Does belowground interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem growth in *Picea abies*?

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ABSTRACT

Mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) frequently over-yield, when compared to respective monospecific stands. Over-yielding is attributed to enhanced resource uptake efficiency through niche complementarity alleviating species competition, for example through enhanced root stratification in mixture. Under severe and frequent summer drought, however, water limitation may become crucial in modifying the prevailing competitive interaction in mixed beech-spruce forests. We hypothesize, therefore, that under drought (H I) inter-specific interaction with beech reduces water accessibility for spruce more than intra-specific conditions, thus (H II) exacerbating drought susceptibility of spruce in terms of reduced photosynthesis and stem growth. Reactions at the organ (leaf, fine root), tree and stand scale were analysed in a mature forest with beech-spruce group mixture. Under inter-specific conditions spruce's fine-root production and depth of water uptake (assessed via $\delta^{18}O$ of xylem water) shifted to shallow, drought-prone soil horizons, in agreement with H I. Overall, lowered fine root production and ramification along with a reduction in long-distance explorative ectomycorrhizal types resulted in decreased soil exploitation in spruce when growing together with beech. Spruce's drought sensitivity was exemplified by a distinct decrease in stomatal conductance, net CO_2 uptake rate and stem growth during periods of water limitation. Notwithstanding, species interaction effects were absent in leaf gas exchange and stem diameter growth, during a six-week summer drought period in 2013 as well as in the extremely dry year of 2003, hence rejecting H II. Based on results from soil moisture measurements and water uptake depth, we interpret the conflicting findings for H I and H II to result from: (i) seasonal shifts between positive (during spring drought) and negative (during summer drought) effects of beech neighbourhood on soil water availability for spruce, possibly overriding each other in their effect on annual stem diameter growth and (ii) the group-wise mixture pattern, where spruce is exposed to competition with beech only along group edges, i.e. laterally only, so that the putatively adverse beech effect on water accessibility stays limited. Our results suggest, compared to single tree mixture, group-wise mixture of beech and spruce to be a favourable silvicultural option in the face of climate change.

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1. Introduction

Mono-specific Norway spruce plantations (*Picea abies* [L.] KARST.), widely promoted outside their natural distribution in Central Europe (Löf and Oleskog, 2005), have proven to be highly susceptible to biotic and abiotic stresses (Albrecht et al., 2010; Neuner et al., 2015; Rouault et al., 2006). Conversely, mixed-stands that include European beech (*Fagus sylvatica* L.) appear to warrant ecological and socio-economic services to extents similar, or even higher, than monocultures of either species (Ammer et al., 2008; Knoke et al., 2008, 2005; Pretzsch and Schütze, 2009; Pretzsch et al., 2010). The mean periodic stand growth of mixed-stands of Norway spruce and European beech and neighbouring monocultures of both species can be used for quantifying the mixing effects on growth. If the growth of the mixed-species stands equals the weighted mean of the two monocultures this indicates an additive mixing effect, i.e., the behaviour

of the mixed stand can simply be derived from the respective monocultures (Forrester and Pretzsch, 2015). In case the mixed stand's productivity exceeds the weighted mean of the monocultures this indicates a multiplicative mixing effect, i.e., species interactions result in an over-yielding of mixed versus mono-specific stands. Frequently found over-yielding of mixed beech-spruce stands may be attributed to niche complementarity of the two species, fostering resource capture efficiency rather than competition (Pretzsch and Schütze, 2009; Pretzsch, 2014; Pretzsch et al., 2012). Consistently, over-yielding in mixed beech-spruce stands is found in particular on nutrient-poor sites (Pretzsch et al., 2010). Over-yielding per se can increase temporal stability of stand-level growth rate (Jucker et al., 2014a). Such growth responses are in line with broad evidence on the positive effects of species richness on ecosystem functioning in natural species communities (Cardinale et al., 2012; Gamfeldt et al., 2013; Lehman and Tilman, 2000). Nevertheless, despite stabilizing effects of species richness on aggregate community properties, e.g. whole stand productivity, inter-specific competition may destabilize individual species populations (Lehman and Tilman, 2000; Loreau and de Mazancourt, 2013). In mixed spruce-beech forests, climate warming will likely modify competition through increasing water limitation (cf. Pretzsch et al., 2012). Most likely are substantial changes in precipitation and temperature, on global but also on a regional scale (e.g. IPCC, 2013, 2007; KLIWA, 2006). Along with distinctly differing temporal variation in annual precipitation (KLIWA, 2006) both, lengths and frequency of climate extremes such as drought may increase severely (Easterling et al., 2000; Jonas et al., 2005; Meehl et al., 2000) and hence strongly influence growth, stability of forests (Fuhrer et al., 2006). For example, reduced rain interception and enhanced stem run-off in beech as compared with spruce, positively affects soil water recharge in mixed beech-spruce systems as compared to pure spruce stands (Augusto et al., 2002; Schume et al., 2004), however, such effects become less important during prolonged periods without precipitation. In fact, higher productivity of mixed forest systems may be linked to an overall higher water demand (Forrester, 2015), resulting in increased drought stress during dry periods (Forrester, 2015; Gebauer et al., 2012; Grossiord et al., 2014a,b), hence endangering drought sensitive tree species within the community (Gebauer et al., 2012; Grossiord et al., 2014b; Jucker et al., 2014b; Maestre et al., 2009). Consistently, Schume et al. (2004) demonstrated faster and more intense (e.g. reaching deeper depths) soil water depletion during summer drought under mixed beech-spruce than under pure beech or spruce stands. In response to belowground interaction with beech, spruce's root system growth shifted vertically towards more shallow soil depths (Bolte and Villanueva, 2006; Schmid and Kazda, 2001; Schume et al., 2004). In addition, the rather conservative strategy of spruce regarding only limited adjustments of fine root morphology (maintaining or even increasing specific fine root length; Bolte and Villanueva, 2006; Grams et al., 2002) in response to drought in belowground competition with beech, implies disadvantages in water exploitation when competing with beech (Bolte and Villanueva, 2006; Schmid, 2002).

In addition to roots, mycorrhizae function in water uptake. Fine roots of both tree species are associated with ectomycorrhizal (ECM) fungi. With respect to their potential to take up water and nutrients by their external mycelium, ectomycorrhizae have been categorized as exploration types (contact, short- and medium-distance and long-distance types, cf. Agerer, 2001). Long-distance types have the potential to retrieve and transport water via distinct rhizomorphs thus may be effective in mitigating drought stress (Lehto and Zwiazek, 2011). However, under drought there may be a trade-off between carbon-costs for building and maintaining long-distance types (Weigt et al., 2011) and reduced carbon supply

from drought stressed trees which would lead to a relatively lower abundance of long-distance exploration types in carbon limited spruce compared to beech. Thus under drought, resource availability as determined by soil water content (root distribution), and carbon supply via photosynthesis (anisohydric, isohydric strategy) may influence ECM exploration types differently in mixed inter-specific vs. intraspecific situations, respectively.

In view of predicted, exacerbating summer droughts (IPCC, 2013, 2007), basic knowledge about competitive versus facilitative interactions in mature mixed beech-spruce forests is scarce, impeding silvicultural mitigation strategies. In the present study, we therefore hypothesized that under drought (H I) inter-specific interaction with beech reduces water accessibility for spruce more than intra-specific conditions, thus (H II) exacerbating drought susceptibility of spruce in terms of reduced photosynthesis and stem growth. The hypotheses are evaluated based on growth and physiological parameters indicative for stress reactivity in both tree species ranging from ectomycorrhizal exploration types to leaf gas exchange and whole-tree growth dynamics in a mature, group-wise mixed beech-spruce forest. To this end, data originating from a summer drought during 2013 and a retrospective analysis on effects of the distinct drought year 2003 are employed.

