The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe


To cite this version:


HAL Id: hal-03312904
https://hal.inrae.fr/hal-03312904
Submitted on 3 Aug 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution 4.0 International License
The greater resilience of mixed forests to drought mainly depends on their composition along a climate gradient across Europe


© Forest Dynamics and Management, INIA–CIFOR, Crtra Coruina Km 7.5, 28040 Madrid, Spain
© Sustainable Forest Management Research Institute, TUM School of Life Sciences Weihenstephan, Technical University of Munich, Hans-Carl-v.-Carlowitz-Platz 2, 85354 Freising, Germany
© INRAE, University of Bordeaux, BIOECO, F-33610 Castres, France
© Department of Silviculture, Warsaw University of Life Sciences-SGGW, Nowoursynowa 159, 02276 Warsaw, Poland
© Department of Plant Production and Forest Resources, Higher Technical School of Agricultural Engineering of Palencia, University of Valladolid, Spain
© Institute of Forest Biology and Silviculture, Vysatuv Magnus University, Students, 11, Akademija, 53361 Kaunas Dvar., Lithuania
© Laboratory of Functional Ecology, Institute of Biology, University of Neuchâtel, Rue Emile-Arjand 11, 2000 Neuchâtel, Switzerland
© University of Natural Resources and Life Sciences Vienna, Department of Forest and Soil Sciences, Institute of Forest Growth, Austria
© Earth and Life Institute, Université catholique de Louvain, Croix du Sud 2, Box L7.05.09, BE-1348 Louvain-La-Neuve, Belgium
© Latvian State Forest Research Institute Silava, Riga 111, Salaspils, LV 2169, Latvia
© CEFE UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EFHE, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France
© Department for Innovation in Biological Agro-food and Forestry System (DIBAF), University of Tuscia, Via San Camillo De Lellis, SNC, 01100 Viterbo, Italy
© Department of Forest Ecology and Silviculture, Faculty of Forestry, University of Agriculture in Krakow al, 29 Listopada 46 31-425 Krakow, Poland
© Bavarian State Institute of Forestry (LWF), Hans-Carl-von-Carlowitz-Platz 1, D-85354 Freising, Germany

**ARTICLE INFO**

**Keywords:** Tree-ring data, Lloret indices, Mixing effects, Drought event

**ABSTRACT**

Despite growing evidence that diverse forests play an important role in ecosystem functioning, ensuring the provision of different ecosystem services, whether such diversity improves their response to drought events remains unclear. In this study, we use a large tree-ring database from thirty case studies across nine European countries and eleven species, covering from Mediterranean to hemiboreal forests, to test if the growth response to site specific drought events that occurred between 1975 and 2015 varied between mixed and monospecific stands. In particular, we quantify how stands resist those specific drought events and recover after them, thus analyzing their resilience. For each drought event and forest stand we calculated resistance, recovery, resilience and relative resilience and we related the variation in these indices between monospecific and mixed stands with type of admixture, tree species identity, site aridity gradient, stand basal area and stand age. We found a large variability among case studies, even for those that share similar species composition and have similar climates. On average, mixed stands showed higher resistance, resilience and relative resilience to drought events than monospecific stands. However, the beneficial effect of mixtures could not be generalized, being greatly modulated by the type of admixture and tree species identity, and depending on site water supply and stand characteristics, such as basal area and age. The increase in resilience in mixtures compared with monocultures was greater on the conifer-broadleaf admixtures, and to a lesser extent in the broadleaved-broadleaved combinations. The observed response patterns to drought largely varied among the eleven studied species, thus

https://doi.org/10.1016/j.foreco.2020.118687

Received 3 July 2020; Received in revised form 30 September 2020; Accepted 8 October 2020

Available online 28 October 2020

0378-1127/© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).
1. Introduction

Mixed forests, characterized by the coexistence of at least two tree species, represent more than two thirds of the total forested areas on Earth (FAO, 2016). A similar figure was reported for European forests, where the area of monospecific forests decreased in the last years (Forest Europe, 2015, pp 28). Over the last decades there has been a widespread agreement that tree species biodiversity plays an important role in forest ecosystem functioning (Baeten et al. 2013; Grossiord et al. 2014; Grossiord 2019), ensuring the provision of a multitude of ecosystem services (Hooper et al. 2012. Gamfeldt et al. 2013; van der Plas et al. 2016, Pretzsch et al. 2019). Moreover, mixed forests can be more stable to different disturbances, both biotic (Jactel et al. 2017) and abiotic (Anderegg et al., 2018; Pretzsch et al. 2019), while they can increase the temporal stability of community productivity (Jucker et al. 2014; del Río et al., 2017) or even increase such productivity (Jucker et al. 2014; Zhang et al. 2012; Forrester 2014; Pretzsch 2017; Jactel et al. 2018). This will result in higher amounts of carbon stored above- and belowground in mixed forests (Forrester et al. 2006; Epron et al. 2013).

Projected climate during the twenty first century will affect forest ecosystem functioning and associated ecosystem services (Pardos et al. 2015; Ammer 2019). In particular, more intense and long-lasting drought events are expected to strongly impact forests (Bonal et al. 2017, McDowell et al. 2020). In recent decades, a sharp decline in forest growth and survival, induced by more frequent and intense droughts, has already been observed in different types of forests and tree species (Aubin et al. 2016). The functional processes that contribute to drought resistance have been widely studied: alterations in tree architecture partitioning, rooting strategies, photosynthesis depletion, stomatal closure (McDowell et al., 2008; Calama et al. 2013; Pardos et al. 2010). These processes are both dependent on species-specific traits and on environmental conditions (Mitchell et al. 2008; Mayoral et al. 2016). In particular, tree species coexisting in a mixed forest can adopt different strategies (tolerance, avoidance and recovery) to cope with drought (Mayoral et al. 2015; Anderegg and HilleRisLambers, 2015, Aubin et al. 2016). Drought tolerance traits include higher xylem resistance to embolism, lower intrinsic water use efficiency, lower leaf water potential and higher wood density, which correspond to the anisohydric strategy. Avoidance traits are deep roots, rapid stomatal control and regulation of transpiration (to maintain a relatively constant midday leaf water potential as soil water potential and predawn leaf water potential decrease), characterizing the isohydric strategy. Species resistance to drought can be classified along a continuum between anisohydric and isohydric strategies (Martínez-Vilalta and García-Forner 2017; Fu and Meinzer, 2019). Recovery traits, which include abundant carbohydrates reserves, respouting ability and reproductive effort, enable trees to recover following drought-induced decline. Those differential responses to drought are supposed to allow complementarity among species, thereby facilitating the co-existence of species under stressful environmental conditions (Mayoral et al. 2015).

