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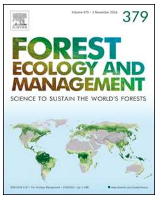

Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect

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ABSTRACT

Tree species mixing has been widely promoted as a promising silvicultural tool for reducing drought stress. However, so far only a limited number of species combinations have been studied in detail, revealing inconsistent results. In this study, we analysed the effect of mixing Scots pine and oak (pedunculate oak and sessile oak) trees on their drought response along a comprehensive ecological gradient across Europe. The objective was to improve our knowledge of general drought response patterns of two fundamental European tree species in mixed versus monospecific stands. We focused on three null hypotheses: (*HI*) tree drought response does not differ between Scots pine and oak, (*HII*) tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture) and (*HIII*) tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions. To test the hypotheses, we analysed increment cores of Scots pine and oak, sampled in mixed and monospecific stands, covering a wide range of site conditions.

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We investigated *resistance* (the ability to maintain growth levels during drought), *recovery* (the ability to restore a level of growth after drought) and *resilience* (the capacity to recover to pre-drought growth levels), involving site-specific drought events that occurred between 1976 and 2015. In monocultures, oak showed a higher resistance and resilience than Scots pine, while recovery was lower. Scots pine in mixed stands exhibited a higher resistance, but also a lower recovery compared with Scots pine in monocultures. Mixing increased the resistance and resilience of oak. Ecological factors such as tree size, site water supply and site fertility were found to have significant effects on the drought response. In the case of Scots pine, resistance was increased by tree size, while recovery was lowered. Resistance of oak increased with site water supply. The observed mixing effect on the tree drought response of Scots pine and oak was in some cases modified by the site conditions studied. Positive mixing effects in terms of resistance and resilience of oak increased with site water supply, while the opposite was found regarding recovery. In contrast, site fertility lessened the positive mixing effect on the resistance of Scots pine. We hypothesise that the observed positive mixing effects under drought mainly result from water- and/or light-related species interactions that improve resource availability and uptake according to temporal and spatial variations in environmental conditions.

1. Introduction

Climate change is characterised by increased temperatures and modified precipitation patterns (Schär et al., 2004; Della-Marta et al., 2007; Jacob et al., 2014). Correspondingly, extreme climate events, such as severe droughts, have increased in frequency and intensity, a trend that is predicted to continue in the future (IPCC, 2014). Drought is a particular challenge for forest managers, as it may affect a multitude of ecosystem responses from the molecular, through organ and individual, to the stand level, thereby altering forest ecosystem dynamics (Floret et al., 1990; Chaves et al., 2003; Bréda et al., 2006; Rennenberg et al., 2006; Hamanishi and Campbell, 2011). Drought occurs under low levels of available water, caused by reduced precipitation and/or increased atmospheric evaporative demand combined with low available soil water (Wilhite, 1993). Under drought, trees may reduce stomatal conductance and photosynthesis, and experience carbon starvation (Irvine et al., 1998; McDowell et al., 2008), modified tree allometry (Pretzsch et al., 2012b), enhanced fine root mortality (Deans, 1979; Gaul et al., 2008) or increased defoliation (Carnicer et al., 2011; Poyatos et al., 2013). Possible effects include decreased tree and stand growth (Chaves et al., 2003; Leuzinger et al., 2005; Hartmann, 2011), a higher susceptibility to biotic and abiotic agents (Allen et al., 2010; Griess and Knoke, 2011; Schlesinger et al., 2016) and, ultimately, even tree die-off and mortality (McDowell et al., 2008). The large extent of drought and heat-induced mortality currently observed, pays witness to a global vulnerability of trees and forests to climate change (Allen et al., 2010).

Droughts, such as those reported for the years 1976, 2003 and 2015 throughout Europe (Bréda et al., 2006; Rebetez et al., 2006; Ionita et al., 2017), have had a detrimental effect on tree and stand growth and show that the natural adaptive ability may be overstrained by sudden changes in growing conditions. Growth responses of trees to drought may depend on intrinsic factors, such as species (Zang et al., 2011; Eilmann and Rigling, 2012; Anderegg and HilleRisLambers, 2016; Thurm et al., 2016; Vitasse et al., 2019), provenance (Taeger et al., 2013), competitive status (Zang et al., 2012), age (Thurm et al., 2016) and size (Jucker et al., 2014; Bennett et al., 2015; Serra-Maluquer et al., 2018); as well as extrinsic factors, such as biome type (Vicente-Serrano et al., 2013; Grossiord et al., 2014; Gazol et al., 2017), altitude (Marqués et al., 2016), soil conditions (Thurm et al., 2016), prevalent climatic conditions (Pasho et al., 2011; Dorman et al., 2013; Lévesque et al., 2014; Clark et al., 2016; Gazol et al., 2017), seasonality of the endured drought event (Merlin et al., 2015; Toigo et al., 2015), stand functional diversity (Gazol and Camarero, 2016), stand competition (Dorman et al., 2015; Thurm et al., 2016) and species mixing (Grossiord, 2018).

The mixture of tree species, i.e. the increase in tree species diversity, has been widely proposed as an effective silvicultural tool to counteract the adverse impacts of droughts on tree growth and vitality, thereby stabilising forest ecosystems (Kelty, 1992; Lüpke et al., 2004; Knoke et al., 2008). Empirical evidence suggests that species mixing can improve resource utilisation within stands, thereby reducing tree climate sensitivity (Thurm et al., 2016), as well as stabilising (Pretzsch, 2005; del Río et al., 2017) and increasing stand productivity (Zhang et al., 2012; Pretzsch, 2017). In this light, the conversion of traditional coniferous monocultures into mixed stands of coniferous and broadleaved species has been widely promoted in European forest policy and management (Klimo, 2000; Zerbe, 2002; Kint et al., 2006; Knoke et al., 2008).

Positive mixing effects are commonly explained by the complementary effect hypothesis, according to which complementarity between species can be either caused by reduced competition or facilitation (Ammer, 2019). Complementarity effects depend on the environmental context, which affects the availability of the target resource over space and time. According to the conceptual framework by Forrester (2014), complementarity effects are expected to increase when the mixing of tree species improves the availability, uptake or use efficiency of the limiting resource. Under rich growing conditions (i.e., high nutrient and water availability), where competition for light increases due to larger leaf areas, light related interactions may be more relevant than under poor growing conditions, where the limiting factor is rather related to soil conditions. The influence of average site conditions on mixing effects has often been described by the stress gradient hypothesis, which states that the effect of facilitation is more pronounced on sites with stressful growing conditions, whereas under benign conditions, the effect of competition dominates (Bertness and Callaway, 1994). Complementarity is also expected to be present under temporal changes in environmental conditions, such as during annual drought (Pretzsch et al., 2012a; del Rio et al., 2014; Thurm et al., 2016), when the mixing of tree species with differing ecological traits and resistance behaviours may mitigate negative growth effects.

Despite a rapidly growing interest from the scientific community and a clear trend towards implementing mixed forest management (Knoke et al., 2008; Messier et al., 2013), the effect of tree species diversity on the drought responses of trees and stands is still under debate. A recent review by Grossiord (2018) showed that positive, negative or neutral effects occur, depending on tree species and ecosystems. This inconsistency across studies may be explained by the often limited scope in terms of geographical extent and number of scrutinised species. The apparent lack of generalisable results makes it difficult to develop silvicultural guidelines for forest mixtures. It rather highlights the need for further studies into the effect of species mixing under drought for different species combinations across various site conditions.

In this study we focus on the drought stress behaviour of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus* spp.) in mixtures and monocultures. The latter comprises both pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.), which are considered together to avoid possible taxonomic pitfalls due to potential cross-breeding (Roloff et al., 2008, pp. 506–507). Following Pretzsch et al. (2019), we use "oak" as a generic term summarising both oak species, or their colloquial names "pedunculate oak" or "sessile oak". Despite differences in ecology on marginal sites, pedunculate oak being more adapted to moist or wet sites than sessile oak, while also being more susceptible to drought stress in comparison (Annighöfer et al., 2015), both oak species grow sympatrically across most of Europe (Jones, 1959). Scots pine is known to be well protected against drought due to its imbedded stomata and pronounced waxy layer on the epidermis (Krakau et al., 2013), although its sensitivity to increased temperatures and drought has been a cause for concern regionally (Kölling and Zimmermann, 2007; Galiano et al., 2010). Oak is able to withstand drought due to its deep-reaching taproots that increase the accessibility of water (Praciak et al., 2013). Scots pine is able to regulate its transpiration in an early stage of drought, whereas oak keeps its stomata open for a longer period of time (Irvine et al., 1998). Pronounced stomatal control (Scots pine) and deep reaching rooting systems (oak) generally allow for a high drought avoidance capacity (Levitt, 1980; Aubin et al., 2016). Scots pine and oak have been shown to differ in their drought response in relation to the seasonality of the drought events (Merlin et al., 2015; Toigo et al., 2015; Vanhellemont et al., 2019); Scots pine performs better under spring drought, whereas oak shows a higher resistance under summer drought conditions. Scots pine and oak are economically important due to a wide range of end-use applications (Eaton et al., 2016; Houston Durrant et al., 2016) and the ongoing transformation efforts towards mixed species forests have often seen the introduction of oak into stands traditionally dominated by Scots pine, in particular on

