the rainfall exclusion plots were an exception with a decreasing amplitude above 27°C. The soil water content was strongly reduced, tissues of the phloem could not be fully replenished overnight and stomata were closed. King et al. (2013) found such patterns for the conifer species larch and spruce in the central Swiss Alps. Amplitudes were one-ninth smaller on rainy days and approximately 40% larger when the daily temperatures were between 15°C and 20°C than at temperatures between 5°C and10°C. In accordance with our study, King et al. (2013) stated that the amplitudes of spruce trees began to shrink with increasing drought.

Beech trees showed larger stem radius amplitudes with rising temperature values, also under the extreme drought in the year 2015. Van der Maaten et al. (2013) determined the day-to-day stem radius variations of beech trees located at opposing north-east and south-west exposed

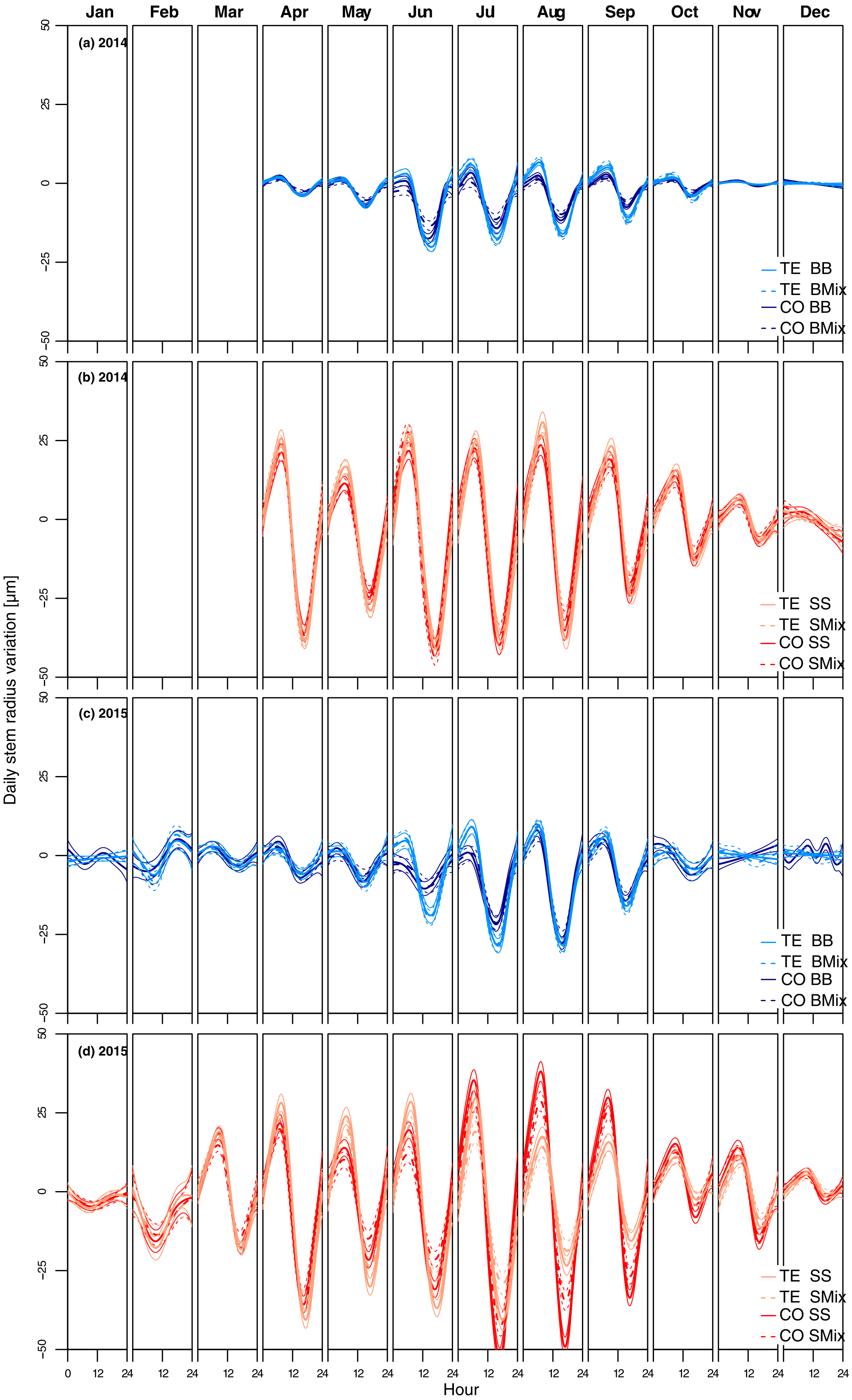

Figure 7. GAMM of daily stem radius variation (amplitude) of each month for the years 2014 (a–b) and 2015 (c–d) separated by spruce (SS, SMix, red lines, panel b and d) and beech (BB, BMix, blue lines, panel a and c), control (CO, dark color) and rainfall exclusion (TE, light color) in intraspecific (BB, SS, solid line) and interspecific (BMix, SMix, dashed line) neighborhood. Lines are cubic smoothing spline fits (bold line) and surrounding lines are 95% confidence intervals (thin lines).

