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Drought Resistance of Norway Spruce (*Picea abies* [L.] Karst) and European Beech (*Fagus sylvatica* [L.]) in Mixed vs. Monospecific Stands and on Dry vs. Wet Sites. From Evidence at the Tree Level to Relevance at the Stand Level

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Abstract: Frequency of drought years is expected to increase through climate warming. Mixed stands have often shown to be more productive than monospecific stands in terms of yield and of resistance against windthrows and bark beetle attacks. Mixture of beech and spruce is of particular interest. However, little is known about its growth reaction to drought. Therefore, we investigated the drought reaction of beech and spruce in mixed vs. monospecific stands along an ecological gradient. In particular, we sought evidence for mixture-related resilience on the individual tree level. Therefore, we quantified the response of tree ring width to drought. Moreover, we attempted to explain the relevance of individual tree response on the stand level by quantifying the stand level loss of volume growth after drought. At the individual tree level, beech was found to be more resilient and resistant in pure vs. mixed stands. Spruce, in contrast, was favored by mixture, and this was especially evident on drier sites. Along the gradient, growth losses at stand level increased in both mixed and pure stands in 2015, with growth gains on the drier sites observed in the same drought year, in accordance with the Stress Gradient Hypothesis. However, the stand level difference of growth loss between mixed and pure stands was not statistically significant. Mitigating mixture effects on the level of the individual tree thus did not become evident on the level of the whole stand.

Keywords: climate change; plasticity; acclimation; ecosystems; legacy effects; biodiversity; drought stress; temperate forests; central Europe

1. Introduction

The long term functionality of forest stands is determined by their capacity to resist and recover after disturbance [1]. Due to climate change, forest ecosystems might be prone to more frequent and severe biotic and abiotic disturbances [2], leading to increased mortality in the future [3,4]. Drier climatic conditions could strongly impact the terrestrial ecosystems by altering their water and carbon cycles [5]. These novel conditions could thus affect forest growth and stability [6].

The growth of forest stands is of general economic interest [7]. Selection of viable tree species, which are both productive and drought tolerant, is therefore crucial. The survivability of forests under more frequent disturbances through future drought events will have both economic and social impacts [8]. Mitigation of climate vulnerability has often been linked to biodiversity as an important component of ecosystem functioning [9]. Within that scope, mixed stands may provide better ecosystem services [10] such as more soil carbon storage [11] and overyielding at stand level [12,13].

However, a specific mixture, which might benefit in terms of yield, may or may not stand resistant under drought conditions, as drought response depends on species combination [14,15]. It may be due to the competitive interaction among trees [16], moreover, it could be subject to site conditions [17]. Thus, it may change along a climate gradient [18]. Several studies have documented drought responses of various species in Europe. A recent study by Steckel et al. 2020 [19] showed Oak and Pine in the mixtures to be more resistant, and Oak to be more resilient than their pure counterparts, where resilience and resistance of Oak improved with site water supply. Thurm et al. 2016 [20] showed Douglas-fir to be faster in drought recovery in contrast to the beech within a Douglas-fir beech mixture. Schwarz & Bauhus 2019 [17] found beech recovering faster with fir admixture. In another study by Pretzsch et al. 2013 [16], beech was found to be more resilient and resistant when mixed with Oak. Resistance, resilience and recovery [21], as well as drought responses, of mixed and pure Norway Spruce (*Picea abies* [L.] Karst) and European Beech (*Fagus sylvatica* [L.]) have also been documented in studies recently [22–24]. Moreover, Pretzsch et al. 2020 [25] reported spruce to be faster acclimated and by 20%–50% less affected within its interspecific neighborhood with beech, while the opposite was true for the beech. Neuner et al. 2015 [26] report a higher survival probability of spruce in mixed stands with beech as compared to pure stands under warmer climate and poor soil conditions. Spruce standalone is prone to biotic as well as abiotic damage [27], especially in drought due to its shallow-rooting system [28,29]. It may, however, experience a reduced drought impact in the mixture [30], as the deep-rooting system of a neighbor like beech [28] might incur benefits by virtue of its hydraulic redistribution effect [9,31,32].

The current state of knowledge about drought responses in mixture considers many mixture types [17]. It means that although there has been a number of investigations, there is still a requirement for investigating drought effects on relevant species mixtures. Even the knowledge about European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) in mixture, although being the most studied mixture type in Central Europe [33], is still unclear in terms of drought stress. Spruce-beech mixture is a frequent one in that region, therefore there is a strong requirement for assessing the specific performance of these species in community under drought events.

Resilience studies have so far focused on the individual tree level (see also Lebourgeois et al. 2010 [34]; Lloret et al. 2011 [21]; Serra-Maluquer et al. 2018 [18]). Such studies have shown the ecological response patterns of individual trees to drought. In particular, they help to understand the underlying physiological mechanisms which govern the drought response of tree ring growth. The Stress Gradient Hypothesis (SGH) [35,36] postulates that facilitative processes among species would become more frequent under more stressful conditions. This phenomenon has been observed repeatedly by empirical studies within plant communities. However, it has not been considered in all the cases. Forest management might thus benefit from measures that promote interspecific facilitation under drought stress and mitigate growth loss and mortality increase. Thus, there is now an additional demand for investigating the relevance of individual tree drought response for future forest management decisions which considers total yield of a stand per hectare. To this end, we additionally investigate resilience and resistance on stand level in mixture vs. monoculture following recent and pronounced drought years, viz. 2003 and 2015. Additionally, we quantify the volume growth losses at the stand level due to these drought years, relative to the pre-drought growth period. Since the reactions might change with different site conditions and water supply, we make our analysis along a climatic gradient across sites in Southern Germany. We first assess the intra- vs. interspecific drought reactions of beech and spruce at the individual tree level in order to look for evidences of species interaction. We henceforth scrutinize the following hypotheses at the individual tree level:

HI: Mixture of European beech and Norway spruce mitigates the negative impact of drought on growth per species.

HII: Such a mitigation of impact through mixture is stronger under drier climatic conditions.

We then quantify the drought responses and additionally, growth losses, at the stand level to find out if there is any mixture effect which emerged due to species interaction at the tree level and if this effect was evident at the total stand level. Therefore, we tested the following hypotheses:

HIII: Mixed stands have a lower growth loss under drought as compared to the weighted mean of the monospecific stands.

HIV: Such a mitigation of growth loss through mixture is larger under drier climatic conditions.

As external responses are reflected in the yearly tree ring formation, we derive the empirical evidence of drought stress from the ring-widths and use basal area increment as the proxy of an individual tree's response to drought. Volume is a more meaningful metric for the forest practices in terms of yield, therefore we take the volume growth per hectare as a proxy of drought response at the stand level.

2. Materials and Methods

2.1. Site Description

The five investigation sites are part of KROOF—the Kranzberg Forest Roof Project. Each of them is a triplet of European beech and Norway Spruce. Such a triplet comprises three rectangular plots which are spatially located close to one another and have similar site conditions. One of these plots is a monospecific stand of spruce, the other one is a monospecific beech stand. One further plot is composed of a mixture of these two species [37]. They are fully stocked and even aged, and range in size from 0.2 ha to 0.14 ha. Stand density is also more or less similar across all five investigation sites. These sites are located along a precipitation gradient from dry to moist conditions. That gradient extends along a transect from North-West (Lower Franconia) in Arnstein to South-East Bavaria in Traunstein (see Figure 1). Mean annual precipitation over the period of twenty years (1999–2018) ranges from 694 mm year^{-1} in Arnstein to 1200 mm year^{-1} in Traunstein (mean of the sites 932 mm year^{-1}). Correspondingly, mean annual temperature ranges from 9.3 to 8.9 °C (mean of the sites: 9.02 °C), respectively [38]. Soil substrates are Limestone, Tertiary Sand and Moraine, with the main soil types being Luvisol and Cambisol. For geographical information, see Table 1.

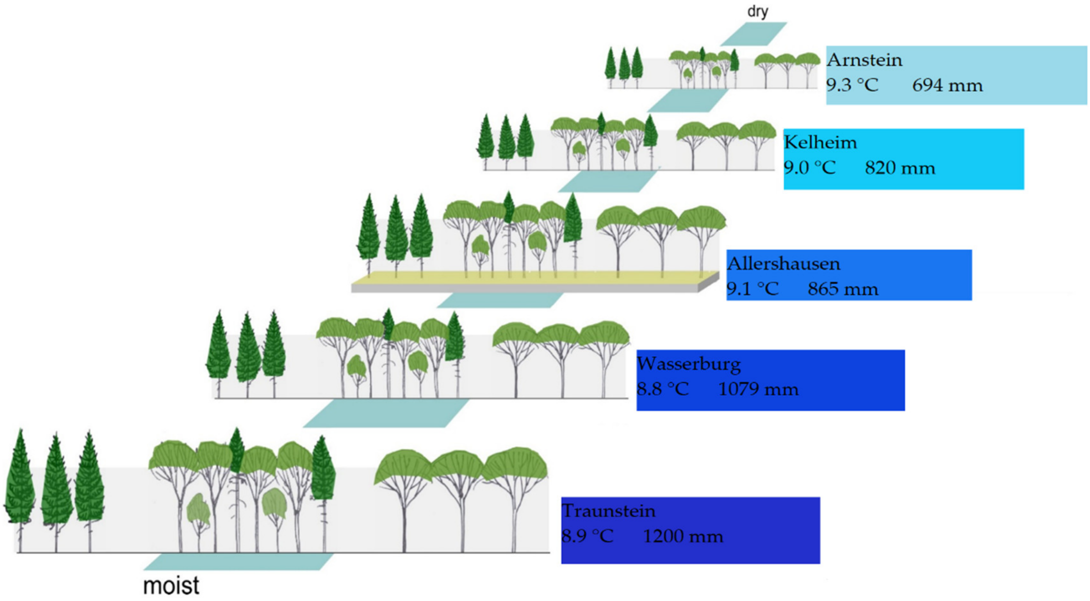

Figure 1. Modified Figure, excerpted from Pretzsch et al. 2015 [37]. From light to dark blue: dry to moist site conditions. Climate data (1 × 1 km raster grid) from Deutscher Wetterdienst (DWD 2019) [38].