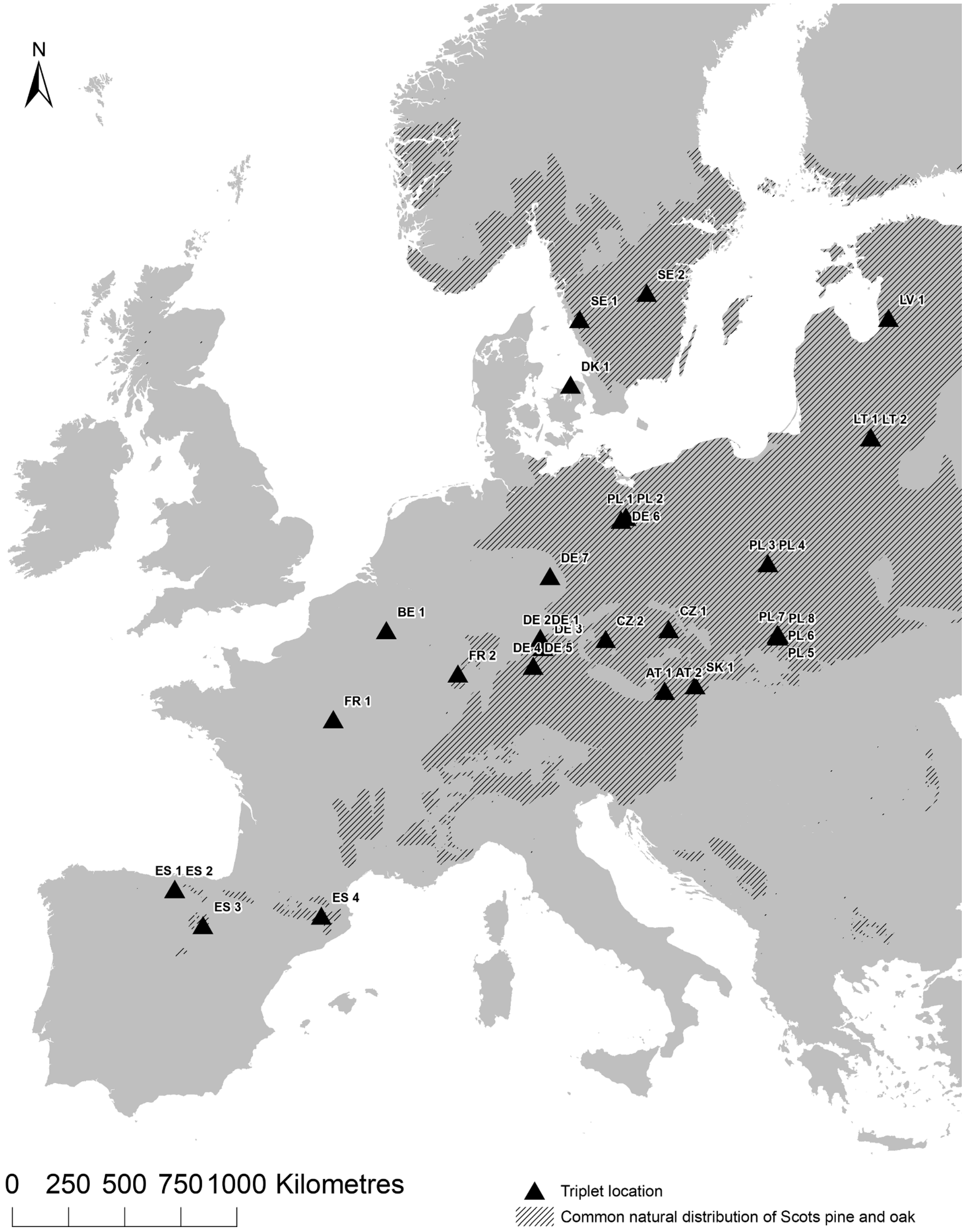

Fig. 1. Location of the 33 Scots pine-oak triplets (black triangles). The hatched area represents the common natural distribution of Scots pine and oak according to EUFORGEN (www.euforgen.org) (EUFORGEN, 2009a–c).

dry sites at lower elevations (Zerbe, 2002; Schröder et al., 2007; Noack, 2011).

Scots pine and oak mixtures are likely to increase in importance under adaptive forest management due to their high drought resistance compared with other economically important tree species, such as Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) (Spellmann et al., 2011; Zang et al., 2011; Albert et al., 2015). However, there is also evidence that this mixture used to be more common in the past, particularly under warmer growing conditions (Björse and Bradshaw, 1998). Empirical studies suggest productivity gains resulting from the mixture of Scots pine and oak (Brown, 1992; Toïgo et al., 2015; Lu et al., 2016; Lu et al., 2018; Pretzsch et al., 2019; Steckel et al., 2019), providing additional incentive for forest owners to establish and manage such forests.

Despite the growing importance of Scots pine-oak mixtures for European forest management under climate change, only a limited number of regional studies (Merlin et al., 2015; Toigo et al., 2015; Bello et al., 2019b; Nothdurft and Engel, 2019) have tried to shed some light on their actual ability to withstand drought stress, reporting both neutral, positive and even negative mixing effects.

The objective of this study was to improve our knowledge of general drought response patterns of two fundamental European tree species in mixed versus monospecific stands. By focusing on the mixture of Scots pine and oak across a comprehensive ecological gradient, covering 33 study sites across 12 European countries, we hope to contribute to a more robust and transferable understanding of the general growth responses under drought stress. For assessing tree drought responses, we considered basic components of tree growth stability (McCann, 2000), as quantified by drought response indices proposed by Lloret et al. (2011): '*resistance*' (Rt), '*recovery*' (Rc) and '*resilience*' (Rs).

To address the research objective, we tested the following null hypotheses:

HI: *Tree drought response does not differ between Scots pine and oak.*
HII: *Tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture).*
HIII: *Tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions.*

2. Material and methods

2.1. Study area and sites

This study is based on 33 triplets located along a comprehensive ecological gradient through Europe, reaching from nutrient-poorer and drier sites, to nutrient-richer and moister sites (Table A1). A more detailed description of the site selection process and experimental design is outlined in previous studies, focusing on stand structure and productivity (Pretzsch et al., 2019; Steckel et al., 2019).

Each triplet entails three rectangular plots, representing a mixed Scots pine-oak stand and two monospecific stands of each species respectively. The plots represent even-aged, fully stocked stands that exhibit a more or less mono-layered structure (see Table A2 for an overview of the stand characteristics).

The study area covers the overlap of the natural distribution of Scots pine and oak well, reaching from the south-western region in northern Spain to the northern and eastern regions in Sweden and Latvia respectively (Fig. 1). The highest concentration of study sites is found in Central Europe, covering Austria, Czechia, Germany, Poland and Slovakia. Table A1 gives an overview of the prevalent site characteristics for each triplet. The triplets are located at elevations of between 27 and 1635 m a.s.l. (mean = 334 m a.s.l.). The stands mainly grow on cambisols or arenosols, originating from sand or sandstone, but also from fylite, granite, limestone, marlstone or shale/loess. The variation in site fertility is reflected by the species-specific site index (Scots pine: $SI_{S.pi}$, oak: SI_{oa}), quantified by the height, hq (m), of the tree with the quadratic mean tree diameter at age 100. Site indexing was carried out by use of common yield tables (Wiedemann, 1948; Jüttner, 1955), which appear suitable, as they are based on long-term experiments, encompassing a broad range of site conditions (Pretzsch et al., 2019). These hq values range from 17.5 to 36.9 m (mean = 28.1 m) for Scots pine and from 14.8 to 36.0 (mean = 25.8 m) for oak in the analysed monocultures. The mean annual temperature ranges from 6.6 to 10.8 °C (mean = 8.4 °C) and the annual precipitation total from 493 to 1267 mm (mean = 694 mm) (Fig. A1).

2.2. Data collection and preparation

All field work was carried out at the end of the growing season in 2017 using a standardised protocol (Steckel et al., 2019). All living and dead trees with a diameter at breast height (dbh, cm) ≥7 cm were included in the survey (see Table A2 for mean tree characteristics). Two increment cores were taken from at least 20 dominant living trees per species and plot, from north and east cardinal directions. Where available, 10 additional living trees per plot were sampled, covering the rest of the diameter distribution (see Table A3 for an overview of cored trees).

Annual ring widths were measured from each increment core using standardised dendrochronological techniques (Speer, 2010). Cross-dating of the raw ring width series was performed for each plot, guided by narrow ring widths in species-specific pointer years (Schweingruber et al., 1990). Broken and otherwise unreadable cores were neglected.

2.3. Calculation of basal area increment

For the analysis of tree growth responses to drought, the tree basal area increment (bai, cm^2) was used. It was calculated based on the mean annual ring width of both increment cores as $bai_n = (d_n^2 - d_{n-1}^2) * \pi/4$, where d_n is the tree diameter at breast height (dbh) for year n, calculated from the cumulative ring widths for each year. The bai was used as basis of assessment, as it is a two-dimensional measure that is known to better reflect tree growth of the whole tree (volume) rather than the one-dimensional growth of tree ring width (Biondi and Qeadan, 2008).

2.4. De-trending procedures

To remove the long-term trends dependent on age as well as the medium-term oscillations due to past thinning activities, we standardised the bai series using a double de-trending procedure (Thurm et al., 2016). For this, the individual raw bai series were first standardised using the Hugershoff function (Hugershoff, 1936) to eliminate any age-related trends. In a second step, the resulting index values were further de-trended by applying a smoothing cubic spline, fixed by 15 years with a 50% frequency-response cut-off to remove any thinning effects. The detrended bai series were subsequently used to quantify tree drought responses.

To assess the reliability of the de-trended bai series, the appropriate descriptive statistics were computed by use of the R-package dplR (Bunn, 2008) (Table A3). The mean interseries correlation (Rbar) is commonly used to measure the strength of the common growth signal within each chronology (Wigley et al., 1984). In our case, mean Rbar values of between 0.42 and 0.44, indicated a good common signal on average among the individuals sampled in each species-composition group (Table A3). The Expressed Population Signal (EPS) was used to measure the reliability of chronologies (Lindholm et al., 1999). On average, EPS was >0.90 for Scots pine and oak in the studied mixtures and monocultures (Table A3). These values are well above the threshold of EPS > 0.85 introduced by Wigley et al. (1984), indicating that the sampled trees accurately represented the hypothetical population.

