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Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe

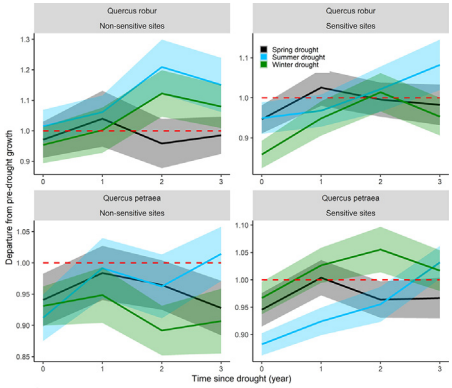
Arun K. Bose [a,b,*], Daniel Scherrer [a], J. Julio Camarero [c], Daniel Ziche [d], Flurin Babst [e,f], Christof Bigler [g], Andreas Bolte [h], Isabel Dorado-Liñán [i], Sophia Etzold [a], Patrick Fonti [a], David I. Forrester [a], Jordane Gavinet [j], Antonio Gazol [c], Ester González de Andrés [c], Dirk Nikolaus Karger [a], Francois Lebourgeois [k], Mathieu Lévesque [g], Elisabet Martínez-Sancho [a], Annette Menzel [l,m], Burkhard Neuwirth [n], Manuel Nicolas [o], Tanja G.M. Sanders [h], Tobias Scharnweber [p], Jens Schröder [d], Roman Zweifel [a], Arthur Gessler [a,q,1], Andreas Rigling [a,q,1]

[a] WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
[b] Forestry and Wood Technology Discipline, Khulna University, Khulna, Bangladesh
[c] Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, Apdo. 202, Zaragoza E-50192, Spain
[d] Faculty of Forest and Environment, Eberswalde University for Sustainable Development, 16225 Eberswalde, Germany
[e] School of Natural Resources and the Environment, University of Arizona, Tucson, USA
[f] Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA
[g] ETH Zurich, Department of Environmental Systems Science, Forest Ecology, Universitätstrasse 22, 8092 Zurich, Switzerland
[h] Thünen Institute of Forest Ecosystems, Alfred-Moeller-Str. 1, Haus 41/42, 16225 Eberswalde, Germany
[i] Forest Genetics and Ecophysiology Research Group, E.T.S. Forestry Engineering, Universidad Politécnica de Madrid (UPM), Madrid, Spain
[j] Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, CNRS, Univ Montpellier, Univ Paul Valéry Montpellier 3, EPHE, IRD, 1919 route de Mende, F-34293 Montpellier, Cedex 5, France
[k] Université de Lorraine, AgroParisTech, INRAE, Silva, 54000 Nancy, France
[l] Technische Universität München, TUM School of Life Sciences, Freising, Germany
[m] Technische Universität München, Institute for Advanced Study, Garching, Germany
[n] DeLaWi Tree-Ring Analyses, 51570 Windeck, Germany
[o] Departement Recherche et Développement, ONF, Office National des Fôrets, Batiment B, Boulevard de Constance, Fontainebleau F-77300, France
[p] Institute of Botany and Landscape Ecology, University of Greifswald, Soldmannstr.15, 17487 Greifswald, Germany
[q] Institute of Terrestrial Ecosystems, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

HIGHLIGHTS

- *Quercus petraea* and *Q. robur* responses to extreme droughts were examined.
- Growth was more related to precipitation compared to temperature.
- Droughts occurred in previous winter and current spring had greater impact.
- Neither species able to recover the pre-drought growth levels to spring droughts
- Long-term growth-climate relationship measured the responses to extreme droughts.

GRAPHICAL ABSTRACT



Growth trajectories during drought (year 0) and 1-3 years after drought. The shaded areas represent mean ± standard error. Sensitive and non-sensitive sites represent the sites where radial growth is significantly and not-significantly correlated with climatic factors, respectively. Red dashed line indicates no change in growth during and after droughts.

* Corresponding author at: WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.
E-mail address: arun.bose@wsl.ch (A.K. Bose).

[1] A. Gessler and A.R. contributed equally to this work.

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ABSTRACT

Recent studies have identified strong relationships between delayed recovery of tree growth after drought and tree mortality caused by subsequent droughts. These observations raise concerns about forest ecosystem services and post-drought growth recovery given the projected increase in drought frequency and extremes. For quantifying the impact of extreme droughts on tree radial growth, we used a network of tree-ring width data of 1689 trees from 100 sites representing most of the distribution of two drought tolerant, deciduous oak species (*Quercus petraea* and *Quercus robur*). We first examined which climatic factors and seasons control growth of the two species and if there is any latitudinal, longitudinal or elevational trend. We then quantified the relative departure from pre-drought growth during droughts, and how fast trees were able to recover the pre-drought growth level. Our results showed that growth was more related to precipitation and climatic water balance (precipitation minus potential evapotranspiration) than to temperature. However, we did not detect any clear latitudinal, longitudinal or elevational trends except a decreasing influence of summer water balance on growth of *Q. petraea* with latitude. Neither species was able to maintain the pre-drought growth level during droughts. However, both species showed rapid recovery or even growth compensation after summer droughts but displayed slow recovery in response to spring droughts where none of the two species was able to fully recover the pre-drought growth-level over the three post-drought years. Collectively, our results indicate that oaks which are considered resilient to extreme droughts have also shown vulnerability when droughts occurred in spring especially at sites where long-term growth is not significantly correlated with climatic factors. This improved understanding of the role of drought seasonality and climate sensitivity of sites is key to better predict trajectories of post-drought growth recovery in response to the drier climate projected for Europe.

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1. Introduction

The frequency and severity of extreme droughts have increased in Europe (Spinoni et al., 2018; Vicente-Serrano et al., 2014) and elsewhere in the world (Spinoni et al., 2014) leading to significant changes in resource availability and altering the overall boundary conditions that are crucial for tree performance in forests (Arneth et al., 2010; Matías and Jump, 2015; Richardson et al., 2018). However, despite years of numerical empirical studies and meta analyses, uncertainties remain about the magnitude of influence of extreme droughts on tree growth (Gazol et al., 2017; Zang et al., 2014), post-drought patterns of tree growth recovery (Anderegg et al., 2015; Ovenden et al., 2021; Zweifel et al., 2020), and processes determining the post-drought recovery trajectories (Gazol et al., 2020; Gessler et al., 2020). These uncertainties are causing concerns given the projected increases in the frequency and severity of extreme droughts (Dai, 2012; Vogel et al., 2020).

The trajectories of post-drought growth recovery can vary across tree species (Anderegg et al., 2015; Peltier et al., 2016), sites (e.g., sensitivity to climate mediated by elevation or latitude and water table depth) (Huang et al., 2018; Kannenberg et al., 2019a), drought characteristics (frequency, duration, intensity, timing, and seasonality) (Bose et al., 2020a; Peltier and Ogle, 2019; Serra-Maluquer et al., 2020), and stand density resulting from forest management (Bose et al., 2018; Sohn et al., 2016; Trouvé et al., 2017). For example, Anderegg et al. (2015) showed that species with low hydraulic safety margins could not recover the growth that declined during droughts over a four-year post-drought period, while Kannenberg et al. (2019a) reported weaker recovery of diffuse ring-porous species compared to ring-porous species. By separating the seasonality of drought occurrence, Huang et al. (2018) showed that when droughts occurred in dry seasons trees were not able to recover their growth during a three-year post-drought period. The important role of drought seasonality has also been identified for *Quercus* species dominated ecosystems in the Mediterranean regions where spring drought had a larger impact on leaf production and photosynthesis compared to autumn drought (Misson et al., 2010a) and on radial growth compared to summer drought (Camarero et al., 2015; Gavinet et al., 2019). In addition to drought seasonality, Huang et al. (2018) demonstrated that climate sensitivity of sites (i.e., sites where tree radial growth is significantly correlated with climatic variables) strongly controls the post-drought growth recovery. These authors showed that trees across species were in principle able to show rapid recovery to droughts that occurred in wet seasons, while this did not happen when they were growing at climatically sensitive sites.

