



Climate warming predispose sessile oak forests to drought-induced tree mortality regardless of management legacies

Any Mary Petritan^{a,*}, Ion Catalin Petritan^b, Andrea Hevia^{c,d}, Helge Walentowski^e, Olivier Bouriaud^{f,g}, Raúl Sánchez-Salguero^{d,*}

^a National Institute for Research and Development in Forestry “Marin Drăcea”, Eroilor 128, 077190 Voluntari, Romania

^b Transilvania University, Strul Beethoven 1, ROU-500123 Brasov, Romania

^c Dept. de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería Universidad de Huelva, Palos de la Frontera 21819, Spain

^d Dept. Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Crta. Utrera km. 1, 41013 Sevilla, Spain

^e HAWK, University of Applied Sciences and Arts, Faculty of Resource Management, Bisgenweg 1a, 37077 Göttingen, Germany

^f University Stefan cel Mare of Suceava, Strada Universității 13, Suceava 720229, Romania

^g Institut National de l'Information Géographique et Forestière, Laboratoire d'Inventaire Forestier, 54000 Nancy, France

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ABSTRACT

Climate warming-related drought could become a major driver of large-scale forest dieback. However, little is known about how past management legacies modulate the climate-growth responses during recent dieback episodes in central European oak forests. Here, we examine the role played by past management –unmanaged old-growth vs. managed forests– in recent tree mortality events occurring in *Quercus petraea* (Matt.) Liebl. stands across large areas of western Romania. We analyze how stand structure (tree size, competition) and climatic factors (drought, temperature and precipitation) drive tree radial growth patterns in neighboring standing dead and living trees. We analyzed basal area increments (BAI) trends, past management legacies and climate- and drought-growth relationships during the 20th century to distinguish the roles and interactions on recent warming-induced dieback. We observed that temperature rises and changes in atmospheric water demand during growing season led to increasing drought stress during the late 20th century affecting both managed and unmanaged forests. Dead trees from old-growth and managed forests showed lower growth than living trees after dieback onset. In both forests, dead and living trees displayed divergent growth patterns after dry 1980s, indicating that dieback was triggered by severe extreme conditions. Dead trees from managed stands experienced significant stronger growth reductions after 1980s though they experienced less tree-to-tree competition than dead trees in old-growth forest. High stand density negatively drove growth and enhanced climate sensitivity in old-growth stands. Competition acted synergistically with climate warming and drought causing tree mortality regardless of the management legacies in of *Q. petraea* forests. Our retrospective assessment of growth rates in relation with climate and structure changes offers valuable information for further forest conservation and management decisions of *Q. petraea* forests. These findings highlight the importance of past uses legacies driving recent forest dieback in temperate oak forests, making them more vulnerable under forecasted climate-warming related droughts in central Europe.

1. Introduction

Temperate deciduous and broadleaf forests cover large parts of central and southeastern Europe and have an important role in responding to the increasing society demands for multiple forest ecosystem goods and services (European Environment Agency, 2016). However, the structure, growth dynamic, functioning and services of

these forests are substantially influenced by the ongoing climate changes, especially by the rising in temperature and the frequency of extreme events (Allen et al., 2010). These extremes, particularly the so-called “hotter droughts” (Allen et al., 2015), together with the global changes associated disturbances, have induced a widespread forest die-off phenomenon affecting different forests around the world (Allen et al., 2010; Carnicer et al., 2011; Ciais et al., 2005; Seidl et al., 2017). In

* Corresponding authors.

E-mail addresses: apetritan@gmail.com (A.M. Petritan), rsanchez@upo.es (R. Sánchez-Salguero).