2.5. Climate data and identification of drought events

Local meteorological data (monthly mean temperature and monthly precipitation total) were obtained from meteorological stations nearby each triplet. In cases where suitable local station data were not available, gridded data were used as provided by national meteorological services or the CRU (Climatic Research Unit) 0.5°-gridded dataset (Harris et al., 2014).

To characterise the climatic site conditions, we calculated the mean annual meteorological variables (mean annual temperature (T, C°) and annual precipitation total (P, mm)) over a time period of 40 years (1976–2015), based on the acquired monthly data. The De Martonne aridity index (De Martonne, 1926) (DMI, mm $C^{\circ-1}$) (Eq. (1)) characterises the climatic water supply of a given site. It is valued due to its minimal data requirement and high explanatory strength (Bielak et al., 2014; Pretzsch et al., 2015). The greater the index, the better the water supply for plant growth.

$$DMI = \frac{P}{(T+10)} \tag{1}$$

On the analysed sites, DMI ranged from 25.7 to 63.9 mm $C^{\circ-1}$ (mean = 37.9 mm $C^{\circ-1}$) (Table A1), which translates into a range of semi-humid to very humid growing conditions according to the classification by Baltas (2007).

For analysing tree growth response to drought, we selected site-specific drought events that had a negative effect on tree growth. For this purpose, we developed a selection approach outlined in Fig. A2 and briefly described here:

First, we identified negative pointer years (Schweingruber et al., 1990) (i.e., years with remarkable negative growth responses), using the normalisation in a moving window method (Cropper, 1979) as implemented in the R-package pointRes (van der Maaten-Theunissen et al., 2015). For this analysis, we used the default window width of five years. Years were considered when at least 50% of the de-trended bai series of one of the two species in monocultures at a given site showed a negative event that indicated a growth reduction of >0.75 standard deviation below the mean. Secondly, these negative pointer years were compared to drought years, identified by means of the Standardised Precipitation and Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). This procedure should guarantee that only growth depressions associated with drought conditions were considered, rather than those associated with masting, frost events, insect and disease outbreaks or forest pasture. Additionally, it ensures that the observed meteorological anomaly, evident on the system level, is reflected by actual drought stress, suffered by the studied individuals. The SPEI is a multi-scalar drought index that is based on a monthly balance of precipitation and the potential evapotranspiration (PET). In our study, PET was calculated using the Thornthwaite equation (Thornthwaite, 1948). The SPEI was derived for a time scale of six months. Site-specific drought years were selected based on the approach outlined in Potop et al. (2014), i.e., we considered years that displayed at least one month with a SPEI ≤ -1.0 during the growing season, potentially encompassing moderate to extreme drought conditions. The growing season was determined for each site by selecting months with a minimum mean temperature of ≥ 10 °C (Winkler, 1980). Years which were classified as both negative pointer years and drought years, were considered as drought events and used as a basis for the subsequent analysis.

2.6. Measures of growth in relation to drought

Growth responses to selected drought events were assessed based on tree drought response indices proposed by Lloret et al. (2011), calculated from the detrended bai series. To improve readability of the results, we multiplied the indices with 100 and thus, report them in percent (%).

$$Rt = \frac{G_{Dr}}{G_{PreDr}} * 100 \tag{2}$$

$$Rc = \frac{G_{PostDr}}{G_{Dr}} * 100 \tag{3}$$

$$Rs = \frac{G_{PostDr}}{G_{PreDr}} * 100 \tag{4}$$

The resistance index Rt (Eq. (2)) is the ratio between tree growth during the drought event (G_{Dr}) and the mean growth during the pre-drought period (G_{preDr}). It shows the capacity of trees to buffer drought stress; Rt = 100 indicates complete resistance.

The recovery index Rc (Eq. (3)) is the ratio between the mean growth during the post-drought period (G_{postDr}) and G_{Dr}. It describes the tree's ability to restore a level of growth after disturbance; Rc = 100 indicates persistence of the drought growth level, Rc $<$ 100 indicates a further decline and Rc $>$ 100 indicates a recovery from the growth level during drought.

The resilience index Rs (Eq. (4)) is the ratio between the average growth after (G_{postDr}) and before (G_{preDr}) the drought event, thereby measuring the capacity of trees to return to growth rates as experienced before drought; Rs $\geq$ 100 indicates a full recovery or increased growth after the drought event, while Rs $<$ 100 indicates growth decline.

Growth during pre- and post-drought periods (G_{preDr}, G_{postDr}) was calculated as the average growth during the three years before, or after, respectively, the studied drought event. This time frame was used as it represents the best trade-off between a sufficiently long period, to ensure a good estimation of the mean growth before and after the drought event, and the risk of an overlap of pre- and post-drought periods with adjacent drought events.

The analysis of tree drought response was restricted to a 40-year time window (1976 – 2015). This time frame is suitable to ensure low variations in stand structure and composition and to consider a sufficient number of site-specific drought events. As a small number of relatively young stands was included in the data set, we introduced an age threshold of 10 years, i.e. drought events were only considered when the stand age at a specific site was 10 years or above. We considered every drought event as a single stress event for each site. To minimise bias, we excluded drought events that showed an overlap of pre- and post-drought periods with adjacent drought events. The final number of site-specific event years ranged from one to five and is outlined in Supplement material 1. The selected drought events include well-reported European droughts as presented by Spinoni et al. (2015). The year 2015 was considered a remarkable drought event and therefore included in the analysis. Due to the fact that trees were sampled in 2017, the post-drought period was reduced to two years in this specific case.

2.7. Modelling approach

In this study, we applied linear mixed-effects models (Pinheiro and Bates, 2004) to account for nesting in the data. By including not only fixed, but also random effects, we were able to account for pseudo-replication, potentially resulting in false, i.e. too progressive, significances (Crawley, 2013). The random effects included in our models address the inter-correlation of samples caused by spatial clustering of trees within the country, triplet group (each triplet is assigned to one of 24 triplet groups, based on its relative location) and triplet. The inclusion of a random effect on the individual tree level did not yield any advantages when comparing models based on the AIC (Akaike Information Criterion) (Akaike, 1981) and was therefore not considered. A separate model was fitted to each of the analysed drought response indices Rt, Rc and Rs. All fitted models were visually checked for homoscedasticity and normal distribution of the residuals. Statistical analyses were conducted in the statistical environment R, version 3.6.0 (R Core Team, 2019), in particular relying on the function lme from the

Table 1
Results of the linear mixed-effects model regressions from Eq. (5). We test a_1, the fixed effect parameter for the dummy-coded binary variable S (species), which becomes 0 for Scots pine and 1 for oak.

Response variable	Statistic	Intercept a_0	S a_1
Rt (%) – Resistance	Estimate	**83.5*** **	**1.4***
	SE	1.8	0.7
Rc (%) – Recovery	Estimate	**129.1*** **	**−2.8** **
	SE	2.3	1.0
Rs (%) – Resilience	Estimate	**100.6*** **	**1.2***
	SE	1.6	0.6

S: fixed species effect. Values in bold are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Non-significant values are denoted by " ns". The number of observations was always n = 5086.

package nlme (Pinheiro et al., 2019).

Below, we present the model equations used to test the hypotheses HI–HIII:

HI: *Tree drought response does not differ between Scots pine and oak.*

Eq. (5) was used to test the general influence of tree species (Scots pine versus oak) on the tree growth response to drought. For this analysis, we only considered monospecific stands in order to exclude any potential confounding effects resulting from the mixture of both species.

$$Y_{ijklm} = a_0 + a_1 * S_{ijkl} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijklm} \tag{5}$$

In Eq. (5), Y_{ijklm} is the response variable, i.e. the analysed drought response index (Rt, Rc or Rs). The indices represent country (i), triplet group (j), triplet (k), tree (l) and drought event (m) respectively. Coefficient a_1 is a fixed effect parameter for the dummy-coded binary variable S_{ijkl} (species) which becomes 0 for Scots pine and 1 for oak. The terms b_i, b_{ij} and b_{ijk} represent the random intercept effects on the level of country, triplet group and triplet respectively ($b_i \sim N(0, \tau_1^2)$, $b_{ij} \sim N(0, \tau_2^2)$ and $b_{ijk} \sim N(0, \tau_3^2)$). Finally, ε_{ijklm} is an independent and identically distributed error ($\varepsilon_{ijklm} \sim N(0, \sigma^2)$).

HII: *Tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture).*

We used Eq. (6) to test the general influence of stand composition (mixture versus monoculture) on the species-specific tree growth response to drought. This model was fitted for Scots pine and oak separately.

$$Y_{ijklm} = a_0 + a_1 * C_{ijkl} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijklm} \tag{6}$$