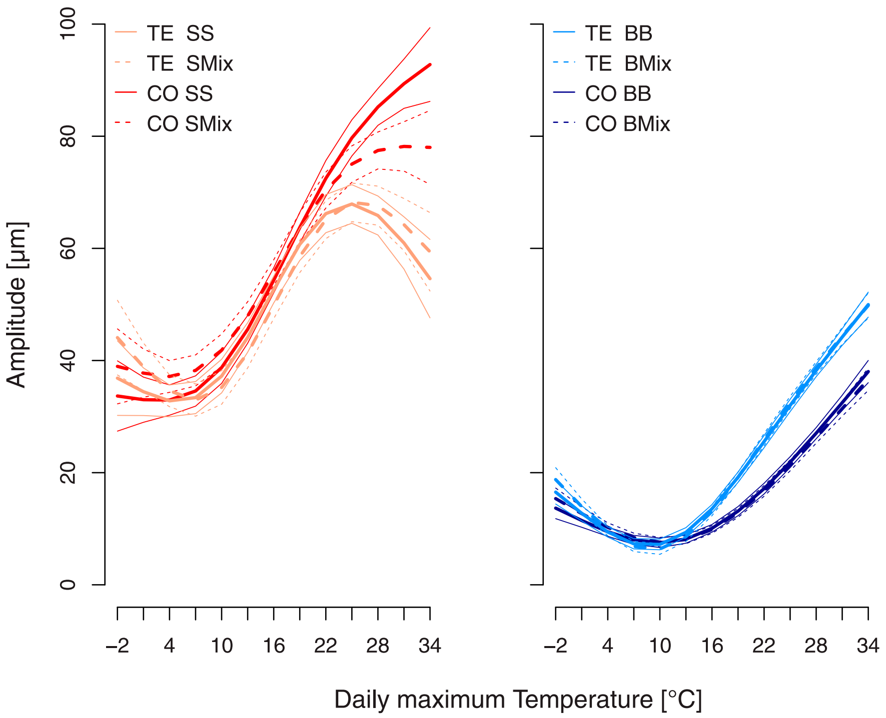

Figure 8. GAMM of the daily stem radius amplitude and daily maximum temperature of the two species spruce (S, red lines, left) and beech (B, blue lines, right) in intraspecific (SS, BB, solid lines) and interspecific (SMix, BMix, dashed lines) environment of the control (CO, dark color) and rainfall exclusion (TE, light color) plots for the year 2015. Bolt lines are the cubic smoothing spline fits with confidence intervals (thin lines).

slopes of a valley in Germany and found a high synchronicity in the daily weather response, despite large differences based on site conditions. This suggests a high flexibility of beech trees under different environmental conditions compared to spruce trees. In consequence, the first hypothesis can be confirmed that Norway spruce reveals a more sensible reaction on dry conditions with a higher tree water deficit than European beech and a decreasing amplitude at extreme drought. With its shallower rooting system, soil water reserves are faster exploited while beech trees reach deeper soil layers with additional soil water reserves. The different phloem thickness of spruce and beech could be an adaption on the different water management strategies and rooting systems.

Influence of inter- and intraspecific competition

The mixing effect on the daily stem radius variations is only visible in the dry and hot year 2015, mainly for spruce trees. They showed a smaller amplitude in interspecific neighborhood in the summer months of 2015 compared to intraspecific neighborhood. We suggest that the reduced amplitude results from an enhanced soil water supply in an interspecific environment. In the summer months, the soil volumetric water content of the rainfall exclusion plots showed higher values for the mixed situation than for spruces in intraspecific neighborhood. Spruce trees in interspecific neighborhood used a lesser amount of stem water due to a higher availability of soil water reserves. The results showed also a decreasing amplitude of spruce trees in intraspecific environment with decreasing soil water reserves at a SVWC of 0.21 $m^3 m^{-3}$. In contrast, the reduced amplitude of spruce trees under strong drought was not observable for spruce trees in interspecific neighborhood.

