

Article

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

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

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

1. Introduction

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

Drought episodes affect physiological processes in trees such as photosynthesis, transpiration, and carbon allocation, which can lead to reduced growth rates and a higher tree susceptibility. The consideration of different tree species is thus crucial due to differences in physiological and anatomical

adjustments to cope with drought events. Therefore, it is important to predict responses of forest tree species to changing environmental conditions in order to understand if silvicultural conversion (e.g., mixtures) are meaningful [2]. Two important indices for depicting the effect of climate change are $\delta^{13}\text{C}$ in tree rings and the radial stem growth of trees [3–5]. Discrimination against ^{13}C ($\Delta^{13}\text{C}$) can be used as an indicator for changes in stomatal conductance and photosynthetic rates and thus reflect changes in soil water content and evaporative demand of trees, even though coupling between leaf physiological processes and incorporated stem cellulose may be dampened [6]. During drought stress, the transpiration rate is reduced by stomatal conductance [7]. In parallel, reduced stomatal aperture reduces the internal CO_2 concentration (C_i) and thus photosynthetic discrimination against $^{13}\text{CO}_2$ at the leaf level. Hence $\Delta^{13}\text{C}$ in tree rings decreases [8]. Another indicator of environmental changes is the reduction in radial growth due to limited water availability. In each particular year, newly formed wood cells reflect the environmental conditions for tree growth. Andreu et al. [9] examined tree-ring widths and $\delta^{13}\text{C}$ chronologies from an Iberian pine forest and concluded that $\delta^{13}\text{C}$ reveals drought stress signals more precisely than radial stem growth. However, the relationship between tree rings and $\Delta^{13}\text{C}$ does not only represent physical archives but also biological processes such as the competition for water and light. Studies by Thurm et al. [10], Pretzsch et al. [11], and Lebourgeois et al. [12] provide evidence based on radial stem growth that species mixture may reduce the climate sensitivity of the species. It is generally accepted that mixed forest stands can improve soil properties [13,14], biodiversity [15,16], and productivity [17,18] at stand level. Complementary resource use allows significant positive effects on yield in mixed compared to monospecific stands [19,20]. Certainly, stands with species mixture are not always more productive than stands with monocultures, as facilitation effects among species are dependent on site conditions, age of the stands, and mixing structure [17,21,22].

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

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

2. Materials and Methods

2.1. Experimental Sites

Four locations in southern Germany were selected to cover a precipitation gradient. The gradient has a northwest–southeast (Arnstein, Parsberg, Wasserburg, Traunstein) extent, with the locations becoming more humid towards the southeast. The precipitation in the growing season (P_{gr}) (April–September) ranged from 320 mm in Arnstein to 850 mm in Traunstein (Table 1; data: Bavarian State Research Center for Agriculture (LfL) [27]). The sites represent a precipitation gradient from the upper colline to sub-mountainous altitudes. The altitudes range from 330 m in the northwest and 600 m in the southeast of Bavaria. Mean annual temperature for the period 1980–2010 ranged between 8.5 to 9.5 °C, with slightly higher temperatures in the southeast. In the year 2003, an extreme climate anomaly occurred in Europe with high temperatures, particularly in August, and long-lasting drought

events. At the investigation plots, the total precipitation in this year was the equivalent of 10 months below the annual average. To calculate resistance and resilience in the drought year 2003, we used values from the years 2000 to 2006, that is three years prior to and post drought.

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

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

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

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

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

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

The sites were selected on the basis of similar soil characteristics, stand density, and comparable stand age. Soil types of the sites are cambisol, with the exception of Arnstein which has a luvisol soil. In September 2014, in order to determine the characteristics of the soils, four soil cores were taken at each plot and divided into five fractions (organic layer, 0–10 cm, 10–40 cm, 40–80 cm, 80–150 cm) to estimate the plant available soil water at field capacity and the cation exchange capacity (CEC) (Table 3). The CEC was high to very high at Arnstein, Parsberg, and Traunstein and between medium and high

at Wasserburg compared to national standards [28]. The two calcareous sites Arnstein and Parsberg compensate for their low soil depth through higher nutrient concentrations. The water storage capacity reflects the gradient and increases from dry to moist sites.

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

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

2.2. Sampling Procedure

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

2.3. Tree Ring Measurements

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

2.4. Carbon Isotope Analysis

To determine the $\Delta^{13}\text{C}$ for the reference period of 2000 to 2006, the cores of the sample trees were mechanically fixed on a wooden holder and prepared with a WSL-core-microtome (WSL, Birmensdorf,

Switzerland). Individual tree rings of both cores (east and north direction) were ripped with a scalpel under a binocular. The years 2000 to 2002, representing the initial period, were pooled. After drying in the dry oven at a temperature of 60 °C, the tree ring samples (mass > 50 mg) were cut into small pieces and processed into a fine powder in sample tubes using a ball mill (Mixer Mill MM2, Retsch, Haan, Germany). Sample mass was always above 50 mg; thus, contamination from sample tube material appeared negligible [35]. Subsequently, aliquots of 2 mg were weighed into tin capsules. For carbon isotope measurements, the samples were combusted to CO₂ using a Euro EA 3000 Elemental Analyzer (Eurovector S.p.A, Milan, Italy). The measurements of the isotope ratio ¹³C/¹²C were carried out using an Isoprime 100 isotope ratio mass spectrometer (GV Instruments Ltd., Manchester, UK).