2. Materials and methods

2.1. Site description and climatic conditions

The study was conducted in a maturing mixed stand of European beech (*F. sylvatica* L.) and Norway spruce (*P. abies* [L.] KARST.) within Kranzberg Forest (FRE 813/1), located in southern Germany/Bavaria (11°39′42″E, 48°25′12″N; 490 m a.s.l.), approximately 35 km north-east of Munich. The mixed stand consists of large groups of beech (4 groups with 150–200 m^2 each) surrounded by spruce (in 2013: spruce 62 ± 2, beech 82 ± 4 years old). For the age series FRE 813 which includes the Kranzberg Forest experiment (FRE 813/1) the long-term over-yielding at the stand level amounts to 1.18 (Pretzsch et al., 2010). Under normal conditions the mixed stand is by 18% more productive than the weighted mean of the two monocultures; both Norway spruce and European beech contribute approximately the same to this over-yielding. In 2010 twelve plots were established with a total area of 1730 m^2 with a mean stocking density of 659 trees per ha and mean basal area of 52 m^2 per ha. The plots include 63 beech with a mean height of 26.1 m and a mean diameter of 28.9 cm at breast height and 53 spruce trees with a mean height of 29 m and a mean diameter of 34.3 cm at breast height. The detailed stand characteristics of the 12 plots are summarized in the supplementary material, Table S 1.

All measurements were carried out within the central area of each plot, comprising the transition between intra-specific spruce (S) and intra-specific beech (B) forming an inter-specific contact zone (MIX). Trees in the intra-specific zones are referred as SS and BB and trees in the inter-specific zone as SB and BS for spruce and beech respectively (cf. Fig. 1). For the present study, all measurements were carried out within the central area of each plot. Soil is a luvisol developed from loess over Tertiary sediments (eutric cambisols, FAO classification). The average annual precipitation (1971–2000) is 785 mm yr^{-1}, with 497 mm during the growing season. The annual mean temperature is 7.8 °C, with 13.8 °C on average during the growing season (for details see Pretzsch et al., 2012). The present study focused on three climatically different years: (i) 2003 with extraordinarily low precipitation and high air temperatures during the growing season throughout Central Europe (Ciais et al., 2005), (ii) 2012 represented by a warm growing season with average precipitation and
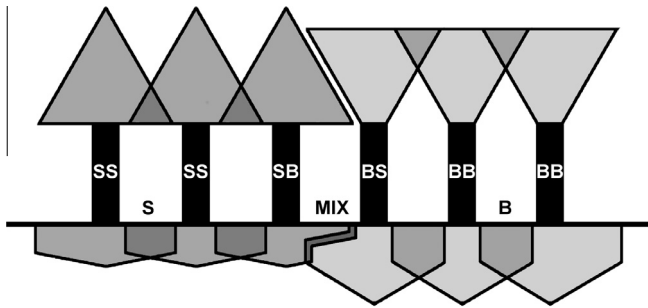
Fig. 1. Schematic illustration of trees with intra- (SS and BB) and inter-specific (SB and BS) competition in the different zones of species interaction (S, MIX and B).

(iii) 2013 with a distinct dry spell in mid/late summer paralleled by high air temperatures (Table 1).

2.2. Soil moisture

Soil moisture (i.e. volumetric soil water content, SWC) was measured via time domain reflectometry (TDR 100, Campbell Scientific, Inc., Logan, Utah, USA). Depending on installation, probe signal integrated SWC either over a soil depth of 0–7 cm or 10–30 cm. At each depth, one TDR probe was installed within each of the three interaction zones of beech and spruce (B, S, and MIX) on each of the twelve plots (n = 12; $n_{total} = 2 \times 3 \times 12 = 72$). Sensor signals of all probes were assessed either monthly during November – April, or weekly during May – October.

2.3. Fine root observation

In 2010, clear acrylic minirhizotron tubes (70 cm long, 6 cm outside diameter) were installed at an angle of 60° from the horizontal to a depth of 60 cm (51 vertical cm). A vertical depth of approximately 50 cm was chosen based on previous research at Kranzberg Forest, as >90% of beech and spruce roots being between 0 and 50 cm (Häberle et al., 2012). Each plot contained six minirhizotron tubes: two in each S and B region, and two within MIX. Each tube was located a minimum distance of one meter from the plot boundaries, and in the case of inter-specific regions, tubes were installed equidistantly from both species. Before installation, minirhizotron tubes were capped at the base with plastic plugs lined with silicon caulk to reduce water infiltration. Tubes, when not in use, were covered with large plastic caps to prevent aboveground water infiltration and light penetration. Beginning in May 2011 and ending in October 2013, contiguous images were taken across the length of each tube using a specialized laparoscopic camera (BTC100X Camera, Bartz Technology, Carpinteria, California). Just prior to leaf emergence (April) and until leaf senescence

(November), images were taken every 10–15 days. During the winter months, images were taken monthly. Images were approximately 15 mm in height, and 18 mm wide. All images were analysed for the depth of fine root production and morphology using *WinRHIZO Tron MF* (Regent Inc., Quebec, Canada). Roots that transected more than one observation window were noted and only counted once. Differences between species' roots were determined by visual inspection of epidermal coloration (spruce: brown, beech: reddish white), along with root tip branching patterns (spruce: alternate branching, beech: herringbone and often opposite branching). Root production was calculated on a per plot basis as the total number of root tips produced per square meter of viewing window.

2.4. Root and mycorrhiza sampling

The sampling campaign was carried out on the 7th and 8th of October 2013. Soil was sampled with a corer of 4 cm diameter to a depth of 25 cm. In each plot two soil cores were retrieved for S and B, but four at the MIX position. The uppermost litter layer, consisting of recently fallen leaves was removed before sampling. Each soil core was separated into an upper organic soil part ($O_{f+h}A_h$, average depth of 0–8.6 cm), in the following referred to as upper soil (UP) and a lower mineral soil part (A_lB_v, average depth of 8.6–25 cm), in the following referred to as lower soil (LO). Within each plot, two samples from each interaction zone and depth were pooled in a plastic bag and immediately stored on ice resulting in a total of eight composite soil samples per plot. Root and soil samples were stored for not longer than 4 weeks in the laboratory at 4 °C until further process. Root samples were manually separated from soil, cleaned in tap water and sorted under a microscope into beech and spruce roots. Fine roots (<1 mm diameter) were cut into pieces of 2 cm length and representative subsamples were taken for analysis of ectomycorrhizal morphotype abundances. Vital mycorrhizal tips were assigned to morphotypes based on similarities of colour and surface properties of the mycorrhizal mantle. We further used the concept of exploration types to categorize the morphotypes according to the extent to which hyphae emanating from the ECM surface exploit the soil as contact, short distance, medium distance smooth, long-distance types according to Agerer (2001).

After morphotyping the fine roots were spread on an acrylic glass trough, filled with water to submerge the roots. A flexible plastic slide of the same format was put on top of the thin water film to fix the roots at the same level by adhesion, taking care of avoiding air bubbles. Roots were then scanned (Epson Perfection 4990 Photo) with a resolution of 1200 dpi at 8 bit greyscale in TIF format. Analysis of the scans was done with the software WinRHIZO (Regent Instruments Inc., Canada). Scaled paper was used to calibrate the Software, background distinction and debris removal was performed manually.