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Europe, the droughts and/or heat waves are expected to be longer and more severe in the future (IPCC, 2019). Thus, a temperature increase from 2.3 °C to 5.3 °C, accompanied by a precipitation reduction and a rise in summer drought events, is projected for the 21st century for central Europe (IPCC, 2019). In addition to climate trends, recent heat-drought induced extreme events (Buras et al., 2020) have increased forest vulnerability, reducing vitality, tree growth and productivity in central European forests (e.g., Stojanović et al., 2015; Thomas et al., 2002). In contrast, the warming conditions contributed to the extension of the growing season length on cold environments (Menzel and Fabian, 1999), to the spread of more thermophilic forest species (Jantsch et al., 2013) as well to increase the forest productivity (Pretzsch et al., 2014). An accelerated forest growth and tree volume rate might contrast with a higher risk of hydraulic failure and mortality of larger trees under increasingly dry conditions (Bennett et al., 2015; Lindenmayer et al., 2016), especially in dense forests of ring-porous oak species (Andersson et al., 2011; Colangelo et al., 2018; McDowell et al., 2008). Besides, the tree growth response to climate change and extreme events could be influenced by tree population density and past forest dynamic (Bottero et al., 2017), including legacies of disturbances and past uses and management which determine the present stand structure (e.g., Sánchez-Salguero et al., 2013, 2015; Sangüesa-Barreda et al., 2015; Stojanović et al., 2017). In this sense, European oak lowland forests were formerly managed by coppicing, which has significantly shaped the present structure and composition of these forest ecosystems (Buckley, 1992). At the early 20th century these coppice forests were abandoned and converted to high stands with significant consequences on tree climate sensitivity to rising temperature and water scarcity (Stojanović et al., 2017). Nonetheless, the understanding of legacy effects of forest management acting as a predisposing (e.g., promoting long-term negative effects on tree-water relations; greater evaporative water loss compared to unmanaged forests) or mitigating (e.g., increasing tree vigor at short-term scale; increasing growing space that promote higher resource acquisition capacity) factor on climate-growth relationships (see Sohn et al., 2016) and its role in current forest dieback processes is still not fully understood (see Camarero et al., 2011).

In order to facilitate forest management decisions, more information about long-term growth trajectories in a changing climate are needed, and possible trade-offs among involved drivers must be considered (Millar et al., 2007; Sohn et al., 2016). An appropriate procedure to gain extensive knowledge on these multidimensional effects could be the “space for time substitution approach”. Through this approach, the study of forests of a region, having climatic conditions like those predicted in the future for another region, will provide knowledge about the ecological adaptation of the species in the respective growing conditions. In this sense, the climate of western Romania was identified as analogous to the forecasted climate for 21st century on large parts of central Germany (e.g., Mellert et al., 2016; Walentowski et al., 2015), and found suitable to indicate future forest development in western Central Europe (Heinrichs et al., 2016). It is expected that climate warming will reduce the prominent dominance of European beech (*Fagus sylvatica* L.), in favor of thermophilous oak species, considered to be more drought-resilient (Cavin et al., 2013; Ciceu et al., 2020; Pretzsch et al., 2013).

Despite the lower climate sensitivity and the increased growth for oaks species during the 20th century (Kint et al., 2012; Rybníček et al., 2016), a massive decline of oaks was observed in central Europe after 1970s (Führer, 1998; Thomas et al., 2002), caused by a combination of biotic (insect defoliation, infection with pathogenic fungi) and climatic factors like summer drought or winter frost (Doležal et al., 2010; Führer, 1998; Mausolf et al., 2018). In temperate forests, forecasted climate warming can affect oaks by modifying length of the growing season (e.g., delay in leaf fall) and the start (e.g., earlier bud bursting), but also by amplifying water stress by rising evapotranspiration rates (Andersson et al., 2011). Many winter-deciduous species, specially ring-porous, are prone to showing an increasing risk of mortality due to carbon starvation

and/or hydraulic failure (Adams et al., 2016). In oak species, hotter-drought damages their photosynthetic activity, reducing their growth and triggering leaf shedding (Barbeta and Peñuelas, 2016). These species have also to rebuild new foliage every early spring before summer drought starts which makes them very susceptible to dry conditions from the previous winter to the early summer (e.g., Colangelo et al., 2018). The impact of climate-induced oak dieback can be also modulated by other extrinsic (e.g., soil conditions, microclimate) and intrinsic (e.g., tree height, competition) factors (McDowell et al., 2008; Colangelo et al., 2017a, 2017b). However, it remains to be answered to what degree past uses legacies, which determine recent tree-to-tree competition (e.g., Sánchez-Salguero et al., 2015), trigger long-term climate sensitivity and contrasting vulnerability to climate warming trends in co-occurring oak trees showing different canopy dieback after droughts. Recent research has provided evidence that drought sensitivity of temperate forests depends partly on how selective cutting or coppicing treatments changed the natural structure of the stands (e.g., Buckley, 1992; Mausolf et al., 2018; Sangüesa-Barreda et al., 2015). To address these questions and to improve our knowledge about the role of land use history in the future vulnerability of central European forests, we take the advantage of recent oak dieback processes identified across western Romania (Ionita et al., 2016) affecting large areas of long-term managed mixed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests as well as neighboring well-preserve natural old-growth (unmanaged) sessile oak mixed forests (see details in Petritan et al., 2012).

