Mixture reduces climate sensitivity of Douglas-fir stem growth

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ABSTRACT

Due to possible positive and compensatory interaction between species, mixed stands are a commonly accepted silvicultural response to reduce risks arising from climate change. Nonetheless, only a few species combinations have been studied more detailed so far revealing variable mixing effects. Here, we analyze the effect of the mixture of Douglas fir and European beech with regard to the species-specific climate sensitivity of growth. We focus on three hypotheses: (i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

To scrutinize the hypothesis we analyzed tree cores from both species taken from pure and mixed stands covering different site conditions and age classes. Tree ring characteristics were used to analyze the differences in climate related long-term growth responses in pure and mixed stands. Short-term responses were investigated by growth reaction indices on individual tree and stand level involving drought events during the years 1950–2010. Linear mixed models were applied to detect effects of ecological co-variables on the indices.

Results reveal that Douglas-fir in mixed stands exhibit a significant improved growing performance compared to pure stands. European beech seems to react indifferently concerning its performance in mixture compared to pure stands.

Differences in drought stress resistance and growth recovery time mainly arose between the species. Douglas-fir showed a significantly lower resistance and required more time to reach again its initial growth level compared to European beech. In mixture we found a trend that Douglas-fir growth recovery time is shortened and extended for European beech.

The analysis along the ecological gradients showed that base-limited soils systems are more drought-tolerant during drought events. Lower basal area as a proxy for reduced stand competition decreased the relative growth loss by drought.

We hypothesize that mainly spatial differentiation in height trigger enhanced diameter growth of Douglas-fir in mixture. Temporal differentiation expressed by deferred phenology attenuates climate sensitivity of this conifer. We conclude that in mixed Douglas-fir and European beech stands the former species is stabilized against climatic impacts. On the contrary, climate sensitivity of European beech is increased.

1. Introduction

An increase in frequency and intensity of ecosystem disturbances such as severe drought events have been observed in many regions of the world (IPCC, 2014) challenging forest management to deal with adaptation issues. In this context species mixing seems to be an effective way to stabilize forests against such impacts (Kelty, 1992; Knoke et al., 2008; Lüpke, 2004). Previous studies focusing on productivity (Forrester, 2014; Toïgo et al., 2014; Vallet and Pérot, 2011) provide evidence, that mixing species modifies resource utilization within a stand. Generally, interactions between combined species seem to be responsible for a change in resource partitioning. Larocque et al. (2013) separate these into interactions resulting in positive (through facilitation and complementarity) or negative (through competition) outcomes. Mainly processes of facilitation and niche differentiation improve the utilization of available resources in mixed stands. Mixing effects are not a constant phenomenon but depend on

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developmental stage of a stand (Binkley and Greene, 1983; Zhang et al., 2012) and on site conditions (Toïgo et al., 2014). According to the stress gradient hypothesis the effect of facilitation is more pronounced on sites with stressful growing conditions whereas under benign conditions competition dominates (Bertness and Callaway, 1994; Callaway and Walker, 1997).

When considering drought events as temporal setbacks of growing conditions it is assumable that in mixed stands comprised by species exhibiting different functional traits and resistance behavior negative growth reactions may also be attenuated. Growth loss or dramatic drop out of one species by a disturbance may be mitigated or even compensated by the second species (Kelty, 1992). Some studies provide evidence that mixture has a positive effect during drought events for at least one species (Lebourgeois et al., 2013; Pretzsch et al., 2013).

In Central Europe forest managers aim at reducing the share of conifer monocultures, mainly dominated by the highly vulnerable Norway spruce (*Picea abies* (L.) H. Karst.) by establishing mixed stands of conifers and broadleafed species (Klimo et al., 2000; Zerbe, 2002). In this context, mixed stands of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) receive increasing attention (Reyer et al., 2010). European beech is one of the most competitive species and would dominate the potential natural vegetation in Central Europe (Bolte et al., 2007; Ellenberg and Leuschner, 2010). Douglas-fir as a non-indigenous species in Europe provides the advantages of having high growth rates and good wood quality and being very adaptable to various site conditions (Kleinschmit and Bastien, 1992). Its growth rates outperform Scots pine (*Pinus sylvestris* L.) and Norway spruce (Hermann and Lavender, 1999; Pretzsch, 2005). Additionally, its drought tolerance seems to be more accomplished compared to other European conifers (Bréda et al., 2006; Eilmann and Rigling, 2012). Complementary characteristics of both species have been described by Hendriks and Bianchi (1995) concerning below ground space occupation and by Thomas et al. (2015) concerning crown stratification.

To enhance knowledge about the effect of mixing Douglas-fir and European beech concerning their resistance against drought, the study analyzed the respective past growth responses of both species. We tested three null hypotheses: (i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

Our analyses of the tree growth performance make use of the comparison of two stand types (pure and mixed) growing on similar site conditions. This enables to detect possible mixing effects on tree chronology characteristics by contrasting intra- and inter-specific competition situations.

In a first step, we use tree ring characteristics to analyze the long term climate response of the trees. Fritts (1976) described the changes of tree chronology characteristics under a gradient from forest interior to semiarid forest border. Trees under harsher conditions built *sensitive* tree rings, with higher mean sensitivity, lower autocorrelation and smaller ring width. In contrast, trees under benign conditions built *complacent* year rings with opposite characteristics. Additionally, Biondi and Qeadan (2008b) showed that tree ring variability computed by the Gini-coefficient varied between different species and between different time periods.

Tree ring chronologies are further used to analyses the short term growth reaction of the species during past droughts event. Pretzsch et al. (2013) could show that resistance of trees is modified in mixture compared to pure stands. We introduce growth recovery time and loss of increment as measure of growth reaction

due to drought, whereas the pre drought growth level serves as reference. Several studies suggest that subsequent years with unfavorable water supply have to be considered when looking at growth recovery time (Eilmann and Rigling, 2012; Hartmann, 2011; McDowell et al., 2008). Therefore, we also take a look at the climate condition after a drought year and link it with the growth recovery time.

We look at both, growth reaction on individual tree and stand level. As growth reaction to drought may be dependent on tree size individual reaction do not allow to scale up to stand level without considering tree size distribution (Mérian and Lebourgeois, 2011). This is even more relevant when comparing pure and mixed stands as tree size distribution may differ between stand types (Pretzsch and Schütze, 2016). By providing relative reaction values, it is possible to explain the biological response patterns of the trees during drought. Absolute growth values on stand level enable a link to forest management.

2. Materials and methods

2.1. Study site and plot set-up

The study was conducted in Central Europe and covered a range of 430 km. Seven different ecological regions were included from "Osteifel" (N 6°44′36.33″, O 50°10′23.86″) in the north west to "Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft" (N 11°51′09.88″, E 48°07′16.78″) in the south east (Fig. 1). The study made use of a triplet experimental setup. Each triplet is composed of a mono-specific stands of Douglas-fir and European beech, respectively and a mixed stand of both species, growing on identical site conditions and exhibiting similar stand age. The plots of a triplet were selected in direct proximity, mostly in the same compartment, to minimize residual effects like soil, tree genetic and management effects. When the plots were not in inside the same compartment, the similarity of the soil was visually checked by a sample with a boring rod. All triplets represented more or less fully stocked and mono-layered forest stands (see Supplementary material 1). General differences in stand density resulted from species-specific, tree size related space occupation (Reineke, 1933) and from mixing effect (Pretzsch and Biber, 2016). By this, comparisons of growth reactions in pure stands of Douglas-fir and European beech as well as in mixed stands of both species under similar growing conditions are enabled. The climate response of the species in mono-specific stands is used to reference possibly deviating response of the species in mixed stands.

The mean annual temperatures between the triplets range from 7.0 to 9.5 °C and from 13.7 to 15.7 °C during the growing period. The mean annual precipitations range from 733 to 1066 mm, and to 322–576 mm in the growing period, respectively (multi annual values from 1981 to 2010) (Deutscher Wetterdienst, 2015). The soil water supply of the triplets, described by a combination of water holding capacity, precipitation and transpiration, ranged from dry to very fresh. The base equipment of the soils ranged from base-poor to base-rich. The age gradient covers three classes: young (approx. 30 years), mature (approx. 60 years) and old stands (approx. 90–120 years). Table 1 gives an overview of the triplet's site conditions and stand parameters.

2.2. Sampling and standardization of tree rings

During the years 2012–2014, in total 1279 trees were sampled by extracting two increment cores from northern and eastern direction from each tree at breast height (1.30 m). Ring widths were measured with digital positiometer (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Cross-dating
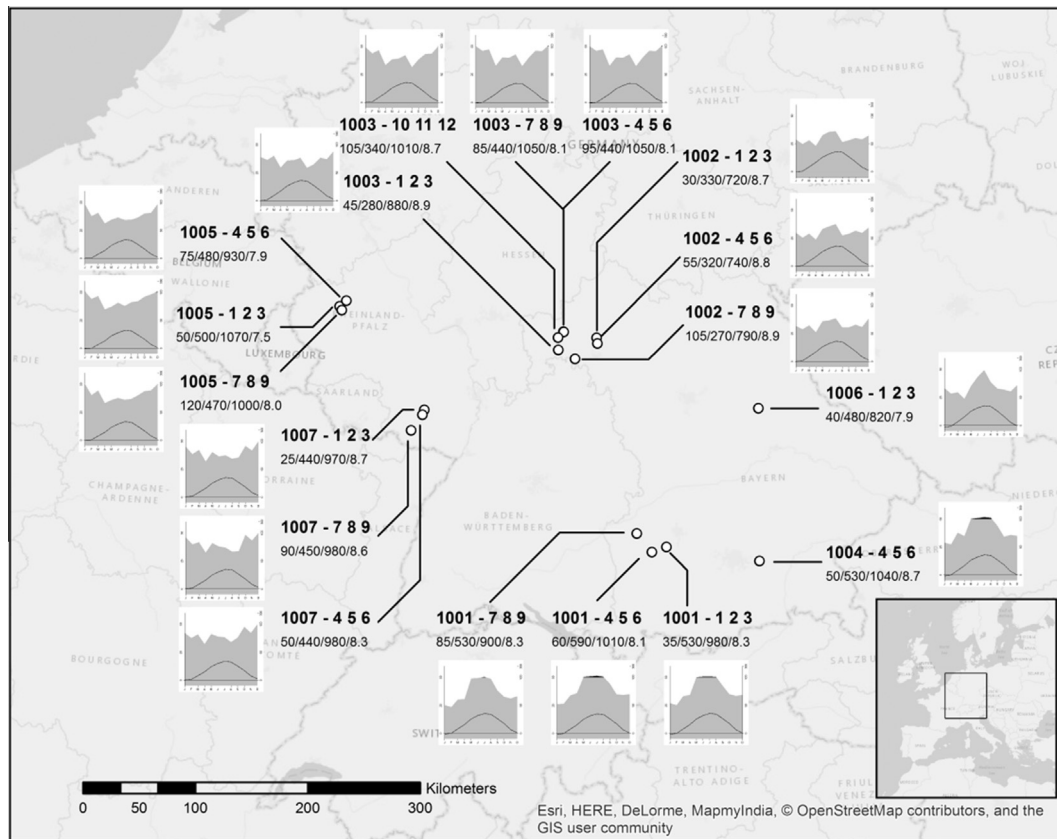
Fig. 1. Location of the 18 triplets in Central Europe (dots) with the associated climate charts according to Walter and Lieth (1967). The experimental trial number results from a four-digit experimental number and a three-digit triplet number. Beneath the experimental trial number, plot information concerning stand age of the triplet, elevation above sea level, annual precipitation sum and mean annual temperature is given.

and synchronization of the tree chronologies were conducted using the software platform TSAP-Win (Rinntech, Heidelberg, Germany). We measured diameter at breast height (DBH) and tree height from all cored tree and from the remaining trees of each plot (n = 1987, see Table 1).

