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ORIGINAL ARTICLE

Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (*Pseudotsuga menziesii*) and European beech (*Fagus sylvatica*)

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Abstract

Key message **The study found an increased investment into stem growth (compared to root growth) if trees were surrounded by a complementary species. This response is consistent with known patterns about root–stem allometry under favorable conditions (humidity and stand density).**

Abstract The study investigated partitioning of resources between roots and stems in mono-species and mixed-species stands of Douglas-fir and European beech at four different sites. We combined tree ring analyses of stems and coarse roots to scrutinize root–stem allometry with a focus on how it is influenced by species mixture and humidity. The results show that allometry in mixed stands changed in favor of stem growth for both species. The greatest relative allocation into stem growth was observed for individual trees which were completely surrounded by trees of the other species. The data indicate that a decrease of stand density, which was used as a proxy for tree competition, has the same effect on allocation. To analyze the influence of humidity, we used a long- and short-term index. Based on these, we can show that allocation changes with general site conditions and annual humidity variations. We found that on both time scales, both species increase resource investment into stem growth if conditions are more humid. Under harsher conditions, allocation shifts into root growth. The findings contribute to understanding the overyielding in mixed stands. Mixing Douglas-fir and European beech leads to the same allocation patterns as an improvement of site conditions. We suggest that for both species, mixture is equivalent to growing on a better site.

Keywords Mixed stands · Root–stem allometry · Density · Site gradient · Complementarity

Introduction

Since long, species mixture is deemed to be a standard measure for improving productivity and stability of forest stands in the practice of silviculture (Liang et al. 2016). The underlying mechanisms behind such mixing effects and the conditions, under which they occur, however, are only partly understood so far. Many studies were conducted to analyze the above-ground overyielding (Binkley and Greene 1983; Bartelink 1998; Amoroso and Turnblom 2006) and the reduced climate sensitivity of stem growth in mixed stands (Pretzsch et al. 2013; Lebourgeois et al. 2013; Jucker et al. 2014). However, for a holistic understanding of the mixing effect, it is essential to investigate the whole system, the aboveground as well as the belowground production.

Several studies could show that an increased resource uptake of the involved species is responsible for the higher productivity often found in mixed stands (Binkley 2003; Forrester et al. 2006b; Thomas et al. 2015). Two mechanisms lead to this increasing uptake, facilitation, and species complementary (Larocque et al. 2013). Facilitation may, i.a., modify resource availability, whereas complementarity means a more efficient use of resources which result from niche differentiations.

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Changes of resource uptake in mixed stands imply shifts of resource allocation among tree compartments (Dieler and Pretzsch 2013). This can be observed by measuring the size of tree compartments or investigating tree allometry (Amoroso and Turnblom 2006; Erickson et al. 2009; Radosevich et al. 2006). The allometry between root and stem size is of particular interest and has been repeatedly examined (Nikolova et al. 2011; Shainsky et al. 1992). Nevertheless, the results about the influence of intraspecific competition show diverse patterns (Poorter et al. 2012) and species-specific analyses, especially for woody plants, seems to be advisable.

In our context of interest, two theories have been advanced to describe the allocation in plants. The first one is the allometric biomass partitioning theory (APT). It describes how organismal attributes change with plant size according to the allometric equation (Peters 1983):

$$\log Y1 = \log \beta + \alpha \log Y2. \tag{1}$$

The variables $Y1$ and $Y2$ in the equation represent the sizes of two interdependent tree compartments, in our case (coarse) root and stem diameter. The parameter α represents the allometric exponent, while β is a scaling parameter. The constancy of α is the major statement of APT. The second theory differs in this assumption. The optimal partitioning theory (OPT) states that plants allocate additional biomass to the organ that takes up the most limiting resource (Bloom et al. 1985; Thornley 1972). Thereby, the allometric exponent α must be variable. Several studies could show plastic responses of tree compartments beyond the predetermined allometric development (Schall et al. 2012; Meier and Leuschner 2008; Nikolova et al. 2011).

From a methodological point of view, the allocation between belowground and above-ground tree compartments can be scrutinized in different ways. The destructive approach excavates whole trees and weighs above-ground and below-ground biomass. Especially for mature trees, this method is extremely laborious and difficult to realize at a large number of trees, which is required for statistical evidence as only one observation per tree is possible. For this reason, we applied a method which compares coarse root and stem diameter growth based on increment borings. The method has already been successfully applied in studies about relationships of site and tree allometry (Nikolova et al. 2011; Pretzsch et al. 2012a, b). It allows for sampling a larger number of trees and to obtain retrospective time series per tree.

In the study at hand, the species mixing effect on root–stem allometry is investigated for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) under mixed and monospecific settings. Previous studies identified an overyielding in mixed stands of both species compared to mono-species stands (Bartelink

1998; Thurm and Pretzsch 2016). Notwithstanding, while complementarity of both species in the crown layer was considered a major effect, there was evidence for additional effects in the root zone. Thurm and Pretzsch (2016) supposed that under harsher conditions, species complementary shifts from the crown stratum into the soil stratum. Drought year analyses, which could show a complementary water use between Douglas-fir and European beech, confirm this assumption (Thurm et al. 2016). In this context, the study at hand intends to supplement the understanding of mixing effects by investigating root–stem allometry and its possible differences due to species mixing.

Based on the existing knowledge, we start from the hypothesis that (1) Douglas-fir and European beech have different root–stem allometry and (2) that mixing both species modifies their allocation into coarse roots and stems compared to their growth in monospecific environments. In this context, we also scrutinize the impact of stand density on allometry. In addition, we formulated the hypotheses that (3) unfavorable general site conditions (low humidity) influence the allocation in favor of root growth, and that (4) short-term droughts have an analogous effect.

Materials and methods

Study area and experimental setup

The study was conducted in spring 2014 on several locations in Southern Germany, which belongs to the warm temperate climate zone. We made use of a triplet experimental setup which has meanwhile turned out an effective method for detecting the mixed stands effects in many studies (e.g., Dirnberger and Sterba 2014; Pretzsch et al. 2015). Each triplet is composed of a pure Douglas-fir stand, a pure European beech stand, and a mixed stand of both species (Table 1). The plots consisted of around 20 individuals in pure stand and 20 individual per species in mixed stands (mean plot size 660 m^2). Each triplet is characterized by homogenous site conditions, and both species have the same age in the respective pure and the mixed stand. Beside these two requirements, the proximity of the plots was a crucial factor. The distance of the plots inside a triplet is on median 90 m (maximum 570 m). Another requirement of the triplet was the structural comparability. The proximity of the plots should ensure the same management regime. Selected were fully stocked stands with very low thinning intensity as confirmed by stump counting. The sampling was made in a managed forest, so totally, unthinned situations could not be found. However, we deemed thinning intensity of the selected stands close to self-thinning, maximum stand density

Table 1 Site characteristics of the four triplets indicating ecoregions (Gauer and Kroiher 2012), climate data (Deutscher Wetterdienst 2015), soil data (Taegger and Kölling 2016) and age