Here we assess how the legacy effects of management influence long-term growth trends and modulate the current climate warming sensitivity during recent dieback processes affecting sessile oak mixed forests of western Romania. We focused on the growth responses to warmer conditions and the effect of past management practices using dendrochronology to reconstruct growth and investigate how the past uses define current temperate oak populations vulnerability. The comparison of growth responses to climate of coexisting living and recent dead trees could advance our understanding of the ecological mechanisms to forecasted warming-related dieback processes. Our specific aims are (1) to describe and compare the inter-annual growth patterns of living and dead trees in contrasting past management history (2) to investigate the relationships among growth patterns and sensitivity to drought and temperature as predictors of recent forest dieback and (3) to determine whether the stand and tree variables (age, size, competition) and past management act synergistically causing differential tree mortality. We hypothesize that managed *Q. petraea* stands would show a higher vulnerability to temperature rise and drought trends than old-growth (unmanaged) forests. We also expect that dead trees would show lower growth rates before death and that the shift in growth patterns would be shaped by changes in tree-to-tree competition and more sensitivity to drought.

2. Material and Methods

2.1. Study area and climate data

The study area includes natural managed (vegetative origin) and old-growth (unmanaged with generative origin) mixed sessile oak forests, in a region located at the transition of the sub-Mediterranean to the Central European temperate bioclimate (Heinrichs et al., 2016). The managed stand is located in western Romania (near to Baile Felix site, Table 1). Before 1948, the year of forest nationalization (Nicolescu, 2010; Unrau et al., 2018), it was managed as simple coppice with a rotation period up to 30–40 years, afterwards this forest is being converted towards high forest by ageing the vegetative regeneration (Nicolescu, 2010). With a mean basal area of the standing trees (both living and dead) with a diameter at breast height (DBH) ≥ 10 cm (G) of 36.1 m² ha⁻¹, the managed site is a mixed oak forest dominated by *Q. petraea* (57% of stand density (N), 57% of G) coexisting with *Quercus cerris* L. (33% of N, 40% of G), and with other tree species like *Carpinus betulus* L., *Sorbus*

Table 1
Main features of the study sites. Values correspond to means \pm standard errors.

Variables	Type of forest	
	Managed	Old-growth
Site name	Baile Felix	Runcu
Latitude (N)	46.93	46.11
Longitude (E)	22.01	22.07
Elevation (m a.s.l.)	200–268 m a.s.l.	540–670 m a.s.l.
Slope (°)	6–10	16
Soil type, soil texture	Luvisol	Cambisols, Luvisol
Mean Annual Temperature (°C)*	9.9 \pm 0.1	9.6 \pm 0.1
Annual precipitation (mm)	498 \pm 11	580 \pm 13
Mean temperature of the hottest month (°C)	20.5 \pm 0.2	20.0 \pm 0.2
Mean temperature of the coldest month (°C)	-1.9 \pm 0.3	-2.1 \pm 0.3
Density (N, trees ha ⁻¹)**	454 (57% s. oak)	438(31% s. oak)
Basal area (G, m ² ha ⁻¹)**	36.1 (57% s. oak)	54.7 (63% s. oak)
Main co-occurring tree species	<i>Quercus cerris</i> L.	<i>Fagus sylvatica</i> L.
Number of sampled trees/ Number of tree cores	112/224	112/162

*Values are calculated from E-OBS climatic data (see Cornes et al., 2018).