Neuner et al. (2015) found that spruces in mixed stands were much less affected by changing climate conditions than spruces in intraspecific competition by means of survival probabilities. This positive mixture effect might be triggered through hydraulic lift by the roots (Dawson 1993; Caldwell et al. 1998; Siqueira et al. 2008; Matyssek et al. 2010), i.e. that water is shifted from deeper to upper soil horizons. When the transpiration at nighttime is low and the tree water potential is high, the roots are surrounded with water from deeper soil layers. If the water potential is lower in the upper soil layer (e.g. under drought) than in deeper soil layers, water emerges from the lower to the upper soil layers, i.e. roots of the surrounding spruce trees can take up the water. Bolte and Villanueva (2006) analyzed the vertical root stratification of beech and spruce trees. They found that beech in mixture with spruce trees rooted in deeper soil horizons compared to monospecific beech, whereas spruce trees keep their shallow rooting system unchanged. The deeper rooting could be a benefit for the beech trees due to a higher water availability and may also reinforce the hydraulic lift effect.

The higher stem radius variations of spruce trees in intraspecific compared to interspecific neighborhood might be also due to the different soil water storages under spruce and beech trees (Rötzer et al. 2017), which affects the soil water conditions in monospecific and mixed species stands. Furthermore, spruce trees benefit with its longer wood formation period (April to August or September) (Bouriaud et al. 2005) from the neighboring of beech trees which have a short growing period (May to August) (Martinez Del Castillo et al.