2.5. Depth of water uptake: sampling and ^{18}O-analysis of soil and xylem water

Beech and spruce xylem as well as soil cores were sampled on the same day in late July 2012 from plots 1–8 (accessible through canopy crane), to interpolate the mean depth of water uptake of tree individuals from the instantaneous $\delta^{18}O$ gradient in soil water and $\delta^{18}O$ of xylem water (cf. Allison et al., 1983; Craig, 1961; Dansgaard, 1964; Dawson, 1993; White et al., 1985). At the time of sampling SWC was close to field capacity. Three soil cores were taken per plot to a depth of 60 cm with a hand soil probe (core diameter 2 cm). In each of the eight sampled plots one soil core was collected at B, S and MIX (n = 8; $n_{total} = 3 \times 8 = 24$). From each soil core, 3 cm sub-samples were taken from four different depths (5 cm, 10 cm, 20 cm, 50 cm). On each plot, twig xylem (twig

Table 1
Precipitation (P) and air temperature (Tair) in 2003, 2012 and 2013 in comparison with the long-term average of 1971–2000. Indexes indicate sums/means based on different periods of the respective year, A: annual, GS: growing season April – September, S: mid/late summer July – August. Bold numbers indicate significant differences from long-term average: sum/mean is below, –, or above, +, the 99% confidence interval of the respective long-term average. Data from Deutscher Wetterdienst (DWD) station "Weihenstephan-Dürnast" (station ID 5404, at about 3 km distance to the study site, 477 m a.s.l.).

	1971–2000	2003	2012	2013
P_a	785 (±88)	524 (**−261**)	786 (+1)	766 (−17)
T_a	7.9 (±0.7)	8.7 (**+0.8**)	8.8 (**+0.9**)	8.4 (**+0.5**)
P_{vp} (Apr–Sept)	497 (±72)	293 (**−204**)	509 (+12)	495 (−2)
T_{vp} (Apr–Sept)	13.5 (±0.7)	16.0 (**+2.5**)	14.9 (**+1.4**)	14.5 (**+1.0**)
P_s (Jul–Sept)	194 (±51)	107 (**−87**)	202 (+8)	97 (**−97**)
T_s (Jul–Sept)	16.8 (±0.9)	19.9 (**+3.1**)	18.5 (**+1.7**)	19.0 (**+2.2**)

sections of approx. 10 cm length and 0.5 cm diameter, bark removed during sampling) from the upper crown was sampled on one intra-specific and one inter-specific beech and spruce tree respectively. Soil and xylem samples were stored in air tight tubes immediately after sampling to prevent evaporation. Samples were stored at −20 °C until further processing. Subsequently, soil matrix water and xylem water was extracted via cryogenic vacuum distillation (cf. Ehleringer and Osmond, 1998) and analysed for their $\delta^{18}O$ signature with an isotope-ratio mass spectrometer (IsoPrime, GV Instruments Ltd., Manchester, UK; MultiFlow 222XL, Gilson Inc., Middleton, USA). Mean depth of water uptake was inferred from the intersection of $\delta^{18}O$ of xylem water and the spline interpolation of the vertical $\delta^{18}O$ profile of soil water.

2.6. Leaf gas exchange

Leaf gas exchange was assessed on one intra-specific and one inter-specific tree per species on each plot accessible by the canopy crane (n = 8), during three campaigns in 2012 (June, July/August and September) and two campaigns in 2013 (July/August and September). Measurements were carried out on sunny days between 9:00 and 14:00 CET within the crown, using sun-exposed, fully developed leaves of beech and one-year-old needles of spruce, by means of a portable infrared gas analyser (LICOR 6400, LI-COR Inc., USA) using appropriate chambers for the respective leaf types (broad leaves: 6400-02B LED light source; conifer needles: 6400-05 Conifer Chamber, LI-COR Inc., USA). Measurements were conducted at saturating photosynthetic active photon flux density ($PPFD_{SAT}$) >1300 µmol photons $m^{-2} s^{-1}$, stable CO_2 concentration of 400 ppm, ambient air temperature and humidity. At each time, measurements were repeated on three pre-selected positions within the sun-exposed crown of the respective tree individual. Gas exchange of spruce was measured on 5 cm long twig sections, averaging approximately 115 needles. In the course of the measurement campaigns in late summer, needles of each measured twig section were harvested and immediately scanned (Epson Perfection 4990 Photo, Epson Deutschland GmbH, Meerbusch, Deutschland) to determine the projected needle surface area. Considering the stomatal distribution in the leaf epidermis (spruce polydirectional, beech unidirectional), gas exchange parameters are expressed on a total needle surface area basis for spruce (conversion factor projected leaf area to total surface area: 3.2; cf. Niinemets and Kull, 1995; Perterer and Körner, 1990) and on a projected leaf area basis in beech.

2.7. Carbon stable isotope composition of leaf bulk material

In parallel with gas exchange measurements, samples of adjacent leaves and one-year-old needles were taken for stable isotope analysis, immediately stored in a cooling box at <4 °C and subsequently dried and ball-milled to a homogenous fine powder. $\delta^{13}C$ of organic leaf matter ($\delta^{13}C_{LOM}$) was determined by mass spectrometry (GVI-Isoprime, Elementar, Hanau, Germany coupled to the elemental analyser EA 3000, Euro Vector, Milan, Italy).

2.8. Tree growth performance

For the analysis of tree growth performance was conducted at the basis of long time series of stem diameter measurements (Astralon D1-K permanent tree girth tapes with Pi-units and vernier scale). Stem diameter data are recorded at the Kranzberg Forest up to 10 times per year since 1997. However, only at 9 out of the 12 plots girth tapes have been installed. Based on these measurements annual basal increments (BAI, $cm^2 yr^{-1}$) were calculated. To eliminate the influence of tree age on the annual BAI values 7-year moving averages were applied. The mean diameter of the spruce trees in 2014 was 37.7 cm (min: 23.2 cm; max: 48.8 cm) while for the beech trees the average was 32.7 cm (min: 20.5 cm; max: 52.3 cm). Indices for resistance, recovery, and resilience, i.e. Rt, Rc, and Rs, respectively, were assessed as detailed by Lloret et al. (2011) and calculated individually for one intra-specific and one inter-specific tree per species on 9 plots (n = 9 for each SS, SB, BS and BB) based on the basal area increment (BAI, $cm^2 yr^{-1}$). 7-year moving averages were employed for:

$$Rt = Dr/PreDr \tag{1}$$

$$Rc = PostDr/Dr \tag{2}$$

$$Rs = PostDr/PreDr \tag{3}$$

PreDr is the index of BAI during 2001/2002 before drought, Dr of BAI during the 2003 drought, and PostDr of BAI during after-drought in 2004/2005. Rt quantifies the decrease from pre-drought to drought, with Rt = 1 denoting unrestricted resistance (otherwise Rt < 1). Rc covers post-drought, with Rc = 1 indicating persistence at low growth (otherwise Rc < 1 denoting decline, but Rc > 1 recovery from drought). Rs represents the ratio between post-drought and pre-drought increment, with ⩾1 for recovery,
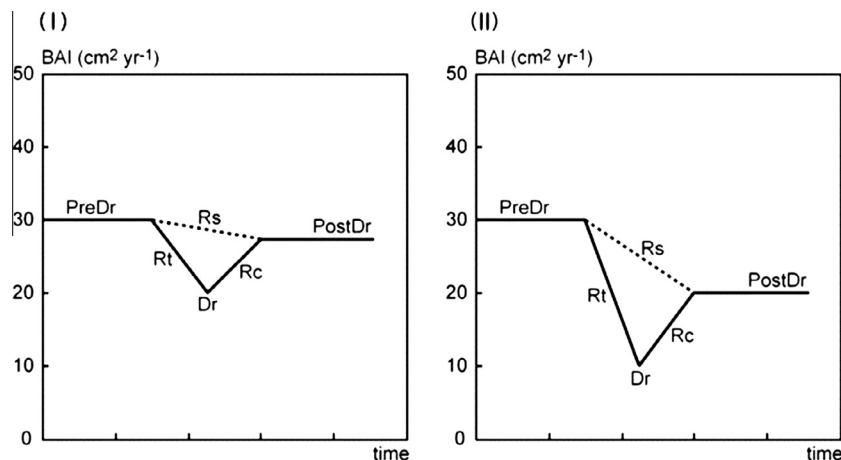
Fig. 2. Course of growth in two different stress events characterized by the growth in the period before drought, PreDr, growth during the drought period, Dr, and growth after the drought period, PostDr (modified after Lloret et al. (2011)). (I) Tree with limited growth decline in response to drought indicated by high resistance and resilience, and medium recovery. (II) Tree with strong growth decline indicated by low resistance, considerable recovery which results in a medium resilience. In the graphs Rt, Rc, and Rs are represented by the gradient of decline from PreDr to Dr, the increase from Dr to PostDr, and the difference in level of PreDr and PostDr, respectively.