** Calculated based on all inventoried standing trees with a DBH \geq 10 cm)

terminalis L., *Tilia cordata* Mill. The mean N of standing trees with a DBH \geq 10 cm was of 454 trees ha⁻¹, with multiple sprout origin. Large dieback phenomenon occurred on this site since 2011, affecting particularly the *Q. petraea* trees. At inventory time, the dead trees accounted 21% of the total standing trees number (91% of them were sessile oaks, with 86 trees ha⁻¹), and 16% of the stand basal area (97% belonging sessile oak, with 5.8 m² ha⁻¹). In the last three decades, the managed forest stand was logged frequently (3–4 times per decade) with sanitary loggings of lower intensity and with one thinning of light-

moderate intensity per decade (8–15% of standing volume). The soil type is a luvisol developed from loess with activity clays. A high quantity of fine pores dead water in such clayey substrates intensifies deficiency of stored available water during dry periods. The studied old-growth forest is one of the few well-preserved natural (unmanaged) mixed sessile oak forests in central Europe (see Petritan et al., 2012) located in the Runcu-Grosi Natural Reserve (Table 1). This old-growth forest is a high forest with N of the all standing trees with a DBH \geq 10 cm about 438 stems ha⁻¹ originated from seed and a mean G of 54.7 m² ha⁻¹ and is dominated by *Q. petraea* (63% of G) followed by other co-dominant species: European beech (36% of G, but 65% of N). This old-growth forest showed a high amount of lying and standing deadwood (240 m³ ha⁻¹, of which 91% is accounted by sessile oak (Petritan et al., 2014), and a high number of large trees (9 trees ha⁻¹ with a DBH \geq 80 cm, and 41 trees ha⁻¹ with a DBH \geq 65 cm). Whereas the maximum DBH of the trees in managed forests reached only 64 cm, in the old-growth forest this was 113 cm. At inventory time, the all species standing dead trees accounted 13% of the N and 14% of the G and was represented especially by sessile oak. The standing dead sessile oaks represent 54% from N (31 trees ha⁻¹) and 86% from G (6.4 m² ha⁻¹) of all standing dead trees. The soils are cambisols and luvisols with medium to high storage capacity for both water and nutrient (Table 1).

The climate in both mixed sessile oaks forests is cool-temperate subcontinental (Kottek et al., 2006). The mean annual temperature varies between 7.9 °C and 11 °C, and the mean annual precipitation between 350 and 825 mm, 283–318 mm of which falls during the growing season in managed and old-growth forests, respectively (Fig. 1, Table S1). The warmest and coldest months are the July (mean temperature about 20 °C) and January (mean temperature about -2.0 °C), respectively, whereas the driest and wettest months are February and March (about 30 mm) and June (about 70 mm), respectively.