Table 1. Geographical information of the five Beech & Spruce triplets.

Site	Code	Age	Geographical Location		E	A	T	P	M	Sub	ST	SI	SI
		(yr)	Lon	Lat	(°)	(m)	°C	(mm yr^{-1})	(mm °C^{-1})			Be (mono)	Sp (mono)
Arnstein	1021	82	09°58′37.20″	49°54′10.80″	-	330	9.3	694	36	LS	LUV	25.4	36.4
Kelheim	1022	89	11°49′19.20″	48°56′08.16″	315	550	9	820	43	LS	CAM	33.4	38.4
Allershausen	1023	72	11°37′18.17″	48°25′53.23″	-	490	9.1	865	45	TS	CAM	32.8	31.5
Wasserburg	1024	61	12°04′22.80″	48°08′31.20″	180	620	8.8	1079	57	MO	CAM	35.3	35.8
Traunstein	1025	67	12°40′19.20″	47°56′20.40″	270	600	8.9	1200	63	MO	CAM	35.0	40.1

Abbreviation: E: exposition; A: altitude above sea level; T: temperature; P: precipitation; M: Martonne Index; Sub: soil substrate; ST: soil type; SI: Site Index of the monospecific stands. Soil substrate LS: Limestone, TS: Tertiary Sand, MO: Moraine. Soil type LUV: Luvisol, CAM: Cambisol. Soil information taken from Schäfer et al. 2017 [24] & Häberle 2020 [39].

Site aridity was characterized by the de Martonne Aridity Index [40], which is defined as:

$$M = P/(T + 10) \tag{1}$$

where P is the annual precipitation sum in mm and T is the mean annual surface air temperature in °C.

Site Index or site productivity was characterized with the quadratic mean height (h_q) of the respective monospecific stands at the age of 100 by referring to the established species-specific yield tables for monospecific spruce (Assmann-Franz 1963) [41] and monospecific beech (Schober 1967) [42]. Although the yield tables serve as a reference only for pure stands, we also considered the same site index for the species' mixed stand counterparts to have a meaningful comparison of the stand characteristics of the species. For this purpose, mixed stands were upscaled to one hectare (see Section 2.3. Stand Level Evaluation).

2.2. Data Sampling and Tree Level Evaluation

379 trees with a minimum of 7 cm diameter were cored in total (19 core samples on average per plot) at breast height of 1.3 m, latest in autumn 2018 using a 5.15 mm increment borer [43]. Trees over the whole tree-size spectrum were cored so that all the size classes could be taken into account for data reconstruction.

Two core samples were taken per each individual tree from the cardinal directions North (0°) and East (90°). The ring width per core and year was measured at a resolution of 0.01 mm with a digital positiometer Type II [44]. The year rings of both cores were cross-dated with the help of identifiable drought years corresponding to notably narrow ring-width. Then, the measured ring-widths (radial increment) from the two cores were averaged per individual tree on a per-year basis.

For the drought analyses at the tree level, a subset of 304 trees was furthermore subsampled out of the 379 cored trees. That somewhat smaller subset comprised of exclusively trees which had been cored as late as in autumn 2018. The cores from this subset thus covered both drought years 2003 and 2015 (see the Introduction section) in order to maintain an identical sample size per drought year and to facilitate the comparison of both drought years by the trees' biological response. The average tree size in 2018 was similar among the species being considered (Table 2).

Table 2. Number of trees cored and subsampled; mean dbh (cm) ± SE in 2018.

	Beech Mixed	Beech Pure	Spruce Mixed	Spruce Pure	Total
All Cored					
N	96	96	94	93	379
Mean dbh	35.4 ± 1.0	31.7 ± 1.0	37.0 ± 1.0	32.7 ± 0.9	34.2 ± 0.6
Min-Max	12.7-60.7	11-54.8	14.6-58.2	13-51.6	11-60.7
Subsampled					
N	77	81	71	75	304
Mean dbh	35.6 ± 1.2	31.7 ± 1.1	36.5 ± 1.1	33.0 ± 1.0	34.1 ± 0.6
Min-Max	12.7-60.7	11-54.8	15-58.2	13-51.6	11-60.7

N: Number of samples; Min: minimum dbh (cm) in the cohort; Max: maximum dbh (cm) in the cohort.

Breast height diameters over bark were measured for a total of 618 trees, including both cored (379) and non-cored (239) trees. Two hundred and ninety-nine out of the total 618 trees (48%) were fitted with permanent diameter measurement tapes. The rest were measured with the normal measurement tapes during the site survey. Individual tree heights were measured for a total of 202 trees using a VERTEX IV Hypsometer [45] and cover the complete range of heights within a stand.

2.3. Stand Level Evaluation

Stand level evaluation of the five triplets was done using the software developed at the Chair of Forest Growth and Yield Science—Technical University of Munich, following the DESER-Norm by Johann (1993) [46]. Breast height diameter over bark, heights of individual trees and species-specific form factors by Franz (1971) [47] were used to calculate individual tree volumes with the help of Equation (2). For extrapolation of these individual tree volumes to the whole stand, they were summed up and upscaled with the help of a multiplication factor which was derived by dividing 10,000 m^2 (1 ha) by the respective plot size. This factor was then multiplied with the sum of individual tree volumes on the plot to get the per hectare volume. Moreover, total tree count and the stand basal area per hectare were extrapolated by multiplying this factor by the total individual tree count present on the plot, and the sum of their basal area, respectively.

$$v = d^2 \, x \, \pi/4 \, x \, h \, x \, f \quad (2)$$

where v, d and h are volume, diameter and height, respectively of an individual tree; f is the species-specific form factor.

Various height curve functions (Freese [48]; Korsuň [49]; Michailoff [50]; Petterson [51] & Prodan [52]) were parametrized based on the height-diameter relationships of the measured data. The parameterization was done specific to each species and to a specific plot. The height of the trees which had not been measured (416 trees) was then calculated from one of the above-mentioned parametrized functions. Calculated stand characteristics for mono as well as mixed beech and spruce have been summarized in Table 3.

To comprehend the stand development over time as dependent on the climatic conditions along the gradient, backward reconstruction of the diameter over bark was performed using an Ordinary Least Squares regression. Using the last known breast height diameter (2018), retrospective diameters were first derived from the tree cores. A log transformed model was fitted between the cumulative diameter increment at the end of a growing season and the breast height diameter at the end of that growing season for each year. The model was then exponentially back transformed (Equation (3)).

$$id_i = a * d^{b}{}_{i\_end} \quad (3)$$

where id_i is the cumulative diameter increment in mm for the year *i*, d_{i_end} is the breast height diameter at the end of the year *i*, in mm. Both *a* and *b* are regression parameters which were estimated from the exponentiated equation. The model assumes a constant bark width over time [53] and an allometric relationship between diameter and diameter increment [12]. Note that for extrapolation to the diameter over bark of the non-cored trees, we accounted for all the 379 tree core samples to provide more stable results for drought responses at the hectare scale. Applying Equation (3), retrospective diameters of the non-cored trees can be easily reconstructed as ($dbh_{i-1} = dbh_i - id_i$).

Individual tree heights were reconstructed using a uniform height curve system first developed by Kennel (1972) [54] and later parametrized by Franz et al. (1973) [55]; see Equation (4). On the plot level, species-specific quadratic mean height was predicted for each retrospective year from the yield tables by Assmann-Franz (1963) [41] and Schober 1967 [42] for Spruce and Beech, respectively.

$$h_i = 1.3 + (d_i/b_0 * d_i + b_1)^3 \tag{4}$$

where h_i is the individual tree height of the year i estimated as a function of breast height diameter d_i of the respective year. Parameters b_0 and b_1 depend on the species-specific age at the plot level, species-specific quadratic mean height (h_q) (retrospective h_q, which comes from the above mentioned yield tables) as well as quadratic mean diameter (d_q) (which comes from the reconstructed diameter) of the respective year. For a more detailed description of the diameter and height reconstruction, see Heym et al. 2018 [53].

After reconstructing the retrospective individual tree heights and diameters, stand level evaluation was done as described earlier.