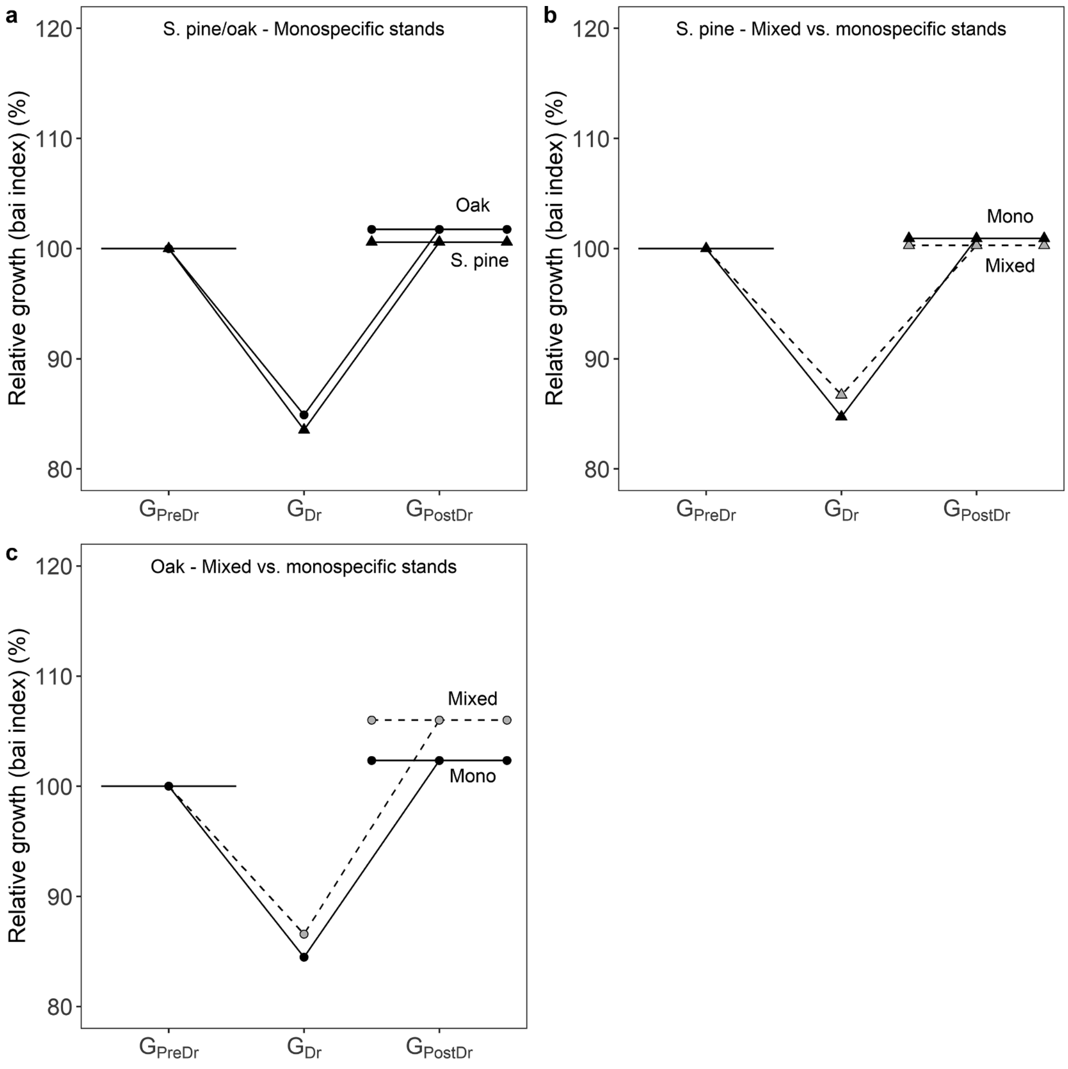

Fig. 2. Estimated growth response to drought (G_{Dr}) as well as growth levels before (G_{PreDr}) and after drought (G_{PostDr}) for Scots pine (triangles) and oak (circles) in mixed (grey symbols, dashed lines) and monospecific stands (black symbols, solid lines) according to Eqs. (5) and (6). Due to the relation to growth before drought, G_{Dr} and G_{PostDr} equal the resistance (Rt) and resilience index (Rs) respectively. a) Comparison of Scots pine and oak trees in monocultures. b-c) Comparison of Scots pine and oak trees growing in mixed versus monospecific stands.

Here, a_1 is a fixed effect parameter for the dummy-coded binary variable C_{ijkl} (stand composition) which is 0 for mixture and 1 for monoculture. The remaining notation is to be understood in the same way as for Eq. (5).

HIII: *Tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions.*

To analyse the influence of ecological growing conditions on the species-specific tree growth response to drought in mixed and monospecific stands, we expanded Eq. (6) further by adding a collection of tree and site-specific ecological variables and their respective interactions with the mixture effect. This leads to the following saturated model that comprises the complete set of possible fixed effects together with the respective interactions (Eq. (7)).

$$\begin{aligned} Y_{ijklm} = {} & a_0 + a_1 * C_{ijkl} + a_2 * ba_{ijklm} + a_3 * SI_{ijk} + a_4 * DMI_{ijk} \\ & + a_5 * (C_{ijkl} * ba_{ijklm}) + a_6 * (C_{ijkl} * SI_{ijk}) \\ & + a_7 * (C_{ijkl} * DMI_{ijk}) + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijklm} \end{aligned} \tag{7}$$

In Eq. (7), tree size is represented by the tree basal area (ba_{ijklm}) at the time of the drought event m. Site-specific information comprises the species-specific site index ($SI_{S.pi}$, SI_{oa}, denoted as SI_{ijk} in the model), representing site fertility, and the De Martonne aridity index (DMI_{ijk}), representing site water supply. The remaining notation is to be understood in the same way as for Eqs. (5) and (6).

Selection of potentially less complex final models nested in Eq. (7) was based on the AIC (Burnham and Anderson, 1998) and biological plausibility of the results. The selection was made with additional help by an automated AIC-based model selection procedure (function dredge from the R-package MuMIn (Barton, 2019)). To address the research question at hand, C_{ijkl} (stand composition) was included a priori in all final models.

3. Results

3.1. Influence of tree species (Scots pine versus oak) and stand composition (mixture versus monoculture) on the tree drought response

Oak trees in monocultures on average showed a greater resistance and resilience compared to Scots pine trees ($p < 0.05$), while recovery was lower ($p < 0.01$) (Table 1, Fig. 2a). Under drought, growth of Scots pine and oak in monocultures was on average reduced to 84% and 85% of the pre-drought period respectively (Table 1, Fig. 2a). Both Scots pine and oak recovered from drought, growing 129% and 126% respectively compared with the growth during drought (Table 1). Scots pine and oak were both resilient to drought, indicated by greater growth after compared to before the stress event, (Rs = 101% for Scots pine and Rs = 102% for oak) (Table 1, Fig. 2a).

Scots pine and oak differed in their reaction patterns depending on stand composition. Scots pine trees showed a greater resistance in mixtures compared with monocultures ($p < 0.01$), although they took longer to recover ($p < 0.001$) (Table 2, Fig. 2b). Oak trees growing in mixtures showed a significantly greater resistance and resilience compared to those in monocultures ($p < 0.001$) (Table 2, Fig. 2c).

3.2. Influence of ecological growing conditions on the species-specific tree growth response to drought

Tree size and site water supply had a significant effect on the growth responses to drought in mixtures and monocultures (Table 3). Larger Scots pine trees were more resistant to drought than smaller ones ($p < 0.001$), but took longer to recover ($p < 0.001$). Site water supply, represented by the De Martonne aridity index (DMI), was associated with greater resistance to drought in oak ($p < 0.01$), but not Scots pine (n.s.). Significant interactions between site variables and the composition effect (C) indicate that the general mixing effect on tree drought response presented in 3.1 was not constant along the studied ecological gradient. In particular, for oak the mixture-advantage in terms of resistance and resilience increased with site water supply ($p < 0.001$) (Table 3, Fig. A3b,f). In contrast, species mixing was not favourable for increasing recovery of oak on sites with higher site water supply ($p < 0.05$) (Table 3, Fig. A3d). Furthermore, the mixture benefit regarding resistance of Scots pine decreased with increasing site fertility ($SI_{S.pi}$) ($p < 0.05$) (Table 3, Fig. A4a).

4. Discussion

Our results indicate that the drought responses were species specific (Scots pine versus oak) (Table 1, Fig. 2a) and depended on stand composition (mixture versus monoculture) (Table 2, Fig. 2b-c). Moreover, we found that the analysed ecological factors influenced the general growth response to drought, while also modifying the observed mixing effect (Table 3, Fig. A3, Fig. A4).

The revealed growth responses to drought are well substantiated, owing to the meticulous identification process of independent site-specific drought events, the comprehensive study area as well as the detailed information on tree- and site-specific characteristics. Although no physiological or hydrological measurements were available for this study, our results provide indications for inferring the underlying mechanisms and causes that drive the observed reaction patterns.

During the studied drought events, neither Scots pine nor oak were resistant to drought, as indicated by growth reductions of 16% and 15% respectively in monocultures (Table 1, Fig. 2a). This result was expected, as drought events were identified by negative pointer years. However, the observed magnitude of growth reduction can be seen as representative of the average drought intensity experienced during the selected drought events and allows a comparison of drought responses between species and composition types. The observed reductions in growth were only slightly less than reported by Merlin et al. (2015) for Scots pine and oak, but considerably lower than found for other economically relevant tree species such as European beech and Norway Spruce (Pretzsch et al. 2013, Metz et al., 2016), thereby confirming a relatively high drought resistance of both species studied. However, because we used a double stage detrending that was independently applied in an extra step prior to regression modelling, it is possible that our smooths led to an underestimation of the magnitude of possible climate-related effects. Furthermore, differing criteria for selection of drought events may explain differences between the studies.

Table 2

Results of the linear mixed-effects model regressions from Eq. (6). We test a_1, the fixed effect parameter for the dummy-coded binary variable *C* (stand composition), which becomes 0 for mixture and 1 for monoculture.

Species	Response variable	Statistic	Intercept a_0	C a_1
Scots pine	Rt (%) – Resistance	Estimate	$\mathbf{86.7}^{***}$	$\mathbf{-2.0}^{**}$
		SE	2.4	0.7
	Rc (%) – Recovery	Estimate	$\mathbf{123.7}^{***}$	$\mathbf{4.9}^{***}$
		SE	2.7	1.0
	Rs (%) – Resilience	Estimate	$\mathbf{100.3}^{***}$	0.6^{ns}
		SE	1.9	0.7
Oak	Rt (%) – Resistance	Estimate	$\mathbf{86.6}^{***}$	$\mathbf{-2.1}^{***}$
		SE	2.6	0.6
	Rc (%) – Recovery	Estimate	$\mathbf{129.8}^{***}$	-1.6^{ns}
		SE	3.7	1.0
	Rs (%) – Resilience	Estimate	$\mathbf{106.0}^{***}$	$\mathbf{-3.7}^{***}$
		SE	1.6	0.6

C: fixed composition effect. Values in bold are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Non-significant values are denoted by " ns". The number of observations was always $n = 5167$ for Scots pine and $n = 5120$ for oak.