If drought weakens the capacity of trees to return to pre-drought growth levels or slow down the recovery process (i.e., leads to retarded recovery), resistance of trees (i.e., their capacity to buffer the stress and maintain growth) to subsequent droughts may decrease (Bose et al., 2020a). Such retarded recovery, that is the reduction in capacity of trees to regain the growth of non-stress conditions (Ovenden et al., 2021), within reasonable time can increase the mortality risk under upcoming stress (DeSoto et al., 2020; Gea-Izquierdo et al., 2021b). However, in contrast to retarded recovery, rapid recovery associated with compensatory growth has also been observed among trees of woody angiosperms (Anderegg et al., 2015; Huang et al., 2018). Compensatory growth refers to the situation where growth rates directly after a drought event are higher than the pre-drought level and may occur when competition is reduced as a result of drought induced mortality of neighbouring trees or coexisting species, or as a consequence of intrinsic physiological processes related to preferential carbon allocation (Cailleret et al., 2017; Gessler et al., 2020). While competition release might increase resistance to subsequent droughts, compensatory stimulation that comes with larger xylem conduits could make trees more susceptible to recurring droughts (Trugman et al., 2018).

Among woody angiosperms, deciduous oak species (*Quercus* spp.) have increasingly been recognized as relatively drought tolerant due to their deep-penetrating roots and strong stomatal control which allows them avoiding water loss during transpiration (Gea-Izquierdo et al., 2021a; Tessier et al., 1994). Among the deciduous, ring-porous oak species, *Quercus petraea* (Matt.) Liebl., and *Quercus robur* L. are the most abundant species in Europe (Haneca et al., 2009). *Q. robur* is typically found in mesic sites across floodplains and valleys of large European rivers, lowlands and rocky sites, while *Q. petraea* is more common across drier regions (Madrigal-González et al., 2017). Among the two species, *Q. robur* has a higher water requirement and displays lower water use efficiency, and is thus, more sensitive to drought stress (Arend et al., 2011; Epron and Dreyer, 1993; Ponton et al., 2002; Vivin et al., 1993). Several recent studies demonstrated that deciduous oaks are dominating the understories of southern European conifer forests, where conifer dieback may be accelerating successional dynamics (Galiano et al., 2010; Gea-Izquierdo et al., 2021a; Rigling et al., 2013). However, an opposite finding such as an increased vulnerability of *Quercus* species to extreme droughts (Ripullone et al., 2020; Urli et al.,

2015) as well as drought associated tree mortality have also been reported (Colangelo et al., 2017). Most of what is known about tree growth responses to extreme droughts of *Q. petraea*, and *Q. robur* comes from regional studies (e.g., Friedrichs et al., 2009a; Martínez-Sancho et al., 2018; Mérian et al., 2011; Scharnweber et al., 2011; Tumajer and Treml, 2016; Urli et al., 2015; van der Werf et al., 2007; Vanhellemont et al., 2019; Vitasse et al., 2019) but see Gil-Pelegrín et al. (2017). While these studies yielded many insights, they were typically limited to regions or countries and did often not quantify the post-drought growth recovery trajectories. The exceptions are Zang et al. (2012) who studied post-drought growth recovery of *Q. robur* in southern Germany and Dorado-Liñán et al. (2019) studied post-drought growth recovery of *Q. petraea* in Mediterranean region. Consequently, tree-ring width analyses across the distribution range in Europe are required to better assess the climatic effects on tree growth under drought but also the recovery performances in the years after drought.

Using a network of tree-ring collections from 100 stands covering a large part of the distribution of the two *Quercus* species in Europe, our main objectives were (i) to determine how water availability and air temperature control interannual variations in radial growth. Specifically, we asked if there are any elevational, longitudinal or latitudinal trends in terms of radial growth responses with the changes in temperature, precipitation, and water balance. Considering the drought tolerant traits such as deep-penetrating roots and strong stomatal control in deciduous oak species, we also (ii) wanted to know which growth mechanisms *Q. petraea* and *Q. robur* employ to cope with extreme droughts: whether they buffer the stress and maintain the levels of predrought growth or if they show the capacity to recover the growth that was declined during the drought events. We also (iii) aimed to assess whether the patterns of post-drought growth recovery vary with the season of the drought occurrence and climate sensitivity of sites. If so, we wanted to determine how drought seasonality and climate sensitivity of sites affect the direction and the magnitude of post-drought growth recovery.

2. Methods

2.1. Study region

The study region spans in Europe from 41.21° N to 54.33° N and from 21.21° E to 3.07° W (Fig. 1), an area dominated by temperate ecosystems. The climate varies largely, with mean annual temperatures and total annual precipitation sum for years 1980–2010 ranging between 5.75 and 13.85 °C (mean 9.58 °C) and 450 and 1541 mm (mean 765 mm), respectively. While temperatures decrease steadily with increasing latitude and elevation, precipitation displays a longitudinal west-east gradient, with sites closer to the Atlantic Ocean subjected to higher precipitation than more eastern sites, particularly in winter and spring.

2.2. Tree-ring data

We compiled tree-ring width data (RW) of *Q. petraea* and *Q. robur* from 100 different sites (64 *Q. petraea* sites and 36 *Q. robur* sites) (Table SM1) along an approximately 2500 km long latitudinal gradient from northern Spain (41.21° N, 3.07° W) to north eastern Germany (54.33° N, 21.21° E) (Fig. 1). We relied on RW chronologies that are already published (n = 88 sites; Table SM1) (Babst et al., 2013; Fischer and Neuwirth, 2012; Friedrichs et al., 2009b; Granda et al., 2018; Harvey et al., 2020; Lebourgeois, 2006; Martínez-Sancho et al., 2018; Mérian et al., 2011; Schneider, 2011; Schröder, 2015), as well as chronologies from unpublished studies (n = 12 sites; Table SM1). For

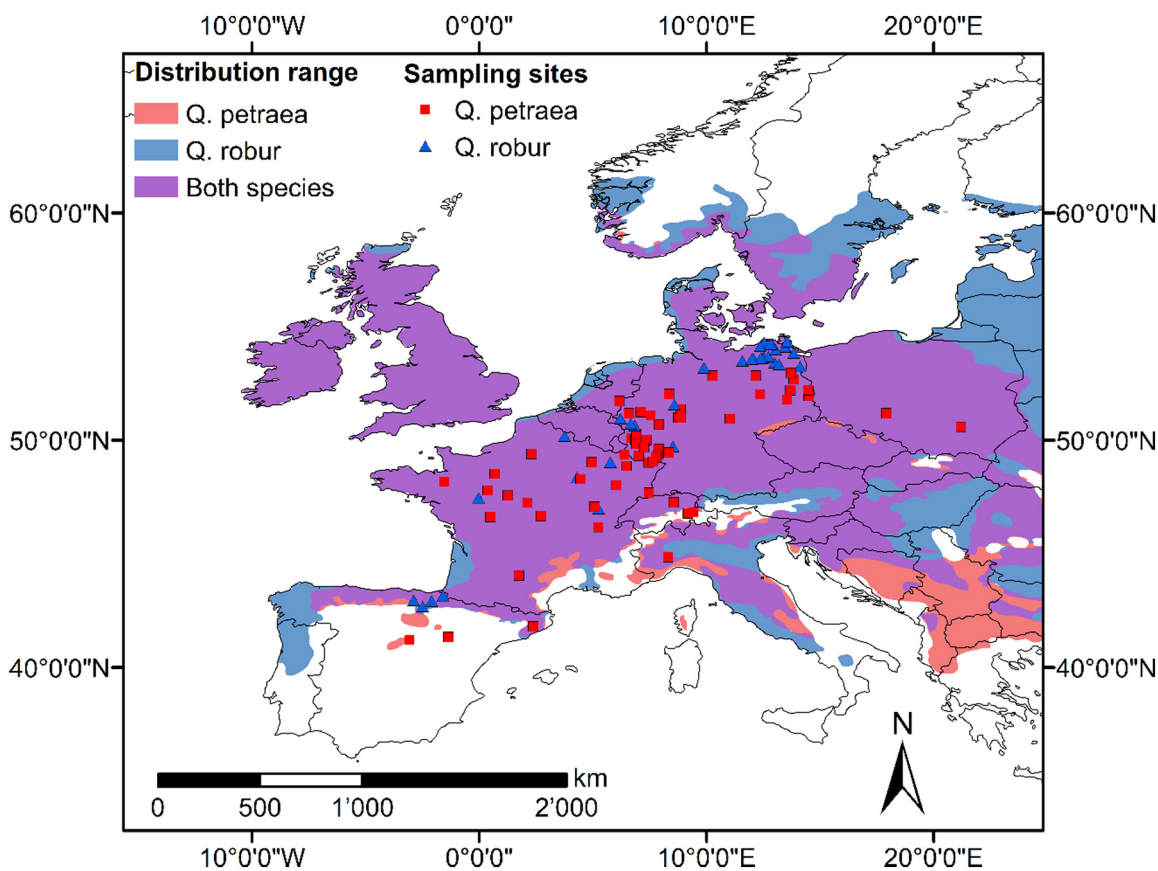

Fig. 1. Location of the 64 *Quercus petraea* and 36 *Q. robur* study sites distributed along the latitudinal gradient that ranged from central Spain to northern Germany with their natural distribution range.
(Source: www.euforgen.org.)

