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Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability

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Abstract

The future performance of native tree species under climate change conditions is frequently discussed, since increasingly severe and more frequent drought events are expected to become a major risk for forest ecosystems. To improve our understanding of the drought tolerance of the three common European temperate forest tree species Norway spruce, silver fir and common beech, we tested the influence of climate and tree-specific traits on the inter and intrasite variability in drought responses of these species. Basal area increment data from a large tree-ring network in Southern Germany and Alpine Austria along a climatic cline from warm-dry to cool-wet conditions were used to calculate indices of tolerance to drought events and their variability at the level of individual trees and populations. General patterns of tolerance indicated a high vulnerability of Norway spruce in comparison to fir and beech and a strong influence of bioclimatic conditions on drought response for all species. On the level of individual trees, low-growth rates prior to drought events, high competitive status and low age favored resilience in growth response to drought. Consequently, drought events led to heterogeneous and variable response patterns in forests stands. These findings may support the idea of deliberately using spontaneous selection and adaption effects as a passive strategy of forest management under climate change conditions, especially a strong directional selection for more tolerant individuals when frequency and intensity of summer droughts will increase in the course of global climate change.

Keywords: climatic extremes, common beech, intrasite variability, Norway spruce, populations, resilience, silver fir, tree ring

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Introduction

With the human influence on climate becoming increasingly apparent (IPCC, 2013), the consequences of altered temperature and precipitation regimes for trees and thus for forest ecosystems are vividly discussed. In Europe, the rise in mean annual temperature by already more than 1.1 °C compared to the preindustrial average exceeds the global mean increase of 0.78 °C (IPCC, 2007, 2013). At the same time, the average length of summer heat waves over Western Europe has doubled and the frequency of hot days has almost tripled (EEA, 2012). In forests, drought is a major constraint to plant growth and productivity, as it is for most terrestrial plant communities (e.g. Churkina & Running, 1998; Luyssaert *et al*., 2010). The direct consequences of drought and secondary damages for forests range from losses in productivity and increased mortality rates on stand level to regional forest die-offs covering several million hectares (Ciais *et al*., 2005; Allen *et al*., 2010). Accordingly, increasing frequency and intensity of summer drought is generally understood as one of the major challenges for forest ecosystems associated with anthropogenic climate change (Bolte *et al*., 2009; Lindner *et al*., 2010).

Uncertainties due to climatic risks have always affected forestry decisions. However, the projected changes, which will exceed past variability (Luterbacher *et al*., 2004) and frequency of extremes (Schär *et al*., 2004; IPCC, 2013) by far, challenge current heuristics of forest management and call for integrative concepts. A core element of any alternative management strategy is the profound knowledge about the tree species' responses to altered climatic conditions (Bolte *et al*., 2009). One of the most prominent approaches toward

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assessing the future potential of a species are studies on its retrospective performance, in terms of growth, mortality and reproduction (Bolte *et al.*, 2009).

Dendroecological studies usually rely on a strong common growth signal of a population of trees, which is achieved by averaging the individual trees' series of radial increment growth to a chronology (Fritts, 1976). This procedure removes large parts of tree-specific variability in increment growth stemming from differences in social class (Martin-Benito *et al.*, 2008; Zang *et al.*, 2012), age (Carrer & Urbinati, 2004; Dorado Liñán *et al.*, 2011), genotype, and other factors that are comparably hard to quantitate, such as microsite differences and small-scale exogenous and endogenous disturbance pulses (Cook, 1990). Consequently, the large body of tree-ring studies on growth response to increasing temperatures and drought episodes predominantly promotes insights about general, population-wide responses, but less so about the bandwidth of responses of individual trees in terms of intrasite variability. Typically, biogeographical patterns of drought responses are revealed by chronology-based studies, and their intersite variability is mainly explained by macro-climate and local modifications of large-scale drought events (e.g., Huang *et al.*, 2010; Zang *et al.*, 2011; Subedi & Sharma, 2013).

More recently, the bandwidth of responses within populations has gained increasing interest with the demonstration of adaptive climatic differentiation among individuals of the same population (Jump & Penuelas, 2005; Jump *et al.*, 2006; Eveno *et al.*, 2008; Sthultz *et al.*, 2009). With selection pressures on populations altered by rapid climate change, more frequent drought episodes will favor directional selection for drought-resistance (Hoffmann & Sgrò, 2011), especially since intrapopulation variability in the response to climate has been connected to different water use strategies on the level of individuals (Morán-López *et al.*, 2014). In this context, the distribution of different response types within a population sample can give further insight regarding the adaptability of a local population, and is – additionally to the information about the averaged, species-specific response – of pivotal interest for assessing a species' adaptability in general.

Tree growth can be a first estimate for the selection for drought adapted species and genotypes. The growth decline in response to drought is generally used as a measure for the loss in vitality (Dobbertin, 2005), with prolonged, drought-induced episodes of reduced growth increasing mortality (Bigler *et al.*, 2004, 2006, 2007). The potential consequences of a directional selection process are complex, and include declines in general plant fitness through loss of chromosomal diversity (Jump & Penuelas, 2005), or adverse effects due to variations in the susceptibility to other climate extremes (Reusch *et al.*, 2005) and perturbations (Sthultz *et al.*, 2009). Furthermore, provenance studies have frequently identified higher drought tolerance in trees to be associated with lower relative growth rates (Rose *et al.*, 2009; Taeger *et al.*, 2013). This is confirmed by the generally lower growth rates at the warm and dry margins of the species' distributions (Loehle, 1998), where populations are directionally selected for drought tolerance. Fast growing trees within a population reveal a higher susceptibility to drought stress (Morán-López *et al.*, 2014). Since most provenance studies focus on populations as a whole, the current knowledge about the relationship of drought tolerance and growth rates within populations is rather limited.