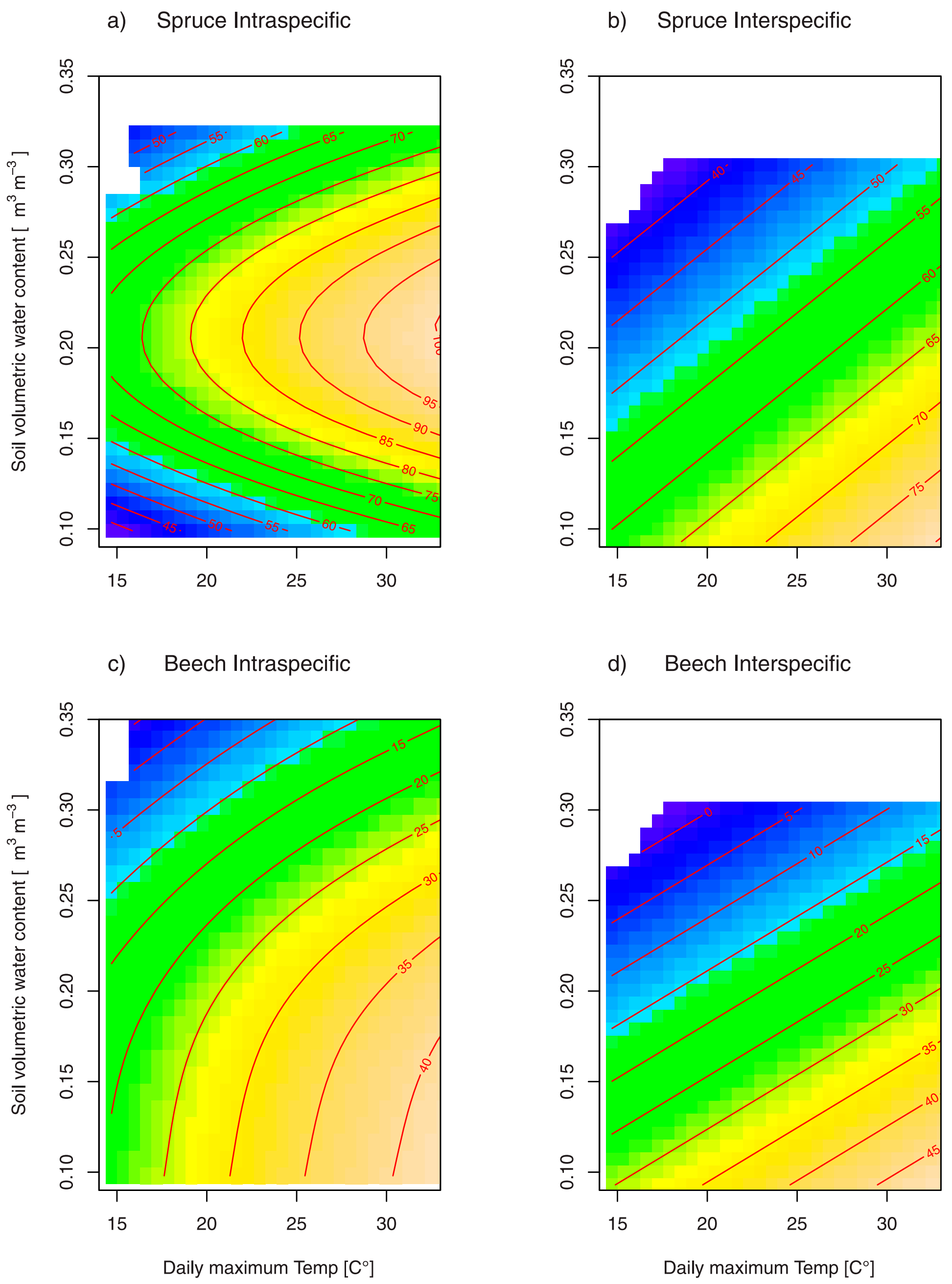

Figure 9. Mean daily amplitudes of spruce (above) and beech (below) in intra- and interspecific neighborhood depended on daily maximum temperature and soil volumetric water content in the summer months (June–September) 2015 within a GAMM model (Table A3). The contour lines show that the amplitudes depended on the maximum temperature and soil moisture.

2016). In April, spruce trees grew without water competition of beech (Thurm et al. 2016).

Schume et al. (2004) provide evidence for such a temporal partitioning of water utilization by beech and spruce trees and illustrated that mixed stands extracted a higher percentage of water from deeper soil layers than the corresponding monospecific stands. Forrester et al. (2010) found that at the leaf scale, the water use efficiency was higher for mixed than for monospecific stands as a result of an increasing photosynthetic capacity of the canopy.

In interspecific neighborhood, a higher percentage of soil water could be observed under strong aridity, which had a positive influence on the tree water status in interspecific environment. Thus, the second hypothesis can be confirmed, i.e. that interspecific neighborhood reduces the use of stem water especially under soil water shortage. For beech trees, only small differences could be detected with a higher tree water deficit and therefore a higher amplitude in interspecific neighborhood. This could be explained through the lesser intraspecific competition and self-thinning dynamics in monospecific stands under dry and poor conditions with more heterogeneous structures. The competitive release caused by mixture with spruce is thus lower (Pretzsch 2009).

Influence of climate

To estimate the climatic influence on the daily stem radius amplitudes of spruce and beech, we tested the variables temperature, precipitation, VPD and soil water content. For Norway spruce, investigations of Oberhuber et al. (2015) could find a relationship between the tree water deficit and VPD for spruce saplings but not for mature trees. He concluded that the mature trees had a more extensive root system and/or a greater water storage capacity. The different environmental conditions while the investigation period led to no relationship in the study period. Similar to our findings, other studies (Zweifel et al. 2005; Köcher et al. 2012; King et al. 2013; Van der Maaten et al. 2013) also found species-specific responses of the stem radius variations with climate. The found that relationships between soil water content and precipitation and the daily stem radius variations match well with results of Deslauriers et al. (2003, 2007), Drew et al. (2008), Ehrenberger et al. (2012) and Brinkmann et al. (2016). Deslauriers et al. (2007) described a highly water-dependent relationship on daily maximum radial stem shrinkage of *Picea abies*, *Pinus cembra* and *Larix decidua* in a timberline ecotone. The water content-related stem diameter variations were largely determined by soil water and VPD, in accordance with Ehrenberger et al. (2012) who also described the soil moisture and VPD as the main determinants of water-related stem radius changes in *Quercus robur*. Brinkmann et al. (2016) found an equal response of *Fagus sylvatica*, *Picea abies*, *Acer pseudoplatanus* and *Fraxinus excelsior* in their relative maximum tree water deficit to the onset of declining soil moisture in the field at Längeren, Switzerland. In this study, spruce trees were most sensitive to decreasing soil moisture or increasing midday maximum tree water deficit. This sensitive behavior of spruce could also be found due to higher tree water deficit at high temperatures and under strong drought. Next to precipitation and soil moisture, King et al. (2013) found a substantial effect of temperature and cloud cover on the diurnal stem radius cycles of *P abies* and *Larix decidua* along a natural temperature gradient in the central Swiss Alps.

Hereby, the highest amplitudes can be seen in the summer months, when temperature is high, while the smallest amplitudes were found in the winter month when the temperature is low. A higher temperature leads to higher transpiration rates and thus increasing stem contraction with a higher demand for water from the soil. If the soil water content is low and the temperature extremely high, the stomata close for protection against dehydration. In consequence, the amplitude decreases due to the absence of soil water for recharging the phloem cells of the bark. This results in a reduction of the carbon gain which may lead to lower stem radius growth (Deslauriers et al. 2007; Steppe et al. 2015).