To calculate $\Delta^{13}\text{C}$, the long-term changes in the atmospheric ¹³CO₂ signal were corrected for: $\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{atmosphere}} - \delta^{13}\text{C}_{\text{plant}})/(1 - \delta^{13}\text{C}_{\text{plant}}/1000)$ [3]. The Belemnite of PEE-Dee-formation from North-Carolina, USA was used as the standard: $\delta^{13}\text{C} (\text{‰}) = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \cdot 1000$, with $R = ^{13}\text{C}/^{12}\text{C}$. The isotopic fractionation enrichment of ¹³C relative to ¹²C isotope is described through the simplified equation of Farquhar et al. [36]: $\Delta^{13}\text{C} = a + (b - a) (c_i/c_a)$. The c_i/c_a indicates the leaf internal to atmospheric CO₂ concentration. The constant a gives the kinetic fractionation of ¹³CO₂ during diffusion (4.4‰). The constant b describes the discrimination by CO₂-fixation of the carboxylating enzymes (29‰). Both stomatal conductance and photosynthesis rate determine c_i and thus discrimination of ¹³C during photosynthesis [8].

2.5. Climatic Site Conditions

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

2.6. Data Analysis and Statistics

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

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

$$y_{ijk} = a_1x_{1ijk} + a_2x_{2ijk} + a_3x_{3ijk} \dots a_nx_{nijk} + b_{i1}z_{1ij} + b_{i2}z_{2ij} \dots b_{in}z_{nij} + \varepsilon_{ijk}$$

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

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

3. Results

3.1. Ring Width Variations and Tree Ring $\Delta^{13}\text{C}$ Signatures

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

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

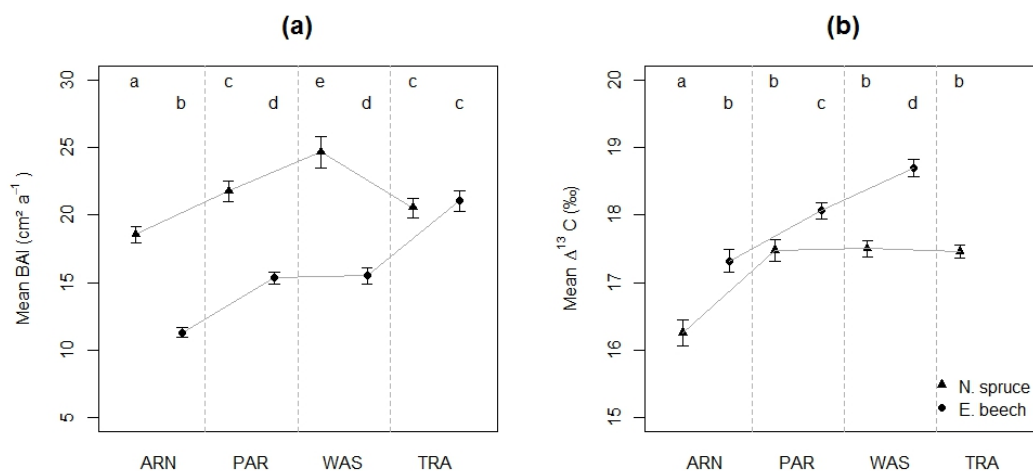


Figure 1. Mean basal area increment (a) and $\Delta^{13}\text{C}$ signatures (b) of spruce trees (triangles) and beech trees (circles) from the dry site Arnstein to the moist site Traunstein. The means of the years 2000 to 2006 were used. Significances are represented by the letters a to e, calculated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

The mean basal area increment index (BAII) in Figure 2 shows the detrended data over the reference period (2000–2006). The figure gives an overview of the data of BAI and $\Delta^{13}\text{C}$ in the period before and after the drought year 2003. The decreased BAI and $\Delta^{13}\text{C}$ in the year 2003 can be

seen in most cases. The drop in 2003 is calculated and evaluated through the results for resistance (RT). For $\Delta^{13}\text{C}$, beech trees of the mixed stands reveal a higher discrimination compared to the same species in a monospecific environment. In contrast, spruce trees had a higher discrimination in a monospecific environment.