In order to extract the climate related growth reaction from the chronologies the individual tree core series were standardized. Here, we use basal area increment (BAI) series instead of ring width series for detrending and statistical analyses, because the BAI as a two-dimensional measurement, better reflects three-dimensional growth of the whole tree (volume) than the one-dimensional growth of tree ring width (Biondi and Qeadan, 2008a; LeBlanc, 1990). The BAI for each individual tree was calculated using the mean radial increment of both cores. A double detrending procedure was applied to standardize BAI time series (Holmes et al., 1986). This two-stage curve fitting (see example in Appendix A) was used to eliminate the deterministic age trend at first. Due to the nature of BAI age trend we applied a Hugershoff function (1936) instead of a negative exponential function or linear regression, usually used for detrending. For the second detrending procedure, a cubic spline was applied because residual growth trends from forest trees strongly depend on

competition and release of competition through thinning. The wavelength of the cubic spline was fixed by 15 years with a frequency response of 0.5. A 15 year window was used as it covers a usual time interval of thinning activities.

To quantify the long-term growth behavior of both species in pure and in mixed stands, we used five standard tree ring characteristics (Biondi and Qeadan, 2008b; Fritts, 1976; Speer, 2010). The mean basal area increment (Mean), calculated as mean value for each tree chronology, provides a measure of the general growth potential. The Gleichläufigkeit (GLK) describes the intra-specific conformity of the tree chronologies within a sample stand. The first-order autocorrelation (AC) indicates to what extent the increment of year n correlated with year n−1. In terms of sensitivity we calculated mean sensitivity (MS), which quantifies the year-to-year variability. AC indicates the existence of low frequency variability in tree ring chronologies which is triggered for instance by physiological processes leading to a lag in response to climate conditions. MS is a measure of high frequency variability and is regulated by short term shifts in climate related growing conditions (Fritts, 1976). Lastly, the Gini coefficient (GINI) represents a quantitative measure of the heterogeneity of increment in tree ring chronologies. GINI, MS and GLK where calculated based on index

Table 1

Stand and site characteristics of the 18 triplets sampled between 2012 and 2014 (Survey) indicating ecoregions (Gauer and Kroiher, 2012) and climate data (Temp - mean annual temperature, Prcp - mean annual precipitation sum) (Deutscher Wetterdienst, 2015), base-richness (Base), water supply (Water) and plant available water capacity (PAWC) (Landesforst Rheinland-Pfalz, 2014a; Taegger and Kölling, 2016), diameter at breast height (DBH) and tree height (Height) refer to the quadratic mean diameter tree, number of cored trees. Base-richness is ranked from very base-poor (1) to very base-rich (5) and water supply is ranked from very dry (1) to very fresh (7).

Experimental trial	Triplet	Ecoregion	Temp [°C]	Prcp [mm]	Base	Water	PAWC [mm]	Stand age [year]	Survey	Douglas-fir						European beech					
										Pure			Mixed			Pure			Mixed		
										DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees
1001	1 2 3	Tertiäres Hügelland	8.3	977	3	7	192	33	2013	26.2	23.8	19	24.7	22.4	22	13.9	18.9	26	13.5	16.3	17
	4 5 6	Tertiäres Hügelland	8.1	1011	3	7	130	60	2013	45.1	32.3	20	53.1	35.7	14	23.3	22.3	37	19.3	22.0	18
	7 8 9	Tertiäres Hügelland	8.3	898	3	7	214	85	2013	74.0	44.9	18	62.0	39.4	17	38.3	28.1	20	25.8	27.7	13
1002	1 2 3	Fränkische Platte	8.7	718	4	3	210	29	2013	18.2	20.3	22	14.0	16.5	16	8.7	14.3	19	10.7	16.9	23
	4 5 6	Fränkische Platte	8.8	740	4	3	200	54	2013	28.3	27.3	24	36.2	29.9	17	15.2	22.3	19	17.0	21.2	30
	7 8 9	Fränkische Platte	8.9	792	4	3	210	103	2013	58.0	43.4	17	75.4	46.8	9	53.6	39.3	14	36.2	35.2	17
1003	1 2 3	Spessart	9	878	2	7	144	43	2013	32.9	29.2	19	34.2	27.3	16	15.4	19.8	24	15.1	17.3	27
	4 5 6	Spessart	8.1	1054	3	4	154	95	2013	64.1	49.2	8	63.1	44.7	5	35.6	35.6	16	29.7	35.8	20
	7 8 9	Spessart	8.1	1054	3	4	154	85	2013	55.2	41.2	10	78.6	38.2	5	30.9	31.8	17	29.9	29.9	19
	10 11 12	Spessart	8.7	1012	2	6	144	105	2013	63.9	41.8	13	80.8	43.5	4	42.4	29.1	17	36.4	30.2	11
1004	4 5 6	Schwäbisch-Bayerische Schotterplatten und Altmoränenlandschaft	8.5	1044	4	7	132	49	2013	27.6	26.2	18	29.9	25.0	14	21.3	22.6	21	15.6	23.2	18
1005	1 2 3	Osteifel	7.5	1066	3	6	171	49	2014	36.7	31.4	28	45.7	31.2	14	16.4	17.7	21	15.2	18.0	25
	4 5 6	Osteifel	7.9	926	3	6	155	75	2014	46.4	36.4	16	73.7	38.7	5	28.1	24.8	25	22.1	21.5	23
	7 8 9	Osteifel	8	1000	3	6	155	119	2014	70.3	49.0	12	83.2	40.9	4	37.0	29.9	18	23.2	22.0	16
1006	1 2 3	Frankenalb und Oberpfälzer Jura	7.9	821	3	5	156	37	2013	26.6	24.9	25	30.2	24.7	23	17.9	19.0	22	17.2	19.7	8
1007	1 2 3	Pfälzerwald	8.7	974	2	5	146	26	2012	11.5	13.0	22	9.1	10.0	15	9.0	11.4	20	7.8	9.0	15
	4 5 6	Pfälzerwald	8.3	980	2	5	193	51	2012	26.4	29.8	20	23.0	24.1	16	16.6	17.7	23	17.9	21.0	18
	7 8 9	Pfälzerwald	8.6	981	2	5	172	92	2012	62.5	43.4	20	69.8	46.2	15	38.2	33.1	20	33.6	32.9	20
		Total (min-max)	8.4 (7.5–9.0)	940 (718–1066)				66 (25.7–119.0)		41.2 (11.5–74.0)	33.3 (13.0–49.2)	331 (8.0–28.0)	49.3 (9.1–83.2)	32.5 (10.0–46.8)	231 (4.0–28.0)	25.7 (8.7–53.6)	24.3 (11.4–39.3)	379 (14.0–37.0)	21.5 (7.8–36.4)	23.3 (9.0–35.8)	338 (8.0–30.0)

values, whereas AC were calculated based on measured raw ring width.

The basal area of the stands was calculated by summing up the basal area of all individual trees per plot and afterwards scaled up to 1 ha. Missing basal area increments of not drilled trees were calculated by fitting a function that relates DBH and previous growth rates of drilled trees ($\ln(i_d) = a + b \cdot \ln(DBH)$). All in all, not drilled trees represented less than 15 percent of the whole basal area.

By the calculation for the drought response of the whole stands, the stand increment was detrended by a Hugershoff function.

For the descriptive core statistics and the calculation of the cubic spline we used the package *dplR* (Bunn, 2008, 2010).

2.3. Weather data

The climatic characterization of the sites and the calculation of the drought indices are based on $1 * 1$ km grid of multi annual and monthly precipitation and temperature data (Deutscher Wetterdienst, 2015). The plots of a triplet were mostly located closer than 200 m together, so that climate data were aggregated only for the mixed stand but also used for the whole triplet (for a more detailed view of experimental setup see Thurm and Pretzsch, submitted for publication). The standardized precipitation-evapo transpiration index (SPEI) was used to identify drought years (Vicente-Serrano et al., 2010). The SPEI was calculated for a time scale of 5 month using a Gaussian kernel function. The length of the timescale was deduced from a comparison of drought events and BAI response. Thereafter, the mean SPEI of the growth period from May to September was calculated. As drought years, the seven years (10th percentile) with lowest SPEI during 1950–2010 per triplet were selected (see Supplementary material 2). Thereby, we investigated tree response during extreme drought years as well as during moderate drought years.

To consider different drought stress behaviors of Doulas-fir and European beech, e.g. isohydric or anisohydric traits (Hartmann, 2011; Tardieu and Simonneau, 1998), drought years were classified into three groups. The classification depended on the climate conditions after a drought year. If after a drought year a year with above average dry climate conditions was following, it was classified as *good post-year*. Respectively average conditions after a drought year were classified as *average post-year* and below-average conditions as *adverse post-year*. The selection was done individually for every triplet. Classification concerning a specific drought year may thus vary between sites.

2.4. Drought year analyses

The *drought year analyses* focused on short-term individual trees' response to drought weather events. Secondly, the drought year analysis was performed for the whole stand. Lloret et al. (2011) introduced three indices (resistance, resilience and recovery) describing the performance of trees under drought stress. Here, beside resistance, we used two new indices characterizing the growth reactions (growth recovery time, increment loss due to drought) of individual trees and stands to drought.

The *resistance* (Rt) quantifies the ability of plants to withstand a disturbance. Lloret et al. (2011) defined Rt as the ratio between growth during the drought event and a mean growth level of a reference period prior to the drought event.

For the resilience (Rs), we found different definitions in the literature. Lloret et al. (2011) described the resilience as the ratio of post-disturbance growth level to pre-disturbance growth level. Pimm (1984) refers to resilience as the time a system needs to return to an equilibrium following disturbance. Here, we used resilience in terms of the duration starting in the drought year until

reaching the pre-drought growth level again (Fig. 2). To avoid confusion of ideas the index is named *growth recovery time* (GRT). The index's unit is year units, as possible decimal figures do not represent ratios of a full year.

The index *increment loss due to drought* (Loss) describes the loss of stand growth due to drought in relation to the pre-drought growth level. It is the cumulated loss during the time of recovery.

To provide a value more common in forest practice, basal area increment loss due to drought was transformed into volume loss. Therefore, we fitted a stand volume function (Eq. (1)) for each mixture (*m*, Douglas-fir pure stand, mixed stand, European beech pure stand) at survey point (*p*) with basal area and stand age as independent variables, including their interaction. The coefficients $a_0 \ldots a_3$ of the fixed effect from the single models are shown in Appendix B.

$$\ln(Volume_{mp}) = a_0 + a_1 \cdot \ln(Basal\ area_{mp}) + a_2 \cdot \ln(Stand\ age_{mp}) + a_3 \cdot \ln(Basal\ area_{mp} \cdot Stand\ age_{mp}). \quad (1)$$

As mentioned in chapter 2.2, deterministic age trend that may influence pre- and post-drought growth rates can be removed by double detrending procedures. Additionally, specific weather conditions prior and after drought events, may also affect the index values. To cope with this problem, all indices for drought event identified along the chronologies were pooled assuming to average possible differences in pre- and post-drought weather conditions.