each study site, coordinates, and mean elevation were recorded (Table SM1). We used data from 1689 adult oak trees of which 1107 trees were *Q. petraea* and 582 trees were *Q. robur*. The total number of trees per site varies between 10 and 30 with a mean of 19 trees, and the trees considered in the analysis were at least 70 years old (see details in Table SM1). From each tree, two to four tree-ring width series were included, measured from increment cores extracted at breast height (1.3 m height) and cross-dated following standard dendrochronological procedures (Fritts, 2001).

We examined growth responses to extreme drought events over a 50-year period, roughly from 1960 to 2010, based on the data availability at different sites. However, our studied trees largely differed in terms of age (Table SM1). Hence, ring-width data were transformed into dimensionless ring-width indices (RWI) with both age- and size-related growth trends and lower frequency variation removed from the RW time series (Cook and Kairiukstis, 1990). For this, individual ring-width series were detrended using a 30-year cubic spline with a 50% frequency cutoff (Cook and Kairiukstis, 1990). RWI were obtained by dividing each series by its growth trend (i.e., spline curve values). We retained the high-frequency variability and the first-order autocorrelation since no autoregressive modelling was performed. For developing the site-level tree-ring standard chronology, we averaged the detrended individual RWI series with a Tukey's biweight robust mean (Cook and Kairiukstis, 1990; Fritts, 2001). The individual RWI and averaged chronology were calculated using the *detrend* and *chron* functions, respectively, available from *dplR* R package (Bunn et al., 2018; R Development Core Team, 2018).

2.3. Climate data and identification of extreme drought

We obtained site-specific climate data from the CHELSA V1.2 timeseries (Climatologies at high resolution for the earth's land surface areas) for each site using the latitude and longitude coordinates (Karger et al., 2017). Monthly precipitation sums and monthly mean, maximum, and minimum air temperatures from January to December were obtained. Seasonal temperature and precipitation variables were also computed by averaging monthly values (summer: June–August; autumn: September–November; winter: December–February; spring: March–May). Monthly potential evapotranspiration was calculated using the *Thornthwaite* function of the R package SPEI (Begueria and Vicente-Serrano, 2013). We then calculated the monthly climatic water balance (CWB) by precipitation minus potential evapotranspiration.

For each site, we identified extreme seasonal droughts that occurred in three different seasons (i.e., previous winter, current spring, and current summer) over a 50-year period. The 50-year period starts approximately from 1960 to 2010. However, the range of this period varied across sites due to differences in timing of data collection (see details in Table SM2). These extreme seasonal droughts were identified when the CWB was <1.5 SD (standard deviation) from the mean CWB of a season. The 1.5 SD from the mean CWB captured all extreme dry seasons of all sites. The identified drought years for all sites across three different seasons are provided in Table SM2.

2.4. Data analysis and statistics

For determining the seasonal climate sensitivity of the annual radial growth (i.e., seasonal climate-radial growth relationships), we calculated Pearson correlation coefficients between site-level RWI and seasonal (i.e., spring, summer, autumn, and winter) climate data (mean temperature, precipitation sum, and mean CWB). We considered current and previous year spring (March–May), summer (June–August), and autumn (September–November), and previous year winter (December–February) mean temperature, sum precipitation, and mean CWB. Based on the results of this analysis, we characterized sites that had significant correlation ($p < 0.05$) with one or more of those climatic variables as "sensitive" and sites that had no significant correlation with any of those climatic variables as "non-sensitive" sites. The idea of characterizing each site by long-term climate sensitivity (i.e., growth-climate relationship) was for quantifying if the legacy of climate sensitivity has any role in determining tree responses to extreme drought events (Huang et al., 2010).

For quantifying the magnitude of the effects of CWB on RWI of *Q. petraea* and *Q. robur* and for assessing its variation with geographical parameters (elevation, latitude, and longitude), we determined the "effect size" for each site by the slope of the linear model between RWI and CWB for a 50-year period. This is a common statistical approach used by large-scale analysis for quantifying the "effect size" of any treatment (e.g., Bose et al., 2021; Forrester, 2019; Vitasse et al., 2019). We performed this analysis separately for each of the three most important seasons (i.e., previous winter, current spring, and current summer). We then fitted a linear model between the "effect size" of CWB on RWI and elevation as well as between "effect size" of CWB on RWI and latitude or longitude.

For understanding whether *Q. petraea* and *Q. robur* maintained the pre-drought level of tree growth during drought events, we quantified the ratio between growth during a drought period and growth during the preceding non-drought period, representing thus the capacity of the trees to maintain growth during drought. This is termed as "resistance" by Lloret et al. (2011). We also quantified the growth reaction following the drought period ("recovery") by the ratio between growth during the post-drought period and growth during the drought period. Finally, we quantified the ratio between growth during the post-drought period and growth during the pre-drought period for quantifying "resilience", that is the capacity of trees to recover and regain the growth of the pre-drought period (Lloret et al., 2011). We quantified these indices (i.e., resistance (RT), recovery (RC), and resilience (RS)) for all identified droughts in the three seasons (i.e., current spring, current summer, and previous winter). We limited the pre-drought and post-drought periods to a maximum of three years. However, when we did not have drought-free three-years-lasting pre- and post-drought periods, we adjusted the pre- and post-drought periods to one or two years based on the data availability. Identified drought periods are presented in Table SM2 of the supplementary information. We averaged RT, RC, and RS of all droughts of a site. We excluded drought periods when we do not have data of pre- and post-drought years. We carefully ensured that the selected pre- and post-drought periods are free of excessively dry years. This is executed for avoiding the potential bias generated by the indices (Schwarz et al., 2020).

For examining the post-drought tree growth recovery trajectories (PDG), we quantified the temporal trajectories of departure from pre-drought growth levels during and after drought. This allowed us to examine the change in radial growth from drought to post-drought years relative to pre-drought period (Kannenberg et al., 2019a). We thus characterized the influence of drought as a departure from pre-drought growth in the period after a drought episode. We quantified this for all droughts for each site and averaged them to obtain a site-level index separated for current spring, current summer, and previous winter drought.

We used drought free 1–3 years period prior to drought events as the "reference-level of growth". We did not quantify the "reference-level of growth" (often characterized as "predicted growth") following the procedure suggested by several recently published studies (e.g., Anderegg et al., 2015; Kannenberg et al., 2019a; Kannenberg et al., 2019b; Wu et al., 2018). These studies quantified predicted growth based on the relationship between RWI and climatic factors such as precipitation, water balance, and air temperature. We recognized based on our data that although this procedure provides useful indices for sites where tree growth is significantly correlated ($p < 0.05$) with climatic factors, it cannot be reliable for sites where climatic factors are not significantly correlated with growth. In our dataset, RWI of 28 sites out of 100 sites were not significantly correlated with mean annual as well as seasonal (winter, spring, summer, and autumn) precipitation,

temperature, and water balance of current and previous year. Therefore, we did not use the index suggested by those studies.