but <1 for decline and low resilience. Fig. 2 exemplifies Rt, Rc, and Rs for moderate response to episodic drought (I) and strong growth reduction (II).

2.9. Statistical data analysis

The effect of intra- and inter-specific competition on temporal dynamics of soil water depletion during the 2013 drought was assessed via regression analysis. Three-parametric exponential decay functions were fitted through the overall means (12 plots) of soil water content (SWC) of the respective soil depth under S, B and M conditions (Sigmaplot, release Version 12.5.0.38, Systat Software Inc., 2011) to derive half-time ($T_{1/2}$) of SWC. Significant differences of $T_{1/2}$ were deduced from the 95% confidence intervals (CI-95%) of the respective exponential parameter λ. SWC during spring was analysed for significant differences ($\alpha = 0.05$) between measurement campaigns and intra- versus inter-specific competition using the GLM repeated measures procedure (IBM SPSS Statistics, release Version 21.0.0.0; IBM Corporation, 2012).

$\delta^{18}O$ of soil matrix and xylem water were examined for significant differences ($\alpha = 0.05$) between intra- and inter-specific competition via analysis of variance (ANOVA).

The effect of tree species (beech, spruce), interaction (B and S vs MIX), and year (2012–2013) on mean rooting depth weighted by cumulative root tip production was analysed through three-way ANOVA. Significant predictors were post-hoc analysed via Tukey HSD ($\alpha = 0.05$).

Measures of fine root morphology, assessed by the fine root samples from soil cores, were tested for significant differences by two-way ANOVA using R (R-Development-Core-Team, 2014). Values were log or square root transformed, if necessary, to ensure normality of error and homogeneity of variance. Significant predictors were also post-hoc analysed by means of Tukey HSD ($\alpha = 0.05$). To account for differing amounts of beech and spruce roots in MIX, roots from soil cores of MIX were regarded as one sample without separating species.

Effects on the abundances of ECM exploration types were evaluated using R (R-Development-Core-Team, 2014). The relative abundance of ectomycorrhizae was calculated as the percentage of tips from each exploration type within the total number of mycorrhizal tips in each sample. Differences between the B, S and MIX, soil depths and tree species were examined with the Wilcoxon Rank Sum Test on subsetted data.

Leaf gas exchange and $\delta^{13}C$ were analysed for significant differences ($\alpha = 0.05$) between measurement campaigns and intra- versus inter-specific competition using the GLM repeated measures procedure (IBM SPSS Statistics, release Version 21.0.0.0; IBM Corporation, 2012). Residuals of the calculated models were tested positively for normal distribution (KS-test). For each measurement campaign, the diurnal drift in leaf gas exchange (cf. Zweifel et al., 2002) of spruce and beech was corrected and standardized to 12:00 CET via linear regression (Sigmaplot, release Version 12.5.0.38, Systat Software Inc., 2011).

The group differences between the resistance, recovery, and resilience of Norway spruce and European beech in inter-specific versus inter-specific environment (see Table 2) were scrutinized with the two-sided *t*-test, using SPSS Statistics, Version 21.

3. Results

3.1. Accessibility of soil water for beech and spruce under inter- and intra-specific growth conditions

3.1.1. Annual course of soil water content

Average soil water contents (SWC) of 31.3 ± 2.0 SE%, 31.0 ± 2.2 SE% and 33.3 ± 2.0 SE% in 0–7 cm soil depth and 35.8 ± 1.3 SE%, 34.6 ± 1.7 SE% and 35.7 ± 1.2 SE% in 10–30 cm soil were reached upon saturating precipitation events in 2012 and 2013 for B, S and MIX respectively (data not shown), indicating similar field capacities irrespective of species interaction. Along with rising T_{air} during early spring, soil water under evergreen spruce was gradually depleted, whereas SWC remained near field capacity
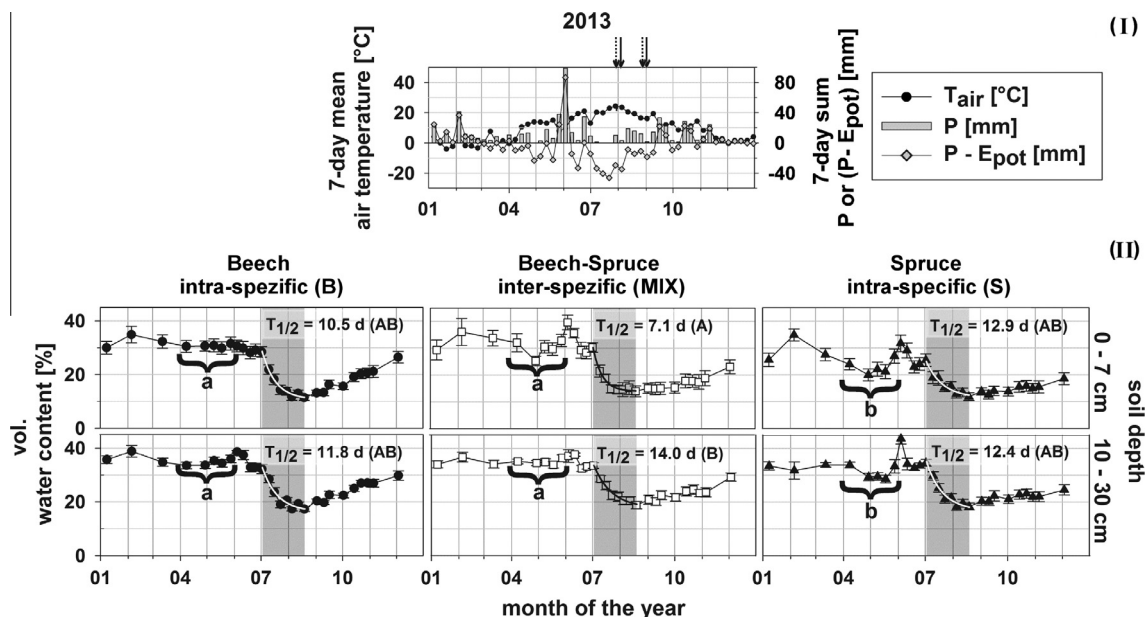
Fig. 3. (I) Climate conditions in 2013 (DWD station 5404): seven-day means and sums of field air temperature (T_{air}, closed circles) and field precipitation (P, grey bars), respectively. Difference between field precipitation and potential evapotranspiration (Penman, 1948) is given by grey diamonds. Arrows indicate dates of leaf gas exchange measurements for beech (broken) and spruce (solid) respectively. (II) Volumetric soil water contents (SWC) in the course of 2013: mean SWC (±SE) at two different depths (0–7 cm; 10–30 cm) under intra- (B; S) and inter-specific (M) conditions. Different lower case letters indicate significant differences ($\alpha = 0.05$) in SWC between species interactions during mid/late spring (8th of April through 28th of May). Half-lifes of SWC ($T_{1/2}$) in different soil depths during the dry period in mid/late summer (2nd of July through 19th of August), derived from regression analysis of the overall mean values at the respective depth of SWC in S, B and M (range of adjusted r^2: 0.98–0.93). Different capital letters indicate significant differences in λ (no overlap of CI-95% of λ) and hence in $T_{1/2}$ between species interactions and soil depths during the dry period.