In Europe, three of the major temperate forest tree species are Norway spruce [*Picea abies* (H.) Karst.], silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.). The isohydric Norway spruce belongs to the economically most important and widest distributed species in Europe and has repeatedly been described as particularly vulnerable to drought (Zang *et al.*, 2011, 2012; Pretzsch *et al.*, 2013; Boden *et al.*, 2014). In contrast, the more anisohydric common beech as the most abundant broad-leaved forest tree in Central Europe (Dittmar *et al.*, 2003) is characterized as more drought-resistant than spruce (Zang *et al.*, 2011; Pretzsch *et al.*, 2013). In direct comparison with Norway spruce, silver fir is described as considerably less vulnerable to drought stress (Becker, 1989; Desplanque *et al.*, 1999; Kölling, 2007; Bouriaud & Popa, 2009), and therefore discussed as a possible alternative for spruce under changing climate conditions (Zang *et al.*, 2011).

This study assesses the variability in tolerance of tree growth against drought events using a comprehensive dendroecological investigation comprising 1760 trees from 86 sites in Southern Germany and Austria. We aim to improve our understanding of the drought tolerance of the three major European temperate forest tree species spruce, fir and beech based on past drought events at multiple sites on a climate cline and to analyze more specifically how variability on the individual level contributes to the tolerance of populations. The data set used in this study is compiled aiming at reducing the variability among the individual trees at a site stemming from site differences and small-scale disturbance pulses. This allows for testing the hypotheses that (i) climate and species drive general patterns in drought tolerance; (ii) drought events amplify the regular variability in growth responses to climate; (iii) individuals with higher drought tolerance are characterized by specific traits, such as smaller relative growth.

Material and methods

Tree-ring data

We used a comprehensive tree ring data set from Southern Germany and Austria (Table S1, Hartl-Meier *et al.*, 2014a,b; Zang *et al.*, 2011), consisting of 1760 trees (750 Norway spruce, 460 silver fir, 550 common beech) from 86 sites. The study area covers the region 47–51°N and 9–15°E, and includes lower mountain ranges as well as Alpine sites. An overview of the sampling locations is given in Fig. 1.

At each site, we selected ten healthy (co)dominant trees per species (hereafter termed population sample) for coring. To reduce variability due to small-scale differences in site conditions, we sampled only in areas where we could either assume approximately homogenous soil conditions throughout, or where we could confirm, following standardized procedures, uniform substrate by repeated soil coring to at least 1 m in depth followed by *in situ* assessment of soil texture. We cored each tree twice at 1.3 m breast height in opposite directions using 5 mm increment borers (Haglöf, Sweden; Suunto, Finland). Using LINTAB series 5 and 6 measuring tables and the TSAP-Win software package (all Rinntech, Heidelberg, Germany), ring widths were measured to the nearest 0.01 mm on each core. We checked cross-dating accuracy both visually and statistically using program COFECHA (Holmes, 1983). The two series of tree-ring widths from one tree were averaged and transformed to basal area increment (BAI) according to Biondi & Qeadan (2008). Lacking a complete record of diameter at breast height, the total basal area for a tree (BA) was approximated as the sum of its annual BAIs.

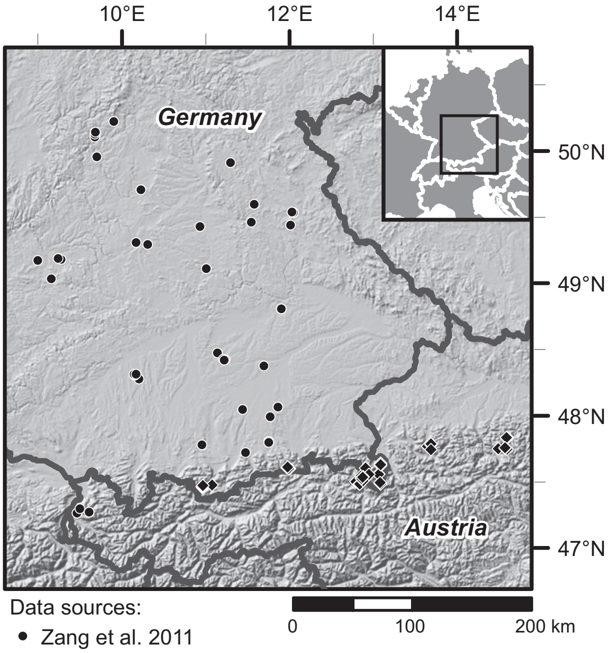

Fig. 1 Map of the investigation area comprising southern Germany and the Alpine area of Austria. The points on the map show the sites where tree-ring data was collected and correspond to the site codes in Table S1.

The tree-ring data were characterized on the level of population samples in terms of mean series length (MSL), expressed population signal (EPS), mean interseries correlation (Rbar), mean sensitivity (MS), and mean BAI (MBAI). EPS, Rbar, and MS were computed for the common time span of 1940–2008 based on raw tree-ring widths, while MBAI was calculated from the BAI series for fixed tree ages of 30–60 years. For each tree, the individual tree age was approximated as the number of rings counted in direction from pith to bark. Real tree age is (partly) underestimated since the pith of the tree was not reached by all cores and the age at which trees reach breast height is varying.

Climatic data

We used temperature and precipitation data from the observational CRU TS 3.2 worldwide data set available on a 0.5° grid (Mitchell & Jones, 2005). Monthly mean temperatures and monthly precipitation sums are available from 1901 and have been aggregated to seasonal means and sums, respectively, corresponding to the summer months of June, July, and August (JJA). Site-specific time series of temperature and precipitation have been constructed by interpolation of the four nearest grid points using inverse distance weighting (Shepard, 1968). The quality of this interpolation from gridded data could be validated for 45 sites using station data and for 39 sites using the HISTALP data set (Auer *et al.*, 2007, see supporting methods M1).