2.4. Detrending Procedures

Prior to our analyses, our core data and the stand level growth needed to be standardized to a dimensionless time series in order to remove any trends caused by the different ages of the five plots or by the tree size as well as stand dynamics [56]. For this purpose we used a smoothing cubic spline function [57–59], which is a flexible smoothing procedure based on polynomials [60]. This was done within the package dplR [61] in statistical program R, version 3.5.3 (*R Studio version 1.2.1335 Build 1379) [62].*

2.5. Quantification of Resistance, Resilience and the Stand Level Growth Losses

Following the method outlined by Lloret et al. 2011 [21], two resilience indices (here denoted by R) viz. Resistance (R_t; Equation (5)) and Resilience per se (Rs; Equation (6)) were investigated. These indices quantify drought reactions based on growth. Within the study at hand, they were applied both at the individual tree level as well as at the whole stand level. At the individual tree level, basal area growth was used as the proxy for growth. For stand level growth we used volume increment per hectare as the proxy for growth, because it is more relevant to forest practice in terms of yield. We chose the well documented recent drought years in the region viz. 2003 and 2015. The mean de Martonne Index for the five sites (Equation (1)) was the least (37 mm °C^{-1}) in both of the drought years, over the twenty years' time period.

$$R_t = Dr/PreDr \tag{5}$$

$$R_s = PostDr/PreDr \tag{6}$$

where R_t is the resistance in the drought year and reflects the growth under drought Dr with respect to the pre-drought growth PreDr. R_s is the resilience per se and reflects the growth levels after drought PostDr with respect to the pre-drought growth PreDr. Minimum value of R_t and R_s is "0," reflecting no growth relative to the pre-drought growth. Value of "1" means that the growth during drought occurred equal to pre-drought growth. Value more than "1" means that more growth occurred relative to the pre-drought growth. The values could be expressed equivalent to percentage, "1" being 100%.

Pre- and post-drought growth were each calculated as mean value of growth over two years. Thus, we deviated from the usual three-year period for calculation (as followed by Pretzsch et al., 2013), since 2018 was also a drought year and post-drought water supply was uniform only within a time window of two years. Therefore, the time length of pre-drought growth calculation was chosen accordingly.

Table 3. Stand characteristics of the five triplets. Values shown in the table are the mean and the min/max values. IG and IV are the mean annual basal area increment and mean annual volume increment from 1999–2018. The rest of the variables show the stand characteristics latest of 2018.

Species	**Age**	***N***	**d_q**	**h_q**	**G**	**V**	**SDI**	**Mixing Proportion**	**IG**	**IV**
	years	(ha^{-1})	(cm)	(m)	($m^2\ ha^{-1}$)	($m^3\ ha^{-1}$)	(ha^{-1})	(%)	($m^2\ ha^{-1}\ year^{-1}$)	($m^3\ ha^{-1}\ year^{-1}$)
Be (mixed)	80	528	31.4	27.8	37	538	686.6	0.59	0.9	17.1
	65–95	308–931	23.7–37.7	23.9–33.7	28.2–46.2	349.9–642.6	574–855	0.41–0.73	0.3–2.2	7.9–32.6
Be (pure)	76	684	27.8	25.9	38	512	745.1		0.8	15.1
	59–100	365–1018	22.4–33.8	21.6–33.4	32.8–45.1	410.9–660.1	593–929		0.3–1.5	9.2–28.4
Sp (mixed)	80	545	36.4	30.6	56	813	980.7	0.41	1.2	21
	65–95	427–699	31.7–44.1	27–34.8	45.8–74.9	622.5–1190.9	839–1217	0.27–0.59	0.5–2.3	12.2–33.3
Sp (pure)	62	787	31.2	27.1	57	758	1073.8		1.5	25.2
	55–75	523–1000	24–35.9	22.2–31.3	45.4–75.6	499.7–1103.1	904–1415		0.5–2.9	12.7–41.4
Be + Sp (mixed)					43	635	791.9		1	18.4
					35.6–46.5	450.1–795.2	701–891		0.5–2	11.1–30

Abbreviations: A: age; *N*: number of trees per hectare, dq: quadratic mean diameter; hq: quadratic mean height; G: stand basal area; V: stand volume; SDI: Reineke's Stand Density Index [63]; IG: mean annual basal area increment; IV: mean annual volume increment.

Total relative volume growth loss at the stand level incurred due to drought was calculated simply by adding up the growth reduction occurred in the drought year and the growth reduction which occurred post-drought during period of recovery, as given in Equation (7). We term it as total relative volume growth loss because the losses or reductions occurred relative to the pre-drought volume growth levels.

$$L = 1 - R_t + 1 - R_s \tag{7}$$

where L is the total relative volume growth loss and could be expressed as a percentage. R_t or resistance at the stand level was calculated using Equation (5) and R_s or resilience per se was calculated at the stand level using Equation (6). L equal "0" reflects no growth losses. $L > 0$ shows that growth losses occurred. $L < 0$ shows the negative growth losses or the corresponding growth gains.

2.6. Statistical Analyses

Statistical analyses were done in statistical program R, version 3.5.3 (R Studio version 1.2.1335 Build 1379*)* [62]. For modelling approach, we used a linear mixed effect model [64] package: nlme *[65]*, accounting for random effects due to spatial variability in the datasets. This model addresses the inter-correlation of samples [19] caused due to either spatial or temporal nesting. We used the site i as the random effect b_i to account for spatial nesting.

For the tree level models, tree j was additionally used to explain the random effects b_{ij} caused due to spatial clustering of trees from different sites and plots. However, addressing random effects at the tree level was also not necessary in most of the cases, as taking it into account either did not affect the model at all or made it worse. Correspondingly, index j and the random effect b_{ij} were not included in such models. In this regard, model selection was based on AIC or Akaike Information Criterion [66]. A difference of AIC > 2 between the models with and without the individual tree as the random effect was the deciding factor for the performance of the model, whether the random effects at the tree level should be taken into account or not, provided that the model with the lower AIC was selected. Saying that, random effect at tree level was accounted for only in the following cases:

1. Tree level resilience per se: Beech in 2003
2. Tree level resistance: Beech in 2015

Moreover, random effects at the plot level were not included in any case and the selection was likewise based on AIC.

2.6.1. Tree Level Models

For the ease of understanding, we wrote a global model of each hypothesis separately (Equations (8)–(11)), accounting for the random effects at each of the above explained level. Tree level random effect was considered only in the above-mentioned cases 1 and 2.

HI: Mixture of European beech and Norway spruce mitigates the negative impact of drought on growth per species.

In order to support our hypothesis HI, we devised the following global model Equation (8) for individual tree level.

$$R_{ij} = a_0 + a_1 * C_{ij} + a_2 * G_{ij} + b_i + b_{ij} + \varepsilon_{ij} \tag{8}$$

Index i represents the site level, index j represents the tree level. Parameter b_i and b_{ij} are the random effects at the site and tree level, respectively. ε_{ij} is the error term. R_{ij} is the resilience index under investigation, C_{ij} is the composition (categorical predictor variable coded as 0 for pure and 1 for mixture), G_{ij} is the individual tree basal area, a_0 and a_1 are the model estimates viz. intercept and slope, respectively. In the case where random effects at the tree level have not been included, index j and the corresponding random effect b_{ij} can be removed from the equation.

HII: Such a mitigation of impact through mixture is stronger under drier climatic conditions.

Equation (9) tests whether the mixing effect is modified by the betterment of the site conditions in terms of water supply and supports the Hypothesis II. Like Equation (8), the model equation explains the random effects at each level.

$$R_{ij} = a_0 + a_1 * C_{ij} + a_2 * M_i + a_3 * (C_{ij} * M_i) + a_4 * G_{ij} + b_i + b_{ij} + \varepsilon_{ij} \tag{9}$$

Index i represents the site level, index j represents the tree level. Parameter b_i and b_{ij} are the random effects at the site and tree level, respectively. ε_{ij} is the error term. R_{ij} is the resilience index under investigation, C_{ij} is the composition (categorical predictor variable coded as 0 for pure and 1 for mixture), additional covariable M_i is the de Martonne Index at the site level, G_{ij} is the individual tree basal area, a_0 and a_1 are the model estimates viz. intercept and slope, respectively. Like Equation (8), tree index j and the corresponding random effect b_{ij} can be removed from the Equation (9) if the tree level random effects have not been included.

2.6.2. Stand Level Models

We use the following stand level model equations.

HIII: Mixed stands have a lower growth loss under drought as compared to the weighted mean of monospecific stands.

After calculating the growth losses with Equation (7), Equation (10) was used to test whether there is a benefit incurred in terms of drought response by the mixture and if the mixture was incurred to lesser total relative volume growth loss than in the pure. Unlike Equations (8) and (9), the model Equation (10) for the stand explains random effects only at the site level.

$$L_i = a_0 + a_1 * C_i + b_i + \varepsilon_i \tag{10}$$

Index i represents the site level. Parameter b_i is the random effect at the site level. ε_i is the error term. L_i is the total relative volume growth loss due to drought year, C_i is the composition (categorical predictor variable coded as 0 for pure and 1 for mixture), a_0 and a_1 are the model estimates viz. intercept and slope, respectively.

HIV: Such a mitigation of growth loss through mixture is larger under drier climatic conditions.