We then modelled site-level RT, RC, and RS as a function of site-level climate sensitivity (two levels: sensitive and non-sensitive), drought seasonality (three levels: spring, summer, and winter), latitude, elevation, and various two-way interactions among these variables. The site-level PDG was modelled as a function of time since drought (0, 1, 2, 3 post-drought years), drought seasonality, site-level climate sensitivity, latitude, elevation, and interactions among these variables.

We developed the best model for each response variable by comparing the Akaike Information Criterion (AIC) weight with the full model. The full model incorporated the additive and interaction effects of all predictor variables mentioned earlier. For this analysis, we used linear mixed-effect models (Zuur et al., 2009) to test the effects of predictor variables (mentioned above), while study site was considered as random factor because repeated measures in different drought periods were performed at each site. The linear mixed-effect models were executed using the *lme* function of the *nlme* package in R (Pinheiro et al., 2014). The post hoc Tukey multiple comparison test was performed to detect the statistical differences using the *lsmeans* function of *lsmeans* package in R (Russell, 2016). We visually verified the assumptions of normality and variance homogeneity of the residuals. We used log transformation of response variables. All analyses were performed in the programming language R version 3.5.3 (R Development Core Team, 2018).

3. Results

3.1. Growth-climate relationships

Precipitation and CWB were stronger climate drivers of growth compared to temperature across the study area (Table 1 and Fig. 2). The current year climate variables (precipitation and water balance) particularly during summer, were more relevant for the growth of the two oak species than previous year summer climate (Table 1). However, climate of the previous winter was the most important variable across the two species (i.e., significantly correlated with the maximum number of sites) (Table 1). Precipitation and CWB had a positive correlation with RWI except for two sites in northern Germany that displayed negative correlations with previous-year summer precipitation. These two sites also showed positive correlations with current year summer precipitation. Regarding the influence of temperature, summer temperature of the previous year showed a significant negative relationship with RWI in 4 out of 64 sites of *Q. petraea* and in 5 out of 36 sites of *Q. robur*. Similarly, previous year spring temperature displayed a significant positive relationship with tree growth in 8 out of 64 sites of *Q. petraea* and 6 out of 36 sites of *Q. robur*, mostly located in northern Germany (Fig. 2). We did not detect any clear pattern of differences between the two species in terms of their climate sensitivity. They displayed a similar climate sensitivity, specifically, 69% and 73% of all sites of *Q. robur* and *Q. petraea* were climatically sensitive, respectively.

3.2. Spatial distribution of correlations between growth and climate

The response to climatic variables showed no significant latitudinal trend with one exception: the effect of the summer water balance on RWI of *Q. petraea* was negatively correlated with latitude (Fig. 3). A higher percentage of *Q. petraea* sites located in the northern part of the gradient had non-significant correlations with climatic variables (Fig. 2). *Q. robur* sites located towards the southern end of the gradient were not significantly correlated with any of our climatic variables. However, northern *Q. robur* sites were more strongly correlated with current year summer precipitation and previous year winter precipitation but not with current or previous year spring precipitation. Spring precipitation had greater association with growth at sites located in the central part of the gradient, i.e., south-western Germany, irrespective of species (Fig. 2). All *Q. petraea* sites located across northern Spain, i.e., near the southernmost limit of its distribution, had significant positive correlation with summer precipitation. However, many of the *Q. petraea* sites located towards the northern end of gradient showed non significant correlation between radial growth and climatic variables examined in this study (Fig. 2). The influence of spring, summer or winter CWB on RWI was not significantly related to elevation of the site irrespective of species (Fig. SM1).

3.3. Growth responses to extreme drought events

For *Q. robur*, growth resistance (RT) to winter droughts was significantly lower at sensitive compared to non-sensitive sites (Fig. 4A). Overall, RT for *Q. robur* was lower at sensitive sites compared to non-sensitive sites irrespective of drought seasonality (Table 2). The RT was significantly lower when droughts occurred in winter compared to summer (Table 2). Tree radial growth recovery (RC) of *Q. robur* was not related to drought seasonality, climate sensitivity of sites, latitude, or elevation (Table 2 and Fig. 4A). Radial growth resilience (RS) was higher across non-sensitive sites compared to sensitive sites (Table 2) and higher after summer droughts at non-sensitive sites than after winter droughts at sensitive sites (Fig. 4A). RS was positively associated with site latitude and elevation (Table 2).

Table 1
Percentage of *Quercus robur* and *Quercus petraea* sites showed statistically significant ($p < 0.05$) positive, negative, and non-significant relationship with different seasonal climatic variables considered in this analysis. Total number of sites for *Q. robur* and *Q. petraea* are 36 and 64, respectively. Note. 'previous' refers to the year previous to tree-ring formation, while 'current' refers to the current year of ring formation. Seasons are summer: June, July, and August, spring: March, April, and May, and winter: December, January, and February. Pearson correlation with a threshold $p < 0.05$ was used for statistical significance.

Climatic variables (units)	*Quercus robur*			*Quercus petraea*		
	Positive-significant	Negative-significant	Not significant	Positive-significant	Negative-significant	Not significant
Previous spring precipitation (mm)	13.9	0.0	86.1	3.1	0.0	96.9
Previous summer precipitation (mm)	11.1	2.8	86.1	6.3	1.6	92.1
Previous winter precipitation (mm)	33.3	0.0	66.7	34.4	0.0	65.6
Current spring precipitation (mm)	27.8	0.0	72.2	26.6	0.0	73.4
Current summer precipitation (mm)	27.8	0.0	72.2	25.0	0.0	75.0
Previous spring temperature (°C)	16.7	0.0	83.3	12.5	0.0	87.5
Previous summer temperature (°C)	13.9	0.0	86.1	6.3	0.0	93.7
Previous winter temperature (°C)	2.8	5.6	91.6	6.3	0.0	93.7
Current spring temperature (°C)	0.0	0.0	100.0	0.0	0.0	100.0
Current summer temperature (°C)	2.8	2.8	94.4	0.0	1.6	98.4
Previous spring water balance (mm)	8.3	0.0	91.7	1.6	0.0	98.4
Previous summer water balance (mm)	13.9	0.0	86.1	7.8	0.0	92.2
Previous winter water balance (mm)	33.3	0.0	66.7	29.7	0.0	70.3
Current spring water balance (mm)	22.2	0.0	77.8	15.6	0.0	84.4
Current summer water balance (mm)	22.2	0.0	77.8	23.4	0.0	76.6

