



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



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We would like to dedicate this work to Prof. Dr. Ulrich Lüttge on the occasion of his 80th birthday.

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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 $\delta^{18}\text{O}$ 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

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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 and 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 its adjustments of fine root morphology (maintaining or even decreasing specific fine root length in response to below ground competition with beech, cf. Bolte and Villanueva, 2006; Grams et al., 2002) 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 Zwiasek, 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 m² 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 m² with a mean stocking density of 659 trees per ha and mean basal area of 52 m² per ha. The plots include 63 beech trees 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). 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

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