Equation (11) tests whether the mixing effect is modified by the improving site conditions in terms of water supply.

$$L_i = a_0 + a_1 * C_i + a_2 * M_i + a_3 * (C_i * M_i) + b_i + \varepsilon_i \tag{11}$$

Index i represents the plot level. Parameter b_i is the random effect at the site level. ε_i is the error term. L_i is the total relative volume growth loss due to drought year, C_i is the composition (categorical predictor variable coded as 0 for pure and 1 for mixture), additional covariable M_i is the de Martonne Index at the plot level, a_0 and a_1 are the model estimates viz. intercept and slope, respectively.

Additionally, resilience per se and resistance at the stand level were also modelled using Equations (10) and (11).

Non-consideration of the Stand Density

We did not consider stand density (SDI) in our stand level models because stands are more or less homogeneous and also have similar density for each individual species across the sites. It also did not have any significant effect on the drought response. The effect of the SDI was checked by computing the analysis of variance on a fitted model, using "anova" function in R software. Additionally, AIC of the models with SDI was also counter-checked using the same approach as outlined in Section 2.6.

3. Results

3.1. Weather Conditions along the Gradient

The average of the de Martonne Index over all sites being considered was 37 mm $°C^{-1}$ in both drought years 2003 and 2015. In drought year 2003, mean temperature averaged over all sites was 9.04 °C. The mean total precipitation of all sites was 695 mm. During the first quarter (January to April) mean temperature over all sites was 2.16 °C and mean total precipitation was 166.6 mm. Within the growing season (May to September), mean temperature was 17.95 °C and mean total precipitation was 341.4 mm.

On the contrary, while the temperature in year 2015 was at 9.74 °C, the mean total precipitation in that year was at 729 mm. The first quarter of year 2015 was warmer viz. at 3.45 °C. During that time period, it was also more favorable in terms of precipitation than 2003, with a mean of 208.4 mm. The growing season of year 2015 was somewhat less warm than that of 2003, viz. at 16.8 °C with a more or less similar mean total precipitation of 352.8 mm. Drought 2015 year was hence markedly less dry than drought year 2003 and even somewhat warmer during the first quarter of the year. See Appendix A for the climatic conditions over the investigation sites.

3.2. Effect of Individual Tree Size on the Drought Response

Tree size had a negative effect on drought response (Table 4, Equations (8) and (9)). An increase from 5 to 10 cm in tree radius corresponded to a modelled decrease in resilience or resistance by 10%. That effect of tree size as a covariable was yielded for both the species, independent of their composition viz. beech (mixed + pure) and spruce (mixed + pure).

3.3. Drought Responses at the Tree Level

HI: Mixture of European beech and Norway spruce mitigates the negative impact of drought on growth per species.

Modelled with Equation (8) (Section 2.6.1), beech and spruce both in mixture and pure stand had a lower relative BAI as compared to the pre-drought growth in the year 2003. There was no benefit from mixture as the resistance values in mixed vs. pure stand of beech and also of spruce were almost similar (Table 4). Spruce thereby had a slightly lower resistance than beech (Figure 2). In contrast, beech in mixed vs. pure stand showed a lower post-drought growth (lower resilience) of −24% ($p < 0.1$) (Figure 2a). Post-drought growth of spruce was similar in both mixed and pure stand (Figure 2c).

However, beech both in mixed and pure stand showed no growth reduction in the drought year 2015. The BAI of beech in that year was even larger than the pre-drought growth levels (Figure 2b, no significant difference between mixed and pure). Growth of spruce in mixture was slightly higher than pre-drought growth (Figure 2d), while it was markedly lower in pure stand. Spruce notably benefited from mixture in terms of resistance. Its growth under drought was 24% higher ($p < 0.01$) in mixed vs. pure stands. Post-drought growth levels of beech in mixture and pure stand remained on the level of pre-drought growth, showing almost similar growth. The post drought growth of spruce was higher than the pre-drought growth (resilience > 1.0), with spruce in mixture showing 20% more ($p < 0.05$) post-drought growth (higher resilience) than in pure stand.

In summary, the drought response of both species being considered was related to mixture. However, both the significance of that relation and its extent depended on drought year and species . After the drought year 2003, beech benefited more in the pure stand. In the year of less severe drought (2015) and the subsequent post-drought, spruce was under benefit in mixture. A mitigating or accelerating effect of mixture was hence species-specific and moreover related to the particular characteristics of the drought year itself and of the two post-drought years. Such a mixture effect was obvious for spruce in the less severe drought year 2015 and over the two years that followed.

HII: Such a mitigation of impact through mixture is stronger under drier climatic conditions.

Resilience (Equation (9), Section 2.6.1) of beech in mixture after drought year 2003 increased under less favorable site conditions along the gradient (see Figure 3). On the contrary, in pure stand the resilience of beech decreased when climatic site conditions became drier (Table 4 under HII, Figure 3a). While the resilience of beech in mixed stand never exceeded the one in pure stands, the regression lines through resilience over site aridity intersect near the lowest de Martonne Index of 25 (Figure 3a). Thus, resilience of mixed beech stands might have become superior to that of pure ones at even drier sites in year 2003. Spruce resilience decreased in both mixed and pure stand as site conditions became less favorable along the climatic gradient. The resilience of the pure stand was close to that of the mixed one at any site aridity being observed (Figure 3a).

In contrast, after drought year 2015, the resilience of beech in mixed vs. pure stand decreased with decreasing site quality, while in case of spruce, it strongly increased (Figure 3b). The resilience of beech in pure stand was nearly the same at any value of aridity after that drought year. On the contrary, the resilience of spruce both in mixed stand and pure stand strongly increased when the site water supply decreased. An important thing to note here is a strong contrasting post-drought growth response of beech and spruce to increasing site aridity when in mixture. Thereby, after drought year 2003, beech seemed to be under benefit in mixed stands. Following drought year 2015, it was, however, spruce in mixture that stood under benefit.

The resistances of beech in mixture and pure stand in drought year 2003 were nearly identical under any value of site aridity being observed. They both decreased as the site quality became less favorable. Same was true for spruce in mixture and pure stand (Figure 3c). In the year 2015, the resistance of beech in mixture again decreased along the gradient towards lower aridity. In pure stand it somewhat increased. Spruce both in the mixture and pure improved in resistance as the site quality decreased. Here in 2015, the growth response especially of beech and spruce in the mixture was remarkably opposite. Spruce had a higher resistance on drier sites in mixture. Contrary was true for the beech in mixture, which had a comparatively lower resistance on drier sites (Figure 3d).

Thus, the effect that mixture had on resistance and resilience along the gradient of site moisture did not depend on the species alone, but notably on drought year and post-drought period being considered. Still, there was clearly a fostering effect of mixture for spruce under drier site conditions in drought year 2015 and its post-drought period.