2.5. Statistics

2.5.1. Tree chronology characteristics

Species-specific chronologies characteristics were used to test for differences of long-term growth behavior between Douglas-fir and European beech in mixed and in pure stands. Therefore, we applied a linear mixed model (Eq. (2)), *lmer* from the R-package *lme4* (Bates et al., 2015). Y_{ij} refers to the mean tree chronology characteristics per plot and species. The mixing types (mixed Douglas-fir, pure European beech and mixed European beech) were included as fixed effects and coded as binary variables, which switch between 1 and 0, depending on which mixing type is fitted.
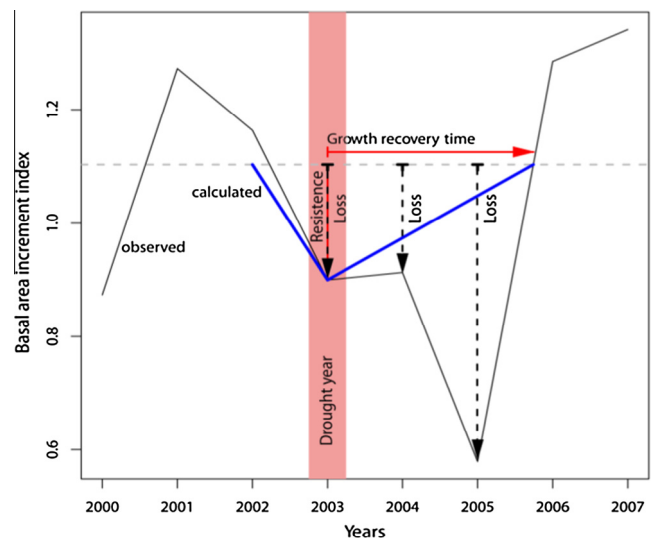
Fig. 2. Schematic illustration of the growth reaction indices used in the analyses (resistance, growth recovery time and increment loss due to drought). The solid black line represents the detrended basal area increment. The bold solid blue line shows the drought response calculated by resistance and growth recovery time, also used in Figs. 5 and 6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$Y_{ij} = a_0 + a_1 \cdot \text{mixed Douglas-fir}_{ij} + a_2 \cdot \text{pure E. beech}_{ij}$$
$$+ a_3 \cdot \text{mixed E. beech}_{ij} + b_i + b_{ij} + \varepsilon_{ij} \quad (2)$$

The indexes i and j represent experimental location and the triplet. a_0 and a_1 represent the coefficients of fixed effects. Random effects are considered with b on experimental location and plot level. The symbol ε represents the independent and identically distributed random error. Results were checked for homoscedasticity and normal distribution. A generalized linear hypothesis test was used for contrasting all mixing type effects, as obtained by the linear mixed model, against each other. We applied the R-package "multcomp" (Hothorn et al., 2008).

In a second step a multivariate analysis of tree chronology characteristics was performed by a Principal Component Analysis (PCA) using the packages "FactomineR" (Husson et al., 2015). It was applied to identify patterns in tree characteristics which are linked to the species, mixing types, age and experimental trial. The four mixing types (pure and mixed Douglas-fir, pure and mixed European beech) of each triplet were addressed individually within the analysis. Mean tree characteristics (mean basal area increment, autocorrelation, mean sensitivity, Gini coefficient and Gleichlaeufigkeit) were included as quantitative variables. Ellipses corresponding to 95% confidence intervals were calculated, based on the coordinates of mixing types, species, age and experimental location.

2.5.2. Drought year analyses

A linear mixed model approach was applied to analyze possible effectors on resistance and growth recovery time and increment loss due to drought on individual tree and stand level. The effectors were separated into two types: plot specific (species, mixing type, post-year conditions) and overarching ecological factors.

With Eq. (3), we tested the effect of plot specific variables at the individual tree level for the resistance and the growth recovery time (YI).

$$YI_{ijkt} = a_0 + a_1 \cdot \text{species}_{ij} + a_2 \cdot \text{mixture}_{ij} + a_3 \cdot \text{species}_{ij} \cdot \text{mixture}_{ij}$$
$$+ a_4 \cdot \text{post-years}_{ij} + a_4 \cdot \text{species}_{ij} \cdot \text{post-years}_{ij}$$
$$+ a_4 \cdot \text{mixture}_{ij} \cdot \text{post-years}_{ij}$$
$$+ a_4 \cdot \text{species}_{ij} \cdot \text{mixture}_{ij} \cdot \text{post-years}_{ij}$$
$$+ b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \quad (3)$$

In addition to Eq. (2), the indexes k and t represent individual tree and drought event, respectively. Additionally, the tree number was considered as random effect. In case of resistance, the dependent effect of post-year and its respective interactions were omitted.

To test the resistance, the growth recovery time and the increment loss due to drought at stand level (YS) we used Eq. (4). The two stand types, European beech pure stand and the mixed stand, are considered as binary variables like in Eq. (2). The Douglas-fir pure stand is represented by the intercept. The post-year factor was omitted on this level completely, because in most cases the weather conditions in 2004 were below average.

$$YS_{ijt} = a_0 + a_1 \cdot \text{pure E. beech stand}_{ij} + a_1 \cdot \text{mixed stand}_{ij} + b_i$$
$$+ b_{ij} + \varepsilon_{ijt} \quad (4)$$

To verify the influence of the ecological factors on resistance and growth recovery time, the following independent variables were taken into account: age, DBH (in case of stand level model the basal area per hectare), relative DBH (ratio of DBH to DBH of the quadratic mean diameter tree per plot), water supply, base-richness, mean annual temperature, annual precipitation sum and in case of stand level model the proportion of European beech (proportion$_{(Eb)}$)(Table 1).

Individual tree level:

$$YI_{ijkt} = a_0 + a_1 \cdot \text{age}_{ijkt} + a_2 \cdot DBH_{ijkt} + a_3 \cdot \text{age}_{ijkt} \cdot DBH_{ijkt}$$
$$+ a_4 \cdot \text{relative } DBH_{ijkt} + a_5 \cdot \text{base-richness}_{ij}$$
$$+ a_6 \cdot \text{temperature}_{ij} + a_7 \cdot \text{precipitation}_{ij}$$
$$+ a_8 \cdot \text{water supply}_{ij} + a_9 \cdot \text{precipitation}_{ij} \cdot \text{water supply}_{ij}$$
$$+ b_i + b_{ij} + b_{ijk} + \varepsilon_{ijt} \quad (5)$$

Stand level:

$$YS_{ijt} = a_0 + a_1 \cdot \text{age}_{ijt} + a_2 \cdot \text{proportion}_{(Eb)_{ijt}} + a_3 \cdot \text{basal area}_{ijt}$$
$$+ a_4 \cdot \text{base-richness}_{ij} + a_5 \cdot \text{temperature}_{ij} + a_6 \cdot \text{precipitation}_{ij}$$
$$+ a_7 \cdot \text{water supply}_{ij} + a_8 \cdot \text{precipitation}_{ij} \cdot \text{water supply}_{ij}$$
$$+ b_i + b_{ij} + \varepsilon_{ijt} \quad (6)$$

Model selection was based on the Akaike Information Criterion (Burnham and Anderson, 1998) and biological plausibility of the results. The selection was made with additionally help of automated model selection (dredge) from the R package MuMln (Barton, 2015), which consider all possible variable combinations.

All statistical analyses were performed in the statistical environment R version 3.2.2 (R Core Team 2015).

3. Results

3.1. Tree chronology characteristics

The analysis of the tree characteristics revealed considerable differences between the mixing types (Fig. 3). In general, the mean basal area increment of Douglas-fir (29.0 cm^2 a^{-1}) was significantly larger than European beech (9.6 cm^2 a^{-1}). Douglas-fir in mixed stands (33.5 cm^2 a^{-1}) showed a significantly higher increment than in pure stands (26.0 cm^2 a^{-1}). Between the increments of European beech in mixture (8.7 cm^2 a^{-1}) and pure stands (10.5 cm^2 a^{-1}) no significant differences were observed. The autocorrelation of tree ring chronologies of Douglas-fir in pure stands (0.68) was highest compared to Douglas-fir in mixed stands as well as to European beech in both stands types. The autocorrelation of European beech in pure stand (0.60) did not differ significantly from Douglas-fir (0.58) or European beech in mixture (0.61).

The patterns of the mixed stands concerning mean sensitivity and Gini coefficient were similar. European beech in mixed stands showed the highest sensitivity (MS = 0.28, Gini = 0.14) whereas Douglas-fir in mixture (MS = 0.24, Gini = 0.12) showed the lowest sensitivity. Douglas-fir in pure (MS = 0.25, Gini = 0.13) and in mixed stands did not differ significantly. The sensitivity of European beech in pure stands (MS = 0.26, Gini = 0.13) did not differ from any mixing type. Concerning Gleichlaeufigkeit a significant interspecific variation was found; Douglas-fir having a higher Gleichlaeufigkeit (pure = 0.63, mixed = 0.64) than European beech (pure = 0.58, mixed = 0.57).