The role of mixed forests in the improvement of individual tree resistance to and recovery from drought (Lebourgeois et al. 2013) has been widely studied in the last years. Results from different authors showed that the benefits of mixture cannot be generalized for all forest types and tree species, noting that the species’ identity could be more important than the number of species in the mixture (Grossiord et al. 2014; Merlin et al. 2015; Pretzsch et al. 2019; Jourdan et al. 2019; Steckel et al. 2020). Furthermore, the benefits of mixtures may also depend on the climatic differences between sites and biomes (Lebourgeois et al. 2013). Although there is evidence that tree diversity regulates drought impacts in forests, it is difficult to draw general conclusions on how such diversity affects the directionality (positive vs negative effects) of forest responses to drought (Grossiord 2019).

At the community level, the beneficial interactions between species in a mixed forest that result in reduced vulnerability to drought can be explained by three different mechanisms, namely resource partitioning (e.g. root stratification or differential stomatal regulation strategies), facilitation (e.g. active hydraulic redistribution, improved soil water and reduced biotic damages during drought) and selection effects (e.g. presence of particularly drought-tolerant species) (Grossiord 2019). According to Forrester and Bauhus (2016), what seems more important to better cope with drought in mixed stands compared to monospecific stands is the coexistence of species with complementary traits that improve water availability, water uptake or water use efficiency and a compatibility with the climatic and edaphic conditions of the site. However, the complementary traits that cause the effect at one site could be different to those that cause the same effect at another site (Baeten et al. 2013). Mixing tree species might on the contrary decrease drought resistance when enhanced tree growth leads to higher evapotranspiration demand (Kunert et al. 2012; Forrester et al. 2016; Grossiord 2019). To this respect, the stress gradient hypothesis postulates that facilitation is more frequent under more unfavourable conditions (Bertness and Callaway 1994; callaway and Walker 1997). This may result in a shift from negative to positive interactions between tree species across a benign to harsh environmental gradient and interannual variations in species interactions (del Río et al. 2014). However, when analysing tree growth facilitation and competition reduction cannot be well distinguished, and only the net effect of species interactions can be observed. Thus, the broader framework proposed by Forrester (2014), which consider simultaneous occurrence of competition reduction and facilitation and different variation patterns with environmental conditions depending on the main limiting factor, is more suitable for interpreting spatio-temporal variation in tree species interactions.

Another issue to consider is whether all the species will benefit from the mixture, or one of them benefits at the expense of the other species. It has been shown that different tree species in mixed stands differ considerably in their response to drought (Pretzsch et al. 2016). While some species show a positive response to drought (i.e., less stressed in mixed stands), others show a negative response (i.e., they are affected by drought even in mixed stands) or even a neutral one, but with potentially different responses along the geographical range of the species (Aubin et al. 2016). Vulnerability to water stress for a given species may also depend on stand basal area (Forrester et al. 2016), stand density (Bottero et al. 2017) and stand age (Sohn et al. 2016). These are important issues to consider when conducting studies across large geographical scales, where local site characteristics, climate conditions, forest management, forest type, tree species assemblages (and their related functional traits) are likely to interact, making the identification of species mixture effects more complex (Grossiord, 2019; Bello et al., 2019).

In this study, we used tree ring data from thirty case studies covering from Mediterranean to hemiboreal forests and eleven tree species to test whether the response of mixed stands to drought events differed to that of monospecific stands. Furthermore, we investigated whether such differential response to drought varied with the type of admixture, tree species identity, site aridity gradient, stand basal area and stand age. For
assessing tree responses to drought, we used the three components proposed by Lloret et al. (2011): resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience (RRs). More specifically we tested the following hypotheses:

**Hypothesis I**: tree growth response to drought events differs between mixed and monospecific stands.

**Hypothesis II**: The benefits of mixture to cope with drought events cannot be generalized to the three types of admixtures found (conifer-conifer, conifer-broadleaved, broadleaved-broadleaved)

**Hypothesis III**: Tree growth response to drought events in monospecific and mixed stands is mediated by the identity of tree species

**Hypothesis IV**: Tree growth response to drought events in monospecific and mixed stands vary along an aridity gradient

**Hypothesis V**: Tree growth response to drought events in monospecific and mixed stands depends on stand characteristics (basal area and age)

2. Material and methods

2.1. Experimental sites

This study was performed using data from 30 case studies spread over 9 countries that represent different European forest stands, including both natural forests and plantations. Stands were located along a gradient from hemiboreal to Mediterranean forests, spanning from central Spain to northern Latvia (Table A1, Fig. 1). Altogether, the case studies cover the main admixtures found across Europe, including conifer and conifer (Pinus-Juniperus; Pinus-Pinus; Pinus-Picea; Picea-Abies; Larix-Pinus; Larix-Picea), conifer and broadleaved (Pinus-Quercus; Pinus-Fagus; Picea-Fagus; Larix-Quercus, Larix-Alnus, Larix-Tilia) and broadleaved and broadleaved (oak-beech). We considered many important tree species for the bioeconomy of European forests such as Fagus sylvatica, Quercus pyrenaica, Quercus petraea, Quercus robur, Quercus pubescens, Pinus sylvestris, Pinus pinaster, Pinus nigra, Picea abies, Abies alba and Larix decidua, with most tree species occurring in several case studies. The studied species showed different functional traits that are described in Table 1.