June, July, and August mean temperature and precipitation are highly negatively correlated across the sites for the time span 1939–2008 ($r = -0.88$), indicating that the sampling took place along a distinct climatic gradient from warm and dry to cool and wet. To simplify further climate-related analyses, JJA temperature, and precipitation along the gradient were aggregated into the De Martonne aridity-humidity index (DMI-JJA, De Martonne, 1926) by calculating precipitation sum (in cm)/(temperature (in °C) + 10). The climatic gradient is then characterized by 70 year long-term means (1939–2008) of DMI-JJA. Note that DMI-JJA values increase from warm-dry to cool-wet conditions. Characterization of drought conditions was validated by the SPEI drought index (Standardized Precipitation and Evapotranspiration Index) using CRU, HISTALP, and local climate station data (see next paragraph).

Tree tolerance

Ratios of growth in drought years to growth during reference periods can be used to describe the impact of these events and the subsequent recovery (Fekedulegn *et al.*, 2003; Zang *et al.*, 2011). Lloret *et al.* (2011) presented a unified framework of tolerance components to describe those growth responses. Here, we used the tolerance components resistance (Rt, the ratio between growth during drought and growth prior to drought), recovery (Rc, the ability to recover relative to the growth reduction experienced during drought) and resilience

(Rs, the after-drought ability to reach performance levels observed prior to drought). All three measures were calculated based on the individual BAI series, namely BAI during drought (Dr), BAI in the respective predrought period (PreDr), and BAI in the respective postdrought period (PostDr) (Figure S2, Lloret *et al.*, 2011) as:

$$\text{Rt} = \text{Dr}/\text{PreDr}$$

$$\text{Rc} = \text{PostDr}/\text{Dr}$$

$$\text{Rs} = \text{PostDr}/\text{PreDr}$$

A three-year period was chosen for both PreDr and PostDr reference (Pretzsch *et al.*, 2013). We selected the pan-European drought years of 1947, 1976, and 2003 with extremely dry summers based on the current literature (Beniston, 2004; Fink *et al.*, 2004; Vautard *et al.*, 2007) as Dr, and pooled the respective tolerance indices for further analyses except for testing ontogenetic effects (see below). Drought conditions were confirmed at all sites for the chosen years using the Standardized Precipitation and Evapotranspiration Index SPEI (Vicente-Serrano *et al.*, 2010; see Figure S1 and Data S1). For characterization of the climate cline, we preferred DMI to SPEI, because due to its standardization the SPEI yields meaningless values close to zero for long-term means. Using common drought years across different sites has the advantage that conditions before and after the drought events are similar, which is crucial for the comparison of tolerance indices. This would not necessarily be the case when, e.g. the driest years on each site were chosen (Martínez-Vilalta *et al.*, 2012).

To assess the general climatic influence on tree tolerance, population sample means of the individual tolerance components were regressed against DMI-JJA using linear regression.

The relationship between the three tolerance components Rt, Rc, and Rs and the predictors PreDr, BA, and tree age at the level of individual trees were tested with linear mixed effects models. We chose a linear mixed effects approach, because the incorporation of random site effects allows interpreting the fixed effect model parameters regardless of a possible large-scale gradient across the investigation area due to climatic differences. Furthermore, we formulated the models with the maximal random effects structure justified by the sampling design to optimize their generalization performance (Barr *et al.*, 2013). We used the site as grouping variable and obtained the general model structure.

$$\begin{aligned}\tilde{T}_{ij} = \beta_0 + \beta_1 \times \text{PreDr}_{ij} + \beta_2 \times \text{BA}_{ij} + \beta_3 \times \text{age}_{ij} + u_{0j} \\ + u_{1j} \times \text{PreDr}_{ij} + u_{2j} + \text{BA}_{ij} + u_{3j} \times \text{age}_{ij} + \varepsilon_{ij}\end{aligned}$$

where $\tilde{T}_{ij}$ is the vector containing a tolerance index (Rt, Rc, or Rs) for tree i and site j, $\beta_0 \ldots\ldots, \beta_3$ are fixed effects associated with the standardized tree-level covariates PreDr, BA and age, $u_{0\text{j}\ldots}u_{3\text{j}}$ denote the random population sample effects associated with the intercept and PreDr, BA and age slopes, and ε_{ij} corresponds to the residuals. The intercept was kept in the model despite standardized variables, since standardization is carried out globally and not on the level of individual population samples.

The influence of PreDr on PostDr was investigated using simpler linear mixed effects models of the form

$$\text{Po}\tilde{\text{s}}\text{tDr}_{ij} = \beta_0 + \beta_1 \times \text{PreDr}_{ij} + u_{0j} \times u_{1j} \times \text{PreDr}_{ij} + \varepsilon_{ij}$$

with fixed effects $\beta_0 \ldots\ldots \beta_1$ and random effects $u_{0\text{j}} \ldots u_{1\text{j}}$ A model with the same mixed effects structure was used to identify a possible relation between tree age and BA.

Assessment of variability in growth response

The variability in growth response to severe drought was assessed using the coefficient of variation (CV) of the individual tree tolerance indices. Since for non-log-normally distributed data the CV does not necessarily correspond to the inequality of the distribution as indicated by e.g. the Gini coefficient (Bendel *et al.*, 1989), all tolerance indices for the individual population samples were tested for log-normality using the Shapiro–Wilk test for normality on the log-transformed data. All distributions displayed log-normal or nearly log-normal distributions at the level of individual population samples, and the close relation of CV to the Gini coefficient of inequality was further approved by their close correlation across all population samples ($r = 0.99$, $P < 0.001$).

Since differently aged stands were assembled in this study, with older stands prominently sampled in higher altitudes and thus under relatively more favorable climatic conditions in severe drought years (Table S1), effects of ontogeny on the CV of tolerance indices might mask the effects of regional climate characteristics. Accordingly, the frequent coincidence of older stands and higher altitudes prevented from testing the influence of tree age on the CV by using MSL as factor. To assess a potential ontogenetic bias, we calculated the CV of tolerance indices separately for each drought year. Thus mean tree ages differed by 27 years (between the events of 2003 and 1976), 29 years (between 1976 and 1947), and 56 years (between 2003 and 1947), respectively.