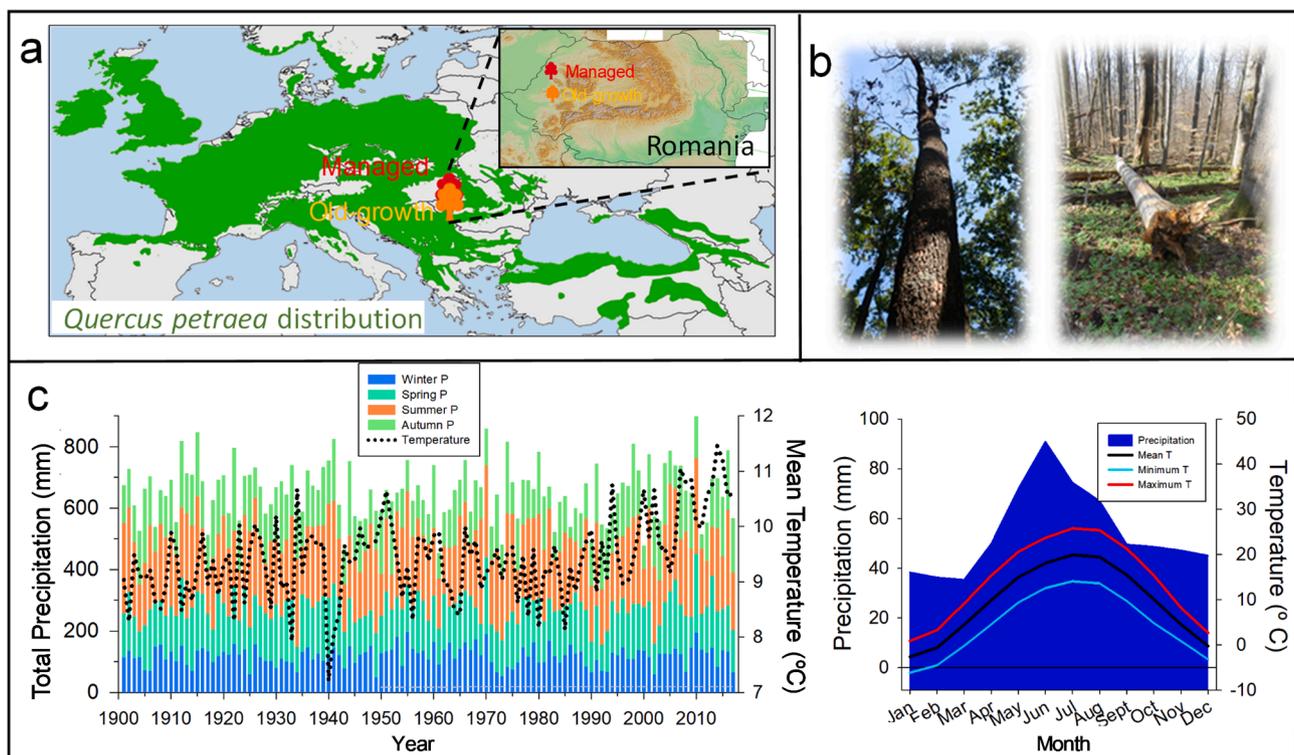


Fig. 1. (a) Location of the study sites in Baile Felix (managed) and Runcu (old-growth) *Quercus petraea* forests in Romania. The upper map shows the distribution of the species (in green) in Eurasia (Eaton et al., 2016). (b) Illustrative pictures of trees showing dieback symptoms at the managed site (left image) and the old-growth site (right image). (c) The left figure shows the regional climate trends of mean annual temperature and precipitation for the studied forests during the 20th century and the right figure shows the climatic diagram. CRU gridded data were used to build the climate series (see Material and Methods). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Field sampling and dendrochronological methods

The fieldworks were carried out in autumn 2013 in the old-growth forest and in 2015 in the managed sessile oak stands (Table 1) and increment wood cores were extracted from a network of six permanent sampling plots (75 × 75 m each plot) established in previous studies (see Petritan et al., 2014). The randomly positioned sampled trees and plots in both sites cover more than 4 ha, making them large enough and well positioned to assess the spatio-temporal dynamics of forest growth. Following Bigler and Bugmann (2003), we sampled 70 pairs of recent standing dominant dead (hereafter D) and living (hereafter L) healthy sessile oak trees of similar size, competition and microsite in each site (Fig. S1). For each tree, at least two cores were collected at breast height (1.3 m) using 5 mm increment borers. Since most of sampled dead trees at the managed stand had recently died (during the last 2–3 years before fieldwork), we also retained the cores of the recently dead trees for the old-growth forest (no longer than 10 years before sampling) (Fig. S2). Wood samples were air dried and sanded with sandpaper of a progressively finer grain until the tree-rings became clearly visible. Tree-rings were measured and cross-dated after scanning at high-resolution to the nearest 0.01 mm using the CooRecorder and CDendro 7.7 semi-automatic software (<http://cybis.se>). In the cases of cores without pith, the rings to the pith were estimated by fitting a template of concentric circles with known radii to the innermost rings and checked using the graphical method developed by Rozas (2003). The visual cross-dating of tree-rings series was checked using the COFECHA program (Holmes, 1983) by comparing the consistency of the different ring-width series with mean site series using moving correlations. A final number of 56 pairs of recently dead and living trees with well cross-dated and reliably age (with less than 10 estimated missing years) from each site was used for the further analyses (Table 2).