In twenty-five case studies out of the total of thirty, plots were organized in triplets. A triplet consisted of a set of three plots that included a two-species mixed stand and the two monospecific stands of the component species of the mixed stand. In the other five case studies (SP1, LI1, LI2, LI3, and LI4), plots were divided between monospecific and mixed stands of the two species were usually arranged in small groups. Plots were located at elevations between 20 and 1400 m a.s.l. (mean = 460 m), with mean annual precipitation ranging from 435 to 1200 mm (mean = 812 mm) and mean annual temperature from 5.6 to 13.5 °C (mean = 8.6 °C) (Table A1).

2.2. Data collection and dendrochronological analyses

Two perpendicular increment cores at breast height were taken per tree. The total number of trees cored was 3,298 trees (Table A2). Annual ring widths were measured from each increment core using standardised dendrochronological techniques (Speer 2010). At the end of the growing season, when cores were taken, different dendrometric variables were measured on each plot, both at tree (diameter at breast height of all trees in each plot) and stand level (mean diameter, mean height, basal area and tree density).

To analyze the effect of drought on tree growth we calculated the tree basal area increment (BAI, cm²), using mean annual ring width of both increment cores:

\[ BAI = \pi \times \frac{1}{4} (d_t^2 - d_{t-1}^2) \]  

where \(d_t\) and \(d_{t-1}\) are the tree diameter at breast height at the end (\(d_t\)) and the beginning (\(d_{t-1}\)) of a given annual ring increment corresponding to rings formed in year \(t\) and year \(t-1\), respectively.

To eliminate the biological growth trends and to produce stationary and residual tree ring width chronologies (Fritts et al., 1990) we used a detrending procedure and an autocorrelation removal with the Friedman supersmooother spline (Friedman, 1984) and autocorrelation modeling. Through this procedure we obtained chronologies of dimensionless indices (CDI), preserving a common variance with interannual time scales. To assess the reliability of the chronologies, we calculated descriptive statistics using ‘dpTR’ R package (Bunn 2010) for each species and plot, including Rbar (mean interseries correlation) and EPS (expressed population signal of detrended BAI series) (Table A2). Rbar has been used to measure the strength of the common growth signal within each chronology (Wigley et al 1984), while EPS is used to measure the reliability of chronologies (Lindholm et al. 1999). In our study, mean Rbar was 0.37, indicating a medium common signal for each species and plot. Mean EPS was 0.88, a value above the threshold of 0.85 indicating that chronologies were reliable and well replicated.

2.3. Climate data

We used climate data on a monthly basis (precipitation, mean, maximum and minimum temperature) for each case study. Climate data were obtained from meteorological stations nearby each case study site. When data were not available, they were obtained from the CGMS database (AGRI4CAST, http://mars.jrc.ec.europa.eu/mars). Monthly data were used to calculate mean annual temperature (\(T^\circ\), °C) and annual precipitation (P, mm) from 1975 to 2015 (see Figure A1 for the relationship between mean annual temperature and total annual precipitation). For characterizing the climatic water supply for each case study, we used the annual De Martonne aridity index (DMI, mm °C⁻¹) (Eq. (2)) and De Martonne aridity index for the summer months (June, July and August) (DMIsummer, mm °C⁻¹) (Eq. (3)), for the period 1975–2015.

![Fig. 1. Location of the 30 case studies across Europe. Species studied in each case study are shown in parenthesis. Aa: Abies alba; Fs: Fagus sylvatica; Pa: Picea abies; Pn: Pinus nigra; Pp: Pinus pinea; Ps: Pinus pinaster; Ps: Pinus sylvestris; Qp: Quercus petraea; Qp: Quercus pubescens; Qr: Quercus pyrenaica; Ld: Larix decidua.](image-url)
Table 1: Environmental and functional characteristics of the studied species.

<table>
<thead>
<tr>
<th>Environmental preferences</th>
<th>Fagus sylvatica</th>
<th>Quercus petraea</th>
<th>Quercus pubescens</th>
<th>Quercus pyrenaica</th>
<th>Pinus nigra</th>
<th>Pinus pinea</th>
<th>Pinus sylvestris</th>
<th>Pinus pinaster</th>
<th>Abies alba</th>
<th>Picea abies</th>
<th>Larix decidua</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environmental preferences</td>
<td>shade tolerant</td>
<td>prefers more shaded environments</td>
<td>more light-demanding</td>
<td>Light demanding</td>
<td>grows preferably in sandy, stony and well-drained soils</td>
<td>More light demand-ding</td>
<td>grows mainly in sandy soils with low water retention</td>
<td>grows better in humid conditions</td>
<td>water uptake in the upper soil layers</td>
<td>Light demand-ding</td>
<td></td>
</tr>
<tr>
<td>Root system</td>
<td>Resprouting ability: capacity to recovery after drought (Mayoral et al. 2015)</td>
<td>shallow root system</td>
<td>preserve its taproot until maturity</td>
<td>deep root system with taproot (Kostler et al. 1968)</td>
<td>Multistratified root system (de-Dios-García et al. 2018)</td>
<td>Deep root system with taproot (Kostler et al. 1968)</td>
<td>Rather shallow root system (Pueh 2003; Filipiak, 1992)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sensitivity to drought</td>
<td>sensitive to drought, but recovers easily after a drought (Jourdan et al. 2019)</td>
<td>less sensitive to drought</td>
<td>lower sensitivity to high temperatures during drought</td>
<td>relatively tolerant to drought although cumulative water deficit constrains their growth in the long term (Sperlich et al. 2011)</td>
<td>dependent on access to a variable groundwater belowground competition is limiting for growth (Roaas et al. 2011)</td>
<td>can profit from sporadic rain events during drought (Marozas et al. 2012)</td>
<td>relatively tolerant to drought for an alpine coniferous species (Jourdan et al. 2020)</td>
<td>falls back after drought, but recovers quickly (Pretzsch, Schütze and Uhl, 2013)</td>
<td>more sensitive to drought than other conifers (Nöthdurf and Engel 2020)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physiological and morphological traits to cope with drought</td>
<td>Stomata opening extended much further into drought: anisohydric behaviour</td>
<td>Maintenance of low osmotic potentials during drought</td>
<td>genetic variability and a high degree of phenotypic plasticity to water availability</td>
<td>Early stomata closure during drought: isohydric behaviour</td>
<td>lower transpiration rates and water potential gradients compared to other pines (Martínez-Vilalta and Pino, 2002)</td>
<td>High plasticity in water use efficiency (Fornes et al., 2018)</td>
<td>Under dry soil conditions, a high degree of stomatal control maintains needle water potential well above the cavitation threshold of the species (Cortés et al. 2012)</td>
<td>Dramatic decrease in photosynthesis (Camarero et al. 2013)</td>
<td>High evaporative transpiration rates (Gazol and Camarero, 2015)</td>
<td>Reduced photosynthesis under mild drought condition (Marozas et al. 2019)</td>
<td>stomatal-limited photo-synthesis, reduced assimilation (Voláš et al. 2020)</td>
</tr>
</tbody>
</table>
Because of its minimal data requirement but high explanatory strength, this index has been widely used to describe drought conditions or aridity of a region (Bielak et al. 2014). The higher the index, more water supply is available for tree growth.