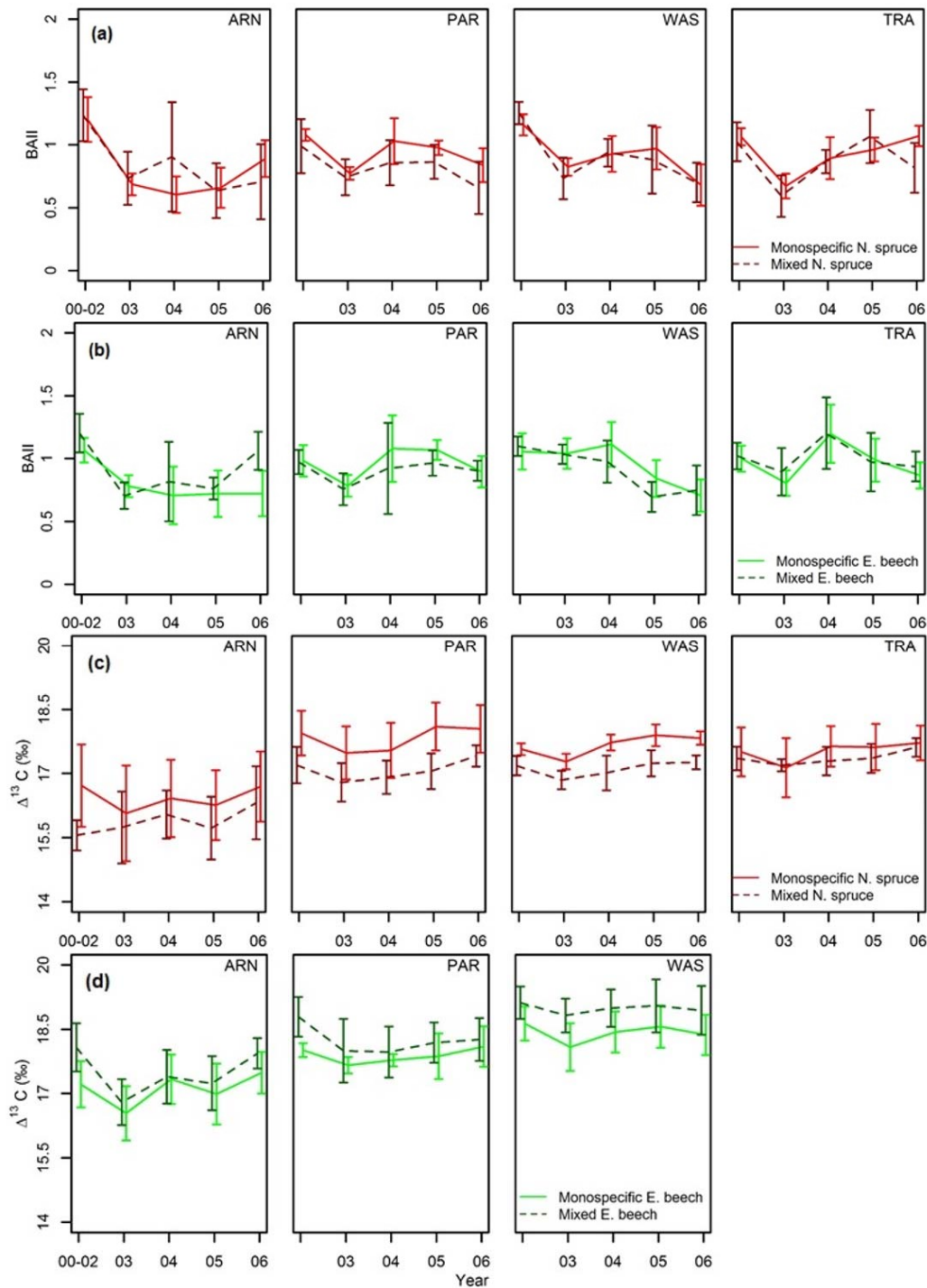


Figure 2. Standardized mean basal area increment (BAII) (a,b) and mean $\Delta^{13}\text{C}$ (c,d) (for the period 2000 to 2006) of spruce and beech in monospecific and mixed neighborhood at the sites Arnstein (ARN), Parsberg (PAR), Wasserburg (WAS), and Traunstein (TRA) with confidence intervals (CI,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

3.2. Species-Specific Differences in Resistance and Resilience

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

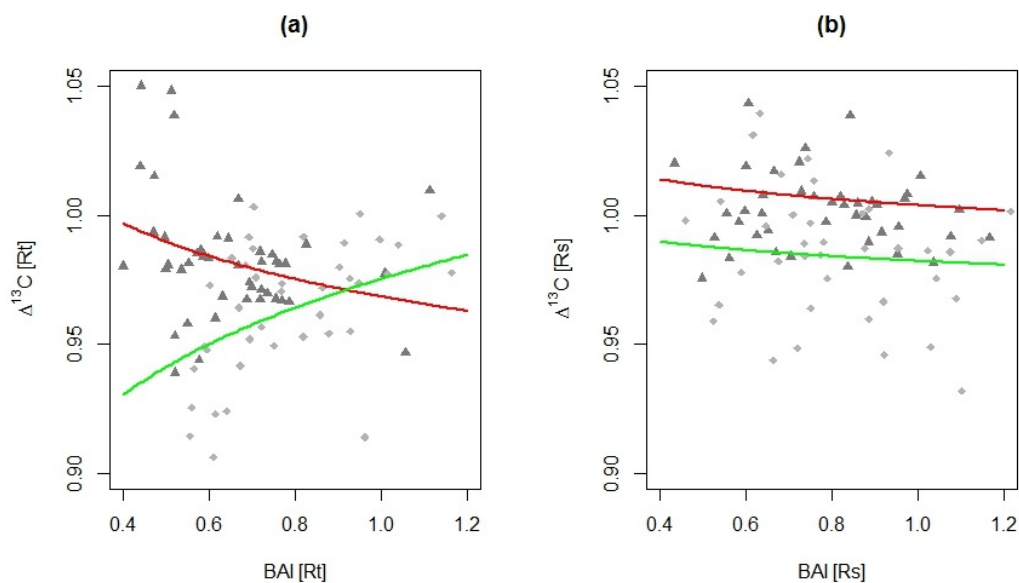


Figure 3. Relationship between the resistance (a) and resilience (b) of the $\Delta^{13}\text{C}$ and BAI of spruce and beech trees in the drought year 2003 (lmer with logarithmic transformation of resistance (RT) and resilience (RS) in the model). Differences are significant between the species for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