The trend due to the geometrical constraint of an increasing volume of wood with rising stem diameter was corrected by converting the tree rings widths into basal area increment (BAI, cm² yr⁻¹), a more biologically meaningful biological descriptor of growth trends (Biondi and Qeadan, 2008). This relatively age-independent measure of radial tree growth in ring-porous oak trees is related to variations in hydraulic conductance (Kint et al., 2012; Colangelo et al., 2018).

To quantify climate- and drought-growth relationships, we first

Table 2

Comparison of tree and stand variables calculated for living and dead *Q. petraea* trees in the Managed and Old-growth sites and summary of the dendrochronological statistics calculated for the basal area increment series in the period 1918–2013, except basal area increment (BAI). Values are means ± SE.

Variables	Managed		Old-growth	
	Living	Dead	Living	Dead
DBH (cm)*	33.3 ± 0.5A	31.4 ± 0.7A	56.5 ± 1.4aB	52.2 ± 1.2bB
Tree height (m)	25.2 ± 0.3aA	23.2 ± 0.6bA	32.3 ± 0.4aB	27.5 ± 0.9bB
Age at 1.3 m (years)	84 ± 1.0A	85 ± 1.0A	184 ± 1.8B	183 ± 1.9B
BAI (cm ²) period 1950–2013	8.1 ± 0.5aA	7.4 ± 0.4bA	14.9 ± 1.1aB	11.9 ± 0.6bB
First-order autocorrelation	0.728 ± 0.010aA	0.667 ± 0.014bA	0.596 ± 0.010B	0.591 ± 0.007B
Mean sensitivity	0.284 ± 0.005A	0.281 ± 0.005A	0.218 ± 0.003bB	0.227 ± 0.003aB
Correlation among trees	0.668 ± 0.022bA	0.774 ± 0.012a	0.789 ± 0.012B	0.768 ± 0.009
EPS	0.981	0.974	0.969	0.986
Time span	1918–2013	1915–2013	1802–2013	1808–2013

* Variables abbreviations: DBH, diameter at breast height; BAI, basal area increment; EPS, Expressed Population Signal. Different letters indicate significant ($P < 0.05$) differences between Living and Dead trees (lowercase letters) and between Managed and Old-growth forests for living or dead trees (uppercase letters) based on Mann-Whitney U test.

removed age- and size-related long-term trends of individual BAI series by converting raw BAI into BAI indices (BAI_i). This was done by fitting a 30 years cubic smoothing spline to raw data to preserve high-frequency growth variability, and then dividing observed by fitted values to obtain dimensionless, standardized BAI indices. The resulting indices (BAI_i) were averaged into a chronology for each site (old-growth vs. managed) per living and dead trees. The resulting mean chronologies (BAI_i) of each site were described for the common period of 1918–2013 by calculating dendrochronological statistic parameters: the first-order autocorrelation of raw width data (AC), the mean sensitivity (MS), the mean correlation between trees (r_{bt}) and the Expressed Population Signal (EPS), which measures the statistical quality of the mean site chronology compared with a perfect infinitely replicated chronology (Wigley et al., 1984). The part of the site chronologies that reached EPS values equal to or higher than 0.85 were regarded as reliable enough for calculating climate-growth correlations (Table 2). Chronology development and standardization were carried out using the *dplR* package (Bunn et al., 2018) in R environment (R Core Team, 2020).

2.3. Structure and competition

For each sampled tree (living or dead) the diameter at breast height (DBH) and total height (H) were measured using tapes and Vertex IV hypsometer, respectively (Table 2). All neighboring trees with DBH larger than 10 cm and recent stumps within a radius of 5 m around each sampled tree were tagged, identified, measured and their social and health status determined. To quantify the potential effect of recent tree-to-tree competition on dieback, we calculated the following competition index (Ci) for each sampled tree (Bigler and Bugmann, 2003; Daniels, 1976):

$$Ci = \sum_j \left(\frac{DBH_j^2}{DBH_i^2} \right)$$

The competition index (Ci) of focal tree i was calculated as the sum of the quotients of DBH_j^2/DBH_i^2 , obtained for all j neighboring trees located within a given radius R from the focal tree i . If a focal tree has zero competitors, the Ci takes a value of 0. The Ci calculation assumed that a high DBH value also implies a high competitiveness of a tree. Correspondingly, trees with a large DBH exert competitive stress on neighboring trees with lower DBH values. Only few recent stumps were identified in the managed plots. The threshold radius above which neighbors were regarded as not competing was estimated to be 5 m following Petritan et al. (2017). This competition index has been previously used in tree-ring studies focused on growth-management associations (see Sánchez-Salguero et al., 2015).