Experimental number	Plot	Ecological region	Geographic position N-longitude	E-latitude	Elevation m above sea level	Mean annual Temperature (1981–2014) (°C)	Mean annual Precipitation (1981–2014) (year mm⁻¹)	Base-richness from base-poor (1) to base-rich (5)	Water supply from very dry (1) to very fresh (7)	Sand (%)	Clay (%)	Silt (%)	Soil types by LUFA	Age (years)	Skeleton section between 60 and 90 cm (%)
1001	4	Tertiäres Hügelland	4393914.11	5343070.81	597	8.1	1011	3	7	55	22	22	Sandy loam	56	48.1
	5	Tertiäres Hügelland	4393968.08	5343012.33	597	8.1	1011	3	7	55	22	22	Sandy loam	64	48.1
	6	Tertiäres Hügelland	4393923.63	5342981.38	588	8.1	1011	3	7	55	22	22	Sandy loam	61	48.1
1002	4	Fränkische Platte	4352612.71	5529925.84	312	8.9	727	4	3	16	59	24	Clay	51	0.6
	5	Fränkische Platte	4352830.72	5530457.12	319	8.8	740	4	3	16	59	24	Clay	54	0.6
	6	Fränkische Platte	4352743.94	5530469.82	319	8.8	740	4	3	16	59	24	Clay	51	0.6
	7	Fränkische Platte	4332272.39	5517554.27	293	8.9	792	4	3	12	56	32	Clay	98	1.8
	8	Fränkische Platte	4332385.63	5517503.25	285	8.9	792	4	3	12	56	32	Clay	102	1.8
	9	Fränkische Platte	4332372.5	5517593.21	272	8.9	792	4	3	12	56	32	Clay	100	1.8
1003	4	Spessart	4323073.04	5541828.39	439	8.1	1054	3	4	31	36	34	Clay loam	85	8.3
	5	Spessart	4322988.25	5542160.09	447	8.1	1054	3	4	31	36	34	Clay loam	88	8.3
	6	Spessart	4323072.25	5542183.9	449	8.1	1054	3	4	31	36	34	Clay loam	87	8.3
Total					410	9	895	4	4	29	43	28		75	

conditions (for a more detailed description of the setup and stand level growth parameter, see Thurm and Pretzsch 2016).

In total, four triplets comprising 12 plots altogether were established. The four triplets were set up in three different ecological regions which range from drier, warmer sites in the ecological region of *Fränkische Platte* to moister, colder sites in the ecoregion *Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft* (see Gauer and Kroiher (2012) for an overview of the German forest ecoregions). The long-term mean annual temperature covers a span of 8.1–8.9 °C with an annual mean precipitation between 727 and 1054 mm. Multiannual and monthly temperature and precipitation data were obtained along a 1×1 km grid of the German Weather Service (Deutscher Wetterdienst 2015). The profundity of soil was always deeper than 1 m (for the skeleton section in soil depth 60–90 cm and the soil type, see Table 1).

Long and short-term humidity indices

For scrutinizing short-term weather effects on root–stem allometry, we used the standardized precipitation–evapotranspiration index SPEI (Vicente-Serrano et al. 2010). It was summarized as an annual value based on the average of monthly SPEI values in the growing period (May–September). The SPEI uses the monthly differences between precipitation and the climatic water balance after Thornthwaite (1948). The input variables of the climatic water balance are monthly mean temperature and geographic latitude. We calculated the climatic water balance at a time scale of 5 months using a Gaussian kernel function, respective for every triplet. The SPEI indexed a time period from 1950 to 2010, whereas the mean weather conditions in this period represent by the index zero and dry conditions represent by negative indices.

As a measure of long-term climate-induced site productivity, the CVP index by Paterson (1956) was brought to bear (Eq. 2):

$$CVP = \frac{Tv \cdot P \cdot G \cdot E}{Ta \cdot 12}. \tag{2}$$

The CVP index is designed to indicate the growth potential of plants just by climate parameters. Greater CVP indices mean better growing conditions. We calculated it for a time span of 30 years (1980–2010). The variable Tv is the mean monthly temperature of the warmest month (°C); P is the sum of the annual rainfall (mm a^{-1}); and G represents the length of the growing period (number of months). Growing season length in Central Europe is mainly determined by temperature (Vitasse et al. 2009). According to Paterson (1956), we attributed months with an average temperature equal to or higher than 3 °C to the

growing period. Ta is the difference between the mean maximum temperature of the warmest month and the mean minimum temperature of the coolest month (°C). The variable E is the so-called evapotranspiration reducer, which Paterson (1956) suggested to calculate by relating the solar radiation at the poles to the radiation at the site of interest. While this is meaningful for differentiating potential plant productivity on a global scale as originally intended by Paterson, we used a modification E' introduced by Gandullo and Serrada (1977) which better reflects the comparably small spatial scope of our study. E' considers the real insolation at the plots by using the local annual sunshine hours per year n_{sun} (Eq. 3):

$$E' = \frac{2500}{n_{sun} + 1000}. \tag{3}$$

The sunshine hours were derived from 1×1 km grid data from the German Weather Service (Deutscher Wetterdienst 2016). In this study, the values of E' fluctuated around 0.97, which represent an average sunshine duration of 1583 h per year.

Sampling and measurement

For this study, we sampled approximately ten dominant trees per species at each plot. At these trees, we measured tree height, DBH, and diameter of the cored root at the position of coring (see below). To quantify the competitive situation of such a tree, we determined the basal area (m^2/ha) in the tree's vicinity with an angle count sampling using a relascope (Bitterlich 1952) with the tree of interest in the center of the sampling spot. The local basal area (local BA) was used as a tree individual competition index. For the counted trees, we recorded also their affiliation to the groups of coniferous (Douglas-fir) and broadleaved trees (European beech). This enabled us to tell whether competition for a given tree of interest was more inter- or intraspecific (cf. Pretzsch 2009) and we get and individual tree mixing proportion (mixing proportion doug, based on proportion of surrounding Douglas-firs). Finally, we adjusted the mixing proportion of European beech with an equivalence coefficient (1.6). Douglas-fir and European beech have different patterns of spatial occupation. Douglas-fir reached greater stand densities, European beech lower. To avoid a spatial overestimation of one species, it was applied the mentioned coefficient. The equivalence coefficient results from the ratio of stand density index from pure Douglas-fir and a pure European beech stand. It was detected in a mixed study of 18 triplets which also used the triplets of the study at hand (for further information, see Thurm and Pretzsch 2016).

For taking stem cores, we applied long-term standard procedures (Pretzsch 2002; Cook and Kairiūkštis 1990).

For the selection and the drilling of the roots, we were geared to a pilot study from Nikolova et al. (2011) which has been successfully applied in several other studies later (Pretzsch et al. 2012a, b). All cores were sampled with a Haglöf increment borer. The stem was cored twice at breast height in North and East directions. The root cores were taken at two tall, lateral structural roots which were excavated. The root coring position was about 60–80 cm from their offset at the trunk. This distance range was chosen a compromise between having the lowest number of missing or discontinuous root growth rings (Krause and Morin 1995) and avoiding strongly eccentric cross-sectional shapes which result from root growth response to wind load (Nicoll and Ray 1996). Nevertheless, many sampled roots show elliptic shapes with the largest radius from the upper edge to the downmost edge and the smallest parallel to the soil surface. To obtain the mean annual growth of the roots, one core was taken from the root's top edge to the center (largest radius) and another one perpendicularly from one lateral root edge to the center (smallest radius). This method also minimizes the amount of year rings which are not hit perpendicularly with the borer. This procedure provided six cores for every tree (two from the stem, two from the first root, and two from the second root). All in all, the data set comprises 175 trees (see Table 2; Fig. 1).