Table 3

Results of the linear mixed-effects model regressions from Eq. (7). We test the effect of ecological factors on the studied tree drought responses in mixtures and monocultures (fixed effect parameters a_1-a_7).

Species	Response variable	Statistic	Intercept	C	ba	SI	DMI	C*ba	C*SI	C*DMI
			a_0	a_1	a_2	a_3	a_4	a_5	a_6	a_7
Scots pine	Rt (%) – Resistance	Estimate	**65.910*****	**−9.858***	**0.007*****	0.594^{ns}	–	–	**0.301***	–
		SE	10.887	4.075	0.001	0.382			0.143	
	Rc (%) – Recovery	Estimate	**132.641*****	**3.849*****	**−0.014*****	–	–	–	–	–
		SE	2.910	1.042	0.002					
	Rs (%) – Resilience	Estimate	**100.289*****	0.633^{ns}	–	–	–	–	–	–
		SE	1.872	0.677						
Oak	Rt (%) – Resistance	Estimate	**69.294*****	**14.517*****	–	–	**0.450****	–	–	**−0.433*****
		SE	5.637	2.827			0.131			0.072
	Rc (%) – Recovery	Estimate	**144.004*****	**−11.669***	–	–	-0.372^{ns}	–	–	**0.261***
		SE	12.017	4.581			0.298			0.117
	Rs (%) – Resilience	Estimate	**98.742*****	**9.985*****	–	–	0.190^{ns}	–	–	**−0.355*****
		SE	6.961	2.774			0.179			0.071

C: fixed composition effect. *ba*: reconstructed tree basal area (cm^2). SI: species-specific site index (m) ($SI_{S.pi}$, SI_{oa}). *DMI*: De Martonne aridity index (De Martonne, 1926) (mm $°C^{-1}$). Values in bold are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Non-significant values are denoted by " ns". The number of observations was always $n = 5167$ for Scots pine and $n = 5120$ for oak.

4.1. Scots pine and oak respond differently to drought

In the studied monocultures, the tree growth response pattern of Scots pine and oak to drought differed significantly. Thus, we reject HI. Resistance and resilience of oak were greater than for Scots pine, suggesting that oak on average had a greater capacity to withstand water stress during the drought events studied and to return to average growth rates as experienced before drought. This finding contradicts Niinemets and Valladares (2006), who assigned greater drought tolerance to Scots pine compared with oak. However, our results confirm a growing body of regional studies that report a more pronounced sensitivity of Scots pine to increased temperatures and drought, suggesting a higher vulnerability compared with pedunculate and sessile oak (Kölling and Zimmermann, 2007; Bello et al., 2019b; Zang et al., 2011) as well as other *Quercus* species (Galiano et al., 2010).

The observed differences in drought response between Scots pine and oak can be attributed to their differing water uptake strategies under drought. Scots pine is characterised by an isohydric strategy, whereas oak is characterised by an anisohydric strategy (Irvine et al., 1998; Zang et al., 2011; Zang et al., 2012; Poyatos et al., 2013; Martínez-Sancho et al., 2017). Under drought, isohydric species are found to reduce water consumption and growth at an early stage by closure of stomata (reduced photosynthesis), whereas anisohydric species continue transpiring until water resources are depleted (McDowell et al., 2008; Domec and Johnson, 2012; Kumagai and Porporato, 2012). Under prolonged water stress, maintenance of transpiration flow in anisohydric plants often requires leaf area control, which reduces water demand (Maseda and Fernández, 2006). Twig abscission is common in oak and enables the trees to avoid runaway embolism (Klugmann and Roloff, 1999). The preventive strategy of isohydric species can reduce stress damage, such as defoliation, loss of fine roots or cavitation of xylem tissue, thereby often resulting in a higher recovery following drought compared with anisohydric species (Leuschner, 1998; Hartmann, 2011). These patterns can be seen as a plausible explanation of the observed species-specific drought reaction, oak exhibiting a significantly higher resistance (i.e., higher productivity), but also a lower recovery than Scots pine.

Differences in resistance behaviour of Scots pine and oak may also arise due to differing seasonal growth dynamics. Oak attains about half of its annual radial growth during spring (Zweifel et al., 2006), when wide earlywood vessels are formed based on reserves carried over from the last growing season. These newly formed vessels are at high risk of cavitation, which may result in water deficit and reduced cell enlargement (Tardif and Conciatori, 2006). In contrast, the growth of Scots pine is concentrated on the summer and early autumn months following needle formation and expansion (Zweifel et al., 2006). Consequently, oak has been found to be more susceptible to spring droughts, whereas Scots pine is more affected by summer droughts (Weber et al., 2007; Merlin et al., 2015; Toigo et al., 2015; Vallet and Perot, 2018; Vanhellemont et al., 2019). Our results may therefore also be related to the generally higher vulnerability of Scots pine to longer summer drought periods and higher mean temperatures, as observed in many regions (Weber et al., 2007). This idea is substantiated by the fact that many of the drought years covered in this study represent well-documented summer droughts, such as for example endured in 1993 (European Drought Centre, 2019), 1996 (Carnicer et al., 2011), 2003 (Ciais et al., 2005; Rebetez et al., 2006; Pichler and Oberhuber, 2007; van der Werf et al., 2007; Lebourgeois et al., 2010; Merlin et al., 2015), 2006 (Merlin et al., 2015) and 2015 (Ionita et al., 2017).

4.2. Stand composition affects drought response of Scots pine and oak

Our results suggest that species mixing can have a significantly positive effect on drought response of scots pine and oak. The resistance of Scots pine was greater in mixture with oak than in corresponding Scots pine monocultures, while recovery was lower. At the same time, resistance and resilience of oak were greater under mixed compared with monospecific stand conditions. Based on these observations, we reject HII. Positive mixing effects are commonly explained by the complementary effect hypothesis (Aarssen, 1997; Loreau, 2000; Loreau and Hector, 2001; Fargione et al., 2007), under which complementarity arises from either facilitation, where one species improves the environmental conditions for another species (Callaway, 2007; Brooker et al., 2008), or reduced competition as a result of niche differentiation (Kelty, 1992; Man and Lieffers, 1999). Both interaction types may be present at the same time and can be difficult to distinguish (Forrester and Bauhus, 2016). Complementary light use, driven by differences in shade tolerance, crown architecture and leaf phenology, can be seen as the prevalent driver of positive mixing effects in Scots pine and oak mixtures under average growing conditions, when water is not the limiting resource (Pretzsch et al., 2019; Steckel et al., 2019). However, as pointed out by Forrester and Bauhus (2016), under periodic drought stress water-related complementarity effects may become more important than under average growing conditions. In this context, oak in mixtures may profit from Scots pine's more conservative stress response strategy, which results in a higher water availability compared to oaks growing with conspecific neighbours (Loreau and Hector, 2001; Pretzsch et al., 2013). Furthermore, spatial stratification of mixed tree species, due to differences in root distribution, architecture or activity, have been shown to improve the exploitation of underground water resources (Schume et al., 2004; Forrester et al., 2010; Schwendenmann et al., 2014). These patterns are likely in the case of Scots pine and oak, as the root morphology differs considerably. The root system of Scots pine is frequently shallow, with no distinct tap root, while oak produces a strong tap root which eventually is replaced by a deep reaching dense system of "heart-roots" (Jones, 1959; Carlisle and Brown, 1968). Furthermore, both Scots pine and oak have been reported to utilise deeper water resources in mixtures compared with monocultures and to exhibit partial niche complementarity for limited water resources (Bello et al., 2019a). Additional complementarity between Scots pine and oak could also arise from seasonal differences in fine root development (Konôpka et al., 2005). Moreover, oak has been shown to exhibit hydraulic lift (i.e., upward hydraulic redistribution) under moderate and severe drought conditions (Caldwell et al., 1998; Jonard et al., 2011; Zapater et al., 2011; Hafner et al., 2017), thereby potentially increasing water availability in the upper soil layers for the admixed species. This form of facilitation is well understood (Neumann and Cardon, 2012; Prieto et al., 2012; Ryel, 2004) and has been hypothesised to be one of the main advantages of mixing oak with other tree species for increased drought resistance (Pretzsch et al., 2013). The admixture of oak may therefore have increased the water availability for Scots pine under drought, resulting in higher radial growth in mixed compared with monospecific stands. The negative relationship between the resistance and recovery of Scots pine suggests a trade-off between both indices, which has also been reported by Gazol et al. (2017) for a wide range of forest types in the Northern Hemisphere and could be attributed to differences in nutrient supply following drought events. Building on Körner (2002), Pretzsch et al. (2013) hypothesise that the more growth and thereby soil nutrient consumption is limited during drought, the more soil nutrients may be available for recovery in the following years. In the case of Scots pine, this means that in monocultures more nutrients may have been available following low growth episodes than in mixtures. Under improving growing conditions (i.e., during post-drought periods), the relationship between Scots pine and oak may on average have changed from complementarity to competition, as suggested by the stress gradient hypothesis (del Rio et al., 2014) and by the complementary inter-specific recovery and resilience pattern observed. For Scots pine, inter-specific competition would then have been greater than intra-specific competition during the post-drought period. In contrast, oak may have experienced a competitive release in mixture compared with monoculture. We assume that when soil water is not the limiting factor, competition for light may become more relevant, resulting in a more asymmetric mode of competition (Hara, 1988; Schwinning and Weiner, 1998; Pretzsch and Biber, 2010; Pretzsch et al., 2018). Under these conditions, oak is more likely to receive a competitive advantage owing to its high crown plasticity (Longuetaud et al., 2013). The stronger resilience of oak in mixtures compared with monocultures could also be caused by a more continuous mineralisation (Pretzsch et al., 2013).