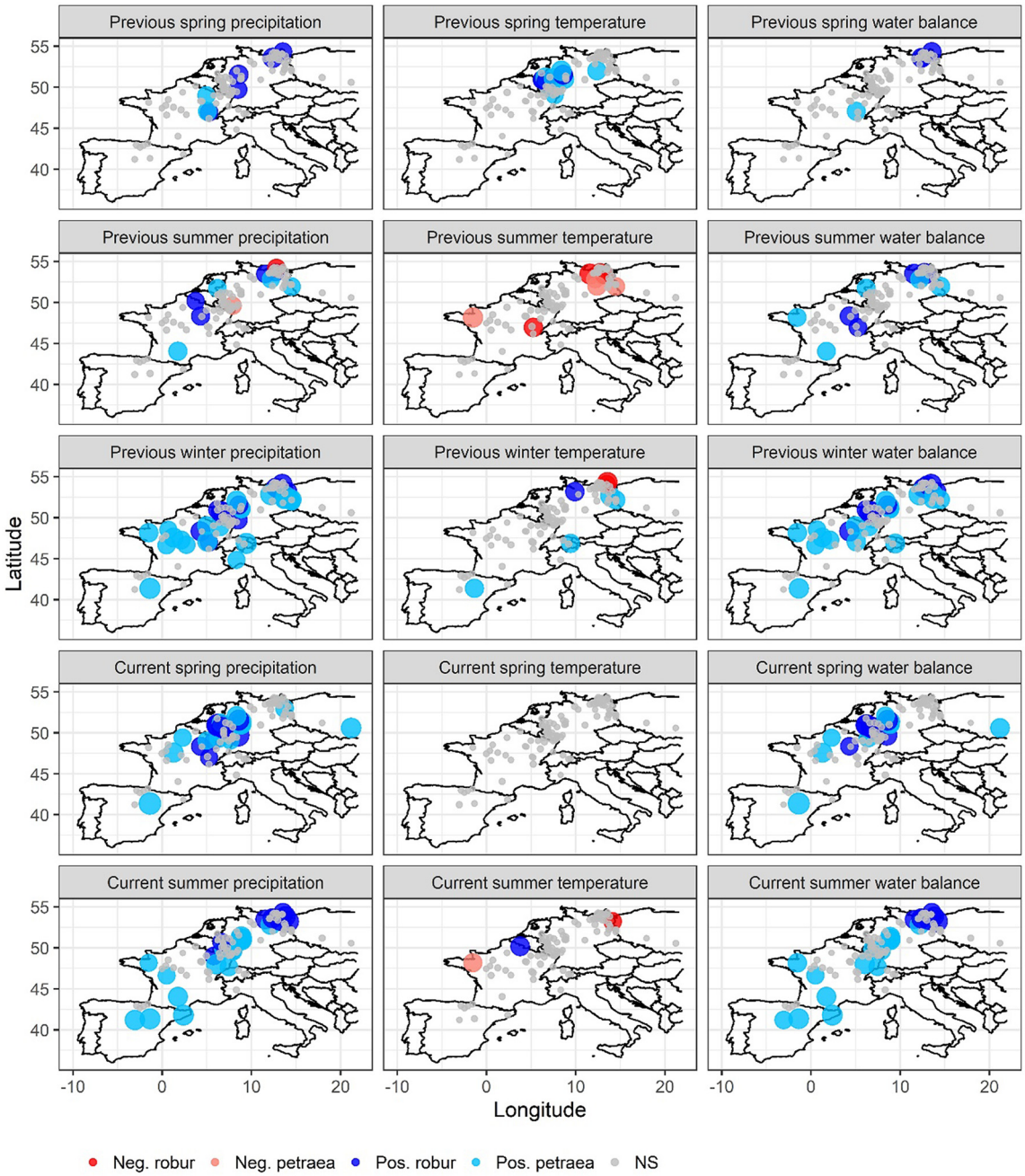

Fig. 2. Seasonal correlations between tree-ring width indices of *Q. petraea* and *Q. robur* with temperature, precipitation, and climatic water balance (precipitation minus potential evapotranspiration). Note. 'previous' refers to the year previous to tree-ring formation, while 'current' refers to the current year of ring formation. Seasons are summer: June, July, and August, spring: March, April, and May, and winter: December, January, and February. Neg. robur: negative correlation with *Q. robur*, Neg. petraea: negative correlation with *Q. petraea*, Pos. robur: positive correlation with *Q. robur*, Pos. petraea: positive correlation with *Q. petraea*, and NS: not statistically significant correlation. Pearson correlation with a threshold $p < 0.05$ was used for statistical significance. Total number of sites for *Q. robur* and *Q. petraea* are 36 and 64, respectively.

For *Q. petraea*, RT was significantly lower after summer droughts compared to spring and winter droughts irrespective of climate sensitivity of sites. However, we detected no significant difference between sensitive and non-sensitive sites and RT was not related to latitude and elevation of the site (Table 2 and Fig. 4B). RC of *Q. petraea* was not related to drought seasonality, climate sensitivity of sites, latitudes, and elevation of the sites (Table 2). The RS of *Q. petraea* was dependent on the interaction between drought seasonality and climate sensitivity of sites (Table 2). For example, *Q. petraea* showed a greater RS to winter droughts occurring at sensitive sites compared to winter droughts occurring at non-sensitive sites (Fig. 4B).

3.4. Post-drought growth recovery trajectories

We observed growth compensation, i.e., higher growth after the drought compared to the pre-drought period, across *Q. robur* sites irrespective of climate sensitivity of sites. However, growth compensation occurred only after summer droughts at both, sensitive and non-sensitive sites, and at non-sensitive sites additionally after winter droughts (Fig. 5A). Overall, post-drought growth was higher across non-sensitive sites compared to sensitive sites of *Q. robur* and after summer droughts compared to winter droughts (Table 3 and Fig. 5A). In contrast to *Q. robur*, *Q. petraea* trees could not fully recover its pre-

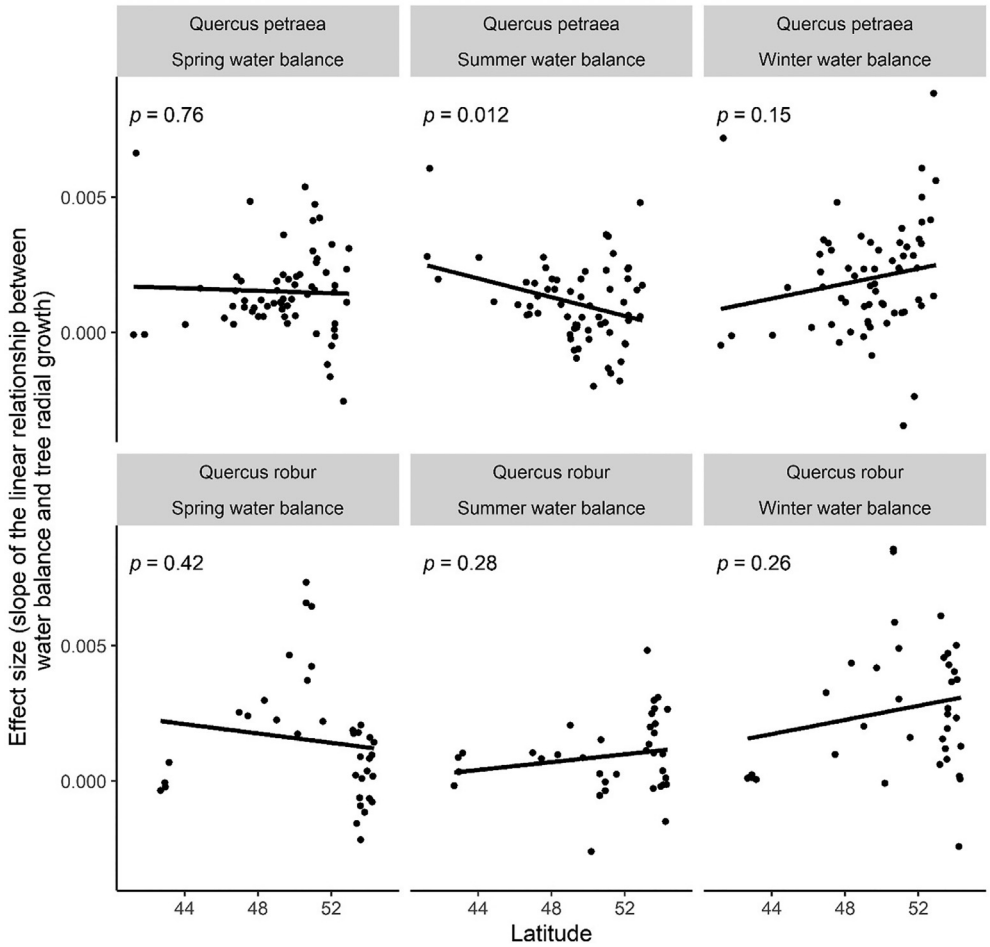

Fig. 3. Effect size (i.e., slope of the linear model) of climatic water balance (precipitation minus potential evapotranspiration) of three different seasons (current spring, current summer, and previous winter) on site-level tree radial growth across latitude (N) of two oak tree species. Total number of sites for *Quercus robur* and *Q. petraea* are 36 and 64, respectively. *p* value indicates the level of statistical significance.

drought growth over a three-year post-drought period at non-sensitive sites (Fig. 5B). However, they were able to fully recover the pre-drought growth level after summer and winter droughts when these droughts occurred at sensitive sites (Fig. 5B). Moreover, growth compensation occurred after summer and winter droughts but not after spring droughts (Fig. 5B). The difference between sensitive and non-sensitive sites for *Q. petraea* was dependent on drought type (i.e., significant interaction between drought type and climate sensitivity of sites) (Table 3).