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

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

3.4. Relationship with Climate Variables

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

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

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

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

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

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

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

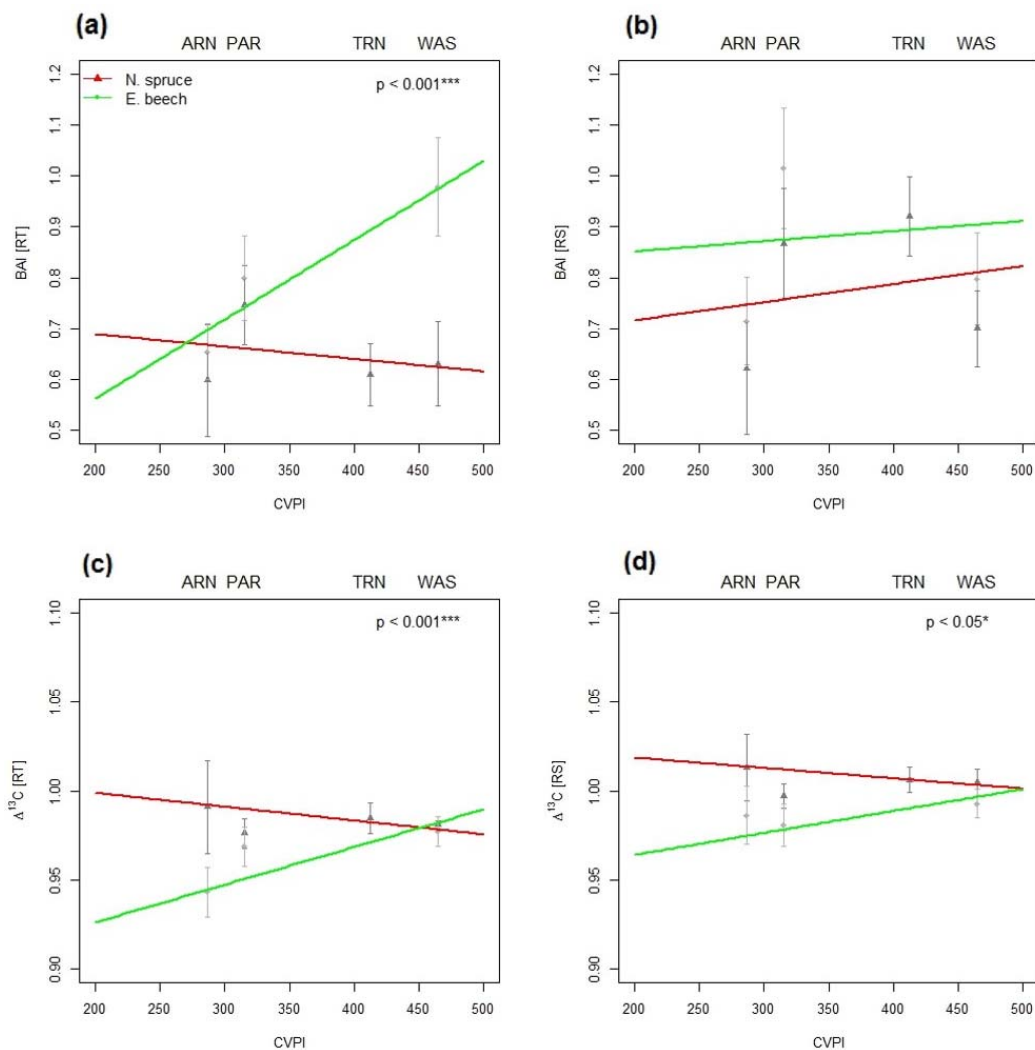


Figure 4. Linear mixed effect model of species and sites relative to the drought period 2003 for the BAI (a,b) and $\Delta^{13}\text{C}$ (c,d) of beech (green line) and spruce (red line), represented by the CVPI, with means of RT and RS and confidence intervals (CI, 95%). The differences between species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

4. Discussion

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

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

In view of the present results, the dendrochemical isotope analysis revealed a clearer signal in drought response among site and stand composition than the dendrochronological tree ring analysis. Likewise, Hartl-Meier et al. [4], Mölder et al. [5], Andreu et al. [9], and Saurer et al. [43] found a strong sensitivity of the C isotopic signatures to climate variables such as precipitation for different species. Tree ring width variations may reflect more local factors i.e., site conditions [9]. The ratio of leaf intercellular and ambient CO_2 concentration and, further, the photosynthetic fractionation of carbon isotopes, generally allow the characterization of environmental effects with the use of $\Delta^{13}\text{C}$ of newly

assimilated organic matter [44]. However, tree ring growth and $\Delta^{13}\text{C}$ in tree rings relationships are not always straightforward, since several factors may concurrently influence isotope fractionation i.e., species-specific differences [3,6].

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

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

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

4.2. Species Interaction in Monospecific Versus Mixed Stands

The influence of the mixture structure of spruce and beech stands has been analyzed in many studies [12,23,56–58] but no common statement could be found in these. Species mixture could lead to positive effects as well as to negative consequences for tree ring growth. For instance, the shading effects of beech or its deep-rooting system and the consequent restriction of water and nutrient supply could have negative effects on spruce [17,59]. Positive effects of beech on spruce might include hydraulic lift by the roots. At night, when transpiration is low and tree water potential high, roots receive water from deeper soil layers. If the water potential is lower in the upper soil layer compared

to deeper soil layers, as in drought situations, water emerges from these layers to the surface layer. This water can be used from the beech tree itself, but also from the surrounding trees [60–62]. This could provide an explanation for the higher resistance of spruce trees in mixture with regard to $\Delta^{13}\text{C}$.

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

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

5. Conclusions

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

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

Appendix A

Table A1. Estimates of the linear mixed effect model of spruce and beech in monospecific and mixed stands along the precipitation gradient (CVPI) (spruce $n = 45$; beech $n = 41$). Standard deviation is represented in brackets. Significance codes: '****' 0.0001 '***' 0.001 '**' 0.01 '*' 0.05 '(*)' 0.1.