The principal component analyses (Fig. 4) showed, that the two axes (PC1 and PC2) performed on tree chronology characteristics explained 53.0% and 23.5%, respectively of the total variance. The descriptive statistic of the PCA can be seen in Supplementary material 3. The similar trend of mean sensitivity (MS) and Gini coefficient (Gini) is evident by the correlation of first dimension (Fig. 4a). Autocorrelation (AC1) was negative correlated to sensitivity. Mean basal area increment (Mean) and Gleichlaeufigkeit showed same correlation on both dimensions. Each of the five tree chronology characteristics were significant correlated to the first
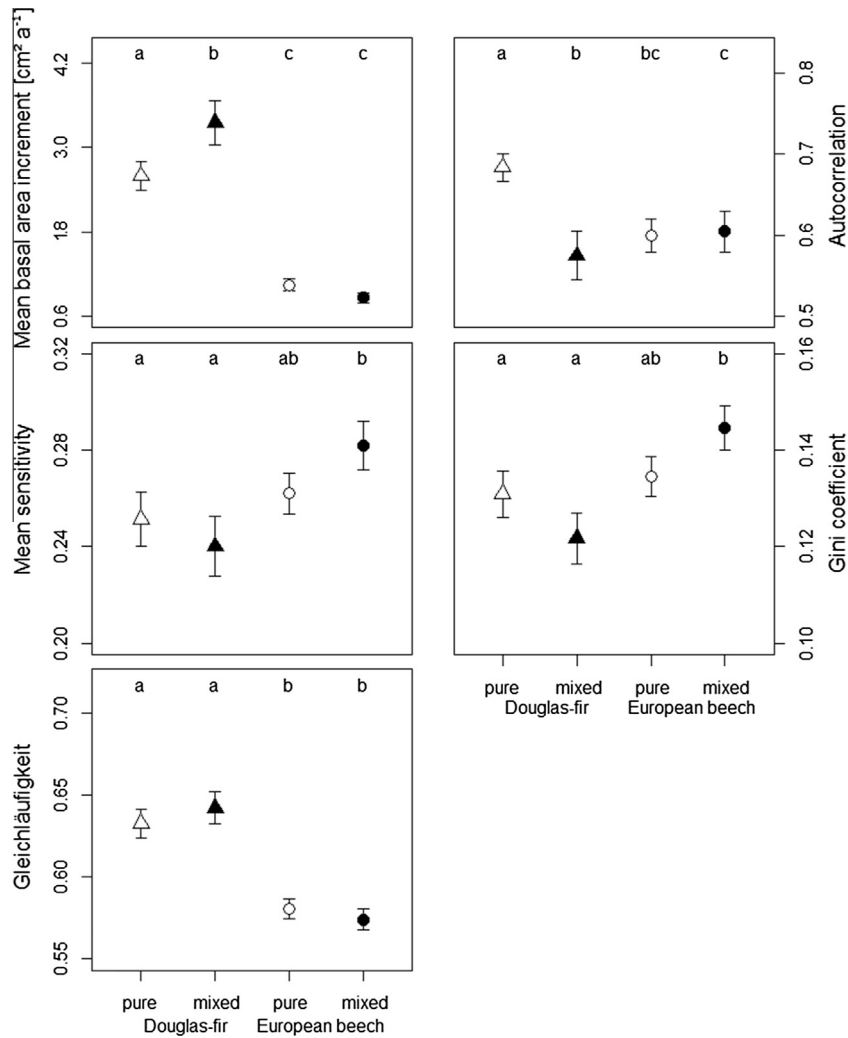
Fig. 3. Statistics of growth series of Douglas-fir (triangle) and European beech (circle) in pure (white) and mixed stand (black) based on 1279 cores. Autocorrelation was calculated on ring width. Mean sensitivity, Gini coefficient and Gleichläufigkeit calculated on double detrended basal area increment indices. Significant differences between the mixing types are indicated by different upper case letters.

dimension and to the second dimension, except for the Gini coefficient.

Each qualitative variables (species Fig. 4d) explained significant differences in tree chronology characteristics, mainly concerning experimental location ($R^2 = 0.57$, $p < 0.001$) and mixing type ($R^2 = 0.35$, $p < 0.001$). The qualitative variables species (Fig. 4b) and mixing type (Fig. 4c) mainly differ by mean basal area increment and Gleichlaeufigkeit. Fig. 4b shows that Douglas-fir and European beech differ significantly in their characteristics. Douglas-fir offered higher mean basal area increment, Gleichlaeufigkeit and autocorrelation; whereas European beech is characterized by lower mean basal area increment, higher sensitivity (MS), and heterogeneity (GINI). Same can be seen in mixing types (Fig. 4c). It is remarkable, that Douglas-fir and European beech differ significantly more in their characteristics in mixed than in pure stands. Young stands differ significantly in their tree chronology characteristics from mature and old stands ($R^2 = 0.08$, $p < 0.05$). They exhibited higher sensitivity, heterogeneity and lower mean basal area increment (Fig. 4d). The PCA showed that younger stands revealed a higher sensitivity. The experimental location was strongly determined by the shift from high autocorrelation to high sensitivity (Fig. 4e).

3.2. Drought year analyses

3.2.1. Individual tree level

The general response of the Douglas-fir and European beech to drought years is illustrated in Fig. 5. The appendant results from the multi comparisons of the linear mixed models are summarized in Table 2. The increment of European beech (resistance = 90.8%) during the drought years dropped significantly less than of Douglas-fir (Rt = 85.5%, $p < 0.001$). No significant mixing effect was existent for both Douglas-fir and European beech. The resistance of both species either in pure or in mixed stands was nearly equal (European beech pure = 90.9, mixed = 90.8, $p > 0.05$; Douglas-fir pure = 85.3, mixed = 85.9, $p > 0.05$). The analysis of plot specific and overarching factors on growth reaction due to drought indicated that the resistance of Douglas-fir was negatively influenced by the DBH and positive by the age (Table 3). This contradiction is solved by the fact that smaller DBH at same age showed a higher resistance for Douglas-fir. The resistance of European beech seemed to be influenced by the social position. Trees with smaller DBH than the basal area tree per plot tended to have a better resistance. Higher base-richness of soils seemed to reduce resistance of both species.
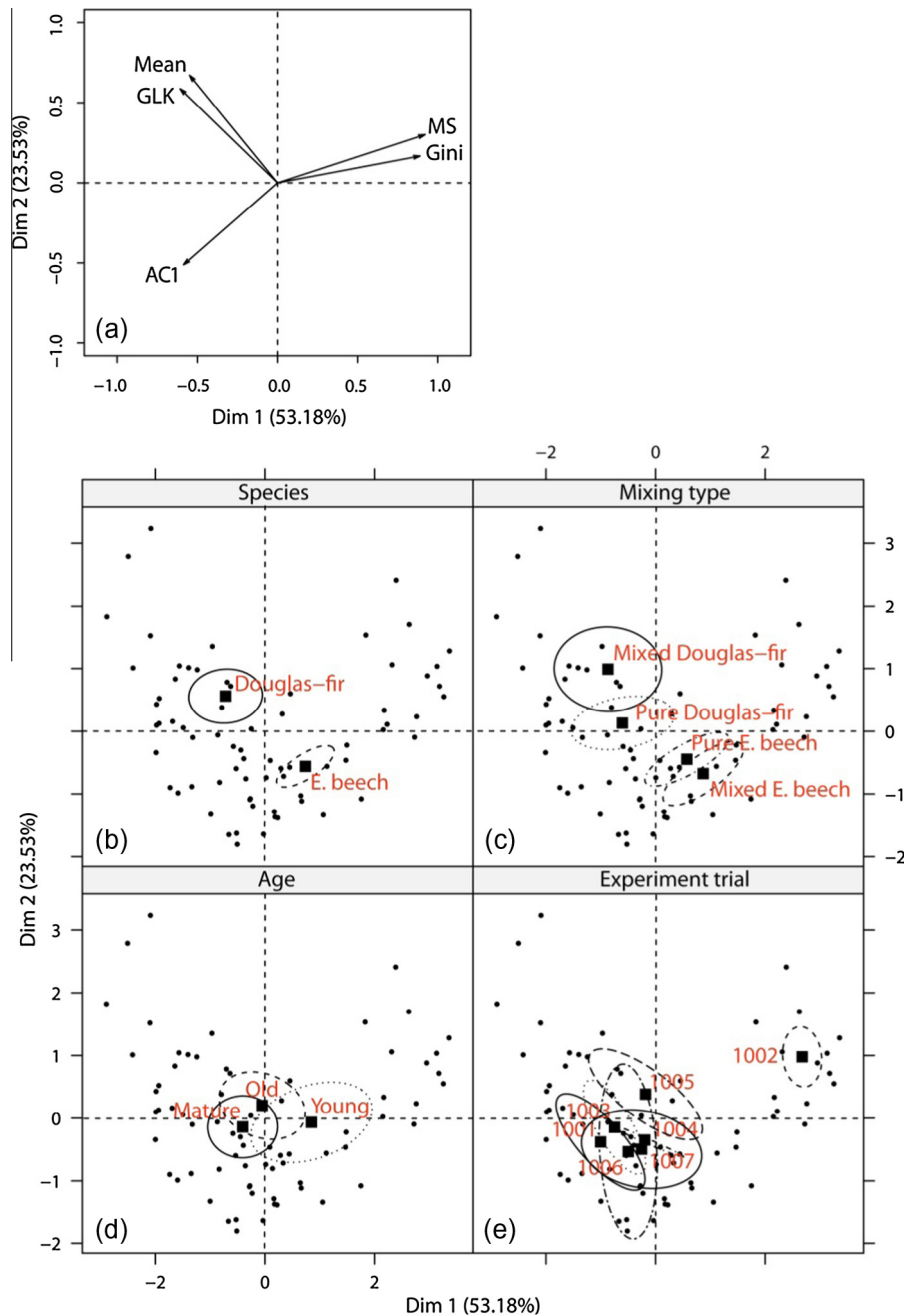
Fig. 4. Principal component analysis (PCA) applied on tree chronologies characteristics for 72 mixing types (Douglas-fir pure and mixed, European beech pure and mixed). (a) The variables factor map indicates correlation and contribution of tree chronology characteristics on the first two axes. (b...e) 95% confidence intervals for average coordinates of species, mixing type, age and experimental trial was depicted by ellipses.

Concerning growth recovery time the analysis showed that European beech (GRT = 1.67) recovered significantly faster than Douglas-fir (GRT = 2.21, p < 0.01) (Fig. 5, Table 2). Mixing species affected the growth recovery time but not significantly. The growth recovery time in mixed stands was shortened for Douglas-fir (pure = 2.33, mixed = 2.01, p > 0.05) and extended for European beech (pure = 1.57, mixed = 1.79, p > 0.05). The growth recovery times of European beech and Douglas-fir in mixed stand range between growth recovery times of both species in pure stand.

The condition of the post-years showed a clear signal for both species; improved weather situation one year after drought, lead to a significant reduction of the growth recovery time (Rs; good = 1.48, average = 2.01, adverse = 2.25, p < 0.01). In case of

adverse post-years the differences of the growth recovery time between European beech (GRT = 1.94) and Douglas-fir (GRT = 2.67) increased (p < 0.001). European beech needed significantly more time to return to its initial yield in mixed stands (GRT = 2.33) than in pure stands (GRT = 1.64, p < 0.05) if dry weather conditions followed a drought event.

Concerning the ecological co-variables only tree age showed a significant effect on growth recovery time for Douglas-fir. Progressive tree age extended growth recovery time (Table 3).

3.2.2. Stand level

Analysis of the stand level reaction showed that the resistance of the European beech pure stands (Rt = 89.5) on drought event
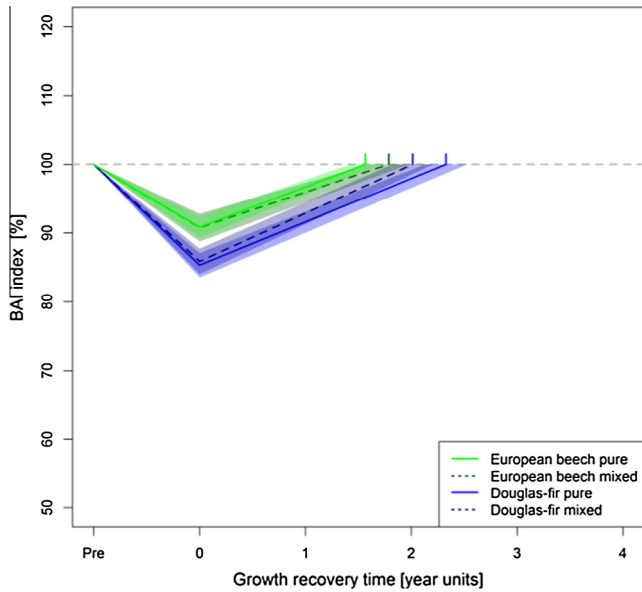
Fig. 5. Mean drought response on individual tree level for all drought events represented by the indices resistance and growth recovery time for European beech (green) and Douglas-fir (blue) in pure (solid) and mixed stands (dashed). The colored bands behind the lines show the respective 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were significantly greater than in mixed stands (Rt = 83.1, p < 0.05) and that of Douglas-fir in pure stands (Rt = 80.8, p < 0.01) (Table 2, see also Fig. 6). The mixed stands range between the European beech and the Douglas-fir pure stands. The analysis of the effect of co-variables indicated an increasing resistance with increasing age and with decreasing proportion of European beech (Table 3). Also base-poorer sites appeared to bear higher resistance.