4. Discussion

Our results showed that drought seasonality is the main climatic factor that controls radial growth (Fig. 2), magnitude of growth decline during drought (Fig. 4), as well as magnitude and direction of post-drought growth recovery (Fig. 5) of *Q. petraea* and *Q. robur* in Europe. We found that over a three-year post-drought period, both species were unable to fully recover the growth that declined during spring droughts (Fig. 5). Moreover, *Q. petraea* trees growing at climatically non-sensitive sites showed slow retarded recovery to spring as well as summer and previous winter droughts over a three-year post-drought period (Fig. 5B). Although extreme droughts with different seasonality differ in drought intensity (Fig. SM2), we did not find any statistically significant effect of drought intensity on the magnitude of growth decline during drought or on post-drought growth recovery. Our study provides evidence that winter water availability before tree-ring formation is more strongly related to radial growth of the two oak species, and that previous winter and current spring droughts induced greater impact on post-drought growth recovery compared to current summer droughts.

4.1. Climate-growth relationships

Our analysis identified common climate signals across the two deciduous oak species from south to north edges of the gradient. Both species showed only minor temperature- growth relationships but displayed strong precipitation- growth associations. However, radial growth of *Q. robur* across the southern edge and central core of the gradient was not related to precipitation or water balance irrespective of the considered season (spring and summer) of the current and previous year and previous year winter (Fig. 2). The weaker role of temperature but stronger impact of precipitation on radial growth have also been reported by other studies such as Friedrichs et al. (2009a) for *Q. petraea* and *Q. robur* in central-west Germany, Harvey et al. (2020) for *Q. robur* in north-west Germany, and Mérian et al. (2011) for *Q. petraea* in western France. Along with these previously published studies our study indicated that climate related drivers for growth in these two oak species do not differ qualitatively from south to north across our 2500 km latitudinal gradient.

Although, several prior studies showed that summer water balance broadly explains the radial growth of oak in central Europe (e.g., Friedrichs et al., 2009c; Neuwirth et al., 2007), we detected greater importance of the previous winter water balance on tree radial growth especially towards the northern part of the gradient. The water

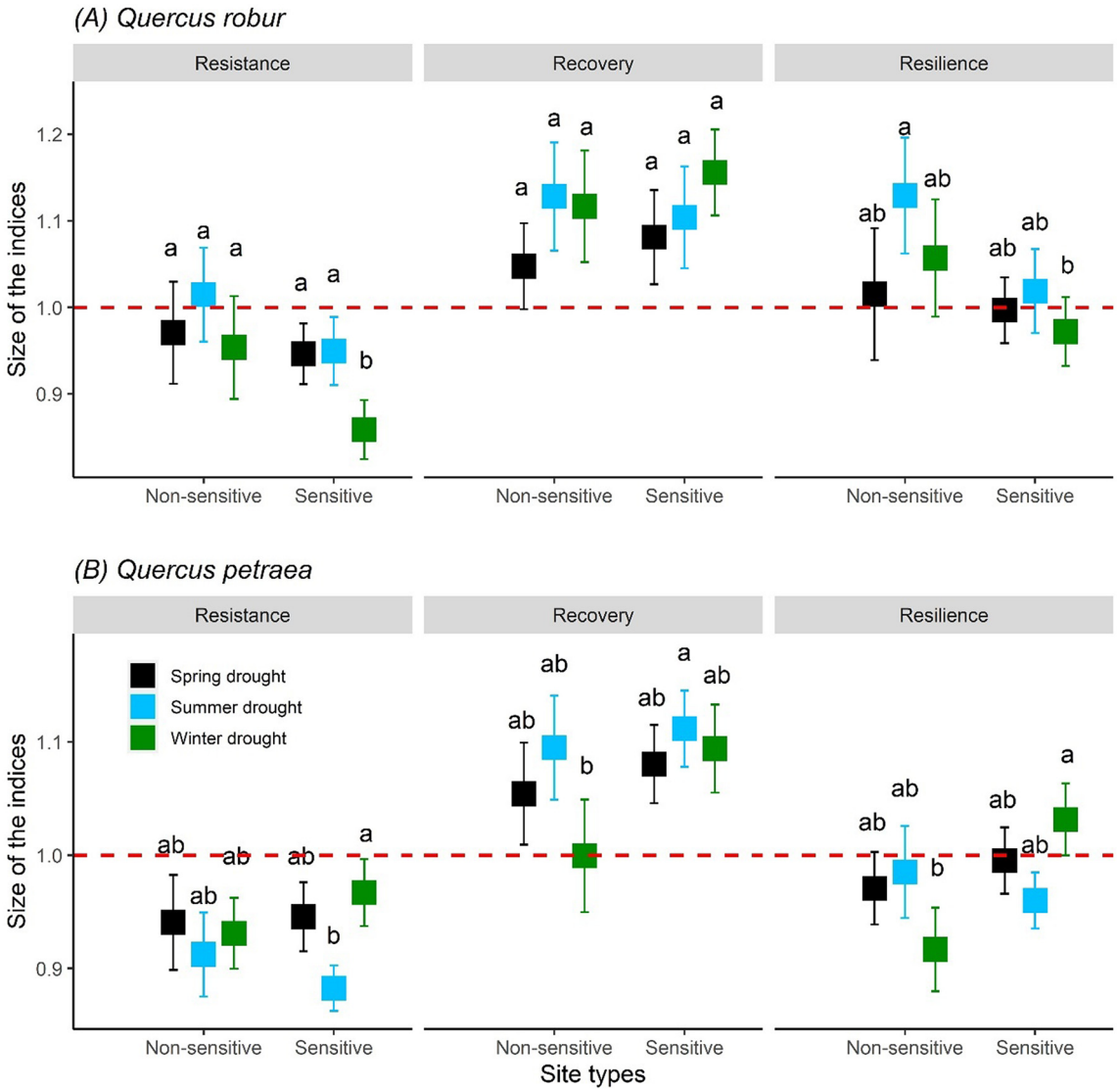

Fig. 4. Site-level resistance, recovery, and resilience of *Quercus robur* (A) and *Q. petraea* (B) to extreme drought events occurred during a 50-year period roughly from 1960 to 2010. The error bars represent mean ± standard error (total number of sites for *Q. robur* and *Q. petraea* are 36 and 64, respectively). Letters on top of the bars show the results (a > b) of the post hoc Tukey multiple comparison test with a threshold <0.05 for statistical significance indicating the differences among the three drought seasons (current spring, current summer, and previous winter) and two site types. Sensitive and non-sensitive sites represent the sites where long-term tree radial growth is significantly and not significantly correlated with climatic factors, respectively. Red dashed line represents no change in growth performances during and after droughts.

availability in winter (December–February) might be related to required physiological activities for the earlywood formation in spring of these two oak species (Matisons and Brūmelis, 2012). For example, González and Eckstein (2003) reported strong relationships between earlywood lumen area of *Q. robur* and moist and cool conditions of late winter and early spring in northwest Spain. Winter water availability is probably the water source that fills up the depleted soil water stores and if there is not sufficient replenishment then the winter water balance will affect tree growth during the growing season (Martin et al., 2018). For example, a recent study conducted in Switzerland on seasonal origin of soil water used by trees reported that deciduous oaks and beech (*Fagus sylvatica*) trees in their growing season were more relying on winter than summer precipitation (Allen et al., 2019). Our analysis lacks information related to soil water at different depths of soil profile and the role of forest management on stand density and species mixture which did not allow us to quantify the influences of these variables on our response variables. We also lack information related to regeneration origin of oak trees. Regeneration origin of *Quercus* species can strongly control the root size and root architectural development, thereby determining the water uptake efficiency during and after droughts (Zadworny et al., 2019). For example, acorn-sown trees develop a deeper and extensive root system compared to coppiced trees allowing a greater access to deep water sources (Zadworny et al., 2021). These deep-rooted trees could show a greater resistance or resilience to droughts compared to coppiced trees.