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

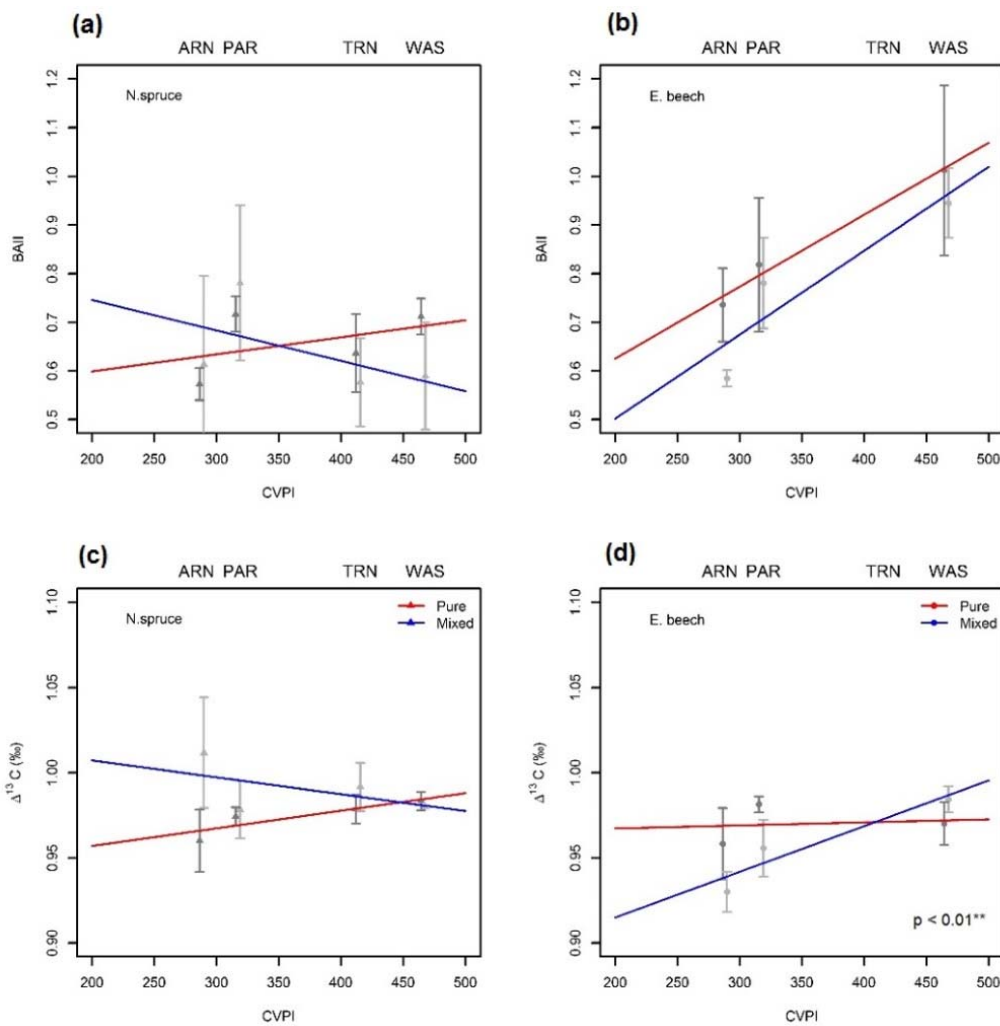


Figure A1. Linear mixed effect model of species and sites relative to the drought period in 2003 for the resistance of spruce and beech of BAI (a,b) and $\Delta^{13}C$ (c,d) in monospecific or mixed environments along the gradient represented by Paterson-index (CVPI).