\[
DMI = \frac{P}{T + 10}
\]

\[
DMI_{\text{summer}} = \frac{P_{\text{summer}}}{T_{\text{summer}} + 10}
\]

In our study, DMI ranged between 19.9 and 66.1 mm °C⁻¹ (mean = 45.9 mm °C⁻¹), and DMI_{summer} from 1.5 to 16.2 mm °C⁻¹ (mean = 8.4 mm °C⁻¹). According to the De Martonne index climatic classification (Baltas 2007), the case studies ranged from semi-dry (in central Spain) to very humid categories (in south-eastern Germany) (Table A1).

2.4. Selection of site specific drought events

To study the effect of drought events on tree growth, we selected for each case study those years with drought conditions that have negatively affected tree growth (namely, site-specific drought events). These site specific drought events had to meet two conditions (see Steckel et al. (2020) for more details): (1) they must be considered as drought years, based on climatic conditions; and (2) they must have significantly reduced tree growth (namely, pointer years).

For this purpose, we first selected drought years using the climate data. Drought years were identified by means of the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) that was calculated using the SPEI R package. This procedure ensures that the observed meteorological anomaly is reflected by drought stress suffered by the individual trees (Steckel et al., 2020). The SPEI is a multi-scalar drought index based on a monthly balance of precipitation and potential evapotranspiration (PET) that estimates the drought intensity, according to its strength and duration. In our study, PET was calculated for a time span of six months using the Thornthwaite equation (Thornthwaite, 1948). An SPEI value below (-1) corresponded to a dry period and SPEI values above (+1) corresponded to wet periods. Following Steckel et al. (2020), we considered drought years those that displayed at least one month with an SPEI ≤ -1 during the growing season. The growing season corresponded to those months with mean minimum temperature above 10 °C.

Secondly, we identified negative pointer years, that is, years that showed a remarkable reduction in tree growth at the individual level. We used the pointerRES R package (Van der Maaten-Theunissen et al., 2015) that uses the normalization in a moving window, relating tree growth in a year to the average growth of a fixed number of preceding years. In our study, we used a window width of four years. Years were considered as pointer when at least 60% of the de-trended BAI series of at least one of the two species in the monospecific plots of each study site showed an episode that indicated a growth decrease of 75% compared to the mean value.

Lastly, in order to confirm that these periods of growth reduction corresponded to drought conditions rather than to other biotic (e.g. pests and diseases) or abiotic (e.g. frosts) factors, we chose years that were both drought years and pointer years. Site specific drought events were then used to evaluate the relationship between the reduction in tree growth and drought in monospecific and mixed stands.

The effect of drought events on tree growth was assessed for the period 1975–2015. As mentioned before, drought events were specific to each case study. The final number of drought events for each case study ranged from one to five (Table A1).

2.5. Growth responses to specific drought events

For each specific drought event and sampled tree, we calculated the tree drought response indices proposed by Lloret et al. (2011): resistance (Rt) (Eq. (4)), recovery (Rc) (Eq. (5)) and resilience (Rs) (Eq. (6)). The resistance index Rt quantifies the ratio between tree growth during the drought event (G_{\text{Dr}}) and the mean growth during some previous years (G_{\text{PreDr}}). Thus, it quantifies the capacity of trees to cope with drought stress, being able to continue to grow during drought. A value of Rt = 100 indicates complete resistance. The recovery index Rc quantifies the ratio in growth between the period after (G_{\text{PostDr}}) and during the drought event (G_{\text{Dr}}). It describes the ability of trees to resume growth after the drought event. A value of Rc = 100 indicates the persistence of the growth level during the drought event, Rc < 100 indicates further decline and Rc > 100 indicates a recovery from the growth level during the drought event. The resilience index Rs quantifies the ratio in tree growth after (G_{\text{PostDr}}) and before (G_{\text{PreDr}}) the drought event. Thus, it measures the capacity of trees to recover the growth rates observed before the drought event. Values of Rs = 100 indicate a full recovery, Rs > 100 an increased growth after the drought event, while Rs < 100 indicates growth decline.

\[
R_t = \frac{G_{\text{Dr}}}{G_{\text{PreDr}}} \times 100
\]

\[
R_c = \frac{G_{\text{PostDr}}}{G_{\text{Dr}}} \times 100
\]

\[
R_s = \frac{G_{\text{PostDr}}}{G_{\text{PreDr}}} \times 100
\]

The Lloret indices have been used for a large variety of research topics, across a large number of species, which cover different growth characteristics, forest types and climatic regions. Although widely used, there has been some critique regarding the interpretation of the results using these indices due to the hypothesized trade-off between recovery and resistance, not being clear which of these two indices is more important to overall resilience (Schwarz et al. 2020). Complementing these three indices with the relative resilience index (RRs) (Eq. (7)) could mitigate these effects, as this index accounts for the damage experienced during disturbance (Lloret et al. 2011). The rationale of RRs is that the ability to achieve the levels of pre-disturbance performance depends on the impact (ie., tree growth reduction) during disturbance. Values of RRs < 100 indicates that the effect of the event persists after disturbance, with lower values indicating decreasing resilience. High resistance to the disturbance reduces to relative resilience, while low resistance increases RRs.

\[
RR_s = \frac{G_{\text{PostDr}} - G_{\text{PreDr}}}{G_{\text{PreDr}}} \times 100
\]

All four indices were obtained from de-trended BAI series for all individual trees. Tree growth for the periods before (G_{prevent}) and after (G_{postevent}) the drought event were calculated as the average growth during the four years before or after the drought event. We used a period of four years because it was assumed to be more robust than results obtained for 2 or 3 years.