Two different baselines for assessing the variability in tolerance metrics were established: one to compare the individual within-population variability in drought response to the respective background variability (i.e. comparing variability during drought events to variability under average conditions), and a second one to compare the within-population variability to a between-population baseline, i.e. the variability expected when taking all population samples into account.

For the first case, the baseline variability was computed by resampling ($n = 1000$) three random years as Dr for the calculation of tolerance indices and respective CV values for all population samples. Paired (according to populations) one-sided Wilcoxon signed rank test were used to globally test the set of all CV of the tolerance indices for the original three drought years for differences from the corresponding medians of all 1000 intrapopulation baseline CV.

For the second case, we used the relationship between geographical distance and CV of tolerance indices. We randomly selected each ten trees across all population samples of a species, calculated the CV of the tolerance indices and recorded their respective mean geographic distance. For each tolerance index, a distance-CV-relation was constructed on 1000 random samples of ten trees. The effect of mean geographic distance on CV of the tolerance indices was tested using linear regression on the distance-CV-relations, and proved in all cases to be positive and significant at the $P < 0.05$ level (an example is given in Figure S4). The expected variability in a given tolerance index for an average population sample was then derived from the linear fit on the respective distance-CV-relation and its parametric 95% prediction interval for the mean distance of 20 m, assumed to represent a good approximation of the mean distance of the trees in a population sample at a given site.

Linear regression models were used to test for relationships between the CV of the tolerance indices of the individual population samples and DMI-JJA. All computations were performed using R version 3.0.1 (R Development Core Team, 2013) with packages *lme4* (Bates *et al.*, 2014), *lmerTest* (Kuznetsova *et al.*, 2013), *reldist* (Handcock, 2011) and *dplR* (Bunn *et al.*, 2013).

Results

General characteristics of tree-ring data

Mean chronology length was 129 years (spruce 122, fir 131, beech 135), with MSL increasing with altitude (Table S1). The overall quality of the chronologies was high, with a mean EPS of 0.90 (spruce 0.89, fir 0.88, beech 0.93), and 82% of all chronologies reaching the critical value of 0.85 (Wigley *et al.*, 1984) (spruce 79%, fir 74%, beech 95%). Chronologies below the 0.85 threshold were not excluded from further analyses, since our analyses focus on three drought years and their preceding/subsequent years, and the dating of these years was assumed to be accurate due to the generally negative deflection of growth associated with these years.

DMI-JJA and altitude were strongly positively correlated ($r = 0.78$, $P < 0.001$), i.e. colder and wetter summers were expected at higher altitudes. For all species, EPS decreased significantly with increasing DMI-JJA, with the weakest relation observed for spruce (spruce: $r = -0.33$, $P = 0.003$; fir: $r = -0.60$, $P < 0.001$; beech: $r = -0.59$, $P < 0.001$). MBAI decreased with DMI-JJA for all species, with the strongest decrease depicted by beech (spruce: $r = -0.50$; fir: $r = -0.48$; beech: $r = -0.53$; all $P < 0.001$). Spruce and fir showed a strong decrease in MS with increasing DMI-JJA (spruce: $r = -0.80$; fir: $r = -0.90$; both $P < 0.001$), while there was no effect of DMI-JJA on MS for beech ($r = 0.00$). No significant correlation between tree age and BA could be observed for fir ($r = 0.03$) and beech ($r = -0.09$), for spruce a significant positive correlation could be detected ($r = 0.31$, $P < 0.001$).

Drought tolerance in relationship with climate

Indices of tolerance to extreme drought events showed clear and consistent relationships to summer climate for Rt and Rc on the population sample level (Fig. 2). For all species, Rt decreased toward the warm and dry end of the gradient (positive correlation with DMI-JJA), with the strongest relation observed for spruce. Since only very few population samples of spruce displayed Rt values above 1.0, a consistent growth decline associated with summer drought was observed, regardless of the regional climatic conditions. For fir and beech, a few population samples displayed Rt values above 1.0, indicating a relative growth increase under summer drought. Population samples with Rt values above 1.0 were distributed rather evenly over the climatic gradient for the latter two species (Fig. 2).

The relation of summer climate and Rc was inverted, with higher Rc values observed toward the warm and dry end of the gradient (Fig. 2). This indicated a quick recovery from the more severe effects in Rt by a relatively faster growth rate after the drought event. The majority of population samples displayed Rc values above 1.0. This means, that only a few population samples displayed progressing growth decline after the drought event.

We did not find a significant correlation of Rs and DMI-JJA for fir and beech, whereas spruce depicted a relatively strong positive correlation of Rs and DMI-JJA implying long-lasting drought effects at the warm-drier end of the gradient (Fig. 2).

A direct comparison of the species along the climatic gradient (Fig. 3) showed generally higher Rt and Rs in silver fir in comparison to Norway spruce and common beech. Spruce consistently showed lower Rt and higher Rc than beech and fir. Furthermore, spruce had the smallest Rs at the warm and dry end of the gradient.

PreDr and PostDr growth were highly positively correlated for all species, with fixed effects estimates of 0.90 for spruce, 0.81 for fir, and 0.88 for beech (all $P < 0.001$). The different components of tolerance were surprisingly differently controlled by PreDr, BA and tree age (Table 1). The strongest influence on Rt was exerted by PreDr in all species, resulting in throughout negative correlations between Rt and PreDr. In spruce and fir, age had no influence on Rt, while BA had a positive effect on Rt, resulting in higher Rt for larger trees. For beech, BA also had a positive effect on Rt, while age had a negative effect, leading to smaller Rt for older trees. In spruce and fir, Rc was predominantly controlled by age, with older trees showing smaller Rc. In beech, age was also negatively associated with Rc, but equally strong effects were exerted by PreDr (negative) and BA (positive). Consequently, this led to an influence of all three parameters on Rs, with PreDr displaying the strongest effect in all species, resulting in trees with low predrought growth rates exhibiting