under still leafless beech (for 2013 see Fig. 3 I, II; data for 2012 is not shown). In the soil layers of 0–7 and 10–30 cm, SWC was significantly lowered, therefore, in S relative to MIX and B. High precipitation at the beginning of June restored SWC almost to field capacity. During the subsequent seven-week dry spell (July 2nd through August 19th, 2013) SWC decreased monotonously. Irrespective of species interaction type, mean SWC reached between 11.4% and 13.9% at 0–7 cm and 17.3–18.8% at 10–30 cm depth towards the end of the dry period. During this period similar amounts of soil water per ground area were consumed from 0 to 30 cm soil depth in B, S and MIX ranging from 48.3 L m^{-2} to 45.2 L m^{-2} respectively. However, half-life analysis of SWC indicated faster depletion at 0–7 cm depth in MIX (T$_{1/2}$ = 7.1 days, corresponding to λ = 0.098 ± 0.013 SE) as compared to S (T$_{1/2}$ = 12.9 days, corresponding to λ = 0.054 ± 0.016 SE) and B (T$_{1/2}$ = 10.5 days, corresponding to λ = 0.066 ± 0.009 SE). In MIX, SWC was depleted significantly faster at 0–7 cm than at 10–30 cm depth (T$_{1/2}$ = 14.0 days, corresponding to λ = 0.049 ± 0.007 SE)
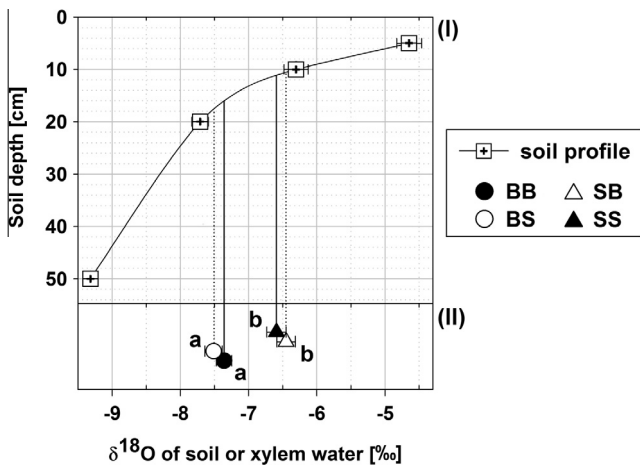

Fig. 4. Vertical profile of the δ^{18}O-signature of soil matrix water (I) and the ^{18}O-signature xylem water (II) of beech (circles) and spruce (triangles) under intra-specific (BB and SS; filled symbols) and inter-specific (BS and SB; open symbols) growth conditions in July 2012. Data of all δ^{18}O soil water profiles was pooled (no significant differences between of S, B, and M). Data points represent mean values ± SE. Different letters indicate significant (p < 0.05) differences in δ^{18}O-signature of xylem water.

3.1.2. Depth of water uptake

No significant differences in the vertical δ^{18}O profile of the soil matrix water were found between B, S and MIX. Averaging the data of all 24 soil cores, the vertical δ^{18}O gradient ranged from −4.6 ± 0.2 SE ‰ at 5 cm depth to −9.3 ± 0.1 SE ‰ at 50 cm depth (Fig. 4 I). δ^{18}O of the xylem water of beech was significantly lower (overall mean, BB & BS: −7.4 ± 0.1 SE ‰) than δ^{18}O of the xylem water of spruce (overall mean SS & SB: −6.5 ± 0.1 SE ‰; Fig. 4 II), corresponding to a lower average depth of water uptake in beech of 16.9 cm compared to spruce of 10.8 cm. δ^{18}O in the xylem water of BS was slightly lower and that of SB slightly higher as compared to the respective intra-specific situation BB and SS. This indicates that, by trend, BS trees take up water from deeper and SB trees from shallower soil horizons as compared to their monospecific counterparts.

3.1.3. Vertical distribution of fine root growth

Significant predictors of average rooting depth (average weighted by cumulative fine root production at the respective soil depth) were species (p < 0.0001) and species interaction (p < 0.005), but not year (p > 0.1). When grown intra-specifically beech produced a greater proportion of roots within deeper soils (54% were deeper than 30 cm) compared to intra-specific spruce root production, which concentrated its roots closer to the soil surface (34% $\leqslant$ 10 cm). In B and S, growing root tips of both tree species were, on average, produced deeper than their inter-specific counterparts in MIX (25.6 vs. 18.9 cm). There was no significant interaction between species and species interaction (species × species interaction, p = 0.1208). This indicates that, integrated over the whole depth profile, both species did respond similar to the mixture and decreased their average rooting depths within mixed soil regions. Additional significant two or three-way interactions between the tested predictors were not found. Integrated over the whole depth profile, fine root production of spruce was strongly reduced in MIX when compared to S. In beech, by contrast, overall fine root production was similar in MIX and B. When analysed in 10 cm depth increments, significant inter- vs. intra-specific differences in fine root production were observed within 0–10 and 11–20 cm depth increments only (Tukey's HSD test, α = 0.05; Fig. 5). In both B and S, a higher abundance of intra-specifically growing root tips were found within 0–10 cm depths when compared to inter-specifically growing root tips. This trend was also observed within 11–20 cm depths in S, but not B (Fig. 5). In B, there
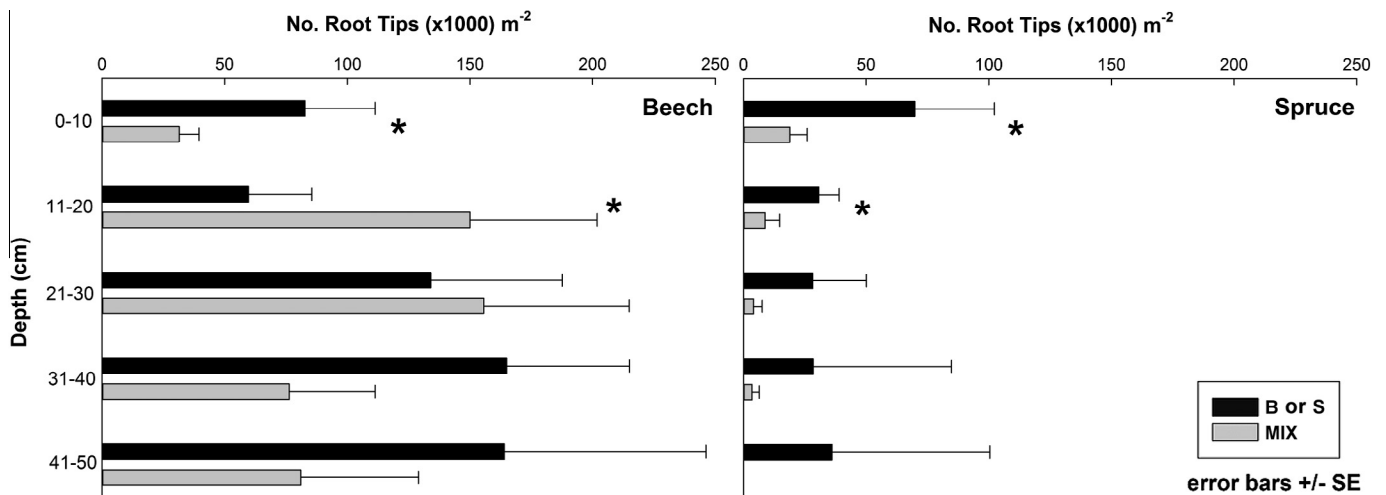
Fig. 5. Cumulative root tip production of *Fagus sylvatica* (beech) and *Picea abies* (spruce) as a function of soil depth (bars represent mean value ± SE). Species interactions: B and S black bars; MIX grey bars. Tukey's HSD test was used to evaluate inter- vs. intra-specific differences in cumulative root tip production within each 10 cm depth increment (α = 0.05). Significant inter- vs. intra-specific differences are denoted by $*$.

was a higher abundance of inter-specifically growing root tips within 11–20 depths, which points to inter-specific complementarity in the vertical distribution of both species' roots.