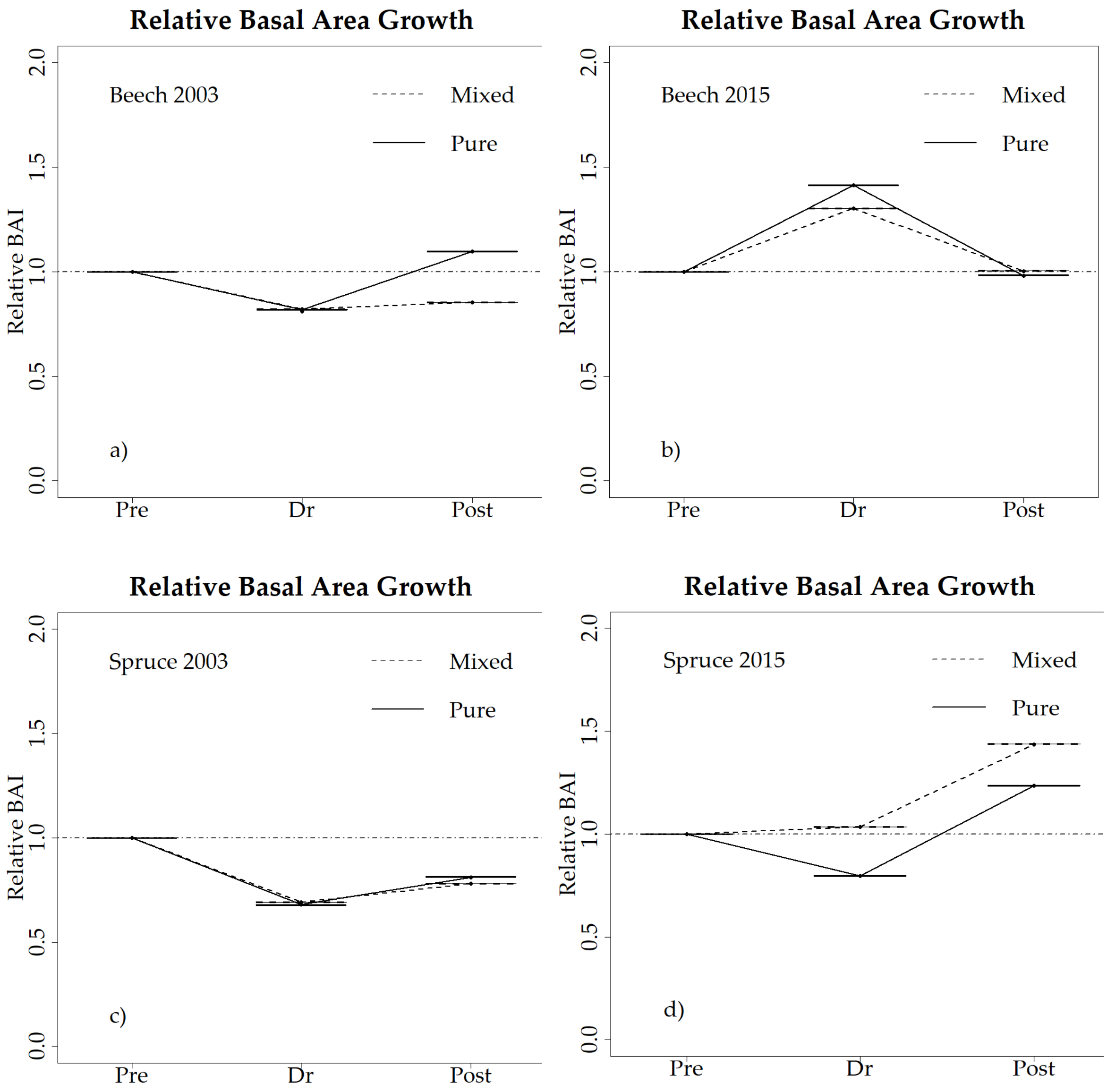

Figure 2. Output of the model Equation (8) showing tree level pre-drought, drought and post-drought growth responses of the beech (**a**,**b**) and spruce (**c**,**d**) in mixed vs. pure, in the two investigated drought years viz. 2003, 2015. The basal area (BA) for modelling in Equation (8) was chosen as a covariable for each species, regardless of the species composition. In the figure above, it has been held as a constant and set to the mean basal area per species in each drought year. Mean BA for beech in 2003 and 2015 was 0.063 m^2 and 0.090 m^2, respectively. Mean BA for spruce in 2003 and 2015 was 0.065 m^2 and 0.094 m^2, respectively. Pre-drought growth levels have been set to 1.0; growth relative to pre-drought is either below 1.0 (showing growth reduction) or above 1.0 (growth gain). N_{beech} (number of samples of beech) was 158 (mixed = 77, pure = 81); N_{spruce} (number of samples of spruce) was 146 (mixed = 71, pure = 75).

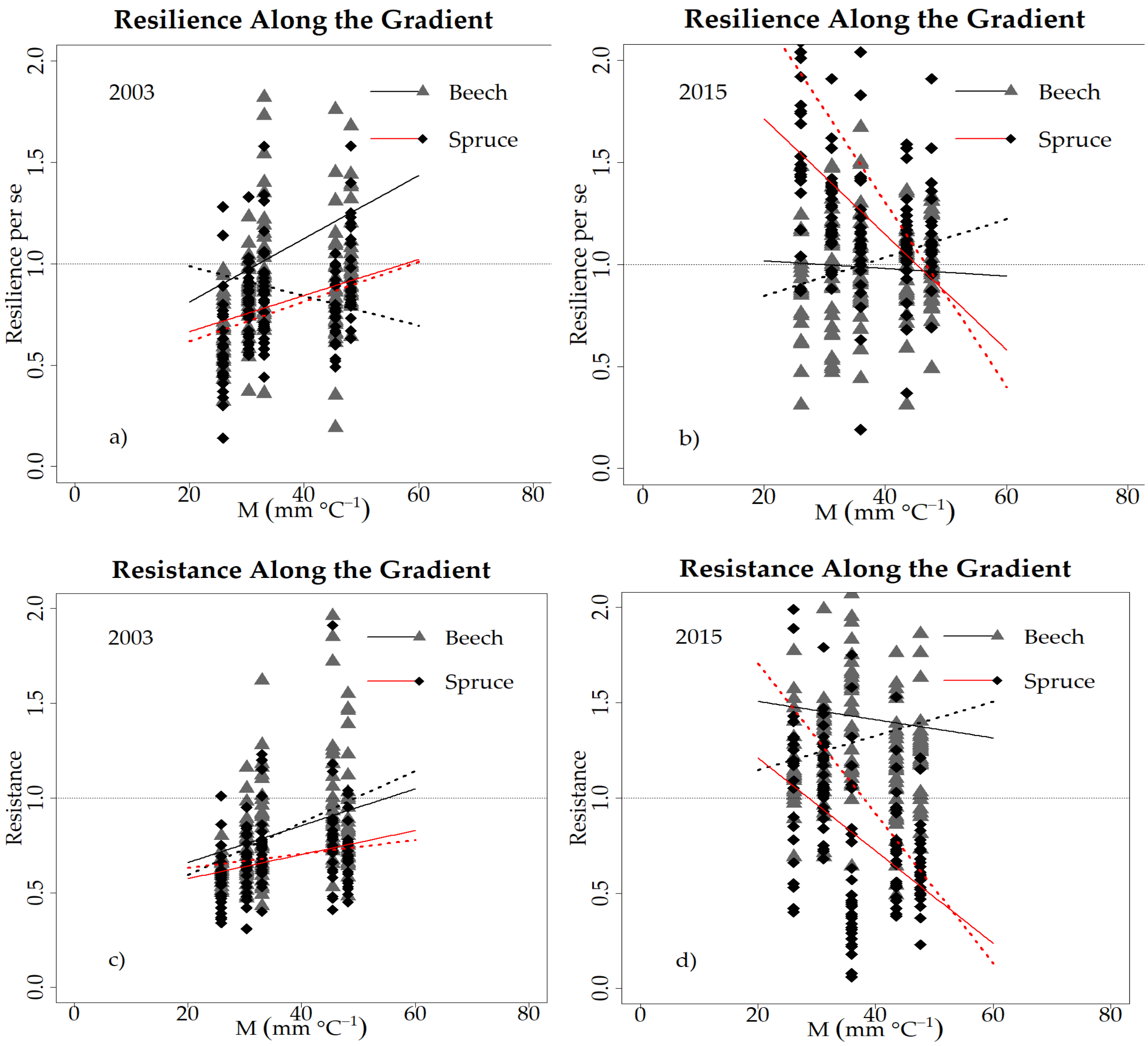

Figure 3. Tree level resilience indices along the ecological gradient (Equation (9)). Black lines indicate beech, red: spruce. Dotted lines represent the mixture. Figure 3(**a**,**b**) illustrate resilience per se in the year 2003 and 2015, respectively. Figure 3(**c**,**d**) illustrate the resistance in the respective drought events. M is the de Martonne Index and represents the sites' water supply along the gradient, in mm °C^{-1}. The basal area (BA) for modelling in Equation (9) was chosen as a covariable for each species, regardless of the species composition. In the figure above, it has been held as a constant and set to the mean basal area per species in each drought year. Mean BA for beech in 2003 and 2015 was 0.063 m^2 and 0.090 m^2, respectively. Mean BA for spruce in 2003 and 2015 was 0.065 m^2 and 0.094 m^2, respectively. N_{beech} (number of samples of beech) was 158 (mixed = 77, pure = 81); N_{spruce} (number of samples of spruce) was 146 (mixed = 71, pure = 75).

Table 4. Results of the Equations (8) and (9) referring to HI & HII, respectively (parameter estimates ± Standard Error (SE)). Estimates could be expressed in percentages as 1.0 = 100%. Estimate a_0 is the intercept and by default shows the resilience or the resistance of the trees in the pure stand. $a_0 + a_1$ show the resilience or the resistance of the trees in mixed stand; estimate a_1 is the effect of mixture, represented by Composition "C"; "G" represents the basal area; "M" represents the Martonne Index. Bold values mark significance at $p < 0.01$, $p < 0.05$ or $p < 0.1$, indicated by "**", "*" and ".", respectively. The effect of tree size as a covariable was yielded for both the species, independent of their composition viz. Beech (mixed + pure) and Spruce (mixed + pure). N_{beech} (number of samples of beech) was 158 (mixed = 77, pure = 81); N_{spruce} (number of samples of spruce) was 146 (mixed = 71, pure = 75).

Tree Level		**Beech**				**Spruce**			
Resilience		**2003**		**2015**		**2003**		**2015**	
HI									
		Value	SE	Value	SE	Value	SE	Value	SE
	a_0	**1.406** **	0.207	**1.034** **	0.055	**0.845** **	0.071	**1.440** **	0.208
C	a_1	**−0.244** .	0.131	0.021	0.053	−0.031	0.037	**0.202** *	0.095
G	a_2	**−4.934** *	2.270	−0.568	0.521	−0.508	0.562	**−2.179** *	1.058
HII									
	a_0	0.869	0.845	**1.094** **	0.188	**0.515** *	0.245	**2.502** *	0.682
C	a_1	0.635	0.606	−0.397	0.263	−0.066	0.156	**0.833** .	0.453
M	a_2	0.016	0.022	−0.002	0.005	0.009	0.006	−0.028	0.018
C*M	a_3	−0.023	0.015	0.011	0.007	0.001	0.004	−0.017	0.012
G	a_4	**−5.924** *	2.280	−0.438	0.523	−0.449	0.562	**−2.336** *	1.054
Resistance									
HI									
	a_0	**0.976** **	0.082	**1.493** **	0.113	**0.796** **	0.047	**1.177** **	0.185
C	a_1	0.003	0.053	−0.111	0.066	0.015	0.032	**0.240** **	0.106
G	a_2	**−2.527** **	0.749	−0.887	0.832	**−1.826** **	0.470	**−4.04** .	1.181
HII									
	a_0	**0.611** **	0.245	**1.66** **	0.497	**0.562** **	0.162	**2.078** **	0.545
C	a_1	−0.147	0.237	−0.635	0.385	0.110	0.133	0.798	0.509
M	a_2	0.010	0.006	−0.005	0.013	0.006	0.004	−0.024	0.014
C*M	a_3	0.004	0.006	0.014	0.010	−0.003	0.004	−0.015	0.013
G	a_4	**−2.339** **	0.755	−0.636	0.899	**−1.775** **	0.470	**−4.05** **	1.169

3.4. Drought Responses at the Stand Level

HIII: Mixed stands have a lower growth loss under drought as compared to the weighted mean of monospecific stands.