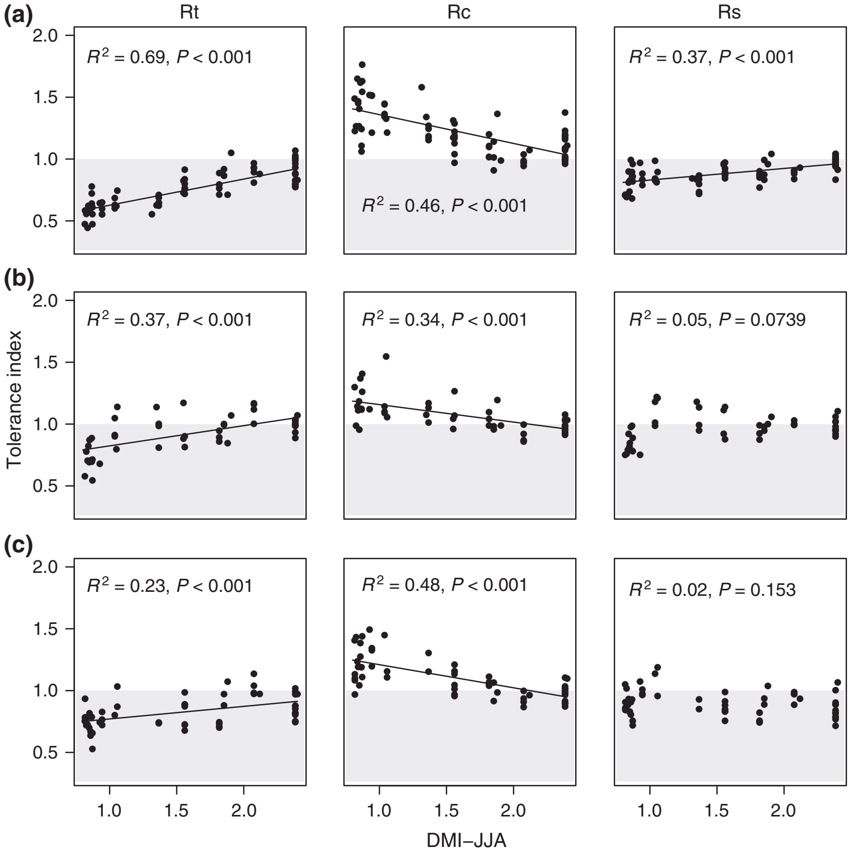

Fig. 2 Correlation of the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) in spruce (a), fir (b), and beech (c) on population sample level with DMI-JJA. Coefficients of determination and significance values correspond to the respective linear model fits. The light gray area represents a relative growth decline (index values < 1).

higher Rs. BA was positively, and age was negatively associated with Rs in all species (Table 1).

Intrapopulation variability in drought years vs. background variability

For all species, the variability in Rt, Rc, and Rs in drought years was significantly higher than the background variability calculated by random selection of event years from the same population samples ($P < 0.05$ in all cases, Fig. 4). The strongest increase from background variability to variability under severe drought conditions was depicted by beech and the weakest increase was found for Rs of spruce.

In spruce and fir, MS, as an integrative measure over all series of a population sample, could explain the variability in the tolerance metrics under drought conditions quite well (Table 2).

Since the study employed differently aged stands, we also tested for systematic ontogenetic effects on the variability in tolerance metrics using the individual drought years separately. Due to the lack of consistent differences in the coefficient of variation in tolerance indices (CV) related to increasing mean tree age (Figure S3), we can discard a potential ontogenetic effect on CV at the population level.

Climatic drivers of variability in tolerance

For spruce and fir, DMI-JJA could explain the variability in tolerance indices at the population sample level (Fig. 5). The variability in all tolerance indices increased with warmer and drier conditions. For beech, only the variability in Rc showed a weak negative correlation with increasing DMI-JJA (Fig. 5).

Relation to expected variability

Most population samples displayed intrapopulation variabilities in tolerance metrics inside the prediction interval for the expected variability based on the intraspecific range (Fig. 5). This means that only few populations displayed either higher or lower variability

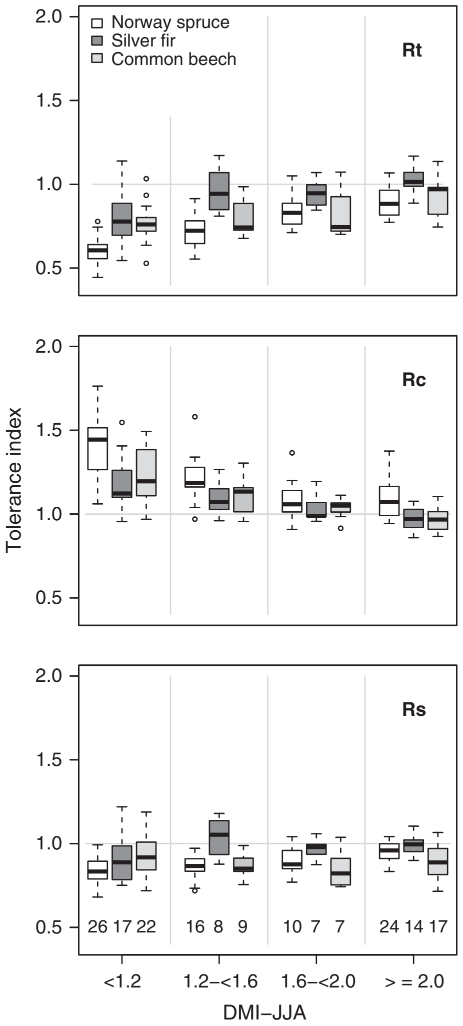

Fig. 3 Comparison of the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) in spruce, fir, and beech along the climatic gradient characterized by DMI-JJA. The numbers under the boxes in the lowest panel indicate the number of observations in each group.

than would be expected from treating the whole data set as one population.

Higher than expected variability occurred only at the warm and dry end of the gradient, most prominently for Rs of fir (Fig. 5), but also for the other tolerance indices of spruce and fir. In beech, higher than expected variability was not observed for Rt and Rc, and only one population showed higher than expected variability in Rs (Fig. 5).