3.1.4. Fine root surface area and branching intensity in the upper soil layers

Irrespective of the species, fine root surface area (FRSA) was higher in the upper soil (UP; overall mean: 3.41 m^2/m^3 ± 0.22 SE) than in the lower soil (LO; overall mean: 1.32 m^2/m^3 ± 0.12 SE; p < 0.001). In UP fine root surface area was highest in B (4.31 m^2/m^3 ± 0.43 SE) and lowest in S (2.63 m^2/m^3 ± 0.28 SE; p < 0.01). Intermediate values were found in MIX (3.29 m^2/m^3 ± 0.23 SE; p$_{Mix\ vs.\ B}$ = 0.10, p$_{Mix\ vs.\ S}$ = 0.36). In LO no significant differences of fine root surface area were found between B (1.37 m^2/m^3 ± 0.23 SE), S (0.94 m^2/m^3 ± 0.15 SE) and MIX

Fig. 6. Fine root surface area (FRSA), extrapolated from soil core data taken in autumn 2013: beech (simple-ruled), spruce (cross-ruled) in the B, S (black) and beech + spruce in MIX (grey) partitioned in upper soil (UP: 0–8.6 cm) and lower soil (LO: 8.6–25 cm). Bars represent the mean values (±SE). Lower case letters indicate significant differences between B, S and MIX in UP and LO (α = 0.05; tow-way ANOVA and the Tukey-HSD test).

(1.34 m^2/m^3 ± 0.20 SE). Irrespective of soil depth highest fine root surface area was found in B (3.0 m^2/m^3 ± 0.36 SE) and lowest in S (1.78 m^2/m^3 ± 0.24 SE; p = 0.001). Fine root surface area in MIX (2.27 m^2/m^3 ± 0.26 SE) did not differ significantly from that in B but was in tendency higher than in S (p = 0.067). In S and B, spruce and beech showed similar UP/LO-ratios of fine root surface area of 2.57 and 2.80, respectively. In MIX, by contrast the UP/LO-ratio was almost three times higher in spruce (4.44) as compared to beech (1.54), indicating a vertical stratification between beech and spruce in response to belowground interaction (Fig. 6).

Fine root branching intensity (data not shown) in spruce was significantly (p < 0.05) lower in MIX (821 tips/m; ±26 SE) as compared to S (984 tips/m; ±54 SE). For beech no significant effect of mixing on fine root ramification intensity was found.

3.1.5. Exploration types of ecto-mycorrhiza

In total 19,103 vital ECM tips were counted and categorized into exploration types. Contact-, short- and long-distance types were found in beech and spruce, whereas medium-distance smooth types were only found in beech. For analysis, exploration types were categorized into two functional groups, concerning their ability to transport water: first, exploration types with distinct rhizomorphs (r+, long distance types) and second, exploration types without rhizomorphs (r−, all other exploration types, for detailed numbers of each exploration type c.f. supplementary material Table S 2). In each tree species and soil depth, ca. 5 times more ECM without rhizomorphs were found (p < 0.001; Fig. 7). For both tree species, relative abundances of ECM groups were not significantly different between upper and lower soil. ECM without rhizomorphs were relatively more abundant in spruce in the upper
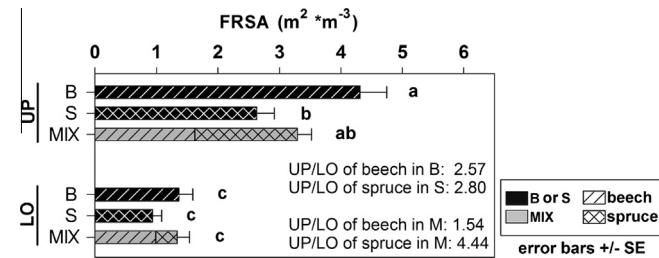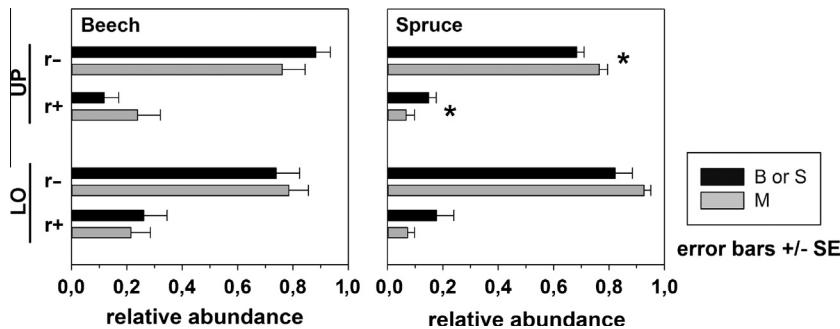
Fig. 7. Relative abundance of ectomycorrhizal exploration types observed in the B, S (black bars) and MIX (grey bars), shown for the upper soil (UP: 0–8.6 cm) and lower soil (LO: 8.6–25 cm). Relative abundance of exploration types with distinct rhizomorphs (r+) and exploration types without rhizomorphs (r−) was calculated as the percentage of tips from each exploration type within the total mycorrhizal tips in every sample. Significant differences (p ⩽ 0.05, similarity percentage test) are indicated by asterisks.
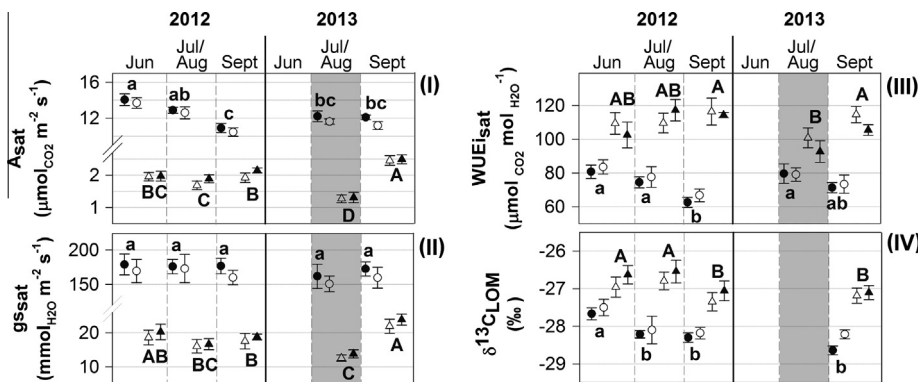
Fig. 8. Leaf gas exchange under saturating light conditions (sat) and ^{13}C-signature of leaves of beech (circles) and spruce (triangles) under intra- (BB and SS, filled symbols) and inter-specific growth conditions (BS and SB, open symbols) in June, July/August and September of 2012 and 2013. The measurements during the dry spell in 2013 are shaded in grey. Mean values (±SE) are shown of (I) assimilation rate (A$_{sat}$), (II) stomatal conductance (gs$_{sat}$), (III) intrinsic water use efficiency (WUEi$_{sat}$) and (IV) δ ^{13}C in leaf organic matter (n = 8 each). Different letters indicate significant differences (p < 0.05) between estimated marginal means (GLM repeated measures) of the different measurement campaigns for beech (lowercase letters) and spruce (capital letters).

soil in MIX compared to S (92% ± 4 SE vs. 82% ± 3 SE; p < 0.05), while ECM with distinct rhizomorphs were relatively less abundant (8% ± 4 SE vs. 18% ± 3 SE; p < 0.05). There were no significant differences among ectomycorrhizal groups of beech in the upper, and in beech as well as spruce in the lower soil.