Our findings of an average positive effect of mixing Scots pine and oak are in line with several studies reporting positive diversity effects in terms of tree growth response under drought stress for other species combinations (Lebourgeois et al., 2013; Pretzsch et al., 2013; Metz et al., 2016; Gazol et al., 2017; Mölder et al., 2019). Furthermore, our results are supported by previous studies that reported a positive effect of species mixing on drought stress reduction in oak (del Rio et al., 2014; Bello et al., 2019b) and those who highlight the advantages of admixing oak with other tree species, such as European beech (Pretzsch et al., 2019). In contrast to our findings, neutral (Merlin et al., 2015; Toigo et al., 2015; Bello et al., 2019b) and negative mixing effects (Bello et al., 2019b; Nothdurft and Engel, 2019) have also been reported in Scots pine-oak stands. However, spatial variations in the interactions between tree species regarding growth have been reported for many forests, suggesting that the use of data from limited parts of the species distribution for deriving general mixing effects may be misleading (Forrester, 2014). The before mentioned Scots pine-oak studies are based on a rather small sample of environmental growing conditions, whereas our results reflect the growth behaviour of Scots pine-oak mixtures across a large portion of the natural distribution area. Furthermore, methodological differences, such as limiting the sampling to dominant trees, may explain why these results differ from ours.

4.3. Tree size and site conditions modify species-specific drought responses in mixed and monospecific stands

Based on our observations, we can reject HIII as there was clear evidence that tree size and site conditions significantly affected the growth response to drought in the analysed mixtures and monocultures. Larger Scots pine trees were significantly more resistant than smaller trees, while the opposite pattern was found with regard to recovery (Table 3). The greater growth reduction of smaller Scots pine is likely an effect of dominance, as small Scots pine trees growing in an understory canopy position may compete for light, water and nutrients. In particular, larger trees may have more extensive root systems, increasing the competitive performance under drought conditions (Zang et al., 2014). Our findings are in line with other reports for Scots pine (Pichler and Oberhuber, 2007) and other tree species (Orwig and Abrams, 1997; Vose and Swank, 1994; Martín-Benito et al., 2008), where growth reductions due to drought were greater for understory than for overstory trees. In contrast, other studies have failed to find any significant influence (Bello et al., 2019b), or have reported a negative effect of tree size on drought resistance, arguing that larger trees show a greater vulnerability to hydraulic stress and experience higher radiation and evaporative demand due to exposed crowns than smaller trees (Zang et al., 2012; Bennett et al., 2015; Merlin et al., 2015; Serra-Maluquer et al., 2018). Methodological differences in the definition of tree size classes and the measures for quantifying growth responses to drought may explain the conflicting results as well as the variability in soil and climatic conditions. Contrary to some studies (Jucker et al., 2014; Ledo et al., 2014), we did not find any indication that tree size modified the effect of stand composition on the tree growth response to drought.

Site conditions modified the drought response of both species. We found that the resistance of oak increased with site water supply. This result confirms a previous study by Pretzsch et al. (2013) that reported increased resistance along the gradient of water supply for Norway spruce, European beech and sessile oak. More importantly however, we found that site water supply significantly increased the positive effect of species mixing regarding resistance and resilience of oak (Fig. A3b,f). Consistent with our results, a strong dependence of drought stress reduction on site conditions in mixtures has been reported from different regions in Europe (Forrester et al., 2016; de Streel et al., 2019). Such as demonstrated by Nothdurft and Engel (2019), resistance of Scots pine and oak can also be negatively affected through mixing within certain climate ranges. As observed on the studied sites, species mixing increased resistance and resilience of oak over most of the water supply gradient. However, on the driest sites, resistance of oak was estimated to be lower in mixtures compared with monocultures. This may be seen as indicative of the fact that trees may be more acclimated to drought stress on dry sites, resulting in less pronounced growth reactions (Lévesque et al., 2013), thereby limiting complementarity effects. However, in drought prone environments, the complementary advantage may also be replaced by competition (González de Andrés et al., 2018), unless net water-use partitioning or water-related facilitation take place (Grossiord et al., 2014). Following the conceptual framework by Forrester and Bauhus (2016), we can hypothesise that in the case of oak, complementary light use may be important, in particular on mesic and moist sites, where water is not the limiting resource. Previous studies along the analysed transect (Pretzsch et al., 2019; Steckel et al., 2019) solidify the importance of reduced light competition as the main driver of stand-level overyielding. In these studies, oak was found to exhibit significantly longer and wider crowns in mixtures versus monocultures, thereby promoting light capture. In contrast, the negative influence of site fertility on the mixing effect regarding resistance of Scots pine under drought (Fig. A3a) suggests a stronger dependency on water-related complementarity effects (Forrester and Bauhus, 2016). Our results confirm studies which report that species mixing does not always improve the response to drought stress, but instead varies in its effect in accordance with temporal and spatial variations in environmental conditions (Grossiord et al., 2014; Forrester et al., 2016; Bonal et al., 2017; de Streel et al., 2019).

The findings of our study are of importance for forest managers seeking to mitigate adverse effects of climate change. By being able to predict under which conditions the mixture of two given tree species is favourable and under which conditions it may be disadvantageous, forest management strategies can be optimised. Current climate projections indicate that sites in Southern Europe and large parts of Western Europe will have lower water supply (higher temperature, lower or constant precipitation) by the end of the 21st century, while conditions are likely to remain more constant in Northern Europe and parts of Central Europe (higher temperature, higher precipitation) (Jacob et al., 2014). These scenarios foresee that a substantial proportion of European forests will be located on sites with an annual water supply of less than 30 mm $^{\circ}C^{-1}$. The climate is also likely to become increasingly variable, meaning more frequent and severe droughts in many parts of Europe (Spinoni et al., 2018). These projections, combined with the results from our study, seem to indicate that mixing of Scots pine and oak might especially be recommendable on many sites in Northern Europe and parts of Central Europe, where future average water supply is not expected to decrease severely, but drought events may still increase in frequency and intensity.

5. Conclusions

Our study provides support for species mixing as a valid management option to reduce the drought vulnerability of European forest ecosystems. Based on our results, mixtures of Scots pine and oak can play a considerable role in shaping climate-smart forests along a wide range of ecological growing conditions. We were able to consolidate previous findings that emphasise the facilitative effect of oak on admixed species. It should therefore be considered as a stabilising component under adaptive forest management. However, oak also benefitted significantly from the admixture of Scots pine over most of the studied ecological gradient, in particular on sites with higher average site water supply. Our research highlights the importance of considering a broad range of environmental growing conditions when comparing the performance of mixtures versus monocultures and demonstrates the possibilities and limitations of the ecological concept of complementarity. The results corroborate previous works that report a good complementarity of Scots pine and oak, proposing this species mixture as a promising option under climate change. However, both species are currently pressured in many European regions due to close-to-nature management schemes that promote more competitive shade tolerant species such as European beech. Silvicultural intervention to increase light availability may often be required to ensure the continuance of oak in particular.

Authors' contribution

M. Steckel initiated the study, performed field and increment core measurements, managed the data, carried out the analysis and wrote the manuscript. H. Pretzsch and M. del Río initiated the study and reviewed the manuscript. All authors provided field data and increment core measurements and improved the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Figs. A1–A4
See Tables A1–A3

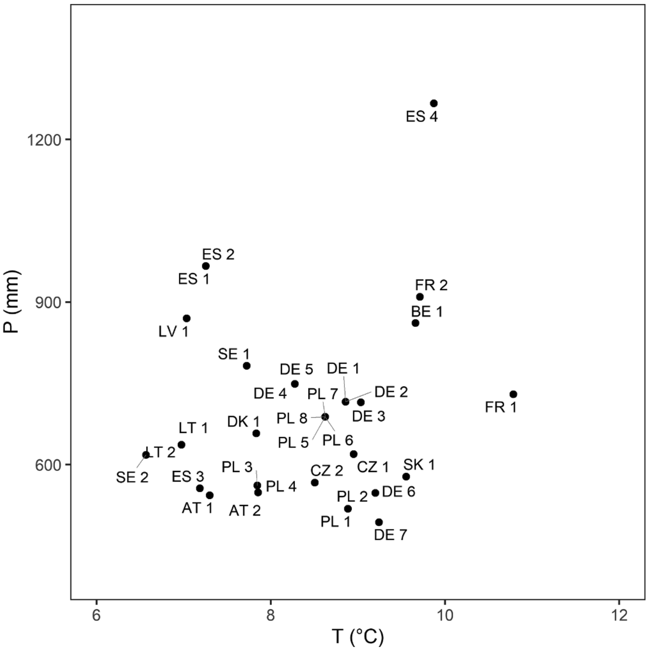

Fig. A1. Location of the 33 Scots pine-oak triplets within the climatic gradient covered. *T*: mean annual temperature (°C). *P*: annual precipitation total (mm). Reference period climate data: 1976–2015.