Ring width measurements were made using a digital positiometer after Johann (1977) (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Measurements of cores stops when tree rings run non-perpendicular. For cross-dating and synchronization of the tree chronologies, we used the software platform TSAP-Win (Rinntech, Heidelberg, Germany). The analyses of root–stem allometry base on relating diameter change between roots and stem. Diameters were calculated backwards by subtracting the measured increments from the diameter at survey time. This annual backward diameter calculation was only done for the time span which was covered by both increment cores per sampling point.

To extract the climate signal in root and stem growth, we detrended the basal area increment of the tree compartments in two steps, as described in detail Thurm et al. 2016). In a nutshell, the first detrending step relied on fitting a Hugershoff increment function (1936). For the second step, we fitted a cubic spline with a wavelength of 15 years.

Statistical analyses

The basic allometric model (cf. Eq. 1) we used for relating root and stem diameter (droot and dstem) can be written as follows:

$$\ln(\text{droot}) = a_0 + a_1 \cdot \ln(\text{dstem}). \tag{4}$$

The coefficient a_0 represents the scaling parameter, and a_1 is the allometric exponent.

To answer our research questions, this model was extended to incorporate several explanatory variables of interest (see below) and fitted to the data. For taking into account the nested data structure (triplet, plot, tree, and root), we applied linear mixed models. Model selection was based on the Akaike Information Criterion (Burnham and Anderson 1998, 2004) and biological plausibility of the results.

At first, we tested for a general difference in the root–stem allometries of Douglas-fir and European beech. To this end, the fixed effect *species* coded as binary variable (1: European beech, 0: Douglas fir) was introduced:

$$
\begin{aligned}
\ln(\text{droot}_{ijklt}) = {} & a_0 + a_1 \cdot \ln(\text{dstem}_{ijklt}) + a_2 \cdot \text{species} + a_3 \\
& \cdot \ln(\text{dstem}_{ijklt}) \cdot \text{species} + b_i + b_{ij} + b_{ijk} \\
& + b_{ijkl} + \varepsilon_{ijklt}
\end{aligned}
\tag{5}
$$

where $a_0 \ldots a_n$ represent the coefficients of the fixed effects. Random effects b are considered triplet i, plot j, tree k, and root level l. The index t stands for the year a measurement belongs to. The symbol ε represents i.i.d. errors. If the estimate of a_2 differs significantly from zero, this suggests species-specific allometric scaling factors. If, however, a_3 differs significantly from zero, we have to assume species-specific allometric slopes.

Further models were fitted separately for Douglas-fir and European beech. Related to the second research question, the influence of the mixture on allometry, we applied the Eq. 6. The fixed effect *mixture* was included as a binary variable (0: pure stand, 1: mixed stand):

$$
\begin{aligned}
\ln(\text{droot}_{ijklt}) = {} & a_0 + a_1 \cdot \ln(\text{dstem}_{ijklt}) + a_2 \cdot \text{mixture}_{ij} + a_3 \\
& \cdot \ln(\text{dstem}_{ijklt}) \cdot \text{mixture}_{ij} + b_i + b_{ij} + b_{ijk} \\
& + b_{ijkl} + \varepsilon_{ijklt}.
\end{aligned}
\tag{6}
$$

Similar to the binary variable species in Eq. 5, the parameters a_2 and a_3 indicate mixture effects on the scaling factor and the allometric slope, respectively.

In addition, to refine the view on species mixing effects, we investigate the shift of allocation by introducing the individual mixing proportion doug as a continuous variable. The proportion ranged between 0 and 1. The value 0 means the individual tree is completely surrounded by European beech and 1 surrounded by Douglas-fir:

$$
\begin{aligned}
\ln(\text{droot}_{ijklt}) = {} & a_0 + a_1 \cdot \ln(\text{dstem}_{ijklt}) + a_2 \\
& \cdot \text{mixing proportion doug}_{ijk} + a_3 \\
& \cdot \ln(\text{dstem}_{ijklt}) \\
& \cdot \text{mixing proportion}(df)\text{doug}_{ijk} + b_i + b_{ij} \\
& + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt}.
\end{aligned}
\tag{7}
$$

To investigate, whether there is also a pattern of stand density, we fitted a model with local BA:

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot local\ BA_{ijk}$$
$$+ a_3 \cdot \ln(dstem_{ijklt}) \cdot local\ BA_{ijk} + b_i + b_{ij}$$
$$+ b_{ijk} + b_{ijkl} + \varepsilon_{ijklt}.$$

(8)

The short- and long-term climatic influences on root–stem allometry were analyzed based on Eqs. 9 and 10. Fixed effects are the standardized precipitation–evapotranspiration index *SPEI* and the Paterson index CVP, respectively. Because the influence of mixture turned out non-significant on long-term scale, we omitted it in Eq. 10:

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot SPEI_{ijt} + a_3$$
$$\cdot mixture_{ij} + a_4 \cdot \ln(dstem_{ijklt}) \cdot SPEI_{ijt} + a_5$$
$$\cdot \ln(dstem_{ijklt}) \cdot mixture_{ij} + a_6 \cdot SPEI_{ijt}$$
$$\cdot mixture_{ij} + a_7 \cdot \ln(dstem_{ijklt}) \cdot SPEI_{ijt}$$
$$\cdot mixture_{ij} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt}$$

(9)

$$\ln(droot_{ijklt}) = a_0 + a_1 \cdot \ln(dstem_{ijklt}) + a_2 \cdot CVP_{ij} + a_3$$
$$\cdot \ln(dstem_{ijklt}) \cdot CVP_{ij} + b_i + b_{ij} + b_{ijk}$$
$$+ b_{ijkl} + \varepsilon_{ijklt}.$$

(10)

All statistical analyses and graphics were conducted with the statistical environment R version 3.2.2 (R Core Team 2015). Linear mixed models were fitted with *lmer* from the R-package *lme4* (Bates et al. 2015). The significances of the coefficients were tested with an F Test with Satterthwaite's approximation (Kuznetsova et al. 2015) from the R-package *lmerTest*.

Results

Species-specific root–stem allometry

The average age of the sampled trees was approximately 59 years (Table 2). However, Douglas-fir was on average 7 year younger, it was 4.4 m higher in pure stands than European beech in pure stands. In mixed stands, the height difference was amounted to even 7.9 m between Douglas-fir and European beech. Douglas-fir had a 9.2 cm greater diameter in pure stands and a 21.5 cm greater diameter in mixed stands than European beech. Overall, the DBH ranged from 19.6 to 95.9 cm and from 9.5 to 63.9 cm for Douglas-fir and European beech, respectively. We found the same pattern of size differences for the root diameters. The average coarse root diameter of Douglas-fir was 13.1 cm (pure = 12.2 cm; mixed = 14.0 cm) and 8.9 cm for European beech (pure = 9.3 cm; mixed = 8.4 cm).