The climate specification of 2003 represented an extreme drought year for all triplets and an adverse post-year in 2004 for most of the triplets. Only in case of four triplets a year with good or average weather conditions followed 2003. Concerning the drought year 2003 growth recovery time did not differ significantly between the stands. Douglas-fir pure (GRT = 2.50) and mixed stands (GRT = 2.53) tended to recover relatively faster, whereas European beech pure stands (GRT = 3.06) needed more time to return to their initial level. In contrast to the positive influence of age on resistance, a higher age extended the growth recovery time. Also improved water supply characteristics of soils extended growth recovery time.

The loss of increment caused by the drought year 2003 was on average 50% of the long-term growth level, independent of species or mixture (Table 4). But reflecting the general growth levels absolute basal area increment loss due to drought was highest in Douglas-fir pure stands. The loss increased in plots with higher stand density (basal area per hectare) (Table 3). Additionally, base-poverty, higher precipitation and warmer temperatures led to a lower increment loss due to drought.

Table 2
Mean values, estimates and significance levels of the multiple comparison of the parameters used in the models (Eqs. (3) and (4)) to estimate resistance and growth recovery time. As independent variable we used species, mixture and post-year (effect of the weather condition on year after drought year). Minor differences between the measured and estimated data arose, because of the random effects. Significant pairs are printed in bold.

	Variables	Pairs (A - B)	Mean		Multiple comparison	
			A	B	Estimate	P-value
Individual tree level (1950–2010)						
Resistance	**Species**	**Douglas-fir - E. beech**	**85.5**	**90.8**	**−5.27**	**0.00****
	Mixture	Mixed - pure	89.0	88.4	−0.30	0.88
	Species:Mixture	Douglas-fir mixed - Douglas-fir pure	85.9	85.3	−0.66	0.79
	Species:Mixture	E. beech mixed - E. beech pure	90.8	90.9	0.07	0.98
Growth recovery time	**Species**	**Douglas-fir - E. beech**	**2.2**	**1.7**	**0.41**	**0.00****
	Mixture	Mixed - pure	1.9	1.9	−0.05	0.80
	Post-years	**Average - adverse**	**2.0**	**2.2**	**−0.38**	**0.01****
	Post-years	**Average - good**	**2.0**	**1.5**	**0.46**	**0.00****
	Post-years	**Adverse - good**	**2.2**	**1.5**	**0.85**	**0.00****
	Species:Mixture	Douglas-fir mixed - Douglas-fir pure	2.0	2.3	−0.22	0.37
	Species:Mixture	E. beech mixed - E. beech pure	1.8	1.6	0.12	0.60
	Species:Post-years	Douglas-fir good - E. beech good	1.8	1.3	0.30	0.11
	Species:Post-years	Douglas-fir average - E. beech average	2.2	1.9	0.31	0.14
	Species:Post-years	**Douglas-fir adverse - E. beech adverse**	**2.7**	**1.9**	**0.63**	**0.00****
	Mixture:Post-years	Mixed good - pure good	1.5	1.5	0.05	0.85
	Mixture:Post-years	Mixed average - pure average	1.8	2.2	−0.32	0.24
	Mixture:Post-years	Mixed adverse - pure adverse	2.3	2.2	0.12	0.61
	Species:Mixture:Post-years	Douglas-fir mixed good - Douglas-fir pure good	1.7	1.8	0.10	0.75
	Species:Mixture:Post-years	E. beech mixed good - E. beech pure good	1.4	1.3	−0.01	0.97
	Species:Mixture:Post-years	Douglas-fir mixed average - Douglas-fir pure average	1.9	2.4	−0.41	0.24
	Species:Mixture:Post-years	E. beech mixed average - E. beech pure average	1.8	2.0	−0.22	0.50
	Species:Mixture:Post-years	Douglas-fir mixed adverse - Douglas-fir pure adverse	2.4	2.9	−0.35	0.27
	Species:Mixture:Post-years	**E. beech mixed adverse - E. beech pure adverse**	**2.3**	**1.6**	**0.60**	**0.04***
Stand level (2003)						
Resistance	Species:Mixture	Douglas-fir pure stand - Mixed stand	80.8	83.1	−2.40	0.45
		Douglas-fir pure stand - E. beech pure stand	**80.8**	**89.5**	**−8.70**	**0.00****
		Mixed stand - E. beech pure stand	**83.1**	**89.5**	**−6.30**	**0.05***
G. recovery	Species:Mixture	Douglas-fir pure stand - Mixed stand	2.5	2.5	0	0.9
		Douglas-fir pure stand - E. beech pure stand	2.5	3.1	−0.6	0.1
		Mixed stand - E. beech pure stand	2.5	3.1	−0.5	0.2

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

Table 3
Estimates for ecological parameters with effect on resistance, growth recovery time and increment loss due to drought separated for individual tree level and stand level. Signifcant estimates are in bold. Hyphens indicate that the respective independent variable was neglected in the model (Eqs. (5) and (6)). The lower part of the table provides information about the quality of the model.

Independent variables:	Dependent variables						
	Individual tree level (1950–2010)				Stand level (2003)		
	Resistance (%)		Growth recovery time (year units)		Resistance (%)	Growth recovery time (year units)	Loss due to drought (%)
	Douglas-fir	E. beech	Douglas-fir	E. beech			
DBH	**−0.415*** (0.064)				–	–	–
Rel DBH		**−0.131*** (0.019)			–	–	–
Basal area per hectare							**0.004*** (0.002)
Mixing proportion of E. beech	**–**	–	–	–	**8.150*** (3.016)		
Age	**0.164**** (0.054)		**0.017*** (0.004)		**0.135*** (0.056)	**0.022**** (0.007)	
Base-richness	**−4.407*** (0.203)	**−4.016 .** (1.775)			**−4.225 .** (2.196)		0.012 (0.007)
Water supply					**0.378*** (0.135)		
Precipitation							**0.001*** (0.001)
Temperature							0.132 (0.124)
Intercept	**106.288*** (6.494)	**114.199*** (5.728)	**1.579*** (0.198)	**1.658*** (0.144)	**85.394*** (7.545)	−0.18 (0.755)	−2.241 (1.444)
Observations	1556	2242	1556	2242	54	54	54
Log Likelihood	−7237.847	−10805.140	−3827.272	−5502.645	−195.076	−90.51	−21.146
Akaike Inf. Crit.	14491.690	21624.280	7666.543	11015.290	404.152	193.019	58.293
Bayesian Inf. Crit.	14534.490	21664.280	7698.642	11043.860	418.075	204.953	74.204

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.
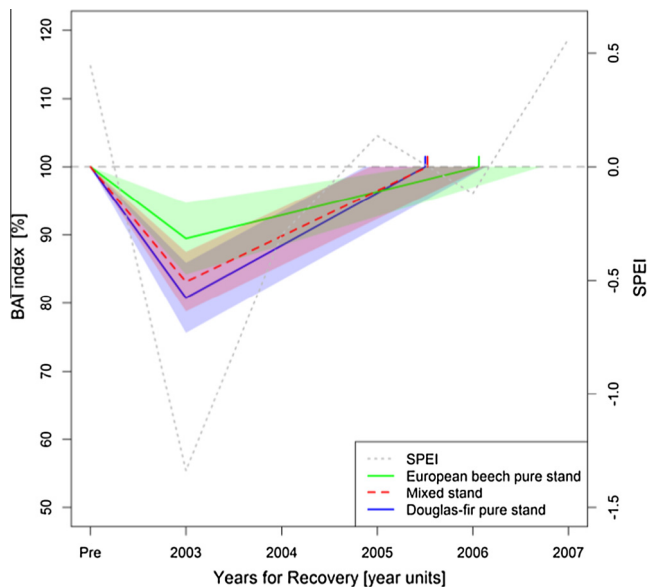
Fig. 6. Mean drought response on stand level to drought event 2003. The response is represent by the indices resistance and growth recovery time for European beech (green solid line) and Douglas-fir (blue solid line) pure stands and for the mixed stands (red dashed line).The grey dashed line represents the average standardized precipitation-evapotranspiration index (SPEI) for all triplets. The colored bands behind the lines show the respective 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Tree chronology characteristics

As expected, mean basal area increment of Douglas-fir was higher than for European beech. Individual growth of Douglas-fir in mixture overtopped the increment of Douglas-fir in pure stands. This is conform with the results of a previous study, based on the same sample plots (Thurm and Pretzsch, submitted for publication). The authors reported that overyielding in Douglas-fir – European beech stands is realized mainly by Douglas-fir. They assumed that higher productivity of Douglas-fir in mixture results from an improved growth on individual tree level. Niche complementarity, fostered by improved resource utilization, may lead to accelerated growth of species in mixture (Vandermeer, 1989). Structural diversification, through dominant Douglas-fir and inferior European beech, as observed here in mixed stands (Thurm and Pretzsch, submitted for publication), enables an increasing utilization of incoming light (Thomas et al., 2015). Studies of Hendriks and Bianchi (1995) and Thomas et al. (2015) supposed that roots of Douglas-fir dominate in the top soil, whereas those of European beech spread into deeper soil layers. This may promote Douglas-fir by better access to nutrient because the uppermost soil layer is the dominant area of decomposition and mineralization of organic matter (Thomas et al., 2015). Species-specific basal area increment varied stronger between European beeches in pure mixed stands than for Douglas-firs, as indicated by the pattern of Gleichlaeufigkeit. This may result from a higher variation in diameter and tree heights for European beech compared to Douglas-fir (Pretzsch and Schütze, 2016).

Table 4
Absolute and relative loss of increment at stand level for the drought year 2003. SD represents the standard deviation. The significant differences were tested by a multiple comparison of the linear mixed models and are indicated by letters. The loss of volume increment was calculated on the independent variables basal area increment, age and their interaction (Eq. (1)).

Mixing type	Loss of basal area increment ($m^2\ ha^{-1}$)	SD		Relative loss of basal area increment (%)	SD		Loss of volume increment ($m^3\ ha^{-1}$)	SD
Douglas-fir pure stand (1.60 $m^2\ ha^{-1}\ a^{-1}$)	0.82	0.49	a	0.52	0.29	A	15.13	11.11
Mixed stand (1.29 $m^2\ ha^{-1}\ a^{-1}$)	0.65	0.35	ab	0.50	0.25	A	11.12	6.10
E. beech pure stand (0.91 $m^2\ ha^{-1}\ a^{-1}$)	0.45	0.44	b	0.50	0.32	A	6.54	5.48
Total	0.64	0.45		0.50	0.28		10.93	7.56

Growth responses of large trees, who dominated the stand, are less influenced by competition. Their growing performance is stronger connected with the weather conditions than the suppressed trees (Chhin et al., 2008; Piutti and Cescatti, 1997). The calculation of the Gleichlaeufigkeit with a conglomeration of large and small trees results in a declined Gleichlaeufigkeit.