Due to drought year 2003, the weighted mean of both monospecific stands at the average of all sites incurred 31.6% volume growth loss (at $p < 0.01$, Equation (10), Section 2.6.2). The mixed stand differed very marginally in growth loss from the mean of the monospecific stands. It incurred almost the same growth losses, which were slightly less at 31%. In contrast to 2003, 2015 would be characterized by small growth gains in both mixed and monospecific stand (Figure 4b). There was a relative growth gain of 9.8% in the weighted mean of both pure stands. Growth gains of the mixed stand were not significantly different from those of the monospecific stands (4.6% smaller).

In summary, mixed stands in neither of the two drought years had any significant growth benefit.

HIV: Such a mitigation of growth loss through mixture is larger under drier climatic conditions.

The trend of growth losses along the gradient was not the same in the two drought years (Figure 4, Table 5; Equation (11), see Section 2.6.2).

In the year 2003, incurred growth losses, both in the mixed as well as the monospecific stands, were less severe at favorable site conditions and more severe under less favorable site conditions. On the contrary, in the year 2015 both mixed and monospecific stands were even subject to growth gains on the drier sites, with the monospecific stand being under slight benefit there. Growth losses thus were higher at higher site aridity in 2015 ($p < 0.05$) (Table 5).

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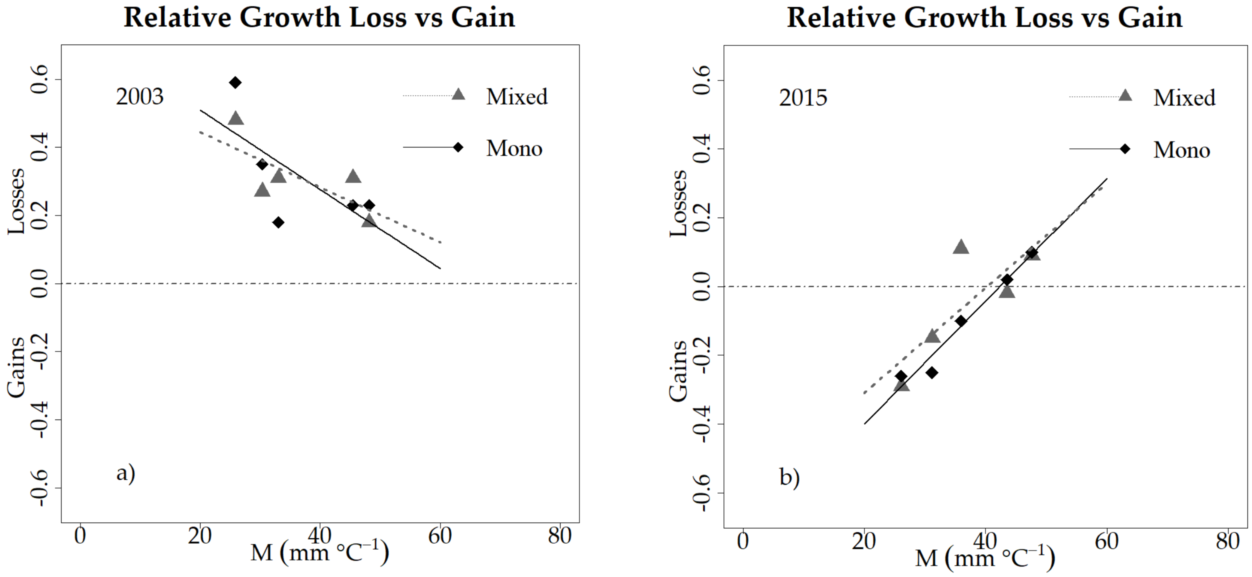

Figure 4. Relative stand volume growth losses along the gradient, modelled with Equation (11) (see Section 2.6.2) for the years 2003 (**a**) and 2015 (**b**). Pure Stand designates the weighted mean of both monospecific stands per site. Value of zero on the ordinate means no growth losses. Value above zero corresponds to growth losses. Value below zero shows growth gains in the year 2015, both by the total mixed stand as well as by the weighted mean of the monospecific stands. N_{mono} (number of observations of monospecific stands) = 5, N_{mixed} (number of observations of mixed stand = 5).

Summarizing, the incurred growth losses were clearly dependent on the drought year and the site conditions. However, the losses do not seem to be affected by the stand composition as both the monospecific and the mixed stands responded similarly to the drought years 2003 and 2015 and with only a marginal difference between the two, indicating that mixed stand was not really much under the benefit more than the pure stand, especially on the dry sites in 2015 where the stands had growth gains.

Table 6 shows a differentiated summary of whether a particular covariable had a positive or a negative effect on the growth response to drought.

Table 5. Resilience, resistance and drought Loss at the total stand level. HIII refers to the estimates of the Equation (10); HIV to the Equation (11) (see Section 2.6.2). Total growth losses around the drought years were determined by Equation (7) (1-RS + 1-RT; Section 2.5) and then modelled with the Equations (10) and (11). Resilience and resistance were also modelled using Equations (10) and (11). Estimate a_0 is the tested response variable for the weighted mean of the monospecific stands; a_1 or composition “C” is the estimate for the total mixed stand; $a_0 + a_1$ represent the resilience, resistance or growth loss in the mixed stand. Bold values mark significance at $p < 0.01$, $p < 0.05$ or $p < 0.1$, indicated by “**”, ”*” and “.”, respectively. Estimates could be expressed in percentages as: 1.0 = 100%. N_{mono} (number of observations of monospecific stands) = 5, N_{mixed} (number of observations of mixed stand = 5).

Stand Level		**Resilience**		**Resistance**		**Growth Loss**	
HIII							
		Value	SE	Value	SE	Value	SE
2003	a_0	**0.884** **	0.042	**0.800** **	0.030	**0.316** **	0.063
C	a_1	0.004	0.034	0.002	0.026	−0.006	0.047
2015	a_0	**1.058** **	0.039	**1.040** **	0.049	−0.098	0.074
C	a_1	0.010	0.022	−0.056	0.028	0.046	0.048
HIV							
2003	a_0	**0.64** *	0.171	**0.617** *	0.113	**0.74** *	0.224
C	a_1	0.107	0.156	0.029	0.126	−0.136	0.221
M	a_2	0.007	0.005	0.004	0.003	−0.011	0.006
C*M	a_3	−0.003	0.004	−0.001	0.003	0.004	0.006
2015	a_0	**1.315** **	0.150	**1.442** **	0.170	**−0.76** *	0.187
C	a_1	0.012	0.124	−0.155	0.146	0.143	0.260
M	a_2	−0.007	0.004	**−0.011 .**	0.005	**0.018** *	0.005
C*M	a_3	−0.000	0.003	0.003	0.004	−0.003	0.007

Table 6. A differentiated summary of the drought responses as per the model Equations (8)–(11), indicating what kind of effect the covariable had on the resilience, resistance or the growth loss (stand level). C stands for composition and indicates the trees in mixture at the tree level. C at the stand level represents total mixed stand. G stands for the basal area, M for the Martonne Index. Plus signs “++”, “+” and “+.” indicate the significantly positive effects at $p < 0.01$, 0.05 and 0.1, respectively. Negative signs “--”, “-” and “-.” indicate the significantly negative effects at $p < 0.01$, 0.05 and 0.1, respectively. N_{mono} (number of observations of monospecific stands) = 5, N_{mixed} (number of observations of mixed stand = 5).

	Tree Level				**Stand Level**		
	Beech		**Spruce**			**Mixed/Mono**	
Resilience	2003	2015	2003	2015	Resilience	2003	2015
Equation (8)					**Equation (10)**		
C	-.			+	C		
G	-			-	G		
Equation (9)					**Equation (11)**		
C				+.	C		
M					M		
C*M					C*M		
G	-			-			
Resistance					Resistance		
Equation (10)					**Equation (10)**		
C				++	C		
G	--		--	-.			
Equation (11)					**Equation (11)**		
C					C		
M					M		-.
C*M					C*M		
G	--		--	--			

Growth Losses	
Equation (10)	
C	
Equation (11)	
C	
M	+
C*M	

4. Discussion

4.1. Species-Specific Drought Response in Mixtures (HI)

Decreased level of precipitation and increased temperatures during severe droughts are mainly the cause of widespread tree mortality as well as growth reduction [67,68], altering the overall forest stand dynamics and energy balance [68]. Adjustment of a tree species to drought is mainly regulated by tree–environment interaction at the organ level viz. regulation of a tree's stomatal conductance. In this regard, trees exhibit isohydric and anisohydric behaviors. Under drought conditions, isohydric tree species would maintain the midday leaf-water potential above a certain threshold by closing their stomata and avoid risking hydraulic failure at the expense of carbon starvation. Anisohydric or risk-taking tree species have a varying leaf water potential (generally lower) and would continue to use water at the risk of hydraulic failure, eventually fixing more carbon than isohydric species [67,69,70].