Table 2 Characteristics of the sampled trees

| Species	Mixture	Number	DBH (cm)			Height (m)			H/d ratio			Root diameter (cm)			Age (years)			LocalBA (m² ha⁻¹)		
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Douglas-fir	Pure	49	47.4	19.6	87.5	35.4	23.0	46.8	72	50	100	12.2	5.7	29.8	56	24	89	52.9	27.6	90.8
	Mixed	41	52.3	28.5	95.9	35.8	26.5	49.2	96	66	181	14.0	5.1	33.6	54	28	96	49.8	28.8	86.4
European beech	Pure	40	38.3	17.0	63.9	31.0	23.9	43.7	81	50	127	9.3	4.9	18.4	65	35	110	44.2	10.4	74.0
	Mixed	45	30.8	9.5	55.4	28.0	17.2	43.2	87	52	148	8.4	5.0	17.5	61	23	108	52.8	36.0	92.2
Total		175	42.2			32.6			72			11.0			59			52.9		
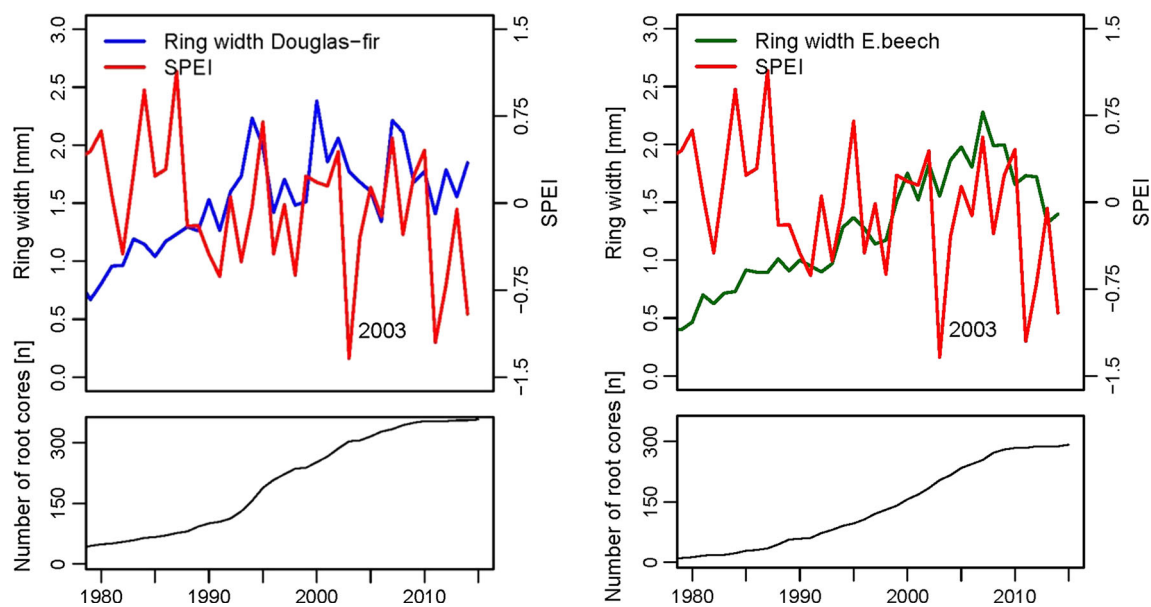
Fig. 1 Ring width chronologies of the lateral roots for Douglas-fir (*blue line*, *left*) and European beech (*green line*, *right*) and the standardized precipitation–evapotranspiration index SPEI (*red line*).

Labeled is the extreme drought year 2003. The *black line* shows the number of available cores in the respective year

The fit results of all linear mixed models shown above are summarized in Table 3. The species-specific model (Eq. 5) indicates that Douglas-fir and European beech significantly differ in their root–stem allocation. European beech has a significantly lower allometric scaling factor but a significantly steeper slope than Douglas fir. We illustrate this result in Fig. 2; up to a DBH of about 26, cm, a typical Douglas-fir invested more resources into coarse roots growth than European beech, at greater diameters, and European beech shows a greater root growth. The inclusion of stand level mixing (dichotomous variable mixture) into the allometric model (Eq. 6, Fig. 3) indicates that Douglas-fir in pure stand has a significant smaller scaling factor than in mixed stands but a significant greater slope. Same effect can be seen for European beech but much it is more pronounced. Both species in pure stands allocate higher biomass portions to the roots if they have DBH beyond about 30 cm (Douglas-fir) and 45 cm (European beech), respectively.

Including mixing proportion at individual tree level gives a clearer view on the shift between root and stem allocation (Table 3, Eq. 7). As shown in the methods section, the proportion of Douglas-fir in the local BA is the variable which was used to this end in the models for both species. Therefore, the highest interspecific competition presented in Fig. 4 is 0.8 for European beech and 0.2 for Douglas-fir. Both species exhibit a significantly higher allocation to stem growth compared to root growth if they compete more against the other species than against their own.

Influence of competition

The 95% of the local BA's arranged between 26.0 m^2/ha and 82.6 m^2/h. Figure 5 shows by means of the fitted Eq. 8, how the trees partitioned resource between root and stem under increasing stand density. The analyses aggregate all trees, independent if mixed or not. The sampled trees in mixed stands show a little bit higher local BA (50.8 m^2/ha) than pure stands (49.1 m^2/ha), but the difference was not significant. The data exhibited that with increasing competition allocation favors root growth relative to stem growth. This pattern was significant for both species but more pronounced for Douglas-fir.

Influence of short-term humidity variation

As shown in the "Methods", the short-term variation of humidity was represented by the SPEI. In the measuring period, the SPEI ranged between −1.58, which was reached in the drought year 2003, and 1.14, which was reached 2002. The SPEI index for all triplets existed from 1998 to 2010 which results in a lower observation account in Table 3. As mentioned in the "Methods", the triplet specific SPEI enables to calculate site-specific minimum and maximum SPEI values. Figure 6 illustrates the allocation pattern of Douglas-fir and European beech in pure and mixed stands. Under humid weather conditions, both species allocate resources in favor of stem growth compared to root growth (Eq. 9). This reaction could be found in pure as well as in mixed

Table 3 Estimated fixed effects for the extended root–stem allometry models (Eqs. 5–10)

Equation	Dependent variable: log(droot)										
	Tree allometry pattern			Competition/density/mixing proportion				Humidity response			
	5	6	6	7	7	8	8	9	9	10	10
Independent variable:	EB - DF	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech
log(dstem)	0.726*** (0.013)	0.633 (0.015)	1.149*** (0.028)	0.506*** (0.027)	1.416*** (0.033)	0.282*** (0.04)	1.501*** (0.087)	0.608*** (0.018)	1.078*** (0.032)	−0.825*** (0.114)	0.058 (0.176)
Species E.beech	−1.990*** (0.109)										
Log(dstem)*species E.beech	0.608*** (0.024)										
SPEI								−0.075** (0.028)	−0.074* (0.031)		
Mixture(pure)		−0.904*** (0.194)	−1.889*** (0.378)					−1.096*** (0.205)	−1.979*** (0.38)		
Log(dstem)*SPEI								0.020** (0.007)	0.025** (0.01)		
Log(dstem)*mixture(pure)		0.267*** (0.025)	0.490*** (0.045)					0.315*** (0.031)	0.522*** (0.052)		
Mixing proportion doug				−1.279*** (0.247)	1.025 (0.549)						
Log(dstem)**Mixing proportion doug				0.390*** (0.043)	−0.338** (0.108)						
Local BA						−0.032*** (0.004)	0.014* (0.007)				
Log(dstem)*local BA						0.009*** (0.001)	−0.003 (0.002)				
SPEI*mixture(pure)								0.072* (0.036)	0.045 (0.045)		
Log(dstem)*SPEI*mixture(pure)								−0.019* (0.01)	−0.016 (0.013)		
CVP										−0.016*** (0.002)	−0.022*** (0.003)
log(dstem)*CVP										0.003*** (0.0002)	0.002*** (0.0003)
Constant	−0.471 (0.144)	−0.104 (0.253)	−1.809*** (0.26)	0.300 (0.277)	−2.773*** (0.215)	1.105*** (0.288)	−3.290*** (0.384)	−0.019 (0.264)	−1.590*** (0.259)	8.403*** (1.259)	10.091** (2.000)