2.6. Data analysis

To test our hypotheses we studied how the four components of the growth response to drought varied as a function of stand composition. Models were fitted separately using Rt, Rc, Rs and RRs response variables. We constructed linear mixed-effect models including case study and drought event as random effects, in order to cope with the lack of independence associated with observations at that level. All fitted models were visually checked for homoscedasticity and normal distribution of the residuals (Zuur et al. 2009, 2010). All statistical analysis were performed using SAS® PROC MIXED.

The different hypotheses were tested by including and checking the level of significance of different continuous or categorical explanatory covariates (see Table A3).
Hypothesis I: Tree growth response to specific drought events differs between mixed and monospecific stands

To test whether there was a general effect of stand composition (mixed vs monospecific) on the response components of tree growth to specific drought events we fitted Eq. (8) to the whole database.

\[ Y_{ijkl} = \mu + SCM_{ijk} + CS_{ik} + D_{il} + \epsilon_{ijkl} \]  

where \( Y \) refers to the response variable (Rs, Rt, Rc or RRs); SCM represents the fixed effect for stand composition (Mixed or Monospecific); CS and D are random effects of case study and drought event, respectively, D being nested into the case study. Finally, \( \mu \) is the intercept of the model and \( \epsilon_{ijkl} \) represents the independent and identically distributed residual error. Subscripts \( i, j, k \) and \( l \) refers to the \( i \)th plot of the \( j \)th case study, for the \( j \)th drought event.

Hypotheses II: The benefits of mixture to cope with drought events cannot be generalized to the three types of admixtures found (conifer-conifer, conifer-broadleaved and broadleaved-broadleaved)

To check whether the effect of stand composition (mixed vs monospecific) on tree growth response to drought events were dependent on the three types of admixtures found (TM, Table A3), we fitted Eq. (9).

\[ Y_{ijkl} = \mu + TM_{ij} + SCM_{ijk} + [TM \times SCM]_{ijkl} + CS_{ik} + D_{il} + \epsilon_{ijkl} \]  

Hypotheses III: Tree growth response to drought events in monospecific and mixed stands is mediated by the identity of tree species

To test this hypothesis we first fitted Eq. (10).

\[ Y_{ijkl} = \mu + Species_{ij} + SCM_{ijk} + [Species \times SCM]_{ijkl} + CS_{ik} + D_{il} + \epsilon_{ijkl} \]  

If a significant effect of the species was detected, we refitted Eq. (8) separately for each species in order to analyze their response in monospecific and mixed stands.

In addition, in order to check the differences in growth response for a given tree species between monospecific and mixed stands, we fitted Eq. (9) separately, for those species that were present in more than one case study (Pinus pinaster, P. sylvestris, Fagus sylvatica, Picea abies, Abies alba, Quercus petraea).

Hypothesis IV: Tree growth response to drought events in monospecific and mixed stands varied along an aridity gradient.

To test this hypothesis we expanded Eq. (8) by adding as explanatory covariate the general De Martonne aridity index during the studied period (1975–2015) at each case study (Eq. (11)):

\[ Y_{ijkl} = \mu + SCM_{ijk} + DMI_{ij} + [SCM \times DMI]_{ijkl} + CS_{ik} + D_{il} + \epsilon_{ijkl} \]  

Hypothesis V: Tree growth response to drought events in monospecific and mixed stands depends on stand characteristics (basal area and age)

To analyze the influence of stand characteristics (basal area and age) at plot level on tree growth response to drought events in mixed vs monospecific stands, we expanded Eq. (8) by adding as explanatory covariates the basal area (BA) and the age (Age) of the plot at the time of the drought event (Eq. (12) and Eq. (13)):

\[ Y_{ijkl} = \mu + SCM_{ijk} + BA_{ij} + [SCM \times BA]_{ijkl} + CS_{ik} + D_{il} + \epsilon_{ijkl} \]  

\[ Y_{ijkl} = \mu + SCM_{ijk} + Age_{ij} + [SCM \times Age]_{ijkl} + CS_{ik} + D_{il} + \epsilon_{ijkl} \]

The full methodology is summarized in Figure A2.

3. Results

3.1. Influence of stand composition (monospecific vs mixed stands) on tree growth response to specific drought events

When considering the whole database with 30 case studies (Hypothesis I) we observed that overall mixed stands showed greater resistance (P-value = 0.0564), resilience (P-value < 0.0001) and relative resilience (P-value = 0.0283) compared to monospecific stands, while no significant differences were detected for recovery (Fig. 2). Interestingly, monospecific stands showed a slight growth decline after the drought event (Rs = 99%), while growth slightly increased in mixed stands after the drought event (Rs = 102%). Despite these general trends, we detected a large variability among case studies, even for those case studies that share the same species composition and have similar climates (Figure A3).

3.2. Influence of the type of admixture (conifer-conifer, conifer-broadleaved and broadleaved-broadleaved) on tree drought response in monospecific and mixed stands

The effect of species mixing on drought responses varied with the type of admixture (Hypothesis II), as stated by the significant interaction effect of stand composition × type of admixture for Rc (P-value = 0.0250), Rt (P-value = 0.0458) and Rs (P-value = 0.0499) (Table A4, Fig. 3). Mixed stands in broadleaved-broadleaved (P-value = 0.0458) and conifer-broadleaved (P-value = 0.0045) admixtures were more resistant to drought than monospecific stands. Resilience in mixed stands was also greater than in monospecific stands for these two types of admixtures (P-value = 0.0696 in broadleaved-broadleaved and P-value < 0.0001 in conifer-broadleaved admixtures). Trees in the three types of admixtures resumed growth after the drought event, but only in the conifer-conifer admixtures did mixed stands show higher recovery (P-value = 0.0289). Mixed stands in the conifer-conifer admixtures showed greater relative resilience compared to monospecific stands (P-value = 0.0510).