Furthermore, the stem growth is closely linked to the turgor pressure of the cambium cells. Modeled data suggest that stem growth is occurring mainly at nighttime, when the water content of the storage tissue increases and the turgor pressure is high (Steppe et al. 2006). If the turgor pressure decreases due to a low water content, cell expansion of the divided cells in the cambial zone will be reduced (Hsiao and Acevedo 1974).

Measurements of stem radius variations reveal unique possibilities to determine the tree water supply in view of changing climate conditions. By using electronical dendrometers, the values are easy to record and can be analyzed for different species, species interactions and site conditions. The extensive information, which can be extracted from these measurements, can be combined with the growth trend for a better understanding of the trees' species-specific behavior under drought stress. Stem radius variations have already been analyzed in former times, but not in view of intra- and interspecific neighborhood within a rainfall exclusion experiment. The stem radius amplitudes showed clear relations with temperature, VPD and soil moisture. Furthermore, species-specific and neighborhood-specific tree water relations under extreme drought situations could be detected. Species mixture could improve the water relations for spruce trees in interspecific neighborhood due to higher soil water availability.

Geolocation information

Kranzberger Forst

11°39′42″E, 48°25′12″N

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix

Table A1. Estimates of the linear mixed-effect models for the daily amplitude of spruce/beech, at throughfall exclusion (TE) and control plots (CO) in relation to VPD and temperature (standard deviations in brackets). Significance codes: “***”: $p < .001$; “**”: $p < .01$; “*”: $p < .05$; “.”: $p < .1$.

	Dependent variable			
	Temperature 2015	Temperature 2014	VPD 2015	VPD 2014
Intercept	7.33	3.05	6.15	4.04
	(5.01)	*(5.04)*	*(5.0)*	*(4.9)*
Amplitude	0.63***	0.55***	15.06***	12.63***
	(0.09)	*(0.12)*	*(1.28)*	*(1.64)*
Species spruce	25.56***	22.13**	28.64***	25.98***
	(5.89)	*(6.29)*	*(5.86)*	*(6.11)*
TE	0.10	−2.29	1.83	2.9
	(6.83)	*(6.83)*	*(6.81)*	*(6.63)*
Amplitude: species spruce	0.98***	1.95***	13.66***	43.36***
	(0.12)	*(0.16)*	*(1.74)*	*(2.22)*
Amplitude: TE	0.58***	0.73***	7.95***	7.18**
	(0.12)	*(0.16)*	*(1.73)*	*(2.23)*
Species spruce : TE	8.01	4.80	3.29	3.22
	(8.66)	*(8.68)*	*(8.62)*	*(8.42)*
Amplitude: species spruce : TE	−1.12***	−0.75***	12.98***	15.97***
	(0.17)	*(0.22)*	*(2.54)*	*(3.07)*
Observations	15,234	14,005	15,234	14,005

Table A2. Estimates of the linear mixed-effect model for the daily amplitude in relation to precipitation at the control plots (CO) in 2015 and 2014 (left site) and soil volumetric water content (SVWC) of all plots for 2015 and 2014 (right site). Standard deviations are in brackets. Significance codes: “***”: $p < .001$; “**”: $p < .01$; “*”: $p < .05$; “.”: $p < .1$.

	Dependent variable			
	Amplitude			
	2015	2014	2015	2014
Intercept	43.38**	34.50***	33.03***	46.51***
	(10.83)	*(4.80)*	*(6.8)*	*(4.4)*
Precipitation	0.05	−0.29***		
	(0.11)	*(0.07)*		
SVWC			44.72**	−50.25***
			(15.5)	*(11.8)*
Observations	8299	6805	2208	1935

Table A3. Estimates of the GAMM model for the daily amplitudes of the year 2015 in relation to the maximum temperature and soil moisture for beech and spruce in an intra- and interspecific environment. Significance codes: “***”: $p < .001$; “**”: $p < .01$; “*”: $p < .05$; “.”: $p < .1$.

	Dependent variable			
	Spruce		Beech	
	Intraspecific neighborhood	Interspecific neighborhood	Intraspecific neighborhood	Interspecific neighborhood
Parametric coefficients:				
Intercept	71.8***	62.4	29.9***	28.7***
Approximate significance of smooth terms:				
s(TempMax)	1.180**	1*	1.5***	1***
s(SoilMoisture)	1.84*	1*	1.8***	1***
Observations	125	125	143	138