Table 3 continued

Equation	Dependent variable: log(droot)										
	Tree allometry pattern			Competition/density/mixing proportion				Humidity response			
	5	6	6	7	7	8	8	9	9	10	10
	EB – DF	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech
Independent variable:											
Number of observations	4433	2512	1921	2512	1929	2512	1929	1994	1482	2512	1929

The numbers in brackets represented the standard deviation of the independent variables (*EB* E. beech, *DF* Douglas-fir, *SPEI* Standardized precipitation-evapotranspiration index, *Local BA* Local basal area, *CVP* Paterson index)

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

stands. The response of Douglas-fir to SPEI in Fig. 6 is almost invisible but this is a problem of scale. However small, the model shows a significant relationship between SPEI and root stem allometry. Obviously, the reaction to short-term humidity fluctuations is very small, but existent. It is all the more surprising that one can separate the reaction to short-term humidity from other effects.

The linear mixed models of the short-term humidity variation (Eq. 9) were significant as well as the models of mixture and local BA (Eqs. 7, 8). Nevertheless, it can be seen that mixture and local BA had a stronger influence on allocation than the SPEI. Only for European beech in mixed stands, a variation of humidity seems to have a large effect.

To clarify, if drought causes contrary responses in root and stem growth or if the allocation of resource is more reduced for one than for the other, we pictured the course of detrended root and stem growth (Fig. 7). A dendrochronological parameter which compared the course of two chronologies against each other is the 'Gleichläufigkeit' (Eckstein and Bauch 1969). The Gleichläufigkeit respects the direction of index (ups and downs) and not the strength of deflection. The Gleichläufigkeit for the mean root and stem growth index was 0.76 between 1990 and 2013. This means 76% of the ups and downs are equal. The year-to-year agreement of root and stem reduced with 1990 because of the decreased number of root chronologies (see also Fig. 1). The 'Gleichläufigkeit' let us suggest that root and stem growth do not have a contrary course.
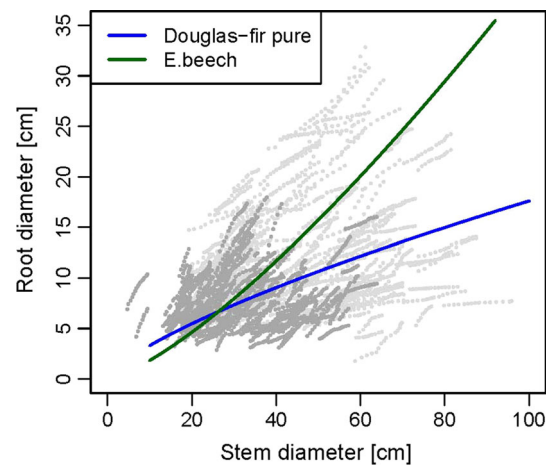

Fig. 2 Root–stem allometry from fitted models according to Eq. 5, and the related, measured, and reconstructed diameter for Douglas-fir (*grey*) and European beech (*dark grey*). Model coefficients can be seen in Table 3
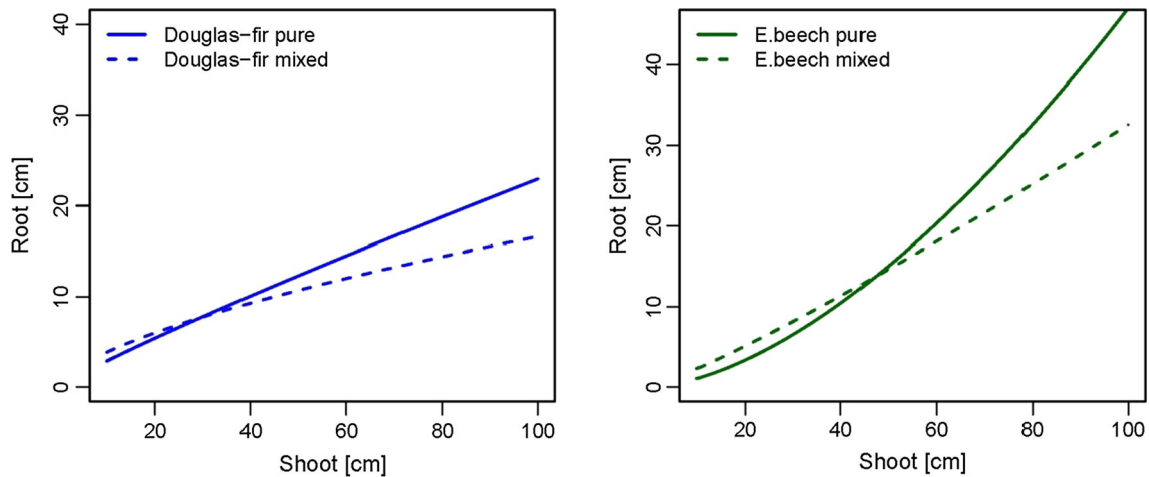
Fig. 3 Root–stem allometry in dependence of stand level mixing type for Douglas-fir (*left*) and European beech (*right*). Model coefficients can be seen in Table 3 and Eq. 6
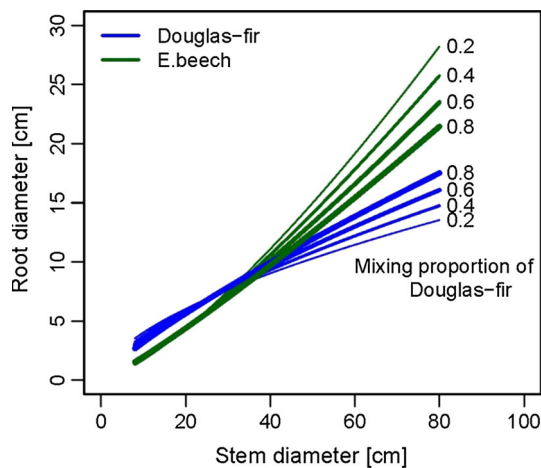

Fig. 4 Root–stem allometry in dependence of interspecific competition represented by mixing proportion of the own species for Douglas-fir (*blue*) and European beech (*green*) related to Eq. 7. Mixing proportions are to be understood as shares of Douglas fir in the local BA. Model coefficient are shown in Table 3
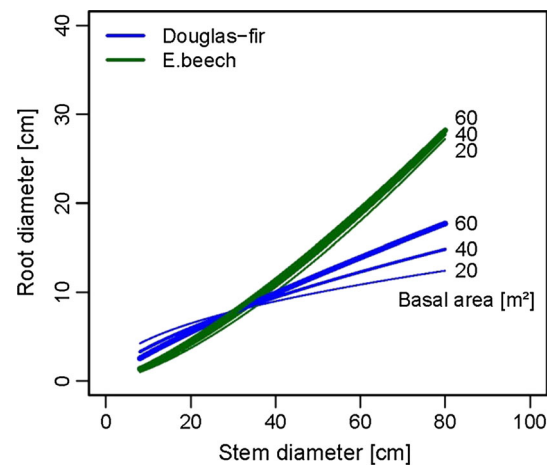
Fig. 5 Root–stem allometry in dependence of local stand density for Douglas-fir (*blue*) and European beech (*green*) according to Eq. 8. Density is represented by local BA which is defined as surrounding basal area of a individual tree. Model coefficients are shown in Table 3