3.3. Influence of tree species identity on tree drought response in monospecific and mixed stands

The effect of drought on tree growth (Hypothesis III) differed between tree species (Table A5). As we detected a large significant effect of the species on the indices, and on the interaction between stand composition and tree species in recovery, resistance and relative resilience, we analyzed the response of each species separately in monospecific and mixed stands (Fig. 4). While recovery, resistance and relative difference differed between species, both in monospecific (P-
value < 0.0001) and mixed stands (P-value < 0.0001), resilience differed between species only in monospecific stands (P-value = 0.0053). The greatest recovery was shown in *Pinus pinea* for monospecific and mixed stands, while the lowest values were observed in *Abies alba* for monospecific stands and for *Quercus pubescens* in mixed stands. The greatest resistance was shown for *Pinus nigra* in monospecific stands and for *Quercus pubescens* in mixed stands, while the lowest values were shown for *Quercus pyrenaica* in monospecific stands and for *Pinus pinea* in mixed stands. Greater resilience was shown for *Quercus pubescens* in monospecific stands and *Pinus pinea* in mixed stands, while the lowest values were shown for *Quercus pyrenaica* for monospecific and mixed stands. Greatest relative resilience was shown in *Pinus pinea*, both in monospecific and mixed stands, while the lowest values were shown for *Pinus nigra* in monospecific stands and for *Abies alba* in mixed stands.

When focusing on the tree species that were present in different admixtures, we found that the species differed in their response patterns to drought (Table A5). *Pinus pinaster* (P-value < 0.0001), *Fagus sylvatica* (P-value = 0.0020) and *Abies alba* (P-value = 0.0579) showed a greater resistance in mixed stands compared to monospecific stands, although *Pinus pinaster* and *Fagus sylvatica* in mixed stands showed lower recovery (P-value = 0.0003 for *Pinus pinaster*, P-value < 0.0001 for *Fagus sylvatica*) and relative resilience (P-value = 0.0262 for *Pinus pinaster*, P-value = 0.0035 for *Fagus sylvatica*). *Pinus sylvestris* (P-value = 0.0357) showed higher resistance in monospecific stands, but lower recovery (P-value = 0.0011). *Pinus pinaster* (P-value = 0.0662), *Picea abies* (P-value = 0.0389), *Pinus sylvestris* (P-value = 0.0148), *Quercus petraea* (P-value = 0.0004) and *Larix decidua* (P-value = 0.0407) showed a significantly higher resilience in mixed stands compared to monospecific stands. *Larix decidua* (P-value = 0.0465), *Picea abies* (P-value = 0.0269) and *Pinus sylvestris* (P-value < 0.0001) showed a significantly higher relative resilience in mixed stands compared to monospecific stands.

If we analyzed in more detail the response to drought of the species according to whether it is accompanied by a conifer or a broadleaved species (Table 2), we found that *Fagus sylvatica* was more resistant in mixed stands, both when mixed with a conifer (P-value = 0.0173) and a broadleaved species (P-value = 0.0261), while the recovery was greater in monospecific stands (P-value = 0.0004 when mixed with a conifer, P-value = 0.0798 when mixed with a broadleaved species). Relative resilience in *Fagus sylvatica* was greater in monospecific stands when mixed with a conifer (P-value = 0.0086). *Pinus sylvestris* resilience (P-value < 0.0001), relative resilience (P-value < 0.0001) and recovery from drought (P-value = 0.0027) only increased when mixed with a broadleaved species, but not with a conifer. *Abies alba* and *Pinus pinaster* resistance to drought increased when mixed with a broadleaved species (P-value = 0.0068, P-value < 0.0001, respectively), but not with a conifer, and the recovery was greater in monospecific stands (P-value = 0.058, P-value < 0.0001, respectively). Relative Resilience of *Pinus pinaster* was greater in pure stands when mixed with a broadleaved species (P-value = 0.0275). Resilience of *Quercus petraea* was greater both when mixed with a conifer (P-value = 0.0075) and a broadleaved species (P-value = 0.0161).

3.4. Influence of the site aridity gradient (De Martonne index) and stand characteristics (basal area and age) on tree growth response to specific drought events in monospecific and mixed stands

Resilience to specific drought events was not constant along the site aridity gradient (Hypothesis IV). Thus, resilience increased under drier site conditions (P-value = 0.0311) (Table A6, Fig. 5). The increase in resilience in drier sites was not significantly different in monospecific compared to mixed stands (non-significant interaction between stand composition and DBH), although a trend to higher resilience was observed in mixed stands in the drier sites (Fig. 5). This effect was found for relative resilience, i.e., higher relative resilience in mixed stands in the drier sites (P-value interaction = 0.0854).

Stand basal area and stand age (Hypothesis V) had also a significant effect on the growth response to drought, both in monospecific and mixed stands (Table A6, Fig. 6). Stands with older trees were more
Fig. 4. Amoeba diagrams for pure and mixed stands representing Resistance (Rt), Recovery (Rc), Resilience (Rs) and Relative Resilience (RRs) for the eleven species studied. The value 1 represents the maximum value observed for Rt, Rc or Rs in pure or mixed stands.
resistant (P-value < 0.0001) to drought, as well as more resilient (P-value = 0.0658) and with greater relative resilience (P-value = 0.0014). Stands with higher stand basal area were also more resistant (P-value < 0.0001) and resilient (P-value < 0.0001) to drought events. The significant interaction between stand age and stand composition for resistance (Rt) (P-value = 0.0545) indicated a greater effect of stand age in mixed stands than in monospecific stands. Regarding recovery (P-value = 0.0135) and relative resilience (P-value = 0.0024), mixed stand showed lower recovery and lower relative resilience with increasing age, while monospecific stands recovery and relative resilience remained relatively constant with age. The significant interaction between stand basal area and stand composition for resilience Rs (P-value = 0.0045) indicated that mixed stands with greater basal area recovered better from drought than monospecific stands.