Autocorrelation is assumed to indicate the existence of low frequency variation in tree chronologies and a higher persistency of growth level from year to year. Here, Douglas fir in pure stands showed highest values of autocorrelation but contrasting low values in mixed stands. LaMarche and Stockton (1974) analyzed the link between autocorrelation in tree ring growth series and needle growth. They showed that needle growth by bristlecone pines (*Pinus longaeva* D.K. Bailey and *Pinus aristata* Engelm.) decreased under negative weather conditions. Consequently, the photosynthetic potential of a tree with perennial needles declined resulting in declined current year ring growth. The influence of the previous year's needles still increase by the fact that the photosynthetic rate of previous year needles can be greater than current year needles (Clark, 1961; Hébert et al., 2011; Hom and Oechel, 1983). In summary, autocorrelation in growth series of conifers having perennial needles should be higher than that of broadleaved species. This can also be seen in a study of silver fir (*Abies alba* Miller) and European beech by Lebourgeois et al. (2014). The low autocorrelation of Douglas-fir which we found in mixed stands might be related to improved resource supply. Douglas-fir seems to be less influenced by the resource store of previous years. Annual variation of the photosynthetic leaf area may be stabilized by higher resource use efficiency in mixed stands.

Sensitivity, here measured by the mean sensitivity and the Gini-coefficient tend to be greater on sites with harsher conditions (Fritts et al., 1965). We observed that European beech showed an increased sensitivity in mixed stands compared to pure stands whereas for Douglas-fir an opposing trend was revealed. This positive mixing effect on sensitivity was also observed by silver fir which growing together with European beech (Lebourgeois et al., 2013). In contrast, the same study could not detect similar effects in a mixture of silver fir and Norway spruce. It might be that the partitioning of water resources varies between pure stands and mixed stands of coniferous and broad-leave trees. Douglas-fir as a coniferous species transpires nearly throughout the whole year (Waring and Running, 1978). The transpiration time of European beech is restricted to the growing period, where the trees carry leaves. During spring times, Douglas-fir in mixed stands profits from higher water availability in spring due to less intra-specific competition than in pure stands. When European beech starts to transpire, water supply is already reduced by Douglas-fir. Moore et al. (2011) observed this temporal partitioning of water utilization by Douglas-fir and red alder. We assume that this is a main reason for the differences in sensitivity between Douglas-fir and European beech in mixed stands. This is also in accordance with the hypothesis that the lower autocorrelation of Douglas-fir in mixed stands is related to a higher independency of previous year resources, which would reflect a facilitation effect by European beech.

4.2. Drought year analyses

4.2.1. Individual tree level

Resistance to drought events of Douglas-fir was generally lower than that of European beech. This is in line with the results of Weigt et al. (2015), who also examined the resistance of European beech and Douglas-fir. But the species-specific differences must be reflected in the context of generally higher absolute increment rates of Douglas-fir, especially in mixed stands. An analysis with the absolute increment values was not appropriate here, because tree age and residual trends may obscure possible responses (also mentioned in chapter 2.4). Resistance in our study did not differentiate between the mixing types. This consists with findings of resistance for European beech admixed to other species (Metz et al., 2016).

Concerning growth recovery time there was also a significant species-specific difference, with longer growth recovery time for Douglas-fir. The growth recovery time was reduced for Douglas-fir in mixed stands compared to pure stands and extended for European beech, but not on a significant level. These trends are in line with the findings for autocorrelation and mean sensitivity. We assume that trees in pure stands start simultaneously to grow in the subsequent year. In mixed stands Douglas-fir may have an advantage by starting to grow earlier than European beech, providing the chance to replenish its reserves more quickly. Douglas-fir in mixed stands starts to deplete water resources earlier during the growing season and this better access to water may shorten the growth recovery time in the years after drought. In cases where a year with below average water supply follows a dry year the effect of growth recovery time extension for European beech becomes more pronounced and significant. This supports the hypothesis that in mixed stands water resources are temporally more partitioned to Douglas-fir. This would lead to a stabilization effect for this coniferous species. As mentioned in chapter 4.1, a spatially different utilization of water resource by diverging rooting patterns between both species is also possible, but current studies do not enable general statements.

Anderegg et al. (2015) examined the recovery of stem growth after drought on a huge amount of forest sites across the globe and several genera. They found a general recovery time between 1 and 4 years after drought. During the drought year 2003, comparable to the stress conditions considered by Anderegg et al. (2015) the reaction of the trees examined here showed an average growth recovery time of 2.7 years and lies within the reported range.

Our data reveal, that the inter-specific differences of the growth recovery time between single drought event and extended drought periods (adverse post-year) increase. This would lead to the conclusion that Douglas-fir is disadvantaged by extended dryer weather conditions, whereas European beech is better capable to compensate this situation. We suggest, that growth recovery time is a good measure to distinguish between iso- or anisohydric traits of tree species.

Anderegg et al. (2015) drew the conclusion that species with lower safety margin of leaf water potential (isohydric species) tend to slower growth recovery after drought. Similar features were hypothesized by McDowell et al. (2002) stating greater suffering for isohydric species during extended drought periods. From this,

Douglas-fir tends to have a more isohydric character than European beech.

Klein and Niu (2014) recommended to differ iso- and anisohydric characteristics by the stomatal conductance of leaf water potential at 50% of the maximum ($\Psi g_s 50$). According to Woodruff et al. (2008), $\Psi g_s 50$ for Douglas-fir provinces from Wind River Basin of southwestern Washington (USA) range between from -0.75 to -1.25. Stout and Sala (2003) measured a $\Psi g_s 50$ of -4.83 for Douglas-fir var. *glauca*. In the current paper we investigated Douglas-fir var. *viridis*. European beech had a $\Psi g_s 50$ from -2.12 to -3.17 (Aranda et al., 2000; Köcher, 2013). This would strengthen the assumption that Douglas-fir has isohydric and European beech anisohydric traits. The anisohydric strategy and the greater cross section of xylem predisposed European beech for hydraulic failure (McDowell et al., 2008). Nevertheless, several additional factors influenced the risk of hydraulic failure, like tree height, crown disposition and root system which were not all measured here.

The hydric characteristics might also be a reason for the unchanged resistance in mixed stands versus pure stands. In drought years, Douglas-fir stomatal safety margin leads to an earlier stop of water consumption than that of European beech. This enables European beech to use free water resources and prevent a more drastic drop of increment compared to pure stands (Pretzsch et al., 2013).

4.2.2. Stand level

During the drought year 2003 the stand level resistance concerning basal area increment followed the species specific single tree pattern being higher in European beech than in Douglas-fir stands. Mixed stands showed an intermediate response, being only significantly different from European beech stands. Due to the high proportion of Douglas-fir in mixed stands, the value for resistance was closer to the reaction of Douglas-fir pure stands. When comparing the measured resistance in mixed stands with the expected value from pure stands, weighted by the mixing proportion no deviation occurred (Appendix C). Because of the responses of both species (Jucker et al., 2014) no compensatory mixing effect concerning resistance was detectable.

In contrast to the general pattern of the growth recovery time for European beech, in 2003 European beech needed much longer to recover. In this case initial growth level was reached even later than for Douglas-fir. This might be a consequence of the subsequent year 2004 when European beech had a high fructification rate (Konnert et al., 2014; Landesforst Rheinland-Pfalz, 2014b). Eichhorn et al. (2008) observed a decreased stem wood production for European beech in 2004 in North Germany. They detected a shift of biomass production from stem wood to fruits. Heavy 'mast'-years generally lead to a high consumption of reserve stores (Burschel, 1966). This might be a reason for the extended growth recovery time for European beech.

Nevertheless, the relative loss due to drought amounted to around 50% for both species and mixing types. The variation in loss of absolute basal area increment was a result of the diverging levels of increment rates between Douglas-fir and European beech. When reflecting stand volume growth a loss due to drought of 15.1 m³ ha⁻¹ was found for Douglas-fir pure stands, 11.1 m³ ha⁻¹ for mixed stands and 6.5 m³ ha⁻¹ for European beech stands (Table 4). Concerning the loss of volume increment, the absolute differences between mixing types is more pronounced compared to the loss of basal area increment. This bias might be induced by the applied volume estimation function (Appendix B), but is presented here to provide a dimension for the forest management. The presentation of relative and absolute drought responses is a major issue of our study. Relative values provide a biological understanding, whereas absolute values take differences in productivity of tree species into account.

4.3. Changing patters along ecological gradients

The applied statistical models revealed that several ecological variables influence drought response of trees. The response of ecological system to ecological conditions is inherently nonlinear (Burkett et al., 2005). Therefore, we additionally checked the courses of independent variables with generalized additive mixed models. Because crucial variables showed linear or almost linear courses we decided to use linear mixed models for better interpretation.

The observed linear course may result because our study covering as well the current planting area of Douglas-fir and European beech pure and mixed stands in Germany but the potential growing area would be greater. So a greater gradient may show a nonlinear course.

It seems that on fertile sites drought has a more severe impact on growth. Higher base richness reduces resistance of Douglas-fir and European beech at individual tree and at stand level. It is assumed that base limited systems are less influenced by short-term water restriction than water limited systems (Mitscherlich, 1909). On sites with higher water supply the impact of drought events also seems to have a more severe impact in terms of growth recovery time and relative growth loss at stand level. Sergent et al. (2014b) investigated Douglas-fir on different fertile sites and found a better recovery on the more fertile ones. The influence of nutrients can have variable effects (Rennenberg et al., 2006) and is less well understood. Additionally, different proveniences response variable on drought stress (Eilmann et al., 2013; García-Plazaola and Becerril, 2000; Sergent et al., 2014a) and may compensate drought stress an different ways.

Tree age was also a significant co-variable in most models. It seems to trigger a twofold pathway of reaction concerning Douglas-fir. On the one hand resistance is higher with progressive tree age on the other hand growth recovery time is extended. An age-related increase of drought stress sensitivity was found for European larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) by Carrer and Urbinati (2004). They supposed that hydraulic constraints increase with tree age and tree height. The assumption is that the gravitation potential in the hydraulic pathways of plants increases with the height (Matyssek et al., 2010; McDowell et al., 2008). The height growth dynamic of Douglas-fir and its huge hydraulic path length may explain such age-dependent drought sensitivity. We additionally performed a drought year analysis on a small collective of sample trees for which we reconstructed tree heights (not shown in the method and result section). The results reveal a significant interaction between increasing height and decreasing resistance and increasing growth recovery time. We assume that the tree height is a major driver of drought response. This interaction of increasing size and increasing sensitivity could also observed for European beech and silver fir (Mérian and Lebourgeois, 2011) and for Scots pine (Merlin et al., 2015). For Douglas-fir in our study, tree age correlates very closely with tree height. This is not the case for European beech. Because of their shade-tolerant traits, European beech forms a wider range of tree heights at similar age (Pretzsch and Schütze, 2016). Therefore, no correlation of tree age with resistance was found for European beech. The negative correlation of the relative DBH with resistance indicates that trees in lower social classes with lower heights and smaller tree rings have a better resistance. This is conform to the findings concerning size dependent patterns of resistance.