Influence of long-term humidity variation

In comparison with the influence of short-term humidity, the effect of site conditions, expressed through the CVP index, on tree allometry was much more pronounced. The CVP index at the driest site was 497 (ecoregion 'Fränkische Platte'). The site with the most favorable growing conditions (ecoregion 'Spessart') had a CVP index of 676. The models of both species indicate that the allometry of trees is strongly determined by the site-specific growth conditions (Fig. 8, Eq. 10). Douglas-fir as well as European beech invests in root growth under harsher conditions at the expense of stem growth compared to more favorable sites. This response was especially pronounced for European beech.

Discussion

Patterns in root–stem allometry

The study investigated the allometric relationship of root and stem growth. We could show that the allometric exponent was influenced by tree species mixture, mixture proportion, stand density, short-term humidity variation, and long-term site-specific humidity. Thereby, the strength of the influence differed strongly among these variables. The finding of a general variability of the allometric exponent supports the optimal partitioning theory (OPT). This is consistent with results for root–stem allometry from several other studies (Nikolova et al. 2011; Pretzsch et al. 2012b; McConnaughay and Coleman 1999).
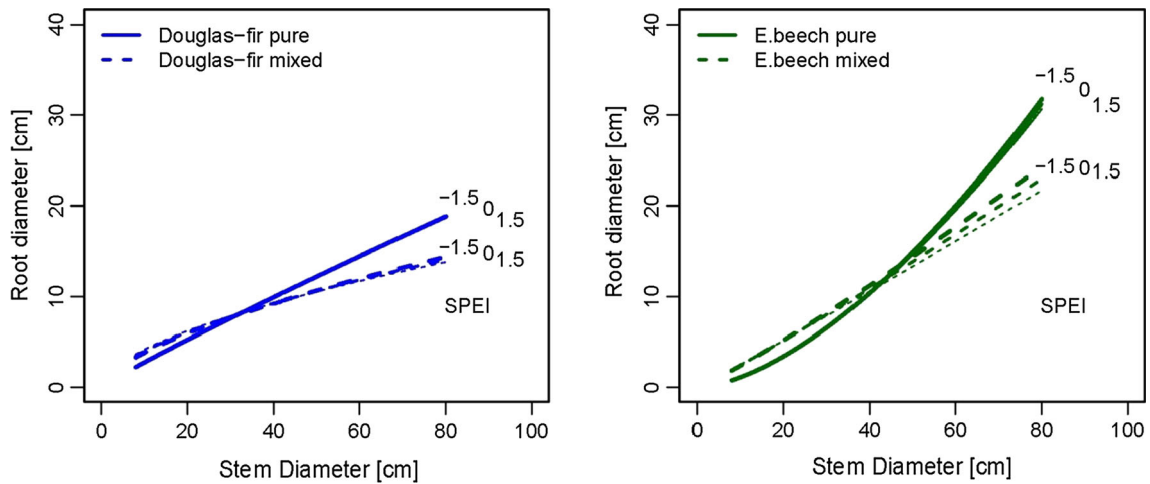
Fig. 6 Root–stem allometry in dependence of humidity in growing period for Douglas-fir (*left*, *blue*) and European beech (*right*, *green*) according to the fitted Eq. 9 Humidity is represented by standardized precipitation-evapotranspiration index SPEI (model predictions shown for SPEI = −1.5, 0, 1.5, corresponding SPEI values et the ends of the lines), although the SPEI effects are very small they turned out significant nevertheless. Model coefficients are shown in Table 3

The pattern of allocation between root and stem was similar for mixture, density and humidity. More favorable conditions lead to a pronounced growth of stem, whereas unfavorable conditions increase growth of roots (see Fig. 9).

Methodological restrictions

Basis of the study is the comparison of stem diameter in breast height and two prominent coarse roots per tree. This method has several advantages to total tree excavation (non-destructive, less resource-demanding, allows sampling mature trees). Nonetheless, the results are diameter comparisons. They cannot be equated with the measured biomasses of above and belowground tree compartments, because in contrast to biomass, they describe resource allocation only indirectly. Another related problem is that we do not know the total number of roots. Therefore, it might be that some of the observed effects are only shifts from individual root increment to a number of roots. This would, however, presuppose that trees changed the structure of their root system. Studies about Douglas-fir where entire root systems were excavated, found out that for this species the number of coarse roots per tree is nearly equal (Mauer and Palátová 2012), going along with a uniform structure of the root system (McMinn 1963). It seems
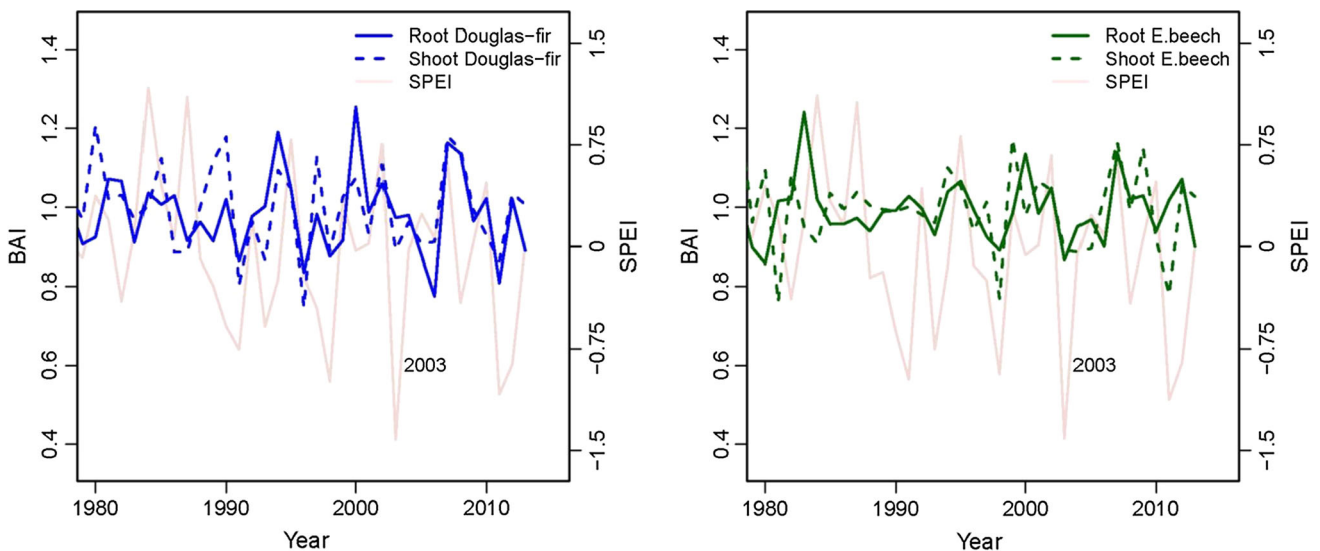

Fig. 7 Detrended root and stem chronologies for Douglas-fir (*blue line*, *left*) and European beech (*green line*, *right*). The standardized precipitation-evapotranspiration index SPEI is added as *red line*. *Labeled* is the extreme drought year 2003

plausible that trees can modify their structural composition within certain limits only. Therefore, we assume that tree species mixing does not lead to significantly different of root numbers.