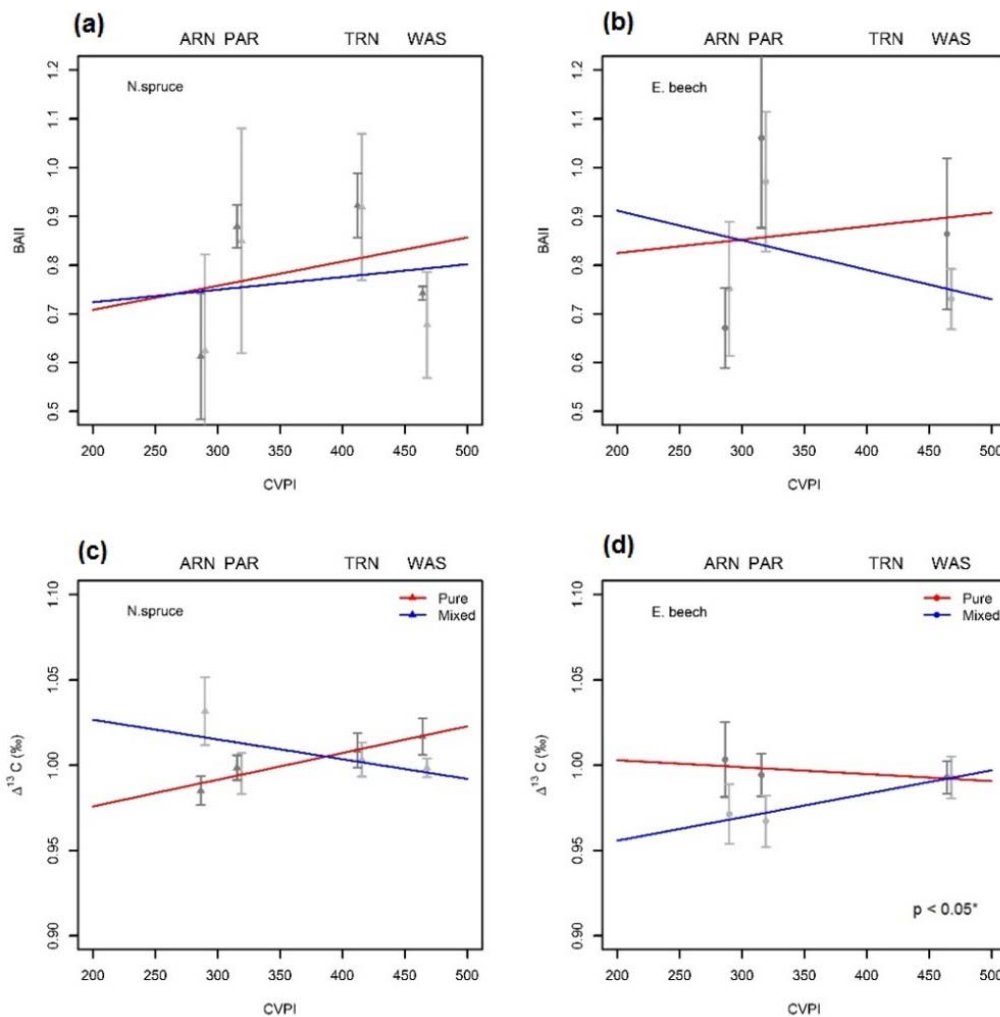


Figure A2. Linear mixed effect model of species and sites relative to the drought period in 2003 for the resilience of spruce and beech of BAI (a,b) and $\Delta^{13}\text{C}$ (c,d) in monospecific or mixed environments along the gradient represented by Paterson-index (CVPI).

References

1. Ciais, P.; Reichstein, M.; Viovy, N.; Granier, A.; Ogee, J.; Allard, V.; Aubinet, M.; Buchmann, N.; Bernhofer, C.; Carrara, A.; et al. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **2005**, *437*, 529–533. [[CrossRef](#)] [[PubMed](#)]
2. Bolte, A.; Ammer, C.; Löf, M.; Madsen, P.; Nabuurs, G.-J.; Schall, P.; Spathelf, P.; Rock, J. Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scand. J. For. Res.* **2009**, *24*, 473–482. [[CrossRef](#)]
3. McCarroll, D.; Loader, N.J. Stable isotopes in tree rings. *Quat. Sci. Rev.* **2004**, *23*, 771–801. [[CrossRef](#)]
4. Hartl-Meier, C.; Zang, C.; Büntgen, U.; Esper, J.; Rothe, A.; Göttelein, A.; Dirnböck, T.; Treydte, K. Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest. *Tree Physiol.* **2015**, *35*, 4–15. [[CrossRef](#)] [[PubMed](#)]
5. Mölder, I.; Leuschner, C.; Leuschner, H.H. $\delta^{13}\text{C}$ signature of tree rings and radial increment of *Fagus sylvatica* trees as dependent on tree neighborhood and climate. *Trees* **2011**, *25*, 215–229. [[CrossRef](#)]
6. Gessler, A.; Ferrio, J.P.; Hommel, R.; Treydte, K.; Werner, R.A.; Monson, R.K. Stable isotopes in tree rings: Towards a mechanistic understanding of isotope fractionation and mixing processes from the leaves to the wood. *Tree Physiol.* **2014**, *34*, 796–818. [[CrossRef](#)] [[PubMed](#)]

7. Bréda, N.; Huc, R.; Granier, A.; Dreyer, E. Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* **2006**, *63*, 625–644. [[CrossRef](#)]
8. Farquhar, G.D.; Ehleringer, J.R.; Hubick, K.T. Carbon Isotope Discrimination and Photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **1989**, *40*, 503–537. [[CrossRef](#)]
9. Andreu, L.; Planells, O.; Gutiérrez, E.; Helle, G.; Schleser, G.H. Climatic significance of tree-ring width and $\delta^{13}\text{C}$ in a Spanish pine forest network. *Tellus B* **2008**, *60*, 771–781. [[CrossRef](#)]
10. Thurm, E.A.; Uhl, E.; Pretzsch, H. Mixture reduces climate sensitivity of Douglas-fir stem growth. *For. Ecol. Manag.* **2016**, *376*, 205–220. [[CrossRef](#)]
11. Pretzsch, H.; Schütze, G.; Uhl, E. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biol.* **2013**, *15*, 483–495. [[CrossRef](#)] [[PubMed](#)]
12. Lebourgeois, F.; Gomez, N.; Pinto, P.; Mérian, P. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manag.* **2013**, *303*, 61–71. [[CrossRef](#)]
13. Ammer, C.; Bickel, E.; Kolling, C. Converting Norway spruce stands with beech—A review of arguments and techniques. *Austrian J. For. Sci.* **2008**, *125*, 3–26.
14. Binkley, D. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. *Can. J. For. Res.* **2003**, *33*, 2274–2279. [[CrossRef](#)]
15. Smith, K.W. Bird populations: Effects of tree species mixtures. In *The Ecology of Mixed-Species Stands of Trees*; Cannell, M.G.R., Malcolm, D.C., Robertson, P.A., Eds.; Blackwell: Oxford, UK, 1992; pp. 233–242.
16. Gotelli, N.J.; Colwell, R.K. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **2001**, *4*, 379–391. [[CrossRef](#)]
17. Pretzsch, H.; Dieler, J.; Seifert, T.; Rötzer, T. Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in stands with different spatial mixing patterns. *Trees* **2012**, *26*, 1343–1360. [[CrossRef](#)]
18. Morin, X.; Fahse, L.; Scherer-Lorenzen, M.; Bugmann, H. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecol. Lett.* **2011**, *14*, 1211–1219. [[CrossRef](#)] [[PubMed](#)]
19. Knoke, T.; Ammer, C.; Stimm, B.; Mosandl, R. Admixing broadleaved to coniferous tree species: A review on yield, ecological stability and economics. *Eur. J. For. Res.* **2008**, *127*, 89–101. [[CrossRef](#)]
20. Kely, M.J. The role of species mixtures in plantation forestry. *For. Ecol. Manag.* **2006**, *233*, 195–204. [[CrossRef](#)]
21. Forrester, D.I. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *For. Ecol. Manag.* **2014**, *312*, 282–292. [[CrossRef](#)]
22. Rötzer, T. Mixing patterns of tree species and their effects on resource allocation and growth in forest stands. *Nova Acta Leopoldina* **2013**, *114*, 239–254.
23. Metz, J.; Annighöfer, P.; Schall, P.; Zimmermann, J.; Kahl, T.; Schulze, E.-D.; Ammer, C. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob. Chang. Biol.* **2016**, *22*, 903–920. [[CrossRef](#)] [[PubMed](#)]
24. Lyr, H.; Fiedler, H.J.; Tranquillini, W. *Physiologie und Ökologie der Gehölze*; G. Fischer Verlag: Jena, Germany, 1992.
25. Klein, T. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct. Ecol.* **2014**, *28*, 1313–1320. [[CrossRef](#)]
26. Lloret, F.; Keeling, E.G.; Sala, A. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* **2011**, *120*, 1909–1920. [[CrossRef](#)]
27. Bavarian State Research Center for Agriculture (LfL): Meteorological Data from Local Weather Stations. Available online: <http://www.wetter-by.de> (accessed on 16 October 2016).
28. Standortskartierung, A. *Forstliche Standortsaufnahme*, 7th ed.; IHW-Verlag: Eching, Germany, 2016.
29. Häberle, K.H. *Soil Characteristics*, Personal Communication: Freising, Germany, 2016.
30. Leavitt, S.W.; Long, A. Sampling strategy for stable carbon isotope analysis of tree rings in pine. *Nature* **1984**, *311*, 145–147. [[CrossRef](#)]
31. Treydte, K.; Schleser, G.H.; Schweingruber, F.H.; Winiger, M. The climatic significance of $\delta^{13}\text{C}$ in subalpine spruces (Lötschental, Swiss Alps). *Tellus B* **2001**, *53*, 593–611. [[CrossRef](#)]