The mentioned contradiction of the age effect of Douglas-fir at individual tree level is explained when considering the DBH effect. We suggest that the older trees with smaller DBH had higher wood density and form stronger hydraulic pathways bearing better resistance against hydraulic pressure under drought (Hacke et al., 2001).

The PCA indicated a general higher climate sensitivity of younger compared to older stands. As tree chronologies have been analyzed throughout the entire tree age this may reveal a climate change effect on trees' sensitivity. Young stands have faced a greater share of time under recent climate change conditions than older ones. Biondi and Qeadan (2008b) also reported from a species-unspecific change in sensitivity over a time period of 400 years.

Increment loss to drought was linked with stand density. With increasing basal area the stand level loss also increased. This outcome is in line with the findings of Rais et al. (2014), who found higher resistance in Douglas-fir plantation with lower stand density. Lebourgeois et al. (2014) confirmed a negative impact on sensitivity with increasing stand density for European beech and silver fir, as well. Rais et al. (2014) concluded that lower stand density is associated with better availability of soil space and a larger root system of the individual tree.

5. Conclusions

Our study of mixing effects between Douglas-fir and European beech on individual tree and stand level comprised a wide range of site conditions, stand ages, and mixing proportions in Central Europe. The results give evidence that Douglas-fir profits from being mixed with European beech in terms of productivity, drought stress release, and time of growth recovery. The stabilized

(Pretzsch et al., 2014), resource allocation pattern between above and below ground organs (Nikolova et al., 2011; Pretzsch et al., 2012) or wood density (Toïgo et al., 2015) may also change during drought periods. Considering these aspects in future analyses may refine the picture of mixing effect between Douglas-fir and European beech.

Appendix A. Exemplary illustration of the double detrending method for a single European beech tree chronology
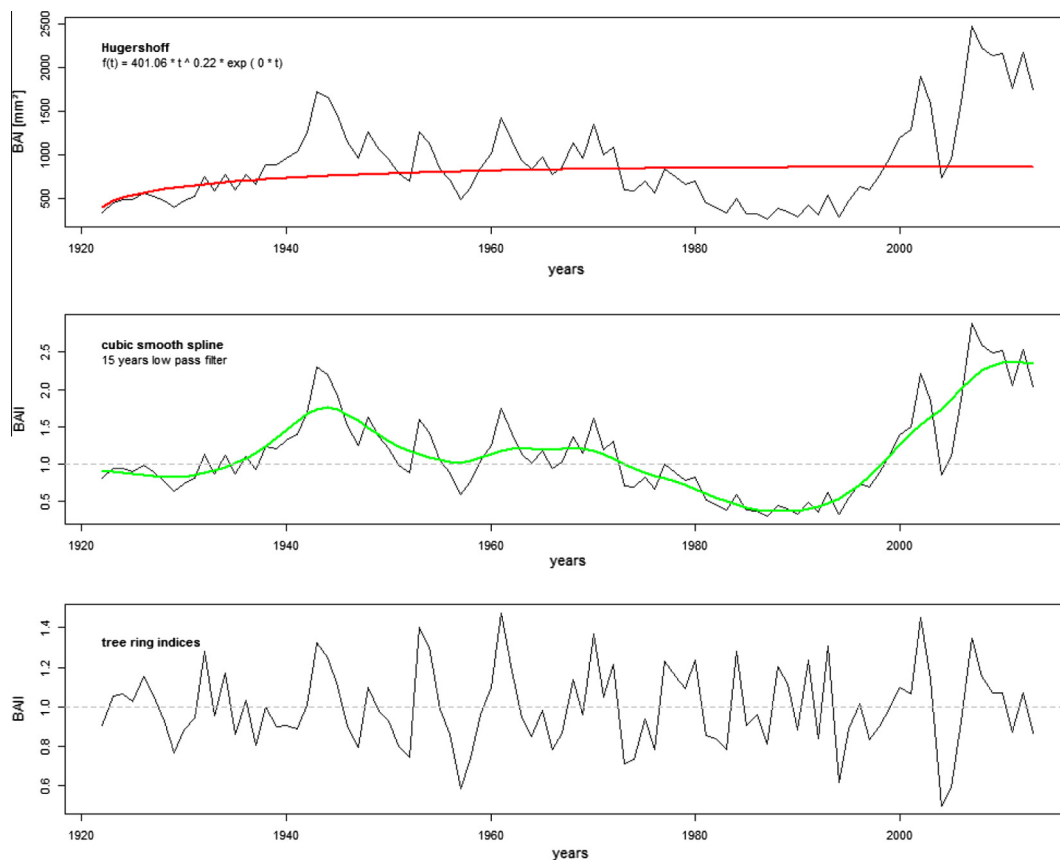
growth of Douglas-fir seems to be on the expense of European beech. Nevertheless, mixed stands with European beech contribute to risk mitigation for the high productive coniferous Douglas-fir.

The study indicate that base limited systems are less affected by drought events and that taller trees have less resistance, both facts are independent from species and mixing type.

The study focused on tree ring information at DBH height. Although the trunk represents a major share of total tree biomass

The figures show the individual European beech No. 1003_11_1 and the steps of double detrending applied to all series of the study. (A) Original basal area increment course (BAI) calculated on the mean of two cores per tree (black line) Growth trend estimated according to Hugershoff equation (red line). (B) Index Series (BAII) (black line) as basal area increment index (BAII) and trend estimated by cubic spline of 15-year wavelength (green line). (C) Resulting basal area increment indices after two step detrending (black line).

Appendix B. Estimates of the regression coefficients (Eq. (1)) and model quality for calculating volume area loss due to drought

The table contains the coefficients a1...a3 of the fixed effects from the model which estimated volume by basal area increment loss. The last row represents the coefficient of determination (R^2).

Mixing type	a0	a1	a2	a3	R^2
Douglas-fir pure stand	0.50	1.78	0.57**	−0.16	0.81
Mixed stand	0.75	−2.58 .	0.50**	0.89*	0.80
European beech pure stand	−0.75	1.31	0.86***	−0.04	0.82

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

Appendix C. Comparison of pure and mixed stands resistance and growth recovery time

This figure shows the comparison of the observed parameter value for mixed stand ($p1.2$ – y-axis) and expected value derived from pure stands ($\hat{p}1.2$ –x.axis). The resistance and growth recovery time of the expected mixed stand was calculated by summarizing the species-specific values of pure stands ($p1, p2$) weighted by the species-specific mixing proportion in mixed stand ($m1, m2$); $\hat{p}1.2 = p1 * m1 + p2 * m2$ (for a more detailed view see Pretzsch et al. (2010)).
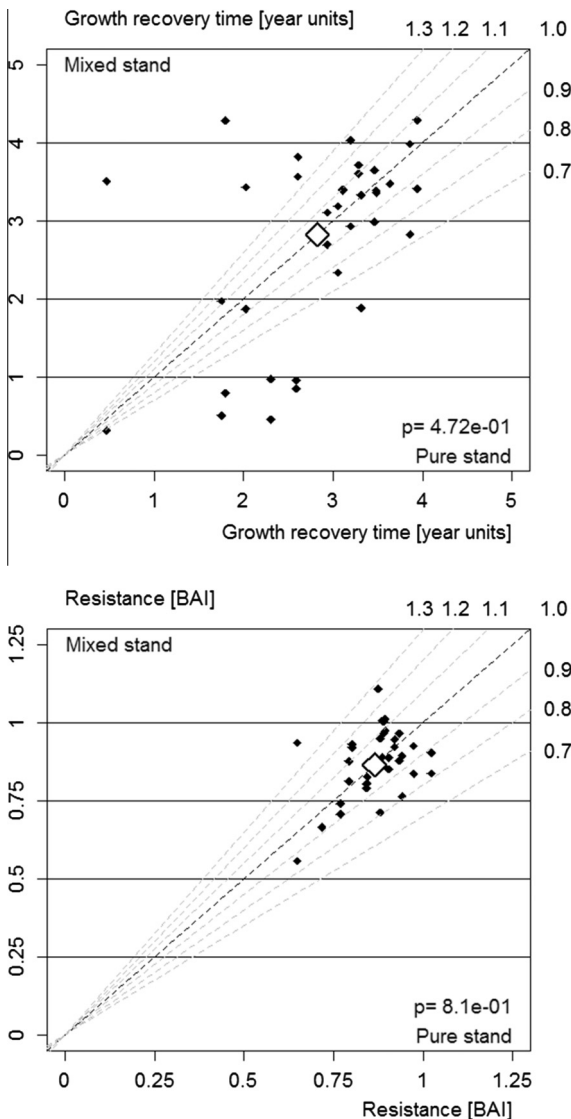
Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.06.020.

References

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., et al., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528–532.

Aranda, I., Gil, L., Pardos, J.A., 2000. Water relations and gas exchange in Fagus sylvatica L. and Quercus petraea (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees 14, 344–352.

Barton, K., 2015. MuMIn: Multi-model inference.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4.

Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193.

Binkley, D., Greene, S., 1983. Production in mixtures of conifers and red alder: the importance of site fertility and stand age. In: Ballard, R., Gessel, S. (Eds.), International Union of Forestry Research Organizations Symposium on Forest Site and Continuous Productivity, pp. 112–117.

Biondi, F., Qeadan, F., 2008a. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Res. 64, 81–96.

Biondi, F., Qeadan, F., 2008b. Inequality in paleorecords. Ecology 89, 1056–1067.

Bolte, A., Czajkowski, T., Kompa, T., 2007. The north-eastern distribution range of European beech a review. Forestry 80, 413–429.

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63, 625–644.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.

Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258.

Burkett, V.R., Wilcox, D.A., Stottlemyer, R., Barrow, W., Fagre, D., Baron, J., et al., 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. Ecol. Complex. 2, 357–394.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer, New York.

Burschel, P., 1966. Untersuchungen in Buchenmastjahren. Forstw Cbl 85, 204–219.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965.

Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. Ecology 85, 730–740.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2008. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. For. Ecol. Manage. 256, 1692–1703.

Clark, J., 1961. Photosynthesis and respiration in white spruce and balsam fir. State University College of Forestry, Syracuse, N.Y. State University College of Forestry at Syracuse University. Technical publication no. 85.

Deutscher Wetterdienst, 2015. Grids Germany-Monthly: Mean Temperature and Precipitation ftp://ftp-cdc.dwd.de/pub/CDC/grids_germany/monthly/, 18 March 2016.

Eichhorn, J., Dammann, I., Schönfelder, E., Albrecht, M., Beck, W., Paar, U., 2008. Untersuchungen zur Trockenheitstoleranz der Buche am Beispiel des witterungsextremen Jahres 2003. Assessment of the drought resistance of beech exemplified by the 2003 extreme weather conditions. Ergebnisse angewandter Forschung zur Buche 3, 109–134.

Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance. Tree Physiol. 32, 178–187.

Eilmann, B., de Vries, S.M.G., den Ouden, J., Mohren, G.M.J., Sauren, P., Sass-Klaassen, U., 2013. Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (Pseudotsuga menziesii (Mirb.)) provenances. For. Ecol. Manage. 302, 133–143.