Several authors found a species-specific, vertical stratification of root systems in mixed stands (Kelty 2006; Forrester et al. 2006a; Bolte and Villanueva 2005). The stratification could be seen in a displacement of fine roots. Two options for this displacement of fine roots in deeper soils are possible: (1) a displacement, realized by sinker roots which branch from the horizontal roots. We should have observed such a reaction when sampling horizontal roots in this study. (2) A greater stratification, in which one species displaces their nutrient uptake into deeper soil layers. This displacement would be generated by an increased growth in heart or tap roots. Douglas-fir as well as European beech feature a heart-root system (Matyssek et al. 2010). Therefore, both species are potentially capable to form a secondary root layer by increase heart-root growth and decrease the growth of the horizontal roots. This would mean that the results we obtained with horizontal roots have to be interpreted in another way, namely, that the mixing effect is not an allocation between roots and stems, but an allocation inside the root system. The retreating species would shift the nutrient transport, respectively, fine root production on these types of roots. Root growth is preferentially favored near the soil surface, because nutrients, soil strength, aeration, and temperature are more favorable there than at depth (Sands and Mulligan 1990). Therefore, stratification without a struggle seems to be not expedient.

A study which was made on a part of our plots found out that out that mixing effects on soil organic carbon and nitrogen concentrations were restricted to the forest floor
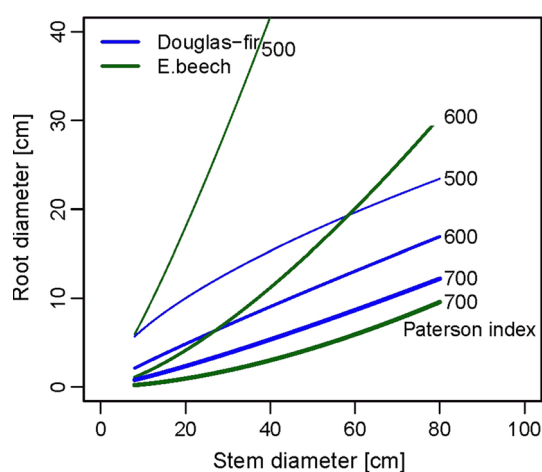

Fig. 8 Root–stem allometry in dependence of long-term site-specific humidity for Douglas-fir and European beech, according to the fitted model after Eq. 10. Humidity at the site is represented by the CVP index by Paterson (1956)

and the uppermost mineral soil (Cremer et al. 2016). A mixture-induced stratification into deeper soil horizons would cause a change of carbon and nitrogen concentrations in these soil layers compared to pure stands. Hendriks and Bianchi (1995) measured root density and biomasses in pure and mixed stands of Douglas-fir and European beech. Their data indicate that both species did not extend their fine root growth pattern in a soil layer, but they have lower root density in mixed stands in the uppermost soil layer (down to 30 cm) compared to pure stands. This would strengthen the assumption of reduced struggle for resources. The data of Hendriks and Bianchi (1995) show a considerable drop of belowground biomass in the mixed stands (25–50%) below what would have been expected from pure stands. This is consistent with our findings of reduced investment into root growth in mixed stands.

Bolte and Villanueva (2005) bring evidence for a root stratification of mixed stands from European beech and Norway spruce. In contrast to our species of interest, European beech and Norway spruce have different root systems which may trigger the stratification. Nevertheless, they also found a reduced fine root biomass in mixed stands.

Humidity

The sensitivity of root–stem allometry to site conditions was pointed out for lodgepole pine *Pinus contorta* (Dougl. ex. Loud) and Douglas-fir by Comeau and Kimmins (1989) and Keyes and Grier (1981). These studies provided evidence that conifers increase stem growth at the expense of root growth under favorable soil moisture conditions. This is a tree individual adaption to site conditions which develops over decades and may explain the great pronounced influence of humidity on root–stem allometry in our results.

The influence of short-term humidity fluctuations was much weaker but also significant in our data. Plants under short-term water-stress may proliferate roots into unexplored regions of soil to unlock water resources and avoid rapid water depletion (Lavelle and Spain 2005). The short allometry response in the current study accords with results from Pretzsch et al. (2012b) for lodgepole pine. They found a more pronounced root growth in a climatically unfavorable period. Nevertheless, growth potential is not excessive in such short periods. Therefore, the reaction cannot compare with a long-term adaptation of allometry (Fig. 8, Eq. 10) to site conditions. In addition, the possibility for unexplored root space in existing stands is not boundless. Easy accessible and favorable root strata are just occupied. The individual trees are restricted in their ability to respond by hardly variable neighbor constellations. That is, another reason why there is only a small possibility to root
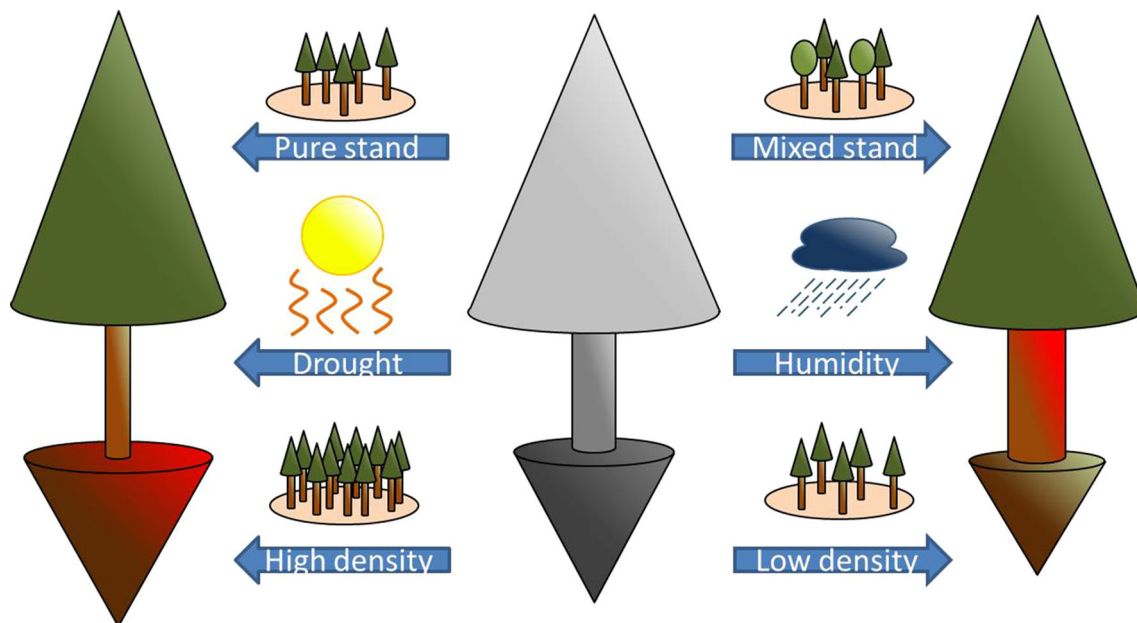
Fig. 9 Comparison of the factors mixing type, humidity and stand density and their influence on root–stem allometry in schematic representation. A gradient from unfavorable conditions to favorable conditions went from *left* to *right* and shift growth allocation from root to stem. The *schematic trees* represents Douglas-fir as well as European beech

extension. In this context, it is interesting that this effect was most pronounced in European beech mixed stands. In a previous study on the same plots, it was found that European beech had limited access only to the soil water storage (Thurm et al. 2016).