4. Discussion

In line with a number of recent studies (e.g. Pretzsch et al. 2013; Metz et al. 2016; Jucker et al. 2016; Steckel et al., 2020), our results using a large database from thirty case studies covering a wide climatic gradient and including eleven common tree species in Europe indicated, on average, a positive effect of mixing on tree growth response to drought, especially on resilience and relative resilience and to a lesser extent on resistance. However, we found a large species-specific variability in growth response to drought in monospecific and mixed stands, being mediated by the type of admixture and more particularly the association of conifers and broadleaves. Moreover, the general positive effect of mixing on resilience to drought was influenced by stand age and basal area, while relative resilience was influenced by stand age. Meanwhile, the resilience along an aridity gradient decreased both in monospecific and mixed stands, although higher resilience to drought was observed in the Mediterranean case study (SP1) characterized by the driest and hottest environment. Additionally, this case study showed higher relative resilience. These findings confirm the general trend towards improved resilience of mixed forests. It is important to note that while these correlative studies are important, they have not proven to be adequate for predicting which mixtures and on which sites certain species will be appropriate (Grossiord 2019). Meanwhile, process-based approaches, including models and carefully designed experiments, can be of great help to predict the growth limitations to climate and species interactions, and therefore these could be used as well (e.g. Pretzsch et al., 2015).

The indices studied displayed different patterns across the case studies. The negative correlation observed between resistance to drought and recovery from drought has been previously reported (Galiano et al., 2010; Thurm et al. 2016; Gazol et al. 2017). According to Steckel et al. (2020) the negative relationship suggests a trade-off between both indices, and could be attributed to more nutrients available following low growth episodes in monospecific stands than in mixed stands. Thus, under the improving belowground resources that follow a drought event, the relationship between species may change from positive to negative, which is in line with the stress gradient hypothesis (Maestre et al. 2009) and Forrester’s framework (Forrester, 2014).

4.1. Monospecific and mixed stands respond differently to drought events

Our results show that tree species mixing can have a significantly positive effect on forest response to drought, which means that trees have greater resistance, resilience and relative resilience when growing with heterospecific neighbours than when growing with conspecifics (Fig. 2). Favourable interactions between heterospecific neighbours in mixed stands generally increase forest resistance to natural disturbances and environmental fluctuations (Pretzsch et al. 2013; Jactel et al. 2017), which suggests that trees might be able to sustain growth even under
suboptimal growing conditions (e.g. del Río et al. 2014; Pretzsch et al. 2013; Forrester 2014). Greater resistance and resilience in mixed stands are mainly explained by two interconnected processes, which are reduced competition through niche partitioning (Jucker et al. 2014) and facilitation (Vandermeer, 1989; Steckel et al., 2020). In terms of niche partitioning, the development of multi-layered canopies in mixed stands, with different crown architecture and phenology, where shade tolerant species can establish below taller, light demanding species, may enable an efficient complementary light use (Binkley et al., 2003; Sapijanskas et al., 2014 and Forrester et al., 2018). This can allow mixed forests to exploit canopy space more efficiently (Molin et al. 2011, Pretzsch 2014; Toigo et al. 2018), thereby maximizing light interception (Ammer 2019), even under drought conditions. Similar belowground complementarity may occur when there is a partitioning in the use of water resources in the soil. Thus, some species that extend their root systems towards deeper soil layers can coexist with others that occupy superficial layers. Underlying facilitation processes such as hydraulic lift and higher functional diversity of the fungal community can also improve water access and use in mixed stands (Grossiord et al. 2014). Higher relative resilience can be interpreted in two ways, as it can reflect either higher buffer capacity to recover or compensating positive effects of the impact via increased neighbour mortality and resource availability to surviving trees (Lloret et al. 2011).

4.2. The benefits of tree mixing to cope with drought events depend on the type of admixture (conifer-conifer, conifer-broadleaved and broadleaved-broadleaved)

The strength of the positive effect of mixed stands on drought response varied considerably with the type of admixture, being mainly observed in conifer-broadleaved admixtures, and to a lesser extent in broadleaved-broadleaved admixtures (Table A4, Fig. 3). Mixed stands formed only by conifers likely exhibit higher competition and niche overlapping due to more similar species traits, whereas in conifer-broadleaved admixtures, belowground partitioning and spatiotemporal niche separation between species may drive complementary or asynchronic response to drought (de Dios García et al. 2018). The trait complementarity between conifer and broadleaved species can result in improved exploitation of underground water resources, as their root morphology and architecture differs considerably (Ammer 2019). Conifers and broadleaves in mixed stands are known to utilize deep water resources more efficiently than in monospecific stands and even exhibit complementarity for limited water resources (Bello et al. 2019). In this type of admixtures, broadleaves (mainly Quercus species) play an important facilitating role. They drive a hydraulic lift under drought conditions, thereby increasing the water available in the upper soil layers (Steckel et al. 2020) that could be more easily used by the shallow root system of the conifers, thus, increasing resistance to drought. Furthermore, different growth dynamics such as the date of budburst, radial growth onset and contrasting patterns of carbon allocation (e.g. Michelot et al. 2012; Zweifel et al. 2006), together with differences in optimum temperature for photosynthesis in broadleaves compared to conifers, may also favour complementarity effects (de Dios García et al. 2018). Conifer-conifer mixtures did not differ in terms of resistance and resilience with monospecific conifer stands, which could be linked to their more similar traits and mainly isohydric behaviour (Table 1). However, these mixtures showed a better recovery than the respective monospecific stands. We can hypothesize that as conifers show in general a drought avoidance strategy (see Table 1 for references), niche complementarity between them may help during the recovery phase.