2.4. Climate-growth relationships

Due to the incompleteness and heterogeneity of local climate data (see Table S1), we used gridded climatic data (mean, maximum and minimum monthly temperatures and total precipitation) to characterize the regional climate trend for the 1901–2017 period. This dataset was downloaded from the Climate Research Unit (CRU, <http://www.cru.uea.ac.uk/es>) and corresponds to interpolated data obtained from instrumental records recorded by a dense network of local meteorological stations, which have been subjected to homogeneity tests and relative adjustments, and finally gridded onto a 0.5° network (Harris et al., 2014). Temporal trends in the CRU monthly temperature and seasonal precipitation were calculated to characterize the regional climate change (Fig. 1c).

To analyze climate-growth relationships, we downloaded the homogenized and quality-checked climate E-OBS v.20 at higher resolution for each forest (0.25° gridded data) for the period 1950–2017 (Cortes et al., 2018), which corresponds to interpolated data obtained from nearby instrumental local meteorological stations (Table S1).

To estimate the effect of drought intensity and duration on radial

growth (BAI) of living and recently dead trees, we used the Standardized Precipitation–Evapotranspiration Index (SPEI), as a multiscalar drought index that accounts for the negative effect of warmer temperatures on water availability by statistically modeling cumulative water balances. The SPEI is calculated using precipitation and temperature data from the same homogeneous and spatially dense dataset of local observatories as CRU climate data (Vicente-Serrano et al., 2010). The SPEI varies from negative to positive values corresponding to dry and wet periods, respectively. The SPEI monthly values were calculated for the study sites considering the 1950–2013 common period and 1- to 24-months long time scales.

To quantify climate-growth relationships between BAI and monthly climate variables from E-OBS database (mean, maximum and minimum temperature; precipitation and SPEI), we calculated bootstrapped Pearson correlation coefficients for the common period 1950–2013. These correlations were calculated from previous August to current October, i.e., during the year of tree-ring formation, as well as for the annual seasons based on previous analyses of the studied species (e.g., Rozas, 2001; Rybníček et al., 2016; Stojanović et al., 2017). To assess whether these relationships were stable through time, we calculated 20-year long moving correlations overlapping by one year, taking into consideration only those climate variables strongly and significantly ($P < 0.05$) correlated with BAI. Comparisons of variables between living and dead trees were assessed using *t* or Mann-Whitney *U* tests in the case of variables that followed or did not follow normal distributions, respectively.

2.5. Drivers of long-term BAI trends

To compare the long-term BAI trends of the living and recently dead trees we used Generalized Additive Mixed Models (GAMMs; Wood, 2006), a flexible semi-parametric approach of characterizing non-linear relationships, as those between the BAI and different explanatory variables like tree age, calendar year and tree size (DBH). GAMMs have been applied to identify the possible differences in growth between the living and recently dead trees in each (old-growth vs. managed) forest (Camarero et al., 2015; Colangelo et al., 2018; Sangüesa-Barreda et al., 2015). To test for the differences in growth trend of coexisting living and recently dead trees on the same site and for the influence of different factors, we built the following GAMMs:

$$BAI_j = s(DBH_j) + s(\text{cambial age}) + s(\text{calendar year}) + Z_j B_j + v_j,$$

where the BAI of the tree *j* (BAI_j) was modelled as smooth function (*s*) of three predictor variables (DBH, cambial age and calendar year). Since the BAI is influenced by the site conditions as well as by the individual growing condition of each tree, tree identity ($Z_j B_j$) was considered as a random effect. We included an error term (v_j) with a first-order temporal autocorrelation (ar1) structure for the serial dependency of BAI values. Calendar year was considered as a covariate and the tree age was entered as a fixed value. BAI was log-transformed [$\log(x + 1)$] prior to the analyses. To determine the GAMMs the *mgcv* package in R was used (Wood, 2017).