We did not detect any statistically significant latitudinal or elevational patterns of radial growth responses with the exception that the effect magnitude of summer water balance decreased with increasing latitude for *Q. petraea* (Fig. 3). This indicates that *Q. petraea* trees growing towards the southern edge of the gradient were more sensitive to summer water balance. This is what we expected based on the current understanding that trees growing at the warm, equatorward margins of the species' distribution range are more sensitive to water stress compared to trees growing towards the core of their distribution (Allen et al., 2015; Urli et al., 2015). The *Q. robur* trees located at the southern edge of the gradient (i.e., in northern Spain) were, however, not sensitive to temperature or precipitation. These sites are located in wetter localities compared to southern *Q. petraea* sites, which

Table 2
Results of the linear mixed-effect models for site-level resistance, recovery, and resilience of *Q. petraea* and *Q. robur* as a function of different variables included in the top-ranked model. The model incorporated the fixed effects of site types (SS: sensitive sites and NS: non-sensitive); drought seasonalities (SmD: current summer drought, SpD: current spring drought, WD: previous winter drought); latitudes; elevation; and interactions among those variables indicated by the sign ×. Significance levels: '***'p < 0.001, '**'p < 0.01, '*'p < 0.05. '-' variable was not included in the top-ranked model. We used the log transformation of the response variables. The analyses were performed separately for each species. Standard errors are provided in the parenthesis.

Predictor variables	Resistance	Recovery	Resilience
Quercus robur			
Intercept	0.002 (0.034)	0.074 (0.032)*	−1.362 (0.372)***
SS vs NS	−0.075 (0.037)*	−0.001 (0.031)	−0.078 (0.029)*
SmD vs SpD	−0.010 (0.025)	−0.026 (0.032)	−0.041 (0.029)
SmD vs WD	−0.099 (0.026)***	0.039 (0.033)	−0.052 (0.030)
Latitude	-	-	0.027 (0.007)***
Elevation	-	-	0.0005 (0.0001)**
Quercus petraea			
Intercept	−0.123 (0.020)***	0.061 (0.022)**	−0.029 (0.026)
SS vs NS	−0.007 (0.020)	0.029 (0.022)	−0.026 (0.030)
SmD vs SpD	0.050 (0.019)**	−0.033 (0.022)	−0.010 (0.037)
SmD vs WD	0.067 (0.021)**	−0.041 (0.023)	−0.073 (0.040)
SS vs NS × SmD vs SpD	-	-	0.040 (0.043)
SS vs NS × SmD vs WD	-	-	0.138 (0.046)**

may reduce the sensitivity to water balance as tree growth sensitivity to moisture is mainly reported for drier sites located at lower elevations (Urli et al., 2015; Vitasse et al., 2019). In addition, a recent study conducted on European beech (*Fagus sylvatica*) reported low drought sensitivity towards the dry distribution margin of the species (Muffler et al., 2020), which is probably due to local adaptation (evolutionary adaptation) at the dry margin (Bolte et al., 2016; Bose et al., 2020b; Cavin and Jump, 2017; Jump and Peñuelas, 2005). Most of these analyses demonstrated that the adaptation capacity of European beech at the dry margin of its distribution facilitates a non-responsive behaviour to water stress. However, this is only true up to a specific stress-threshold after which trees can start to respond with crown dieback and mortality (e.g., Walthert et al., 2021).

4.2. Effect of drought seasonality on growth performance during and after drought

We observed radial growth decline (i.e., resistance below zero) during drought years in both species (Fig. 4). However, the magnitude of growth decline varied across drought seasonality and climate sensitivity of sites. Our analysis showed a greater impact of summer and spring droughts on the radial growth of *Q. petraea* compared to *Q. robur* (Fig. 5). The later species did not experience growth decline in response to summer droughts but only to spring and winter droughts. We observed that *Q. robur* lost almost 20% of pre-drought levels of growth in response to winter droughts at climatically sensitive sites. However, the species showed its capacity to fully recover the pre-drought levels of growth immediately after the drought events (Fig. 5). In contrast to *Q. robur*, *Q. petraea* showed the highest growth decline in response to summer droughts. This species was able to fully recover the growth that was declined in summer drought but not in spring droughts (Fig. 5).

Our results showed that spring droughts had the strongest impact on post-drought growth recovery. None of the two species was able to recover the growth that was declined in response to spring droughts over the three post-drought years. Drought in spring can increase soil dryness and can delay the canopy development and reduce canopy leaf area (Misson et al., 2011). The results from a rainfall exclusion experiment conducted on *Quercus ilex* in Mediterranean forests showed that rainfall exclusion during spring had a stronger impact on leaf-level photosynthesis compared to rainfall exclusion in autumn (Misson et al., 2010a). Studying the same species under similar environmental condition, Camarero et al. (2015) reported a greater decline in radial growth during the year associated with spring and summer droughts compared to years with summer drought only. The strong influence of spring drought on tree growth performances has also been identified by other studies conducted in different forest ecosystems and can be explained because the highest growth peak occur in that season and it is linked to species-specific shoot and leaf phenological patterns (e.g., Dawadi et al., 2013; Martin-Benito et al., 2018; Panthi et al., 2017).

Spring is the most important period of phenological change for the study species and ecosystems and rainfall in that season is strongly related to annual primary productivity (Misson et al., 2010b). Deciduous and ring-porous species such as *Q. petraea* and *Q. robur* are more dependent on winter and spring conditions (Alla and Camarero, 2012), because the onset of the earlywood vessel formation and budburst are related to spring soil water availability (Fonti et al., 2010; Pérez-de-Lis et al., 2016) and the area of earlywood vessels decreases in response to reduced precipitation in the early growing season (González and Eckstein, 2003). Ring-porous species are generally more sensitive to extreme drought events because they usually operate with narrow hydraulic safety margin (Choat et al., 2012). Drought in spring can delay the onset of xylogenesis and reduce the rate of xylem cell production and thus annual growth (Pérez-de-Lis et al., 2016).

Although both oak species showed slow retarded recovery to spring droughts, they showed rapid recovery to summer droughts, in which they grew at higher rate during the post-drought period compared to pre-drought growth rate, indicating compensatory growth responses in both species (Fig. 5). The growth compensation has also been identified across Fagaceae species by Anderegg et al. (2015) and Huang et al. (2018) on global tree-ring network analyses. The growth compensation may result from the population-level mortality which may occur during the drought events and release survived individuals from competition (Cavin et al., 2013). The compensatory growth can also be an inherent physiological reaction or acclimation strategy of trees to compensate for losses during the stress period (Arend et al., 2016; Gessler et al., 2020; Ovenden et al., 2021). For stem radial growth, compensation might also be a result of preferential carbon allocation to rebuild damaged xylem (Trugman et al., 2018).

Our study identified significant differences in terms of post-drought growth recovery between sensitive and non-sensitive sites (Table 2 and Fig. 5). Our non-sensitive sites are associated with higher annual as well as seasonal precipitation and water balance compared to sensitive sites (Fig. SM3). In non-sensitive sites, previous winter droughts had larger impact on post-drought growth recovery of *Q. petraea* compared to sensitive sites. In addition, both *Q. robur* and *Q. petraea* at non-sensitive sites could not fully recover the pre-drought growth rate when they experienced spring droughts. These results may indicate that both species were less adaptive at non-sensitive mesic sites where the long-term tree growth does not seem to be limited by climatic factors. Higher vulnerability to spring droughts at non-sensitive sites might be due to the lack of acclimation traits at these mesic sites. For example, low water-use efficiency on mesic sites (which might be an advantage when water availability is high) can make a tree vulnerable to upcoming water stress (Guehl et al., 1991). Higher growth sensitivity to extreme droughts from mesic sites has also been identified for other deciduous oak species (Orwig and Abrams, 1997). Species adapted and acclimated to mesic sites may compete more intensively for light since water is not a regularly limiting factor and they may also show lower root to shoot ratios (Lloret et al., 1999; Matías et al., 2019). This may suggest that during periods of extreme droughts, competition for water may be more severe on mesic versus xeric sites while trees are not adapted or acclimated to such extreme climatic conditions. Further large-scale studies may focus on intraspecific variations of drought response in *Q. robur* and *Q. petraea* on population level in order to differentiate between climate impact and local adaptation status (Depardieu et al., 2020).