In our study, we found that the type of mixture matters not only at the functional or phylogenetic level (i.e. conifer vs broadleaved) but also at the tree species composition level (Table A5, Fig. 4), pointing out to a species identity effect (Forrester et al. 2016). According to Anderreg et al. (2018) and Fichtner et al. (2020), positive effects of mixing increase with increasing taxonomic diversity of neighbours, mainly, with
species hydraulic traits. Let us focus on the two species (*Pinus sylvestris* and *Fagus sylvatica*) that are most commonly found in the different case studies (Table 2). The positive effect of mixing could be explained by a complementarity effect that arises from facilitation (one species improves the environmental conditions for another species) or reduced competition (niche differentiation), although both types can be present at the same time (Forrester and Bauhus 2016). Thus, the isohydric, drought sensitive *Pinus sylvestris* would benefit from species mixture when growing with anisohydric broadleaved species such as *Fagus sylvatica* or *Quercus petraea*. Furthermore, the differences in the demands for light between the species (e.g. shade tolerance, crown architecture and leaf phenology) could favour their complementarity (e.g. pioneer, shade intolerant *Pinus sylvestris* vs late-successional, shade tolerant *Fagus sylvatica*) (Pretzsch et al. 2015; Pretzsch et al. 2019), although this was not clearly observed in our study. *Fagus sylvatica* was found to exhibit higher resistance to drought when mixed with both conifers (*Picea abies*, *Abies alba*, *Pinus sylvestris* or *Pinus nigra*) and broadleaves (*Quercus petraea* or *Quercus pubescens*), while the recovery and relative resilience was...
greater in monospecific stands compared to mixed stands. Thus, it seems that *Fagus sylvatica* can benefit from the mixture in terms of resistance to drought, irrespective of the type of admixture. It has been shown that *Fagus sylvatica* strongly determines the microclimate when mixed with other species (Heinrichs et al. 2019), usually benefiting more from the mixture than its neighbours. 

4.3. Drought responses in monospecific and mixed stands along the site aridity gradient 

Resilience and relative resilience to specific drought events were not constant along the site aridity gradient (Table A6, Fig. 5). Thus, we observed how both indices increased in those sites with drier conditions, ie, with lower De Martonne index. Several studies have reported drier forests to be more adaptable to the future drought events than the wetter forests (Zang et al. 2014). However, there is not a general consensus, when comparing monospecific vs mixed stands located along an aridity gradient, if the facilitative processes among coexisting species in a mixture will be more beneficial in drought-prone environments (Ruhk et al. 2020). In our study, the increase in resilience to drought events along the site aridity gradient was not significantly different in monospecific compared to mixed stands, although a trend towards higher resilience was observed in mixed stands in the drier sites along the gradient. In particular, higher resilience and relative resilience to drought was observed in mixed stands in the most drought-prone case study, which corresponded to the Mediterranean continental case study SP1 (Table A1), characterized by a high acclimation to high drought stress intensity (de-Dios-García et al., 2015). However, based on our results, the overall pattern we found along the studied site aridity gradient was not consistent with the stress-gradient hypothesis, which suggests that facilitation occur more frequently and are more important under drier sites (Grossiord et al. 2014).

4.4. Stand basal area and age affect growth response to drought in mixed and monospecific stands 

Based on our observations, both basal area and stand age significantly affected the growth response to drought in the studied stands (Table A6, Fig. 6). Stands with greater basal area were more resistant and resilient to drought than stands with lower basal area. This result may suggest that trees in denser plots tend to grow more than expected in drier years, a result that has been previously found in drought-prone sites, resulting in an attenuated effect of competition (Calama et al. 2019).

Older stands were more resistant and resilient to drought, this effect being greater in mixed stands than in monospecific stands. The lower sensitivity to drought with age has been observed in other tree species (Thurm et al. 2016; Carrer and Urbinati 2006). Drought stress may decrease with increasing age as trees get better access to water in deeper soil layers by their extended root systems (Pretzsch et al. 2018). However, it has been also hypothesized that hydraulic constraints increase with tree age, which would lead to an increase in drought stress sensitivity in some tree species (Carrer and Urbinati 2004). The lack of uniformity in trees responses of different ages to drought reflects the complexity of climate-growth relationships.

5. Conclusions 

Overall, tree species mixing seems to provide forests with greater resistance and resilience to drought events, but these average effects cannot be generalized to all types of admixtures. The more resilient mixed-species forests combines conifer and broadleaved species, and to a lesser extent broadleaved and broadleaved species, suggesting the importance of functional traits diversity and complementarity and the general observation that diversity – ecosystem functioning relationships are context dependent (Ratcliffe et al. 2017). In addition, we found that the benefit of mixing species was similar to monospecific stands along the studied site aridity gradient, although a greater resilience and relative resilience to drought was observed in the driest environmental conditions. Last, the observed response patterns to drought largely varied among the eleven studied species. Such complex interactions between species composition and site conditions makes it difficult to predict how tree mixing may improve the resistance and resilience of mixed-species forests to drought. As mentioned before, process-based approaches could be useful for such predictions. Long-term studies are now needed to understand how monospecific and mixed forests can adapt to the more frequent and intense droughts they will experience under climate change.

6. Authors’ contribution

M. Pardos arranged the common database, carried out the analysis and wrote the main body of the manuscript. R. Calama helped with the statistical analysis. R. Calama, M. del Río, H. Jactel and H. Pretzsch reviewed the manuscript. All authors provided data at stand level (field data) and tree level (increment core measurements) for each case study and helped with their comments to improve 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.

Acknowledgements

The study was supported by the ERA-Net SUMFOREST project REFORM “Mixed species forest management. Lowering risk, increasing resilience” (PCIN2017-026) and Marie Skłodowska Curie Actions-RISE, CARE4C. Special thanks to Nuria Simón and Guillermo Madrigal for their assistance building up the common database. All coauthors thank their national funding institutions for supporting the establishment, measure and analysis of core data in the studied plots. Research at the Polish case studies was additionally supported by the Ministry of Science and Higher Education of the Republic of Poland (No W117/H2020/2018).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118687.

References