Our findings reflect the general mechanism of isohydric and anisohydric behavior of spruce and beech, respectively. Beech in general and in monoculture had a higher drought resistance than spruce, reflecting its anisohydric behavior. The response, however, differed in mixture where its growth under drought was less than in monocultures, which was evident in 2015. Spruce, on the other hand, seems to have benefited in the mixture in 2015. This benefit can be attributed to: (1) hydraulic redistribution [71,72] from the deep soil to the shallow soil layer, incurring a growth benefit to the shallow-rooted spruce from the deep-rooted beech; (2) water pre-emption by the spruce before the vegetation period as spruce starts transpiring earlier than the beech while the latter is still leafless [25]. The latter also explains the lesser resistance of beech in the mixture. Post-drought growth responses of spruce for the year 2015 in the mixture were also higher than in pure, and contrary in the case of beech. Different growth responses to drought in 2003 and 2015 could be attributed to a better water availability during the first quarter (January-April) and summer (May-September) of 2015, which in total had higher precipitation than in 2003. Additionally, low resilience of spruce mixed and pure in the year 2003 could be explained by the "growth preconditioning" from the previous drought year [73]. Short- or long-term legacy effects on growth which may persist in the years following drought maybe caused due to hysteric stomatal conductance and previously limited synthesis of non-structural carbohydrates [74] such as starch, which further affects the biomass allocation, and also due to lower water reserves in the soil [75], thus affecting the recovery post-drought. Such legacy effects usually arise due to droughts in the late growing season [75]. If such effects persist over a period of time, whether short term (one year) or long term (more than one year), it establishes an "ecophysiological drought memory" [74] among the trees or stands. In a study by Breda et al. 2006 [76], lower starch content in the spring post-2003 was found to correlate to a large decline of tree twigs and branches in the crown of oaks. The limited synthesis of the non-structural carbohydrates, especially among the isohydric species, likely affect their resin formation and viscosity, altering the physical nature of resin defense against bark beetle attacks [77,78]. Any compositional or quantity change of resin monoterpenes, volatile organic compounds or alkaloids, which are involved in plants' defense [76,78], are also likely to indicate the stressed trees to the bark beetles, due to their olfactory sense [78]. Moreover, higher temperatures during a year might also decrease the generation time of the tree herbivores, leading to increased "voltinism" and eventually more severe outbreaks [77].

In our study, beech in 2003 in the pure stand somehow managed to recover better than the spruce in both mixture and pure. Apart from its anisohydric behavior, presence of vessel elements in the hardwood such as European beech might have allowed a better hydraulic conductivity than the softwood Norway spruce, which lack vessel elements [79].

Although the drought responses in the mixtures were species-specific, our findings partially support HI and are in accordance with the findings of Pretzsch et al. 2020 [25] of the Kranzberg rainfall exclusion experiment, who found spruce in its interspecific neighborhood to be overall more resistant than the spruce in the intraspecific neighborhood. On the contrary, beech acclimated better in its intraspecific neighborhood. In the same study, natural drought occurred in 2003 and 2015 and showed spruce to be 20%–50% less affected within their interspecific neighborhood. On the other hand, beech was 23% more affected in its interspecific neighborhood in terms of relative basal area growth. In another study by Goisser et al. 2016 [80], spruce was found to be 11% more resistant and 6% more resilient in the interspecific neighborhood in terms of stem diameter growth. In the same study, no significant differences were found for the beech but it was 10% less resistant and 1% less resilient than its intraspecific neighborhood.

4.2. Drought Response along an Ecological Gradient (HII)

Although some studies have reported a positive drought response with increasing water supply along the gradient for several species such as pine and oak [19], spruce, fir and beech [73], spruce, oak and beech [16] and Taiwan Pine in subtropical China [81]; others have reported findings in contradiction [5,26]. Moreover, studies from other geographical regions [82] suggested drier forests to be more adaptable to the future drought events than the wetter forests. Our findings using the statistical model Equation (9) revealed that the drought responses were not consistent along the gradient. Beech, for example in the pure stand, had an increasing trend of resilience and resistance along the ecological gradient in the year 2003. One reason for this could be relatively lower water deficits on wetter soils than drier soils, consequently higher soil water potentials which could be exploited by its deeper roots, contributing to an increasing drought resistance and post-drought growth viz. resilience [82].

Responses of species in mixtures in the year 2015 were opposite to each other along the gradient, with spruce being more resilient and resistant on the drier sites than on the wetter sites; contrary was true for the beech, indicating a reduced underground competition (or even facilitation) for the spruce in the mixture as per the “niche complementarity effect” [12,83,84] when water was the limiting factor. For example, when hydraulic redistribution occurs, which is more observable on the drier sites [30], it would benefit shallow rooting spruce. At the same time, spruce is also an interception for the beech on such sites. This interception additionally explains their opposite behavior. Moreover, higher resilience and resistance of spruce in the mixture on the drier sites indicate its acclimation potential for future drought events [30]. Furthermore, differing responses in the year 2003 and 2015, with the drought responses generally better in the latter on the drier sites, hint towards its ability to cope with a changing environment or its “phenotypic plasticity” [85,86].

Our findings for beech in the mixture are partially in accordance with that of Pretzsch et al. 2013 [16] who reported higher resilience and resistance in the mixtures of beech and oak which increased with the increasing water supply. No effect was found in the same study for the mixture of beech and spruce. Zang et al. 2014 [73] found Norway Spruce to be more resistant under the wetter climatic conditions than on the drier sites. Moreover, findings of Neuner et al. 2015 [26] indicate Norway Spruce in the mixed to be more adaptable to climate change in terms of their probability of survival, where they revealed a higher probability of survival of the species in the mixture under the less favorable conditions with lower precipitation and warmer temperatures.

Although the tree size has been positively associated with growth under normal conditions [87,88], responses might differ under drought conditions. Size heterogeneity may play an important role in the whole stand growth post-drought as the smaller trees recover faster [1] and have also been found to be more resilient and resistant than the larger trees [18]. Tree mortality around the globe due to drought conditions has been found to be higher in case of larger trees than that of smaller trees [89,90]. Large trees are reservoirs for half of the global forest carbon but at the same time, more vulnerable to drought [68,91].

For our analysis of the tree size we pooled the trees from the monoculture and mixed culture together in order to generalize the effect of individual tree size in terms of drought, independent of whether they stand in the mixture or pure. Our findings of the tree size's response to drought are in harmony with Serra-Maluquer et al. 2018 [18] and we report increasing drought resilience and resistance with the decreasing tree size and the behavior is consistent for both the species in both drought years. Post-drought growth responses were more pronounced for beech in general, where the decreasing basal area led to a more prominent post-drought growth viz. resilience, than spruce. Smaller tree size of spruce, however, contributed to a generally better resistance than the beech. The reason for larger trees to be more stressed under drought lies in their social position and inherent physiological response to drought due to their height as they are exposed to an elevated atmospheric water demand than the smaller trees [18], the latter being situated under canopy.

4.3. Relevance for Forest Management (HIII & HIV)

How mixed stands get over drought compared with mono-specific stands is most relevant for forest practice [2,15]. As Norway spruce is an economically very important species, its behavior in mixture compared with monospecific stands is of prior interest [92]. If Norway spruce grows similar or even better in mixed compared to monospecific stands under normal or stress conditions this paves the way to keep at least a certain portion of this valuable species even under climate change [25,30].

Recent studies showed that on the long term, mixed stands of Norway spruce and European beech can overyield mono-specific stands [13] and mixing may significantly reduce damages of spruce by bark beetle and storms [7,26]. Jactel et al. (2018) [93] and Liang et al. (2016) [94] found at least on average no significant underyielding of tree species in mixed versus monospecific stands. For forest practice, some percents of overyielding are not too relevant. However, it is important to know how Norway spruce comes off in mixture, e.g., with European beech under drought stress, which is expected to go up under the future climate [92].

Some studies [10,16,19,20] showed a tendency towards higher drought resistance in inter- compared with intra-specific neighborhoods, however other works by Forrester et al. 2016 & Grossiord 2014 [5,95] put this into perspective.

In our study, we found no significant differences between the growth losses of the mixed and monospecific stands, as the better drought response at the tree level (in case of spruce) in the mixture has not shown to be evident at the whole mixed stand level. Perhaps that drought response was balanced out due to beech in the mixture, as it did not perform better in the mixture than in the pure stand, especially in the year 2015, and also post-drought 2003.

Along the gradient, growth losses due to drought in 2003 decreased when sites became more wet for both the mixed and monospecific stands; they decreased on the contrary in 2015 as the sites became drier. Growth gains were thus prominent under 2015 on the drier sites for both the mixed and the monospecific stands, in line with the Stress Gradient Hypothesis [36].