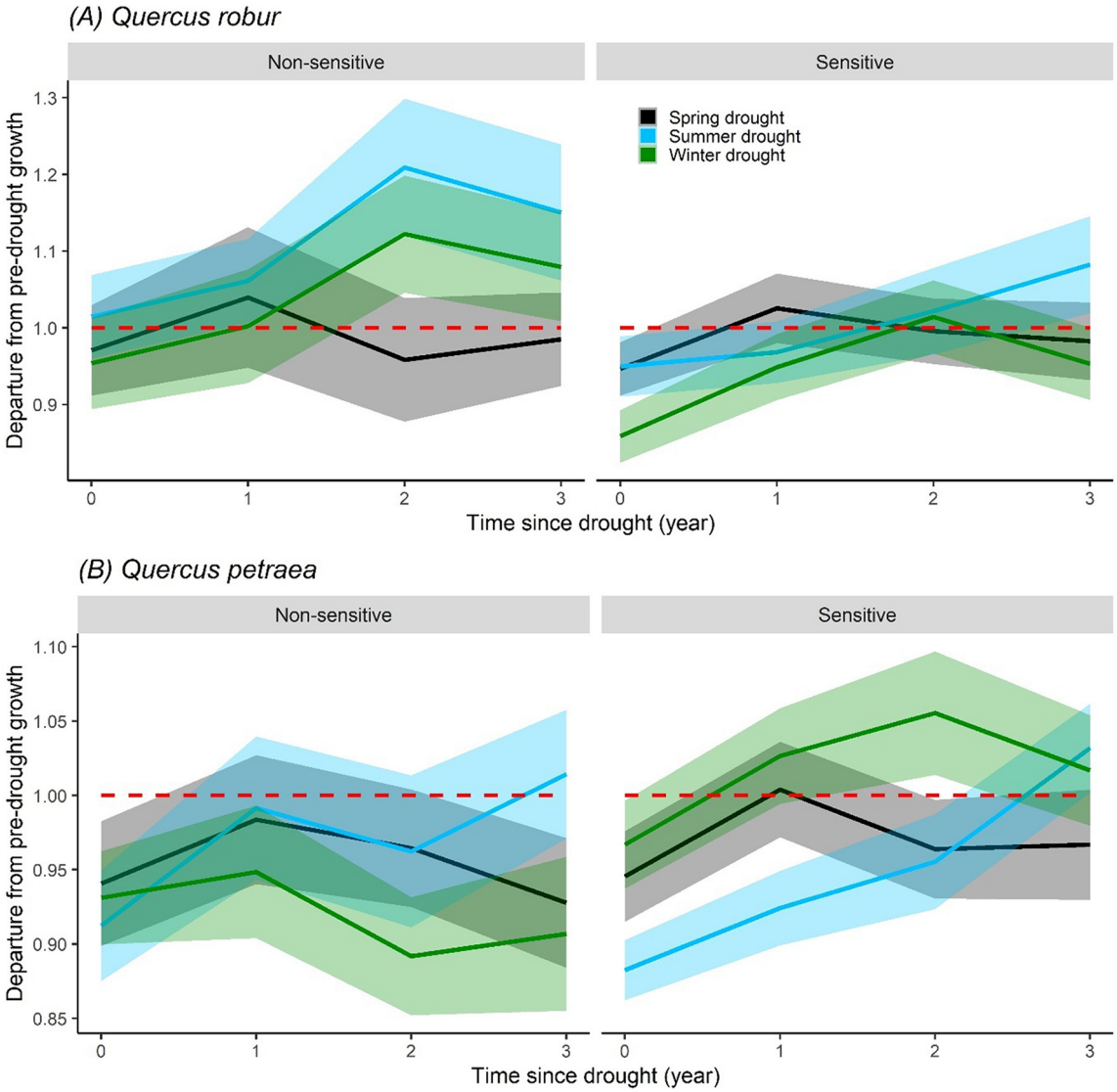

Fig. 5. Radial growth trajectories during drought (year 0) and 1–3 years after drought measured by the departure from pre-drought growth level. Results are presented for *Quercus robur* (A) and *Q. petraea* (B) when droughts occurred in current spring, current summer, and previous winter across climatically sensitive and non-sensitive sites. The shaded areas represent mean ± standard error (total number of sites for *Q. robur* and *Q. petraea* are 36 and 64, respectively). Sensitive and non-sensitive sites represent the sites where long-term tree radial growth is significantly and not significantly correlated with climatic factors, respectively. Red dashed line represents no change in growth during and after droughts.

Table 3
Results of the linear mixed-effect models for site-level post-drought recovery of *Quercus petraea* and *Q. robur* as a function of different variables included in the top-ranked model. The model incorporated the fixed effects of time (drought year, 1st year since drought, 2nd year since drought, and 3rd year since drought); site types (SS: sensitive sites and NS: non-sensitive); drought seasonalities (SmD: current summer drought, SpD: current spring drought, WD: previous winter drought); latitudes; elevation; and interactions among these variables indicated by the sign ×. Significance levels: '***'$p < 0.001$, '**'$p < 0.01$, '*'$p < 0.05$. '-' variable was not included in the top-ranked model. We used the log transformation of the response variables. The analyses were performed separately for each species. Standard errors are provided in the parenthesis.

Predictor variables	*Quercus petraea*	*Quercus robur*
Intercept	−0.090 (0.022)***	−1.247 (0.390)**
Drought year vs 1st year since drought	0.050 (0.013)***	0.053 (0.018)**
Drought year vs 2nd year since drought	0.042 (0.013)**	0.088 (0.018)***
Drought year vs 3rd year since drought	0.061 (0.014)***	0.084 (0.019)***
SS vs NS	−0.020 (0.024)	−0.098 (0.036)*
SmD vs SpD	−0.007 (0.022)	−0.098 (0.034)**
SmD vs WD	−0.055 (0.023)*	−0.082 (0.029)**
Latitude	-	0.024 (0.007)**
Elevation	-	0.0005 (0.0001)**
SS vs NS × SmD vs SpD	0.019 (0.026)	0.082 (0.038)*
SS vs NS × SmD vs WD	0.117 (0.027)***	0.009 (0.035)

5. Conclusion

Our findings support the understanding that moisture availability especially of previous winter and current spring primarily controls the radial growth of *Q. petraea* and *Q. robur* in Europe. The radial growth response to summer water balance was more sensitive towards the warmer, southern margin of the distribution of *Q. petraea* but not of *Q. robur*. This may indicate the higher adaptive capacity of *Q. robur* towards its warmer margin of the distribution or its distribution being restricted to mesic sites with minor drought stress. Our results showed that both species were more vulnerable to spring droughts compared to summer and winter droughts. They showed rapid recovery or even growth compensation after summer droughts but displayed slow retarded recovery in response to spring droughts where none of the two species was able to fully recover the pre-drought growth-level over the three post-drought years. In addition to drought seasonality our study identified the importance of sites' climate sensitivity for determining the post-drought tree growth recovery. Climate sensitivity characterizes the long-term response of trees to climate factors. Our

results indicated that in non-sensitive sites where tree growth is not strongly related to climatic factors *Q. petraea* trees could not fully recover the pre-drought growth level over the three post-drought years. Tree growth in our non-sensitive sites has not been limited by high-temperature or low-precipitation (Fig. SM3), and therefore *Q. petraea* trees might have not been acclimated physiologically (e.g., high water use efficiency) and structurally (e.g., higher root to shoot ratio) to water stress condition. *Q. petraea* trees of non-sensitive sites required longer time to recover the pre-drought growth level compared to sensitive sites is probably due to their long-term mal-adjusted structures. This improved understanding of the role of drought seasonality and climate sensitivity of sites in determining the resilience and post-drought growth recovery of two widely distributed tree species is needed to better predict trajectories of forest ecosystems in response to a warmer and drier climate over the temperate and Mediterranean Europe.

CRediT authorship contribution statement

A.K.B., A.R., A. Gessler, and J.J.C conceptualized the idea and designed the methodology, all authors contributed to the preparation and development of the dataset. A.K.B. and D.S. analysed the data, A.K.B. led the writing of the manuscript with valuable contributions from all authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the research reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.147222.

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