Discussion

Chronology characteristics

Observed reduced mean sensitivity (MS) at wet-cool summer conditions (higher DMI-JJA) for spruce and fir points at decreasing climatic constraints on the year-to-year variability in tree growth (Fritts, 1976). In cool-wet summers, non-climatic factors contribute stronger to year-to-year variability in tree growth, and the common growth signal of the population samples (EPS) is reduced. A decrease in MS with altitude (and thus climatic constraints) in closed stands of Norway spruce and silver fir was also observed by Dittmar *et al.* (2012) in Southern Germany. This is in contrast to well-established relationships between MS and altitude as the basis for climate reconstruction from tree rings where sensitivity and climate signal strength increases with altitude. However, our findings were retrieved at sites from lowlands to below the tree line.

Table 1 Parameters for fixed effects ($\beta_1 \ldots, \beta_3$) in the linear mixed effects models relating tolerance indices resistance (Rt), recovery (Rc) and resilience (Rs) to predrought growth level (PreDr), basal area (BA), and tree age. Reported are the parameter values and the significance of the fixed effects (coded as: *** for $P < 0.001$, **for $P < 0.01$, and *for $P < 0.05$) for the species-wise models (sample size for spruce was 750, 460 for fir, and 550 for beech)

Species	Fixed effects	Rt	Rc	Rs
Norway spruce	PreDr	−0.35***	−0.11	−0.74***
	Age	0.05	−0.50***	−0.44***
	BA	0.29***	0.11	0.66***
Silver fir	PreDr	−0.33***	−0.21*	−0.50***
	Age	0.00	−0.55***	−0.27*
	BA	0.16**	0.19*	0.31***
Common beech	PreDr	−0.48***	−0.36***	−0.92***
	Age	−0.25**	−0.37***	-0.64***
	BA	0.29**	0.29**	0.60***

Species-specific tolerance to drought

All three species compared in this study displayed strong relations between resistance and recovery (tolerance indices Rt and Rc) and summer climate (Fig. 2). The strongest relation was found for Rt in spruce, with a particularly large part of the variance explained by the climatic gradient. In all species, Rt and Rc behaved reciprocal and low Rt values were generally linked to higher Rc values. This resulted in a relatively weak climatic differentiation of the integrating factor of resilience (Rs) in silver fir and common beech (Fig. 3), while for Norway spruce, Rs still followed the climatic gradient notably well (Fig. 2). Most spruce population samples showed a prolonged growth reduction after the three drought years of 1947, 1976, and 2003 as indicated by low Rs (Fig. 2). This confirms the rating of Norway spruce as a particularly drought intolerant species as previously indicated by complementary approaches,

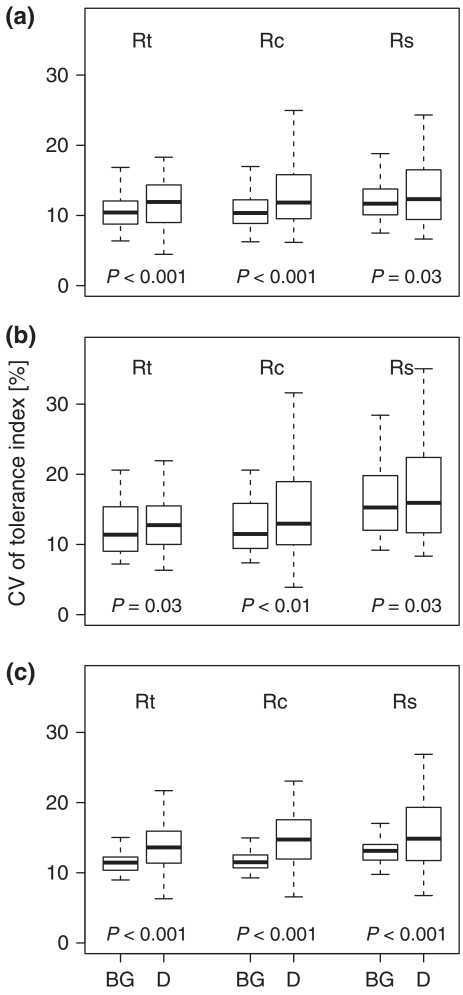

Fig. 4 Comparison of intrapopulation background variability (BG) with variability in drought years 1947, 1976, and 2003 (D) for resistance (Rt), recovery (Rc), and resilience (Rs) in spruce (a, sample size $n = 75$ for all groups), fir (b, $n = 46$), and beech (c, $n = 55$). Significance levels correspond to one-sided paired Wilcoxon signed rank tests.

such as climatic envelopes (Kölling, 2007), simulation studies (Pretzsch & Dursky, 2002), ecophysiological studies (Cochard, 1992), and other dendroecological assessments (Kahle & Spiecker, 1996; Mäkinen *et al.*, 2002; Pretzsch *et al.*, 2013).

The even distribution of resilience (Rs) along the climatic gradient in fir and beech (Fig. 2) indicates full recoveries from the initial impact of drought independent from general climate conditions. Following Galiano *et al.* (2011), a strong growth reduction (in terms of a low Rt) which was also observed toward the warm and dry end of the climatic gradient for the majority of fir and beech populations, is only compensated if Rc is not exclusively dependent on stored carbon reserves, but profits from rebuilt photosynthetic tissue.