Nevertheless, the general patterns of improved root growth in dryer growing periods do not mean that lateral roots get a growth spurt. Stem increment and root increment show a contrary course. Under unfavorable weather conditions, both tree compartments exhibited a loss of growth but absorbed resources will mainly be invested into root growth. This is conformed with the findings of Nikolova et al. (2011) who worked with Norway spruce (*Picea abies* [L.] Karst.).

Mixture and density

Our data showed that an increasing proportion of the admixed species comes with a higher investment in stem growth. Pretzsch and Biber (2016) provide evidence that maximum tree density is higher in mixed stands. Such a more intense crowding might be possible because of a better or complementary nutrient utilization. Pretzsch et al. (2014) showed significant differences in the nutrient content of Douglas-fir and European beech on the whole-tree level. European beech accumulate more potassium and Douglas-fir more phosphor. The combination of different, species-specific nutrient requirements per hectare enables greater supply for the individual. The mixing of complementary species, such as Douglas-fir and European beech,

can likely be seen as an improved resource availability (Bartelink 1998; Thurm and Pretzsch 2016; Thomas et al. 2015). However, an increasing density increased the root–stem ratio in general as also highlighted by Pearson et al. (1984). Species mixing seems to attenuate the competition situation (Piotto 2008).

Our data indicate that increasing age augmented the mixing effect on root–stem allometry. The finding that the mixing effect takes time to appear was also confirmed in other studies (Zhang et al. 2012; Cavard et al. 2011). An increased investment into stem growth with increasing shares of interspecific competition was well pronounced for both species. However, the general comparison of European beech in pure and mixed stands (Eq. 6, Fig. 3) shows that the allocation of stem growth in smaller DBH classes is more pronounced in pure stands than in mixed stand. This allometry first differs when stem size of European beech passes the mean DBH in our plots. Interestingly, we could observe an analogous response in a previous investigation on the same plots, which deals with above-ground biomass productivity (Thurm and Pretzsch 2016). Overyielding of European beech likewise begins when the species reach greater DBH values, in other words, with some delay. Although these responses do not directly match with this study because the study at hand deals with individual tree level data whereas the previous study deals with stand level data, this analogy remains remarkable. When comparing tree allometry in pure and mixed stands, it should be taken into account that DBH distributions in

pure and mixed stands might be different (Pretzsch and Schütze 2016).

A previous study about Douglas-fir and European beech in mixture (Thurm and Pretzsch 2016) and studies about mixing other species (Moore et al. 2011; Pretzsch et al. 2016) could show that overyielding and above-ground structural diversity enhanced soil water availability. Due to partitioning of water resources (Jonard et al. 2011; Forrester et al. 2010), mixed stands may not reach a limit of sufficient water supply, while mono-species stands already do. Therefore, the limiting factor, which drives the overyielding, respectively, the height stratification, shifts from soil to light (Forrester 2014; Pretzsch et al. 2016) and root growth can be reduced in mixed stands.

Seemingly, there is a connection between increasingly differing allometry in pure and mixed stands and overyielding in mixed stands with increasing age. Keyes and Grier (1981) found out that total stand net biomass production (above plus belowground) did not change significantly under a varying site condition gradient but only the partitioning between above and belowground biomass. Maybe, the measured overyielding in mixed stands is partly a partitioning of growth into above-ground biomass with comparable total biomass to pure stands. This is of particular interest because carbon-balance based forest models might overestimate the overyielding in mixed stands.

A physiological adaption against drought is likely to shift allocation in favor of the roots (Bréda et al. 2006). This was clearly confirmed in our study. However, this fact alone would also suggest a declined drought tolerance of mixed stands where we found a decreased root–stem ratio. However, it was found in several studies that mixing tree species can improve their drought tolerance (Lebourgeois et al. 2013; Thurm et al. 2016; Pretzsch et al. 2013). Maybe, the complementary water partitioning between the species in mixed stands (Jonard et al. 2011; Forrester et al. 2010; Thurm et al. 2016) or water pumping property of trees (Aranda et al. 2012) improved the drought sensitivity of mixed species by enhancing the general water supply. But these mechanisms in mixed stands are not well understood so far. In addition, the role of mycorrhizae in the water uptake of trees keeps our interpretation open. Lehto and Zwiazek (2011) mentioned that this could also have an effect on water uptake under stress.

We are aware that there might be complex interactions of stand density, mixture and humidity that influence root stem allometry (Elkin et al. 2015; Guillemot et al. 2015). However, this was not the main focus of the study and we refrained from including them in order to avoid over-complex statistical models.

Wind load and root–stem allometry

Wind stability is another reason for trees to change their root–stem ratio (Coutand et al. 2008; Reubens et al. 2009; Gardiner et al. 2016). In general, stronger wind loads result in a shift in favor of the roots. The decreased investment in roots in mixed stands could suggest a higher risk of windthrow in mixed stands. However, a positive influence of species mixture on wind stability of trees was confirmed by several studies (Mayer et al. 2005; Schütz et al. 2006; Schelhaas 2008). Schelhaas (2008), who investigated the influence of wind on European beech and Douglas-fir found out that a lower height-stem diameter ratio (h/d) of Douglas-fir in mixed stands decreased the risk of wind damage. This different h/d ratio results from a changed competition situation in mixed compared to pure stands (Schelhaas 2008; Thurm and Pretzsch 2016). Abetz (1976) concluded that the predominant species in mixture decreased their h/d ratio whereas suppressed species increased their h/d ratio. Reason is the necessity to grow to light. Thurm and Pretzsch (2016) also observed this pattern of predominant Douglas-fir and suppressed beech with modified h/d ratios in mixed stands. Nevertheless, there seems to be no direct link between h/d ratio and root stem allometry, because the response in h/d went contrary, whereas the allometry pattern based on root stem diameters in mixed stands for both species is similar.

A contrasting point should not go unmentioned in this context: e.g., Röhrig et al. (2006) point out, stand canopy roughness strengthens wind turbulences, and increase the risk of wind damages. In mixed stands as covered by our plots, the great tree height difference between Douglas-fir and European beech would thus predispose Douglas-fir.

Conclusions

The morphological plasticity and adaptability of tree stems and crowns to a given competitive status is rather easy to measure and well known. It affects, among others, growth resilience of the stand, stand stability, and wood quality. Compared with this, the plasticity of the stem in relation to roots is much more difficult to access and, therefore, rather unknown. However, of course, it is also highly relevant, for, many important tree and stand traits, e.g., tree and stand stability against wind, below and above-ground carbon storage, resource use, and tree and stand productivity. Although based on rather rough sampling, we could show a high plasticity and adaptability of the root–stem relationship. Further detailed analyses seem desirable, as they might show to what extent this partitioning affects overyielding in mixed stands, as well as their susceptibility to windthrow or drought compared to pure stands.

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