3.2. Drought response of spruce and beech under intra- and inter-specific growth conditions

3.2.1. Leaf gas exchange and carbon isotope composition

Light-saturated assimilation rate (A_{sat}) and stomatal conductance (gs_{sat}) yielded higher intrinsic water-use-efficiency ($WUEi_{sat}$) and $\delta^{13}C$ of leaf organic matter ($\delta^{13}C_{LOM}$) in spruce (mean $WUEi_{sat}$: 108 ± 2 SE $\mu mol_{CO2}/mol_{H2O}$; mean $\delta^{13}C_{LOM}$: 28.1 ± 0.1 SE ‰) than in beech (mean $WUEi_{sat}$: 75 ± 2 SE $\mu mol_{CO2}/mol_{H2O}$; mean $\delta^{13}C_{LOM}$: 26.9 ± 0.1 SE ‰; Fig. 8). In beech, A_{sat} was lower in late summer (11.2 ± 0.2 SE $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) proceeding leaf-senescence, whereas gs_{sat} remained stable at 168 ± 4 SE $mmol\ m^{-2}\ s^{-1}$ throughout the growing season. Consistently, in beech $WUEi_{sat}$ and $\delta^{13}C_{LOM}$ were lowest in late summer. During the drought in July 2013, beech did not appear to be water-limited, whereas spruce reached its lowest A_{sat} (1.3 ± 0.09 SE μmol_{CO2}) and gs_{sat} (13.2 ± 0.71 SE $mmol_{H2O}$) compared to growing season means (A_{sat}: 2.1 ± 0.06 SE μmol_{CO2}; gs_{sat}: 19.2 ± 0.70 SE $mmol_{H2O}$). Counterintuitively, $WUEi_{sat}$ of spruce was also lowest during the summer drought 2013. Fig. 9 shows that during the intense dry spell in midsummer 2013, the most drought stressed trees (lowest gs_{sat}) diverged from the usual negative correlation between gs_{sat} and $WUEi_{sat}$, indicating photoinhibition perhaps due to the concurrently high insolation. Significant species interaction effects (BB vs BS and SS vs SB) did not emerge from leaf gas exchange and $\delta^{13}C_{LOM}$ analyses.
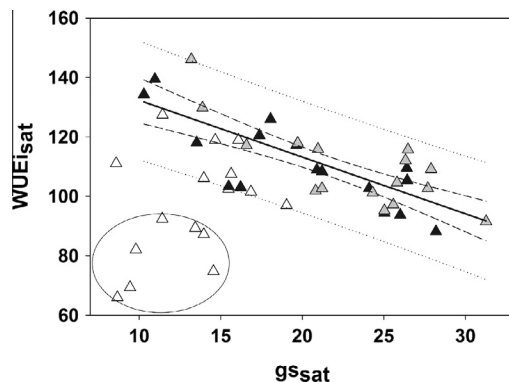
Fig. 9. Intrinsic photosynthetic water-use-efficiency of spruce (calculated from gas exchange data) in relation to stomatal conductance under dry (midsummer 2013: open symbols) and moist conditions (midsummer 2012: filled, black symbols and late summer 2013: filled, grey symbols). Overall regression of $WUEi_{sat}$ vs. gs_{sat} under moist conditions (solid line): $r^2 = 0.59$, p < 0.01, 95% confidence band (dashed line) and 95% prediction band (dotted line). Regression of $WUEi_{sat}$ vs. gs_{sat} under dry conditions in 2013: n.s., due to deviant values at very low gs_{sat} (within circle).

3.2.2. Tree growth performance during the drought year 2003

Using tree ring analyses to retrospectively analyse effect of the drought year 2003 on stem diameter growth dynamics, spruce turned out to be less drought-tolerant than beech (Table 2). Resistance and resilience of spruce (SS) were slightly lower compared to spruce when neighbouring beech (SB), and recovery was higher. Resistance and resilience of beech (BB), on the other hand, was slightly increased and recovery decreased when compared to BS. All these comparisons of species-interaction, however, were not significant. Large species-specific differences between spruce and beech led to significantly lower resistance (−11%) and lower resilience (−20%) of SB compared to BS trees. In general, recovery was higher the more pronounced growth depression was during the preceding drought.

4. Discussion

The present study focused on the drought susceptibility of Norway spruce when grown adjacent to European beech, hypothesizing (H I) that water accessibility for spruce is limited by the presence of beech. As a consequence, (H II) mixture with beech may exacerbate drought susceptibility, reducing spruce's photosynthesis and stem growth.

4.1. Soil water accessibility for inter-specific spruce during summer drought

Before bud break in beech, soil water consumption of evergreen spruce significantly lowered the SWC in S when compared to MIX and B (cf. also Schume et al., 2004). During the drought in late summer of 2013, however, soil water depletion was most rapid in 0–7 cm soil depth of MIX. Relative to S, the enhanced total absorptive surface area of beech and spruce fine roots together (Fig. 6) suggest increased belowground competition in MIX and associated exhaustion of soil water in the upper soil. Fast soil moisture depletion exacerbates drought even during a short absence of precipitation, rapidly conveying high doses of drought stress (Goisser et al., 2013; Zang et al., 2014) in the upper soil depths of MIX. Lower production and FR surface area of spruce roots in MIX in comparison to S may be a result of asymmetric competition belowground. Bolte et al. (2013) observed that spruce had a lower root area index, as well as root biomass when growing in mixture with beech. Therefore, the admixture of spruce, with its distinctly different root growth traits, may favour beech in occupying mixed soils. Our results confirm the observation in previous studies that competition with beech shifts spruce fine roots to the upper, more drought-prone soil layers (Bolte and Villanueva, 2006; Schmid and Kazda, 2001; Schume et al., 2004). Corresponding to the observed shift in vertical fine root distribution, $\delta^{18}O$ analysis of xylem water revealed by trend higher, respectively lower, average depths of water uptake in SB and BS trees as compared to their intra-specific counterparts (SS and BB). Spatial and temporal patterns in fine-root growth of spruce appear to be conservative even under water limitation (Gaul et al., 2008; Mainiero et al., 2010), the more so, if constrained by competing beech (cf. Fig. 6). Considering

Table 2
Indices for resistance, recovery and resilience (means ± se) of stem diameter growth according to Lloret et al. (2011) for spruce and beech growing in inter- versus intra-specific neighbourhood based on 9 trees per species in intra- and inter-specific neighbourhood. P-values denote the significance between SS/SB, BB/BS and SB/BS.