Table 2 Summary of the linear regression models relating the variability in tolerance indices resistance (CV of Rt), recovery (CV of Rc), and resilience (CV of Rs) to the chronology characteristic mean sensitivity (MS) (see text for explanation). Reported are the coefficients of determination (R^2, numeric), and the significance of the ordinary least squares regression (coded as: ***for $P < 0.001$, **for $P < 0.01$, and *for $P < 0.05$) for the species-wise models (sample size was 75 for spruce, 46 for fir, and 55 for beech). All correlations between CV and MS are negative

Species		CV of Rt	CV of Rc	CV of Rs
Norway spruce	MS	0.32***	0.42***	0.36***
Silver fir	MS	0.34***	0.41***	0.37***
Common beech	MS	0.01	0.01	0.01

The different response patterns of spruce and beech along the climatic gradient (Fig. 3) agree with the findings of Pretzsch *et al.* (2013). According to literature, the isohydric spruce reduces water consumption and growth already in an early stage of drought stress through stomata closure (Dobson *et al.*, 1990; Maier-Maercker, 1998), a strategy that avoids damages and allows for a relatively quick recovery. However, our study suggests, that due to resilience varying with site, spruce is only competitive with beech at the cooler and wetter half of the climatic gradient. This insufficient recovery in stem growth from drought stress can be explained by a strong preconditioning of growth through previous-year climate (Zang *et al.*, 2011) and changes in the root-shoot allometry as a direct response to dry conditions (Nikolova *et al.*, 2011). In contrast, the more anisohydric beech maintains a higher stomatal conductivity throughout the drought period, and can thus continue to grow for longer. This strategy risks the hydraulic integrity of the xylem, e.g. by xylem embolism (Geßler *et al.*, 2007). Considerable investments of assimilates into the restoration of the conducting pathway result in slow recovery rates after-drought stress (Pretzsch *et al.*, 2013).

In comparison to spruce and beech, fir generally showed high values of resistance (Rt) and resilience (Rs) across the whole climatic gradient (Fig. 3). This is well consistent with the findings of Elling *et al.* (2009) that healthy fir trees (i.e. especially those not damaged by SO_2 immissions) show a remarkably good drought-resistance in Central Europe.

Aside from increasing severity of drought, there might also be a genetic differentiation along the climatic gradient. Modrzyński & Eriksson (2002) found local adaptation to drought in Norway spruce from southern Poland in terms of earlier bud set and higher root biomass in high-elevational individuals. This is interpreted as a relative advantage of high-elevation

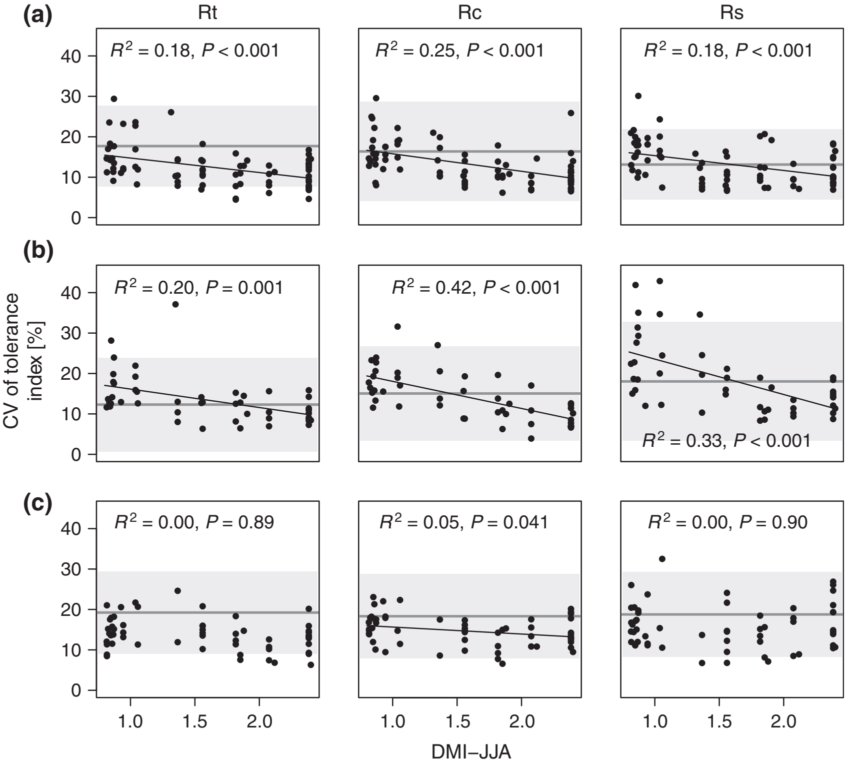

Fig. 5 Correlation of variability in tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) in spruce (a), fir (b), and beech (c) with DMI-JJA. Coefficients of determination and significance values correspond to the respective linear model fits. The dark gray line corresponds to the expected CV at a distance of 20 m, the area shaded in light gray signifies its parametric prediction interval.

ecotypes, when drought conditions will intensify with climate change. On the other hand, King *et al.* (2013) found strong evidence for gene flow in Norway spruce along an altitudinal gradient, possibly counteracting local adaption.

Variability in drought response at the population level

Literature suggests that increasing climatic stress will increase the common climatic signal in tree growth, thus EPS, since the contributions of nonclimatic effects on tree growth are reduced (Fritts, 1976). This rationale is the basis of climate reconstruction using tree-ring proxy data. Also, provenance trials indicate that variation in response pattern with genetics is smaller under generally less favorable conditions (Modrzyński & Eriksson, 2002; Taeger *et al.*, 2013).

However, our study for the first time revealed that we cannot conclude from patterns of climate sensitivity under less favorable climate conditions to patterns in extreme years, since different mechanisms apply when climatic extremes are considered: instead of a more uniform response of the whole population, we found a significant increase in variability in within-population drought responses (Fig. 4). Since variability and inequality were highly correlated at the level of population samples (see Material and methods section), a higher variability in drought responses is linked to a more unequal distribution of the responses. Our finding that the more severe a drought extreme is, the more variability in response can be expected at the population sample level was also confirmed by the comparison along the climatic gradient (Fig. 5). Here, the variability in all tolerance indices (spruce and fir) or Rs (beech) at the population sample level significantly increased from favorable to less favorable conditions. This is consistent with the observation that during low-growth episodes, the inequality in size-increment is increased within stands (Metsaranta & Lieffers, 2008). In addition, this is indicated by a change from size-asymmetric to size-symmetric competition under drought stress (Zang *et al.*, 2012), leading to the development of distinct size hierarchies in the long run (Metsaranta & Lieffers, 2008).