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht: 203 Tabellen, 6, vollst. neu bearb. und stark erw. Aufl. Ulmer, Stuttgart. UTB 8104.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For. Ecol. Manage. 312, 282–292.

Fritts, H.C., 1976. Tree Rings and Climate. Acad. Pr., London.

Fritts, H.C., Smith, D.G., Cardis, J.W., Budelsky, C.A., 1965. Tree-ring characteristics along a vegetation gradient in Northern Arizona. Ecology 46, 394–401.

García-Plazaola, J.I., Becerril, J.M., 2000. Effects of drought on photoprotective mechanisms in European beech (Fagus sylvatica L.) seedlings from different provenances. Trees 14, 485–490.

Gauer, J., Kroiher, F. (Eds.), 2012. Waldökologische Naturräume Deutschlands: Forstliche Wuchsgebiete und Wuchsbezirke – Digitale Topographische Grundlagen – Neubearbeitung Stand 2011. Landbauforschung vTI Agriculture and Forestry Research Sonderheft Nr. 359.

Hacke, G.U., Sperry, S.J., Pockman, T.W., Davis, D.S., McCulloh, A.K., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, 457–461.

Hartmann, H., 2011. Will a 385 million year-struggle for light become a struggle for water and for carbon? - How trees may cope with more frequent climate change-type drought events. Glob. Change Biol. 17, 642–655.

Hébert, F., Thiffault, N., Munson, Alison D., 2011. Field photosynthesis measurements on black spruce (Picea mariana): does needle age matter? Commun. Soil Sci. Plant Anal. 42, 2738–2750.

Hendriks, C., Bianchi, F., 1995. Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. Neth. J. Agric. Sci. 1995, 321–331.

Hermann, R., Lavender, D., 1999. Douglas-fir planted forests. New Forest. 17, 53–70.

Holmes, R.L., Adams, R.K., Fritts, H.C., 1986. Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin with procedures used in the chronology development work including users manuals for computer programs COFECHA and ARSTAN.

Hom, J.L., Oechel, W.C., 1983. The photosynthetic capacity, nutrient content, and nutrient use efficiency of different needle age-classes of black spruce (Piceamariana) found in interior Alaska. Can. J. For. Res. 13, 834–839.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363.

Hugershoff, R., 1936. Die mathematischen Hilfsmittel der Kulturingenieurs und Biologen: Herleitung von gesetzmäßigen Zusammenhängen als Manuskript veröffentlicht, Dresden.

Husson, F., Josse, J., Le, S., Mazet, J., 2015. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining.

IPCC, 2014. Climate Change 2014: Synthesis Report.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., Knops, J., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol. Lett. 17, 1560–1569.

Kelty, M., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M., Larson, B., Oliver, C. (Eds.), The Ecology and Silviculture of Mixed-Species Forests, Forestry Sciences. Springer, Netherlands, pp. 125–141.

Klein, T., Niu, S., 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct. Ecol. 28, 1313–1320.

Kleinschmit, J., Bastien, J.C., 1992. IUFRO's role in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco.) tree improvement. Silvae genetica 41, 161–173.

Klimo, E., Hager, H., Kulhavý, J. (Eds.), 2000. Spruce Monocultures in Central Europe: Problems and Prospects. European Forest Institute.

Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. Eur. J. Forest Res. 127, 89–101.

Köcher, P., 2013. Hydraulic Traits and Their Relevance for Water Use Strategies in Five Broad-Leaved Tree Species of a Temperate Mixed Forest. Niedersächsische Staats- und Universitätsbibliothek Göttingen, Göttingen.

Konnert, M., Schneck, D., Zollner, A., 2014. Blühen und Fruktifizieren unserer Waldbäume in den letzten 60 Jahren. LWF Wissen, 37–45.

LaMarche, V.C.J., Stockton, C.W., 1974. Chronologies from termperature-sensitive bristlecone pines at upper treeline in Western United States. Tree-Ring Bull. 1974, 21–45.

Landesforst Rheinland-Pfalz, 2014a. Forsteinrichtung Rheinland-Pfalz: Basenaustattung, Wasserhaushalt.

Landesforst Rheinland-Pfalz, 2014b. Waldzustandsbericht 2014, Mainz.

Larocque, G.R., Luckai, N., Adhikary, S.N., Groot, A., Bell, F.W., Sharma, M., 2013. Competition theory — science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research. Environ. Rev. 21, 71–84.

LeBlanc, D.C., 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Can. J. For. Res. 20, 1399–1407.

Lebourgeois, F., Eberlé, P., Mérian, P., Seynave, I., 2014. Social status-mediated tree-ring responses to climate of Abies alba and Fagus sylvatica shift in importance with increasing stand basal area. For. Ecol. Manage. 328, 209–218.

Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For. Ecol. Manage. 303, 61–71.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920.

Lüpke, B.v., 2004. Risikominderung durch Mischwälder und naturnaher Waldbau-ein Spannungsfeld. forstarchiv 75, 43–50.

Matyssek, R., Fromm, J., Rennenberg, H., Roloff, A., 2010. Biologie der Bäume: Von der Zelle zur globalen Ebene; 32 Tabellen. Ulmer, Stuttgart. UTB Biologie, Agrar- und Forstwissenschaften, Landschaftsplanung 8450.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., et al., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–739.

McDowell, N.G., Phillips, N., Lunch, C., Bond, B.J., Ryan, M.G., 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiol. 22, 763–774.

Mérian, P., Lebourgeois, F., 2011. Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. For. Ecol. Manage. 261, 1382–1391.

Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. For. Ecol. Manage. 339, 22–33.

Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D., et al., 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. Glob. Change Biol. 22, 903–920.

Mitscherlich, E.A., 1909. Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenertrages. Landwirtschaftliche Jahrbücher 38, 537–552, Parey, Berlin.

Moore, G.W., Bond, B.J., Jones, J.A., 2011. A comparison of annual transpiration and productivity in monoculture and mixed-species Douglas-fir and red alder stands. For. Ecol. Manage. 262, 2263–2270.

Nikolova, P.S., Zang, C., Pretzsch, H., 2011. Combining tree-ring analyses on stems and coarse roots to study the growth dynamics of forest trees: a case study on Norway spruce (Picea abies [L.] H. Karst). Trees 25, 859–872.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307, 321–326.

Piutti, E., Cescatti, A., 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can. J. For. Res. 27, 277–284.

Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.-D. (Eds.), Forest Diversity and Function, Ecological Studies. Springer, Berlin Heidelberg, pp. 41–64.

Pretzsch, H., Biber, P., 2016. Tree species mixing can increase maximum stand density. Can. J. For. Res., 1–15

Pretzsch, H., Biber, P., Uhl, E., Hense, P., 2012. Coarse root–shoot allometry of Pinus radiata modified by site conditions in the Western Cape province of South Africa. South. For.: J. For. Sci. 74, 237–246.

Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., et al., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67, 712.

Pretzsch, H., Block, J., Dieler, J., Gauer, J., Göttlein, A., Moshammer, R., et al., 2014. Nährstoffentzüge durch die Holz- und Biomassenutzung in Wäldern. Teil 1: Schätz-funktionen für Biomasse und Nährelemente und ihre Anwendung in Szenariorechnungen. Allg. Forst Jagdztg 185, 261–285.

Pretzsch, H., Schütze, G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur. J. Forest Res. 135, 1–22.

Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. Plant Biol. 15, 483–495.

Rais, A., van de Kuilen, Jan-Willem G., Pretzsch, H., 2014. Growth reaction patterns of tree height, diameter, and volume of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) under acute drought stress in Southern Germany. Eur. J. Forest Res. 133, 1043–1056.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res 46, 627–638.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R.S., et al., 2006. Physiological responses of forest trees to heat and drought. Plant Biol (Stuttg) 8, 556–571.

Reyer, C., Lasch, P., Mohren, G.J., Sterck, F., 2010. Inter-specific competition in mixed forests of Douglas-fir (Pseudotsuga menziesii) and common beech (Fagus sylvatica) under climate change — a model-based analysis. Ann. For. Sci. 67, 805.

Sergent, A.-S., Bréda, N., Sanchez, L., Bastein, J.C., Rozenberg, P., 2014a. Coastal and interior Douglas-fir provenances differ in growth performance and response to drought episodes at adult age. Ann. For. Sci. 71, 709–720.

Sergent, A.-S., Rozenberg, P., Bréda, N., 2014b. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Ann. For. Sci. 71, 697–708.

Speer, J.H., 2010. Fundamentals of Tree-Ring Research. University of Arizona Press.

Stout, D.L., Sala, A., 2003. Xylem vulnerability to cavitation in Pseudotsuga menziesii and Pinus ponderosa from contrasting habitats. Tree Physiol. 23, 43–50.

Taegger, S., Kölling, C., 2016. Standortinformationssystem BaSIS. AFZ-DerWald, 10–13.

Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. J. Exp. Bot. 49, 419–432.

Thomas, F.M., Bögelein, R., Werner, W., 2015. Interaction between Douglas fir and European beech: Investigations in pure and mixed stands = Wechselwirkungen zwischen Douglasie und Rotbuche: Untersucheungen an Rein- und Mischbeständen. Forstarchiv: forstwissenschaftliche Fachzeitschrift 86, 83–91.

Thurm, E.A., Pretzsch, H., urm and Pretzsch, submitted for publication. Productivity and structural properties of mixed versus pure stands of European beech (Fagus sylvatica L.) and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) depends on environmental conditions. Ann. For. Sci. (submitted for publication)

Toïgo, M., Vallet, P., Perot, T., Bontemps, J.D., Piedallu, C., Courbaud, B., 2014. Over-yielding in mixed forests decreases with site productivity. J. Ecol., pp n/a.

Toïgo, M., Vallet, P., Tuilleras, V., Lebourgeois, F., Rozenberg, P., Perret, S., et al., 2015. Species mixture increases the effect of drought on tree ring density, but not on ring width, in Quercus petraea–Pinus sylvestris stands. For. Ecol. Manage. 345, 73–82.

Vallet, P., Pérot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway spruce: evidence based on large-scale inventory data and a generic modelling approach. J. Veg. Sci. 22, 932–942.

Vandermeer, J.H., 1989. The Ecology of Intercropping. Cambridge University Press, Cambridge [England], New York.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Climate 23, 1696–1718.

Walter, H., Lieth, H., 1967. Klimadiagramm-Weltatlas: Von Heinrich Walter Und Helmut Lieth. G. Fischer, Jena.

Waring, R.H., Running, S.W., 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant, Cell Environ. 1, 131–140.

Weigt, R.B., Bräunlich, S., Zimmermann, L., Saurer, M., Grams, T.E.E., Dietrich, H.-P., et al., 2015. Comparison of δ(18) O and δ(13) C values between tree-ring whole wood and cellulose in five species growing under two different site conditions. Rapid Commun. Mass Spectrom.: RCM 29, 2233–2244.

Woodruff, D.R., Meinzer, F.C., Lachenbruch, B., 2008. Height-related trends in leaf xylem anatomy and shoot hydraulic characteristics in a tall conifer: safety versus efficiency in water transport. New Phytol. 180, 90–99.

Zerbe, S., 2002. Restoration of natural broad-leaved woodland in Central Europe on sites with coniferous forest plantations. For. Ecol. Manage. 167, 27–42.

Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J. Ecol. 100, 742–749.