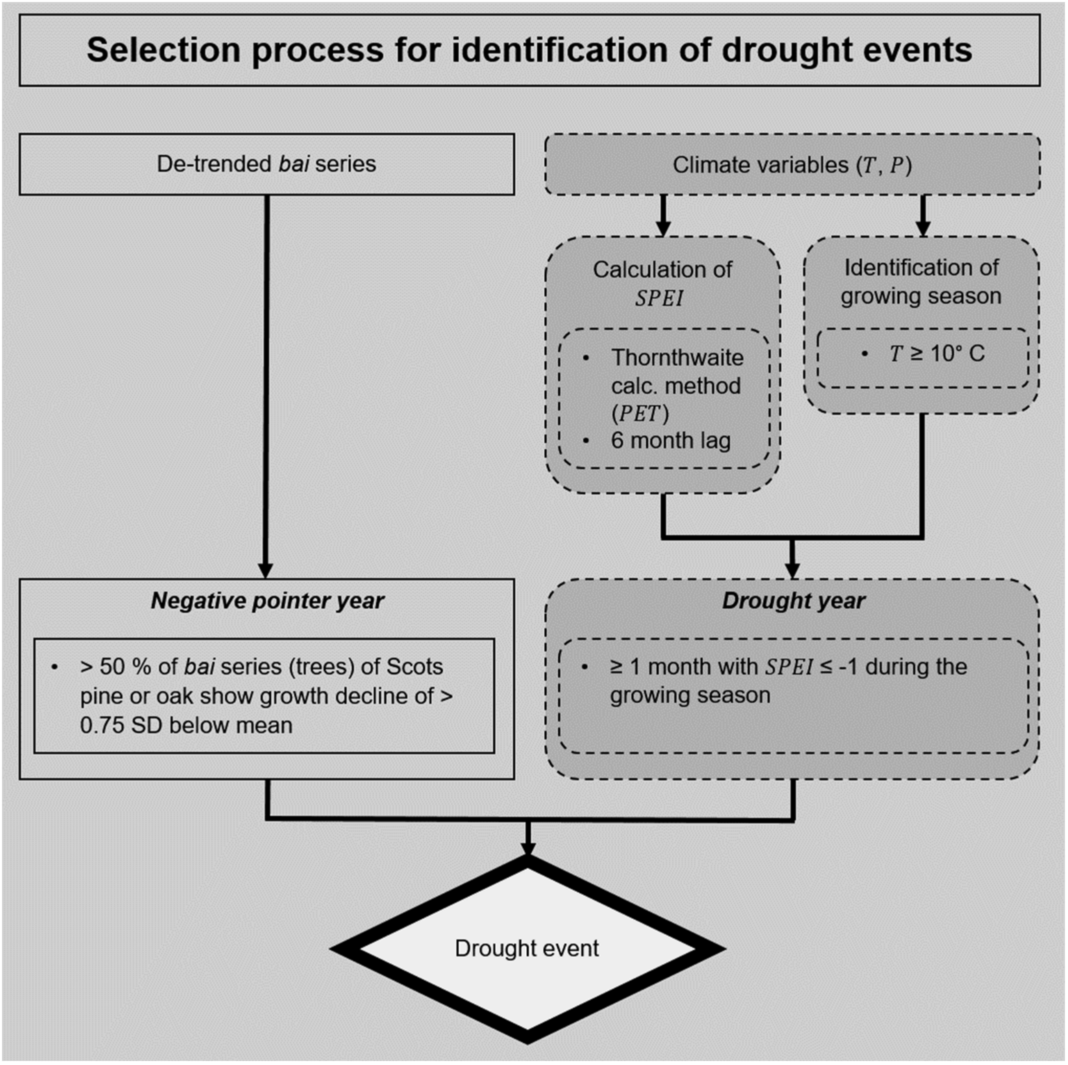

Fig. A2. Flow chart depicting the process for identifying drought events.

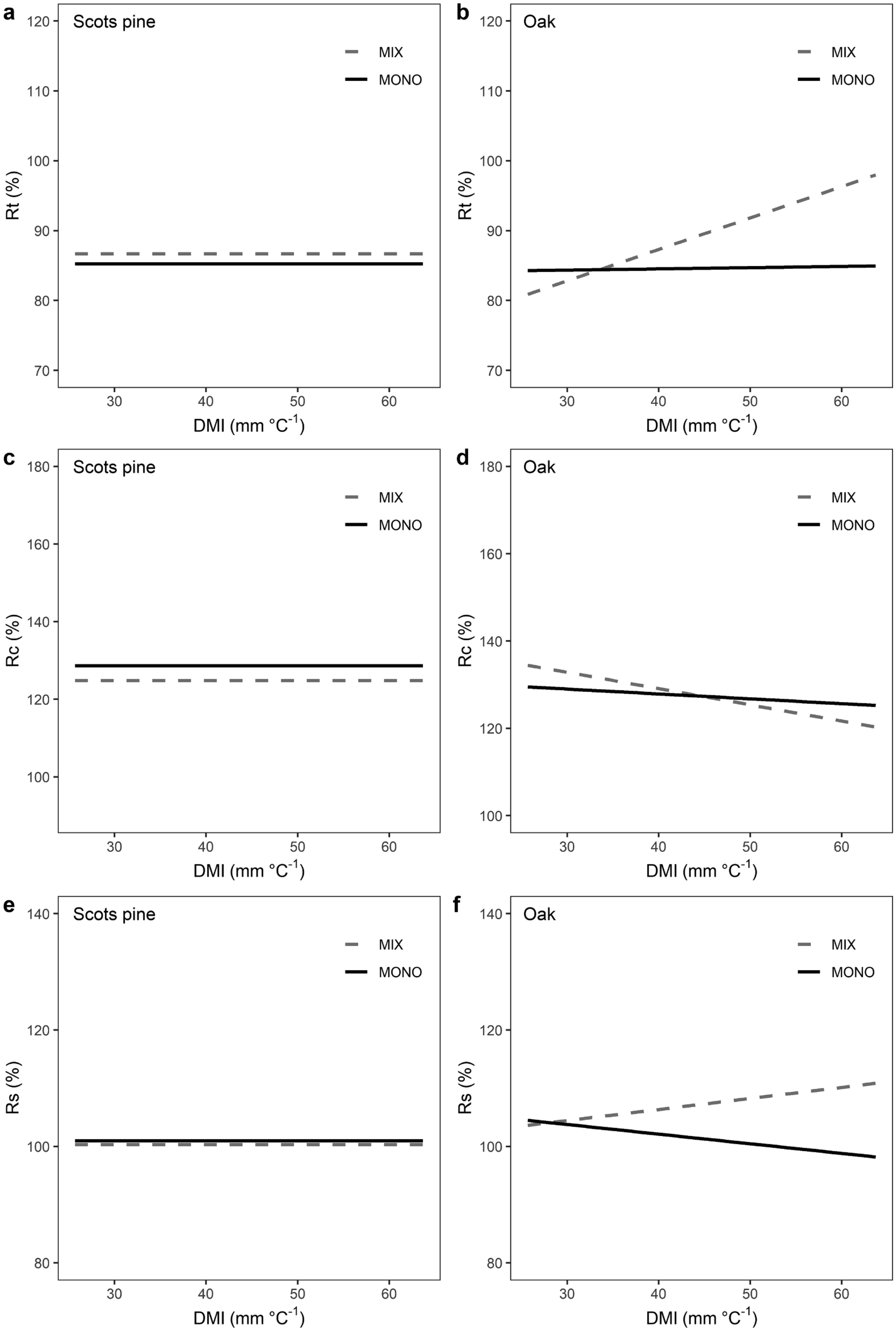

Fig. A3. Effect of the De Martonne aridity index (*DMI*) on the drought response of Scots pine and oak in mixed (dashed grey line) and monospecific stands (solid black line). Lines represent the fixed effect terms from Eq. (7). Variables other than *DMI* were set at the respective means as obtained from the data. a-b) Resistance (*Rt*). c-d) Recovery (*Rc*). e-f) Resilience (*Rs*).

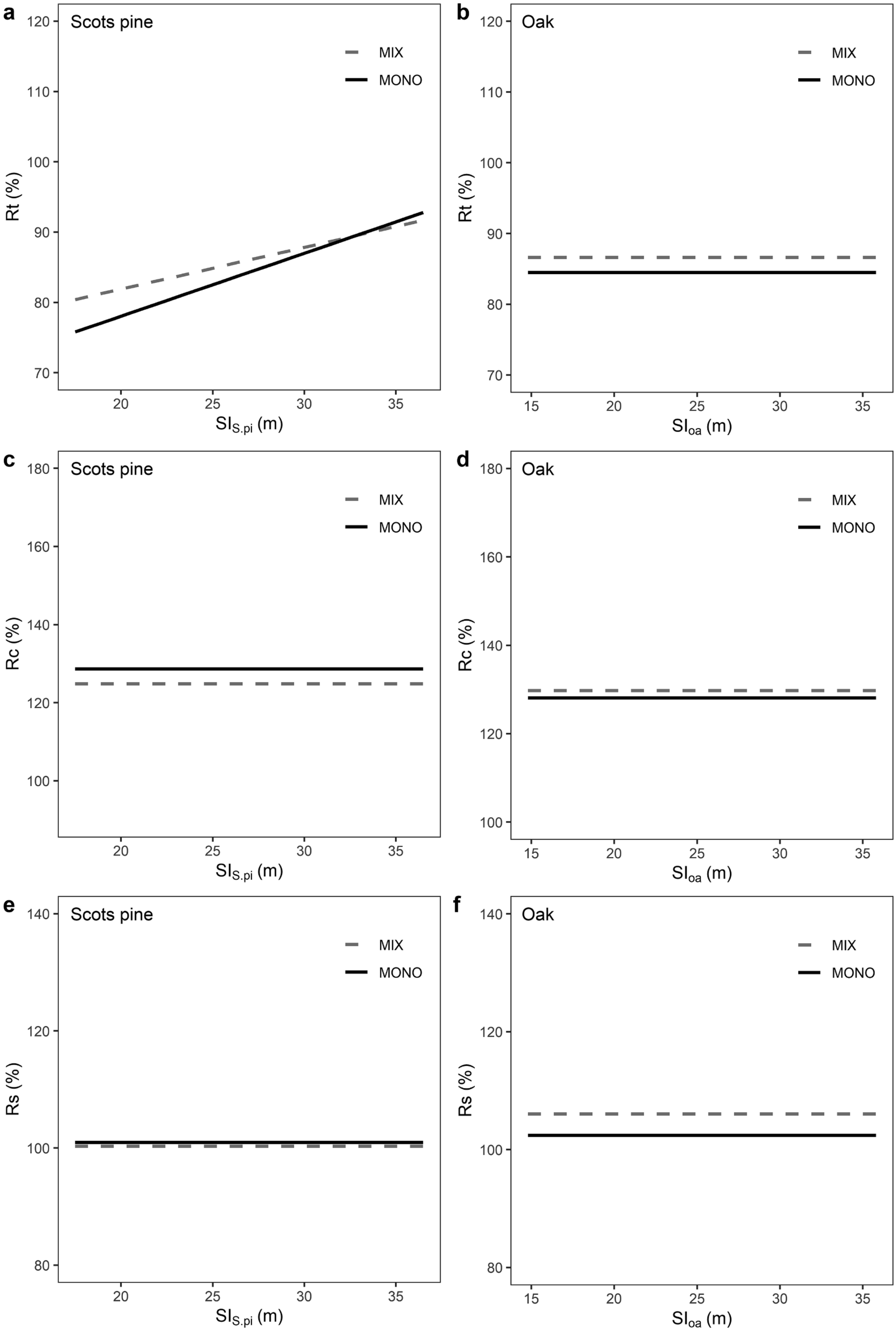

Fig. A4. Effect of the species-specific site index ($SI_{S.pi}$, SI_{oa}) on the drought response of Scots pine and oak in mixed (dashed grey line) and monospecific stands (solid black line). Lines represent the fixed effect terms from Eq. (7). Variables other than SI were set at the respective means as obtained from the data. a-b) Resistance (Rt). c-d) Recovery (Rc). e-f) Resilience (Rs).