32. Biondi, F.; Qeadan, F. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. *Tree-Ring Res.* **2008**, *64*, 81–96. [CrossRef]
33. Holmes, R.L.; Adams, R.K.; Fritts, H.C. *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*; University of Arizona: Tucson, AZ, USA, 1986; p. 184.
34. Hegershoff, R. *Die Mathematischen Hilfsmittel der Kulturingenieure und Biologen: Herleitung von Gesetzmäßigen Zusammenhängen. Als Manuskript Veröffentlicht*; Institut für Forstingenieurwesen und Luftbildmessung an der forstlichen Abteilung der Technischen Universität Dresden: Dresden, Germany, 1936.
35. Isaac-Renton, M.; Schneider, L.; Treydte, K. Contamination risk of stable isotope samples during milling. *Rapid Commun. Mass Spectrom.* **2016**, *30*, 1513–1522. [CrossRef] [PubMed]
36. Farquhar, G.D.; O'Leary, M.H.; Berry, J.A. On the Relationship between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. *Aust. J. Plant Physiol.* **1982**, *13*, 281–292. [CrossRef]
37. Paterson, S.S. *The Forest Area of the World and Its Potential Productivity*; Royal University of Goteborg: Gothenburg, Sweden, 1956.
38. Benavides, R.; Roig, S.; Osoro, K. Potential productivity of forested areas based on a biophysical model. A case study of a mountainous region in northern Spain. *Ann. For. Sci.* **2009**, *66*, 108. [CrossRef]
39. Vanclay, J.K. *Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests*; CAB International: Wallingford, UK, 1994; p. 312.
40. Pretzsch, H.; Rötzer, T. Indicating Forest Ecosystem and Stand Productivity: From Deductive to Inductive Concepts. In *Ecological Forest Management Handbook*; CRC Press Taylor & Francis Group: London, UK, 2016; p. 415.
41. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [CrossRef]
42. Kuznetsova, A.; Brockhoff, P.B.; Christensen, R.H.B. lmerTest: Tests in Linear Mixed Effects Models. R Package Version 2.0-29. Available online: <http://CRAN.R-project.org/package=lmerTest> (accessed on 2 September 2016).
43. Saurer, M.; Siegenthaler, U.; Schweingruber, F. The climate-carbon isotope relationship in tree rings and the significance of site conditions. *Tellus B* **1995**, *47*, 320–330. [CrossRef]
44. Gessler, A.; Brandes, E.; Buchmann, N.; Helle, G.; Rennenberg, H.; Barnard, R.L. Tracing carbon and oxygen isotope signals from newly assimilated sugars in the leaves to the tree-ring archive. *Plant Cell Environ.* **2009**, *32*, 780–795. [CrossRef] [PubMed]
45. Leavitt, S.W. Tree-ring C-H-O isotope variability and sampling. *Sci. Total Environ.* **2010**, *408*, 5244–5253. [CrossRef] [PubMed]
46. Levesque, M.; Saurer, M.; Siegwolf, R.; Eilmann, B.; Brang, P.; Bugmann, H.; Rigling, A. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Glob. Chang. Biol.* **2013**, *19*, 3184–3199. [CrossRef] [PubMed]
47. Kloeppel, B.D.; Treichel, I.W.; Kharuk, S.; Gower, S.T. Foliar carbon isotope discrimination in Larix species and sympatric evergreen conifers: A global comparison. *Oecologia* **1998**, *114*, 153–159. [CrossRef] [PubMed]
48. Zang, C.; Rothe, A.; Weis, W.; Pretzsch, H. Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahrringbreiten. *Allg. Forst Jagdztg.* **2011**, *182*, 98–112.
49. Helle, G.; Schleser, G.H. Beyond CO₂-fixation by Rubisco—An interpretation of ¹³C/¹²C variations in tree rings from novel intra-seasonal studies on broad-leaf trees. *Plant Cell Environ.* **2004**, *27*, 367–380. [CrossRef]
50. Kuptz, D.; Fleischmann, F.; Matyssek, R.; Grams, T.E.E. Seasonal patterns of carbon allocation to respiratory pools in 60-yr-old deciduous (*Fagus sylvatica*) and evergreen (*Picea abies*) trees assessed via whole-tree stable carbon isotope labeling. *New Phytol.* **2011**, *191*, 160–172. [CrossRef] [PubMed]
51. Klein, T.; Hemming, D.; Lin, T.; Grunzweig, J.M.; Maseyk, K.; Rotenberg, E.; Yakir, D. Association between tree-ring and needle delta¹³C and leaf gas exchange in *Pinus halepensis* under semi-arid conditions. *Oecologia* **2005**, *144*, 45–54. [CrossRef] [PubMed]
52. Barbour, M.M.; Walcroft, A.S.; Farquhar, G.D. Seasonal variation in delta¹³C and delta¹⁸O of cellulose from growth rings of *Pinus radiata*. *Plant Cell Environ.* **2002**, *25*, 1483–1499. [CrossRef]