The future unforeseen drought events might be different in their characteristics like the drought years 2003 and 2015. On one hand, the year 2015 had seen relatively lesser precipitation during the mid of the growing season in July (see Figure A1), it had provided better growing conditions in the spring, which was of growth benefit during the start of the tree-ring formation. It also benefited the post-drought growth as the conditions were relatively better during the end of the growing season as compared to 2003. Trees and stands in the drought year 2003, on the other hand, received much less precipitation during the start of the growing season and the growing season itself was relatively dry. Post-drought growing conditions seemed to be affected by the lesser precipitation in the year itself and also during the end of the growing season, affecting the endogenous properties within the tree bodies (as explained in Section 4.1).

If drought years like 2003, however, become more frequent and overlap with each other, this might have a long-lasting effect on the growth in terms of short- or long-term legacy, thus affecting the forest productivity outside the drought years as well. In short, ecological carbon balances would be negative and forests might not be sustainable [74]. Although 2015 was comparatively drier than

2003, it does not mean that such years would not negatively affect the growth of the forests in the future as our results along the gradient indicated differing responses for each species at tree level; as one species benefited on the drier sites, the other did not and it was clearly dependent on the mixture. Growth gains such as in 2015 at the stand level on drier sites might be evident due to one species in the mixture or the pure, but it could still be detrimental for the other species existing in the either of the stands, for example on the drier sites. Such droughts could also have a negative impact on the carbon balance by affecting the tree-ring cell formation within the growing season itself, and drought legacy effects might persist in the following years. This would also affect the stability of the forest productivity in the long run due to the varying growth behaviors of the trees and the stands, responding to the varying climatic conditions each different year and within the year itself.

4.4. Comparison between the Findings at the Tree and the Stand Level

The findings at the tree level reveal the biological responses to the external climate which affect the annual tree ring formation by triggering the inner-lying physiological responses. The width of the tree ring on one hand tells about the growth reduction of an individual in a mixture or a monospecific stand, on the other hand, it may not be assumed as the response of the whole stand to drought as the whole population has not been taken into account. As a result, the growth losses or "yield losses" per hectare cannot be quantified. Our tree level findings report some positive drought responses in the mixture but it was not evident in the whole mixed stand. Growth losses in the mixed stand in the year 2003 were more or less the same (0.6% lesser) as in the monospecific stands; resistance and resilience also being similar. In the year 2015, the monospecific stands were subject to even lesser growth losses (non-significant, −4.6% than that of mixed stands). They were also 5.6% more resistant in the same drought year. Resilience however, was marginally higher in the total mixed stand by 1% in the year 2015. If the mixing effect was not additive [96–98], it was not multiplicative either since the results hardly showed any pronounced evidence of the species interaction at the whole stand level under drought.

4.5. Methodological Considerations

Tree diameter or basal area growth when plotted over age follows a unimodal course [99]. So, when the indices by Lloret at al. (2011) [21] are calculated for drought stress at different ages, they will yield different results, even if the drought stress is similar.

For example, when calculated for years in the increasing part of the curve, the resilience will be generally higher then when calculated for the decreasing phase simply due to the different trend of the curve. If all trees or stands included in an evaluation have the same age and the considered drought years occur at the same tree age, the quantification of Lloret indices viz. resilience, resistance and recovery might be useful, as the bias is always the same and a group comparison between control and stressed trees will yield meaningful results even without detrending [25].

However, in this evaluation we included trees and stands of a broader age span from 55–100 years and considered different drought years which may occur at different tree ages. Therefore, elimination of any age-related growth trends prior to the analyses was crucial.

We did not consider stand density in our stand level models because stands are more or less homogeneous and also have similar density for each individual species across the sites. It also did not have any significant effect on the drought response.

5. Conclusions

Our tree level finding, on one hand, gave us a hint of how the specific individuals within a forest ecosystem could respond to the future changing climatic conditions. Positive mixing effects at the stand level were, however, not pronounced. Even then, the findings at the stand level are important since mixed stands provide other pivotal properties for various ecosystem services, such as aboveground mechanical stability against windthrows and storms, richer biodiversity, protective functions and belowground stability due to diverse root systems. Therefore, it is important to know whether mixed stands might be superior in terms of drought sensitivity of growth and carbon fixation. Our study shows just small differences between the mixed and the pure stand, as the dependency lies on varying site conditions and the scenario of drought, as well as tree size distribution because size matters. Moreover, up to date in our knowledge, this is the second study which tries to quantify the whole stand level drought response; the first one being Thurm et al. 2016 [20]. However, this is the first time we relate the tree level drought response to the whole stand level response of the spruce-beech triplets and pave a way for future research in the topic, as frequency of drought years is expected to increase. Site acclimation and plants' morphological plasticity is more likely to contribute in adaptation to the changing climate and they both need more research. More studies about the suitable species' provenances will help to better comprehend the alternatives for future forest management.

Author Contributions: S.R. wrote and structured the manuscript, analyzed the data, interpreted and discussed the results. W.P. proofread the manuscript, contributed to text in methods and results, and provided consultation in the data analysis. M.H. provided methodological as well as technical guidance in the stand level evaluation and provided his consultation through the process. H.P. initiated the study, conceptualized the study design and provided consultation. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare that they have no conflict of interest.

Appendix A

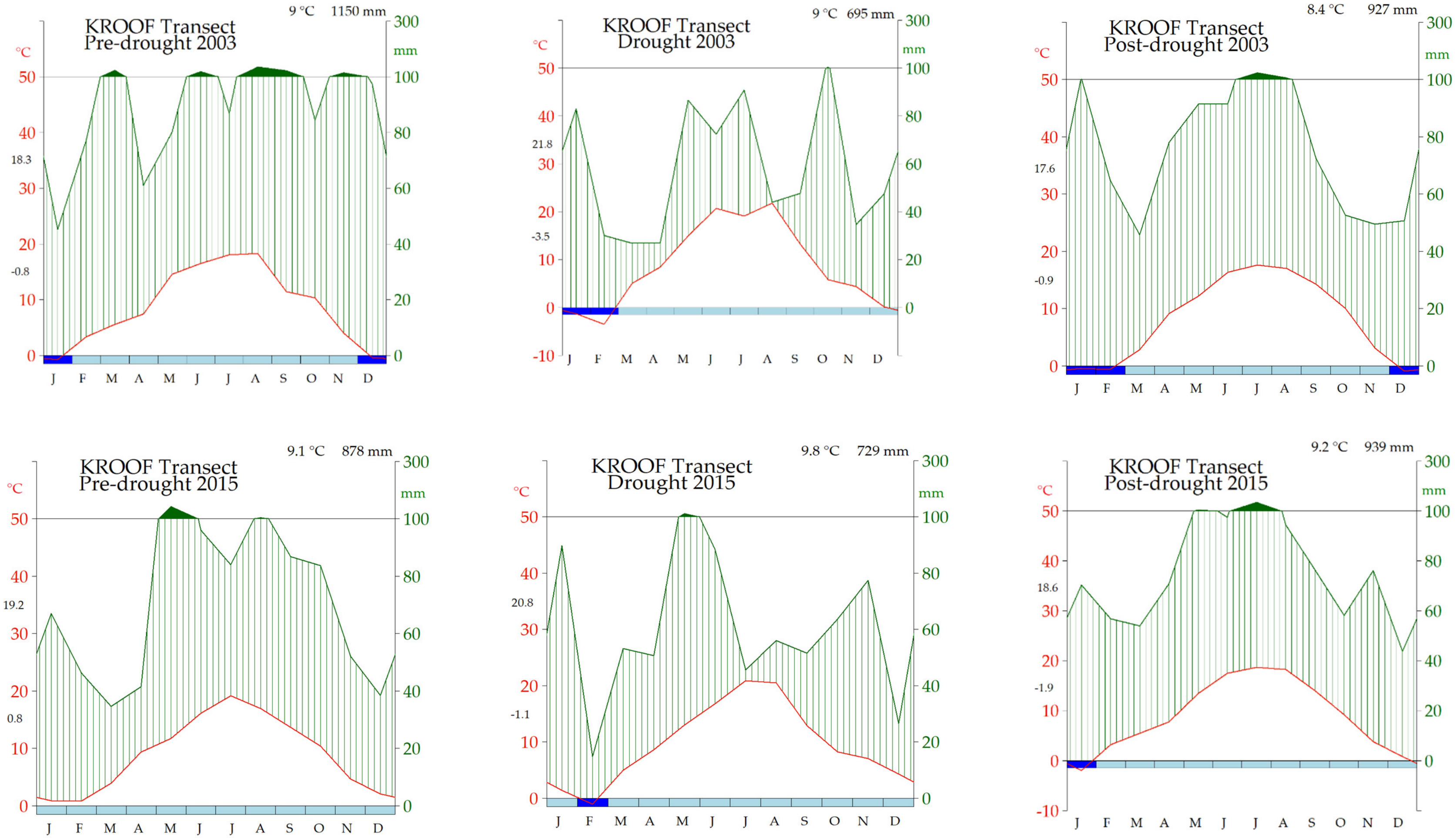

Figure A1. Pre-drought, drought and post-drought climatic conditions shown here as the monthly mean temperature (°C) and the monthly mean precipitation (mm), on the five investigation sites. Climate Diagram after Walter & Lieth 1967 [100], plotted using the R-package "climatol" [101]. Values on top right show monthly mean temperature, and total mean precipitation, for all the five sites. The values in black along the ordinates show the mean maximum and mean minimum temperature in that particular period/year.

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