Table A1
Site characteristics for all 33 Scots pine-oak triplets.

Triplet	Country	E	T	P	DMI	PM	Soil	Texture	SI	
									$SI_{S.pi}$	SI_{oa}
AT 1	Austria	450	7.3	543	31.5	Sand/loam over granite	Cambisol	Loamy sand	24.3	22.6
AT 2	Austria	450	7.9	548	30.8	Sand/loam over granite	Cambisol	Loamy sand	18.6	17.8
BE 1	Belgium	187	9.7	861	43.9	Shale/loess	Cambisol	Clay loam	29.4	24.2
CZ 1	Czechia	265	9.0	619	32.8	Marlstone	Arenosol	Loamy sand	26.4	20.6
CZ 2	Czechia	400	8.5	567	30.7	Fylite	Cambisol	Loamy sand	27.5	25.2
DE 1	Germany	330	8.9	716	38.0	Sandstone	Cambisol	Loamy sand	21.2	21.1
DE 2	Germany	330	8.9	716	38.0	Sandstone	Cambisol	Loamy sand	21.4	19.7
DE 3	Germany	335	9.0	715	37.7	Sandstone	Cambisol	Loamy sand	24.4	23.1
DE 4	Germany	467	8.3	749	41.1	Sandstone	Stagnosol	Silt/clay loam	30.7	28.7
DE 5	Germany	467	8.3	749	41.1	Sandstone	Stagnosol	Silt/clay loam	30.9	30.8
DE 6	Germany	27	9.2	548	28.6	Sand	Cambisol	Loamy sand	28.9	30.8
DE 7	Germany	347	9.2	493	25.7	Sandstone	Cambisol	Loam	20.7	27.5
DK 1	Denmark	40	7.8	658	36.9	Sand	Arenosol	Sand	25.8	28.0
ES 1	Spain	780	7.3	966	56.2	Sandstone	Cambisol	Sandy loam	25.1	24.7
ES 2	Spain	785	7.3	966	56.2	Sandstone	Cambisol	Sandy loam	27.1	22.7
ES 3	Spain	1635	7.2	556	32.5	Sandstone	Leptosol/Cambisol	Loam	24.2	16.3
ES 4	Spain	1149	9.9	1267	63.9	Limestone/marl/sandstone	Regosol	Silty loam	17.5	16.5
FR 1	France	149	10.8	730	35.2	Sand	Planosol	Sandy loam/clay	27.9	26.0
FR 2	France	270	9.7	910	46.2	Sandstone	Cambisol	Loamy sand	29.5	30.3
LT 1	Lithuania	76	7.0	636	37.6	Sandstone	Arenosol	Loamy sand	30.3	29.0
LT 2	Lithuania	80	7.0	636	37.6	Sandstone	Arenosol	Loamy sand	36.9	26.6
LV 1	Latvia	60	7.0	870	51.2	Sand	Retisol	Loamy sand	35.8	28.9
PL 1	Poland	128	8.9	518	27.5	Sandstone	Arenosol	Loamy sand/sand	33.8	27.3
PL 2	Poland	114	8.9	518	27.5	Sandstone	Arenosol	Loamy sand/sand	33.8	26.3
PL 3	Poland	211	7.8	561	31.6	Sandstone	Luvisol	Sand/sandy loam	32.0	29.8
PL 4	Poland	209	7.8	561	31.6	Sandstone	Luvisol	Sand/sandy loam	34.5	29.5
PL 5	Poland	220	8.6	688	37.1	Sand	Arenosol	Loamy sand	34.4	32.0
PL 6	Poland	220	8.6	688	37.1	Sand	Arenosol	Loamy sand	35.9	31.3
PL 7	Poland	200	8.6	688	37.1	Sand	Arenosol	Loamy sand	33.4	29.6
PL 8	Poland	200	8.6	688	37.1	Sand	Gleysol	Loamy sand	32.8	36.0
SE 1	Sweden	110	7.7	782	44.1	Granite	Cambisol	Sandy loam	19.5	24.8
SE 2	Sweden	120	6.6	618	37.4	Granite	Cambisol	Sandy loam	23.6	14.8
SK 1	Slovakia	223	9.6	578	29.6	Sand	Arenosol	Loamy sand	27.7	28.3

E: elevation (m a.s.l.). T: mean annual temperature (°C) (40-year average 1976–2015). P: annual precipitation total (mm) (40-year average 1976–2015). DMI: De Martonne aridity index (mm $°C^{-1}$) (De Martonne, 1926) (40-year average 1976–2015). PM: parent material. Soil: key reference soil group according to FAO WRB classification (IUSS Working Group WRB, 2015). Texture: texture class according to FAO WRB classification (IUSS Working Group WRB, 2015). SI: site index (m) for Scots pine ($SI_{S.pi}$) and oak (SI_{oa}) monocultures, referring to quadratic mean height, h_q, at age 100.

Table A2
Mean tree and stand characteristics of the 33 triplets of mixed and monospecific stands as sampled in 2017. The evaluation for each plot and species is based on the DESER-Norm 1993 by Johann (1993), using evaluation routines developed by the Chair of Forest Growth and Yield Science at the Technical University of Munich (Biber, 2013).

	MP %	Age years	d_q cm	h_q m	N trees ha^{-1}	SDI trees ha^{-1}	BA m^2 ha^{-1}	V m^3 ha^{-1}	PAIBA m^2 ha^{-1} $year^{-1}$	PAIV m^3 ha^{-1} $year^{-1}$
S. pine + oak					773	823	38.7	419	0.6	10.3
					257–2071	*450–1276*	*20.5–59.3*	*110–567*	*0.2–1.1*	*3.9–16.8*
S. pine mixed	49	74	30.9	23.7	349	440	21.9	238	0.3	5.5
	19–80	*42–132*	*19.5–48.9*	*11.9–33.2*	*51–976*	*145–837*	*7.8–36.4*	*72–475*	*0.1–0.6*	*1.6–10.7*
oak mixed	51	74	26.1	21.5	424	383	16.8	181	0.3	4.8
	20–81	*43–130*	*15.7–39.3*	*9.0–29.3*	*117–1263*	*153–769*	*5.8–29.9*	*38–307*	*0.1–0.5*	*1.5–8.2*
S. pine mono		73	28.4	23.1	795	871	41.2	431	0.7	10.4
		41–130	*18.2–39.2*	*10.8–31.2*	*327–2249*	*395–1354*	*18.3–58.6*	*99–622*	*0.3–1.3*	*3.4–15.9*
oak mono		78	27.1	22.1	774	718	32.7	363	0.6	9.1
		40–126	*14.0–40.7*	*9.1–32.3*	*181–2397*	*393–1034*	*20.3–50.6*	*110–648*	*0.2–1.1*	*4.1–14.9*

Stand characteristics are given for the mixed stand as a whole (S. pine + oak), for the species in the mixed stands (S. pine mixed, oak mixed) as well as for the monospecific stands (S. pine mono, oak mono). The means of all 33 triplets are given in plain text as well as ranges (min–max) in italics. MP: mixing proportion, based on weighted SDI (%). Age: stand age (years). d_q: quadratic mean diameter (cm). h_q: quadratic mean height (m). N: number of trees (trees ha^{-1}). SDI: stand density index (trees ha^{-1}). BA: stand basal area (m^2 ha^{-1}). V: standing volume (m^3 ha^{-1}). PAIBA: five-year (2013–2017) periodic stand basal area increment (m^2 ha^{-1} $year^{-1}$). PAIV: five-year (2013–2017) periodic stand volume increment (m^3 ha^{-1} $year^{-1}$).

Table A3
Descriptive statistics for cored Scots pine and oak trees and their respective detrended *bai* chronologies in mixtures and monocultures.

Composition	Statistic	n	dbh	Rbar	EPS
S. pine mixture	mean	27	33.1	0.44	0.93
	sd	6	8.7	0.10	0.06
	min	7	10.0	0.23	0.69
	max	36	62.0	0.66	0.98
S. pine monoculture	mean	26	31.3	0.44	0.94
	sd	5	7.8	0.08	0.02
	min	14	8.0	0.26	0.87
	max	32	61.8	0.66	0.98
Oak mixture	mean	26	28.0	0.42	0.91
	sd	7	9.8	0.15	0.08
	min	7	7.4	0.13	0.68
	max	40	63.3	0.74	0.98
Oak monoculture	mean	27	30.5	0.43	0.92
	sd	4	9.7	0.16	0.08
	min	16	7.3	0.08	0.60
	max	33	70.0	0.72	0.98

n: number of cored trees. *dbh*: diameter at breast height (1.3 m) of cored trees. *Rbar*: mean interseries correlation (average pairwise correlation between all detrended *bai* series). *EPS*: expressed population signal of detrended *bai* series.

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117908.

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