53. Hommel, R.; Siegwolf, R.; Zavadlav, S.; Arend, M.; Schaub, M.; Galiano, L.; Haeni, M.; Kayler, Z.E.; Gessler, A. Impact of interspecific competition and drought on the allocation of new assimilates in trees. *Plant Biol.* **2016**, *18*, 785–796. [[CrossRef](#)] [[PubMed](#)]
54. Zang, U.; Goisser, M.; Häberle, K.-H.; Matyssek, R.; Matzner, E.; Borken, W. Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study. *Z. Pflanzenernähr. Bodenkd.* **2014**, *177*, 168–177. [[CrossRef](#)]
55. Zeide, B. Tolerance and self-tolerance of trees. *For. Ecol. Manag.* **1985**, *13*, 149–166. [[CrossRef](#)]
56. Assmann, E. Waldertragskunde. In *Organische Produktion, Struktur, Zuwachs und Ertrag von Waldbeständen*; BLV Verlagsgesellschaft: München, Germany, 1961.
57. Pretzsch, H. Facilitation and Competition in Mixed-Species Forests Analyzed along an Ecological Gradient. *Nova Acta Leopoldina* **2013**, *114*, 159–174.
58. Jucker, T.; Bouriaud, O.; Avacaritei, D.; Coomes, D.A. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. *Ecol. Lett.* **2014**, *17*, 1560–1569. [[CrossRef](#)] [[PubMed](#)]
59. Goisser, M.; Geppert, U.; Rötzer, T.; Paya, A.; Huber, A.; Kerner, R.; Bauerle, T.; Pretzsch, H.; Pritsch, K.; Häberle, K.H.; et al. Does belowground interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem growth in *Picea abies*? *For. Ecol. Manag.* **2016**, *375*, 268–278. [[CrossRef](#)]
60. Matyssek, R.; Fromm, J.; Rennenberg, H.; Roloff, A. *Biologie der Bäume*; Verlag Eugen Ulmer: Stuttgart, Germany, 2010.
61. Caldwell, M.M.; Dawson, T.E.; Richards, J.H. Hydraulic lift: Consequences of water efflux from the roots of plants. *Oecologia* **1998**, *113*, 151–161. [[CrossRef](#)] [[PubMed](#)]
62. Dawson, T.E. Hydraulic lift and water use by plants: Implications for water balance, performance and plant-plant interactions. *Oecologia* **1993**, *95*, 565–574. [[CrossRef](#)] [[PubMed](#)]
63. Pretzsch, H.; Schütze, G. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: Evidence on stand level and explanation on individual tree level. *Eur. J. For. Res.* **2009**, *128*, 183–204. [[CrossRef](#)]
64. Pretzsch, H.; Schütze, G. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biol.* **2005**, *7*, 628–639. [[CrossRef](#)] [[PubMed](#)]
65. Bolte, A.; Kampf, F.; Hilbrig, L. Space sequestration below ground in old-growth spruce-beech forests—Signs for facilitation? *Front. Plant Sci.* **2013**, *4*, 1–11. [[CrossRef](#)] [[PubMed](#)]
66. Callaway, R.M.; Walker, L.R. Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. *Ecology* **1997**, *78*, 1958–1965. [[CrossRef](#)]
67. Maestre, F.T.; Callaway, R.M.; Valladares, F.; Lortie, C.J. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* **2009**, *97*, 199–205. [[CrossRef](#)]
68. Malkinson, D.; Tielbörger, K. What does the stress-gradient hypothesis predict?: Resolving the discrepancies. *Oikos* **2010**, *119*, 1546–1552. [[CrossRef](#)]
69. Pretzsch, H.; Block, J.; Dieler, J.; Dong, P.H.; Kohnle, U.; Nagel, J.; Spellmann, H.; Zingg, A. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann. For. Sci.* **2010**, *67*, 712. [[CrossRef](#)]
70. Tardieu, F.; Granier, C.; Muller, B. Water deficit and growth. Co-ordinating processes without an orchestrator? *Curr. Opin. Plant Biol.* **2011**, *14*, 283–289. [[CrossRef](#)] [[PubMed](#)]