Parameter	Spruce				SS/SB	Beech				BB/BS	SB/BS
	SS	se	SB	se	p	BB	se	BS	se	p	p
Resistance	0.43	0.08	0.54	0.04	0.073	0.75	0.08	0.65	0.08	0.139	<0.001
Recovery	1.43	0.32	1.27	0.17	0.251	1.20	0.10	1.35	0.32	0.251	0.144
Resilience	0.62	0.07	0.68	0.09	0.333	0.89	0.08	0.88	0.07	0.689	<0.001

the high drought susceptibility of spruce at Kranzberg Forest (Nikolova et al., 2009) such response seems counter intuitive, as it exposes large parts of the spruce root system to overall drier conditions in the upper soil layers. However, input of beech litter may be beneficial for neighbouring spruce, as it can significantly alter the topsoil properties (i.e. reduced humus accumulation and acidity) and hence nutrient release from litter decomposition and nutrient cation mobility (Goettlein et al., 2012; Rothe et al., 2002). Reduced fine root branching intensity of spruce roots in the presence of beech may result from enhanced nutrient availability (Meyer, 1987), indicating a strategic shift from intense soil exploitation to selective foraging with extending roots (Waisel et al., 2002). In mixture with beech, spruce enhanced its share of ECM without rhizomorphs while lowering the proportion of ECM with distinct rhizomorphs. The latter produces 15 times more biomass, at least, of external mycelia with higher C demand than needed by other types (Rygiewicz and Andersen, 1994; Weigt et al., 2012, 2011). Hence, in mixture with beech, ECM that exploit the nutrients of the beech litter at lower carbon costs may be favoured. Genera with long distance type ECM, conversely, can increase the plant water uptake due to an up to 15-fold extension in hyphal length and a 3-fold increase of the absorbing surface (Lehto and Zwiazek, 2011; Rousseau et al., 1994; Weigt et al., 2012).

In view of the natural distribution of spruce, on nutrient-poor sites and under humid climates (i.e. with only short-term drought, Schmidt-Vogt, 1987; Spiecker, 2000), root dominance in upper soil, high capacity for selective foraging in combination with highly efficient nutrient uptake through fungal partners, appears to be an effective and hence highly competitive strategy for pre-emption of nutrients from litter mineralization and soil water upon drought (Craine and Dybzinski, 2013; Schmid, 2002). During extended periods without precipitation, however, shallow rooting in drought prone upper soil horizons, reduced intensity of soil exploitation and lower water absorbing ECM-surface area of spruce in response to inter-specific competition with beech limits the accessibility to deep soil water (Craine and Dybzinski, 2013) as well as the capacity for water extraction from dry soil. With regard to summer drought, present results hence corroborate H I that the presence of beech roots reduces water accessibility for spruce through (i) a shift of spruce fine roots to shallower, drought prone soil depths and (ii) reduced association with ECM fungi of the long-distance type.

4.2. Drought susceptibility of leaf gas exchange and stem growth in spruce under intra- and inter-specific neighbourhood

Stomatal control of transpiration and water-use-efficiency of carbon assimilation is crucial for plant survival and growth performance, especially under drought (Chaves, 1991). Being one of the earliest responses to water limitation (Flexas and Medrano, 2002), reduced stomatal conductance can serve as indicator for drought stress (Medrano et al., 2002). However, characteristic differences in the drought sensitivity of stomatal response may occur between species with different ecological strategies in controlling internal water relations (i.e. being isohydric versus anisohydric, cf. McDowell et al., 2008). In line with present results regarding stomatal conductance and BAI, spruce has often shown to be more drought-susceptible than beech (Pretzsch et al., 2013; Zang et al., 2011), despite spruce's xeromorphic foliage. Spruce apparently employs an isohydry strategy (Lyr et al., 1992), reducing stomatal conductance at early stages of soil drought. Needle xeromorphism may, hence, be a feature to preserve water in the tree, once the stomata have closed. By contrast, beech may follow an anisohydric strategy, with a less sensitive regulation of stomatal conductance to soil drought during prolonged dry spells compared to spruce (Leuschner, 2009). Consistently, spruce operates at higher WUEi than beech (Fig. 8). However, during midsummer 2013, drought-

related reduction of stomatal conductance in spruce resulted in decreased rather than increased WUEi. Stomatal closure under high insolation, exacerbates photo-oxidative (Foyer et al., 1994a, 1994b) as well as temperature stress (Lin et al., 2012). Especially both stresses in combination may exacerbate photoinhibition (Gamon and Pearcy, 1990; Sage and Kubien, 2007), hence being responsible for the reduced WUEi of photosynthesis in drought stressed spruce. Such response illustrates the high susceptibility of spruce to such weather conditions.

Dobbertin (2005) suggests reduced carbon allocation to stem growth as one of the most drought-sensitive responses at the whole tree level. Results of the meta-analysis by Poorter et al. (2012) corroborate such assumption for a wide range of species. Thus, especially the LLoret-indices for resistance, Rt, and resilience, Rs, based on stem diameter growth (Fig. 2) seem appropriate for scrutiny whether water stress and growth reduction of spruce is more severe in mixture with beech than under intra-specific conditions. The group comparison between the indices Rt, Rc, and Rs (Table 2) reveals both whether inter-specific neighbourhood modifies the drought stress reaction compared with intra-specific conditions and to what extend drought stress is modified by different neighbouring tree species. Of special interest are Rt and Rs as they reflect the trees ability to avoid and overcome growth reductions by drought which, in the long term, mean a loss of their fitness and competitiveness within the population.

The comparison reflects the generally higher drought resistance and resilience of European beech compared with Norway spruce (Pretzsch et al., 2013). In contradiction to H II we found no exacerbation of drought stress and growth reduction in mixed compared with monospecific environment. There is even a nearly significant (p = 0.073) increase of drought resistance of Norway spruce when growing in neighbourhood of beech (Table 2, first line). Despite supported concerns about negative effects of beech on accessibility of soil water for spruce (H I, supported), we found no evidence of increased drought susceptibility in leaf gas exchange or BAI in spruce when growing in the neighbourhood of beech, thus rejecting H II.

5. Conclusions

Concerns about negative effects of beech on accessibility of soil water for spruce when growing in mixture (H I) were supported. Interacting with beech, spruce produced roots predominantly within shallower, drought prone soil horizons. Moreover association with ECM fungi of the long-distance type was distinctly reduced. However at the whole-tree level, our results provided no evidence of increased drought susceptibility of spruce trees grown in a group-wise mixed spruce-beech forest thus rejecting our second hypothesis (H II). The conflicting findings regarding H I and H II are interpreted to result from two aspects: (i) seasonal shifts between positive and negative effects of beech-spruce interaction and (ii) the group-wise mixture pattern of the investigated forest stand. Our results suggests that especially in the case of spring drought, evergreen spruce may benefit from reduced competition for water and hence higher SWC when growing in mixture with deciduous beech (cf. Fig. 3). Carrying forward the results from long-term observations (Del Río et al., 2013) and forest growth modelling (Forrester and Tang, 2016), shifts between positive and negative effects of species-interaction in beech-spruce stands may not only occur inter-annually but also intra-annually, possibly overriding each other in their effect on annual BAI. To disentangle interfering intra-annual mixture effects on tree growth, continuous measurements of stem diameter growth appear to be necessary. In addition, due to the group-wise mixture pattern, inter-specific spruce individuals are only partially exposed to beech competition.

Thus, adverse neighbourhood effects of beech on accessibility of soil water for spruce (cf. Section 4.1) prevail single-sided, which may also explain that only small differences in $\delta^{18}O$ of xylem water and hence estimated average depth of water uptake were observed between SB versus SS and BS versus BB. In line with the results of Pretzsch et al. (2012), we conclude that the group-wise mixture pattern, exposing spruce individuals to beech competition only partially, i.e. single-sided, buffer the putatively adverse neighbourhood effect of beech on drought susceptibility of spruce. In comparison to single tree mixture, group-wise mixture of beech and spruce appears to be the favourable silvicultural option in the face of climate change.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.05.032.

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