The comparison of observed vs. expected (horizontal lines in Fig. 5) individual level variability for the population samples showed a remarkable and significant increase in variability for some populations of spruce and fir at the warm and dry end of the climatic gradient. Consequently, the observed high resilience of fir under these conditions must stem from some extremely well performing trees that outweigh other, poorly performing trees in the population samples. This is supported by the observation that during low-growth episodes the increased inequality in size-increment is caused by a few, extraordinarily fast growing individuals (Metsaranta & Lieffers, 2008).

For all species and sites, growth rates prior and after-drought events were highly positively correlated. Thus, effects of disturbance or mortality of neighbor trees on observed tree tolerance should be of minor importance. Lloret *et al.* (2011) interpret such a correlation as an effect of robustness: trees that are more robust due to microsite conditions and intrinsic factors (physiological state, genetics) are able to perform better after stress periods.

Variability in drought response at the individual level

At the level of individuals, we found a considerable relationship between high tolerance against drought and low-growth rates prior to drought (Table 1). While high growth rates are intuitively associated with benefits for the fitness of trees, Bigler & Veblen (2009) showed decreased longevity of conifers connected to increased early growth rates. Martínez-Vilalta *et al.* (2012) found a link between high growth rates prior to drought and high-drought susceptibility. This is interpreted as a reduced investment in defense, and structural disadvantages such as decreased root-shoot ratio or decreased mechanical stability. Bigler & Veblen (2009) also confirm this relationship for different tree ages. Equally in our study, the average growth rate for the first 30 years of each trees' life is a similarly good predictor for tolerance to drought as the growth immediately preceding the drought event (PreDr, $P < 0.001$ for all species, data not shown). Higher PreDr growth rates can therefore be interpreted in terms of structural maladaptation to extreme drought.

The sole focus on above-ground stem growth is an important shortcoming of the tolerance indices used. Since relatively low above-ground growth rates could also be due to an increased root to shoot allocation ratio, smaller above-ground growth could consequently be linked to improved water uptake and the possibility to shut down photosynthesis later (Comeau & Kimmins, 1989; Nikolova *et al.*, 2011; Pretzsch *et al.*, 2012). Our finding of lower growth rates being associated with increased resistance to drought events is further confirmed by provenance studies, where highly drought-resistant origins show reduced above-ground growth rates (Rose *et al.*, 2009; Taeger *et al.*, 2013).

Although we sampled only (co)dominant trees, tree size had a positive effect on all tolerance indices, with the strongest influence on Rt and Rs (Table 1). Dominant trees are more likely to compete successfully for resources, such as water. These findings are well consistent with studies on Norway spruce, that demonstrate smaller growth reductions in drought years of dominant trees as compared to suppressed ones (van den Brakel & Visser, 1996; Zang *et al.*, 2012).

Recovery from drought events also depended on tree age, however, opposite to the effect of tree size described above. Younger trees recovered better and thus showed higher resilience to drought. The literature on ontogenetic changes in climate sensitivity is ambiguous, pointing at either no consistent change across age classes (Carrer & Urbinati, 2004; Esper *et al.*, 2008), or at a declining sensitivity with increasing tree age (Szeicz & MacDonald, 1995; Rozas *et al.*, 2009). However, most of the studies relating tree age to climate sensitivity focus on long-term growth-climate relationships, but not on climatic extremes. For drought extremes, a higher tree age has been associated to lower resilience in the growth response (Martínez-Vilalta *et al.*, 2012). In the case of drought, decreasing resistance with age can be interpreted as a decreasing capability to compensate for the loss in reserves due to reduced photosynthetic capacity (Yoder *et al.*, 1994) or ontogenetic changes in root structural traits (Rozas *et al.*, 2009).

Implications for ecosystem management

The unequivocally lower drought tolerance of Norway spruce, especially at the warm-dry end of the climatic gradient suggests a rethinking of this species' suitability in future forests, especially where climate and soil conditions reinforce extreme drought episodes in the future (Boden *et al.*, 2014). Drought events amplify the regular diversity in growth responses to climate, and lead to more heterogeneous and variable response patterns in forests stands. Despite the careful sampling design, we cannot exclude microsite effects on individual tree growth interacting with possible genetic traits. But generally, trees with a (genetically or microsite derived) predisposition to lower above-ground growth rates could in the long-term be favored by directional selection under aggravating summer droughts. This is also supported by recent findings on the coupling of growth and drought susceptibility of forest trees in the Mediterranean (Martínez-Vilalta *et al.*, 2012; Morán-López *et al.*, 2014). On the other hand, rising temperatures, higher atmospheric CO_2 concentrations, and increasing availability of nutrients through atmospheric deposition have led to accelerated tree growth during the 20th century in Europe (Spiecker, 1999). As indicated by our results, this trend may favor structural maladaptation to drought-induced physiological stress, and can therefore contribute to the destabilization of forest stands under climate change by lowering the resilience of growth response to drought events. Consequently, whether the idea of deliberately using spontaneous selection and adaption effects as a passive strategy in forest management (Bolte *et al*., 2009) is supported by the strong diversity in drought response at the population level can only be decided after further investigations. A special focus on the interaction between microsite and genetic influence on the linkage between age, growth rate and resilience of tree growth to drought and other important facets of performance under drought such as regeneration and mortality on individual and population level is of primary importance in this regard.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Validation of interpolated climate data against station data and the HISTALP data set.
Data S2. Verification of drought conditions at the sampled sites.
Figure S1. SPEI values for all sites, calculated from gridded SPEI data and from local station data and the HISTALP data set.
Figure S2. Response to drought characterized by growth in the periods before the drought event, during, and after the drought event.
Figure S3. Testing for ontogenetic effects on variability in tolerance indices.
Figure S4. Exemplary distance-CV-relation for the mean geographic distance of 10 randomly selected trees and the CV for a tolerance index.
Table S1. Location and elevation for all sampling sites, and characteristics of tree-ring chronologies for the sampled species.