In a second step, to test whether trees with contrasting declining status (living vs. dead trees) show different growth responses to several drivers (e.g., climate, drought, age, competition), generalized linear mixed-effects models (GLMM) were separately fitted to BAI data of living and dead trees for the managed and old-growth study sites considering the period 1950–2013. We adjusted linear mixed-effects models assessing competition or tree size (considered here as a proxy of the past management), and climatic variables (maximum temperature, precipitation and SPEI) as fixed effect factors. BAI was log-transformed [$\log(x + 1)$] prior to the analyses. The predictor variables were introduced as fixed effects and tree identity and tree age as random effects. We used selected monthly and seasonal temperature, precipitation and SPEI data as climatic predictors of BAI according to the

results of climate-growth relationships (see Section 2.3). We included a first-order temporal autocorrelation (ar1) structure for the BAI values. Residuals of the models were checked for normality, homoscedasticity and temporal autocorrelation. The effects of climate, drought and competition on BAI were tested and compared with a null model considering BAI as a constant. We also evaluated the existence of multicollinearity among fixed effects by calculating the variance inflation factor (VIF), which was always lower than three, suggesting no redundancy problems among predictors (Zuur et al., 2009). We used an information-theoretic approach for multi-model selection based on minimizing the Akaike information criterion (AICc) (Burnham and Anderson, 2002). The AICc combines the measure of goodness of fit with a penalty term based on the number of parameters (*k*) used in the model, i.e., it selects the most parsimonious models. We also calculated Δ_i , which is the difference in AICc with respect to the best-fitting model, and the Akaike weights W_i (i.e. the relative probability that model *i* would be the best-fitting model for the observed data). We considered a selection of models with substantial support to be those in which the AICc between models was less than two (Zuur et al., 2009). The linear mixed-effects models were fitted with the *nlme* package (Pinheiro et al., 2016) in R (R Core Team, 2020).

3. Results

3.1. Climate and growth patterns

Long-term regional meteorological data showed a significant positive trend of the mean annual temperature ($r = 0.29$, $P < 0.05$, mean rate $+0.01$ °C year⁻¹) (Fig. 1c) as well as for spring, summer and autumn temperatures (Fig. S3), whereas precipitation did not reveal any clear trend (Fig. 1c and S3). We detected a positive mean temperature shifts in the 1980s showing transitions to warm periods, emphasized the beginning of the longest warmer and dry period since 1900s (Fig. 1c and S3). The stronger increase was found during summer (the mean annual rate of the 1980–2017 was with $+0.54$ °C greater than mean of the whole period), follows by spring temperature ($+0.45$ °C). According to the spring and summer precipitation data and SPEI values, the most severe regional droughts occurred in 1943, 1962, 1987, 1990, 1993, 2000, 2003 and 2012 (Fig. 1c).

Living trees were taller than recently dead trees in both forests and thicker only in old-growth forest (Table 2). There was no significant difference in tree age between dead and living trees in both forests (Table 2). While in the old-growth forest half of the dead trees formed the last growth ring maximum three years before the sampling year (Fig. S2), in managed forest almost all the dead trees formed the last growth ring one to two years before, and more than 50% died during the sampling year.

Mean BAI values after 1950s were higher in living than in dead trees in both sites (Table 2) and higher in old-growth than in managed stands. The mean correlation among tree-ring series was higher in dead than in living trees in managed forests indicating a higher responsiveness to climate, in contrast to old-growth forests. Living trees had higher values of first-order autocorrelation than dead trees in both forests, significantly only in managed one. Mean sensitivity was higher in dead trees and lower for old-growth forests, indicating a higher inter-annual variability of radial growth (Table 2). In all cases the EPS was above the 0.85 threshold indicating a well-replicated population chronology for the studied period (Table 2).

3.2. BAI response to climate and drought

Both sites showed significant association between the intensity and severity of drought and tree-ring growth, with significant ($P < 0.05$) higher values in dead than living trees and significant ($P < 0.001$) stronger correlations in managed than in old-growth forests (Fig. 2). We found a positive and significant relationship between SPEI recorded at

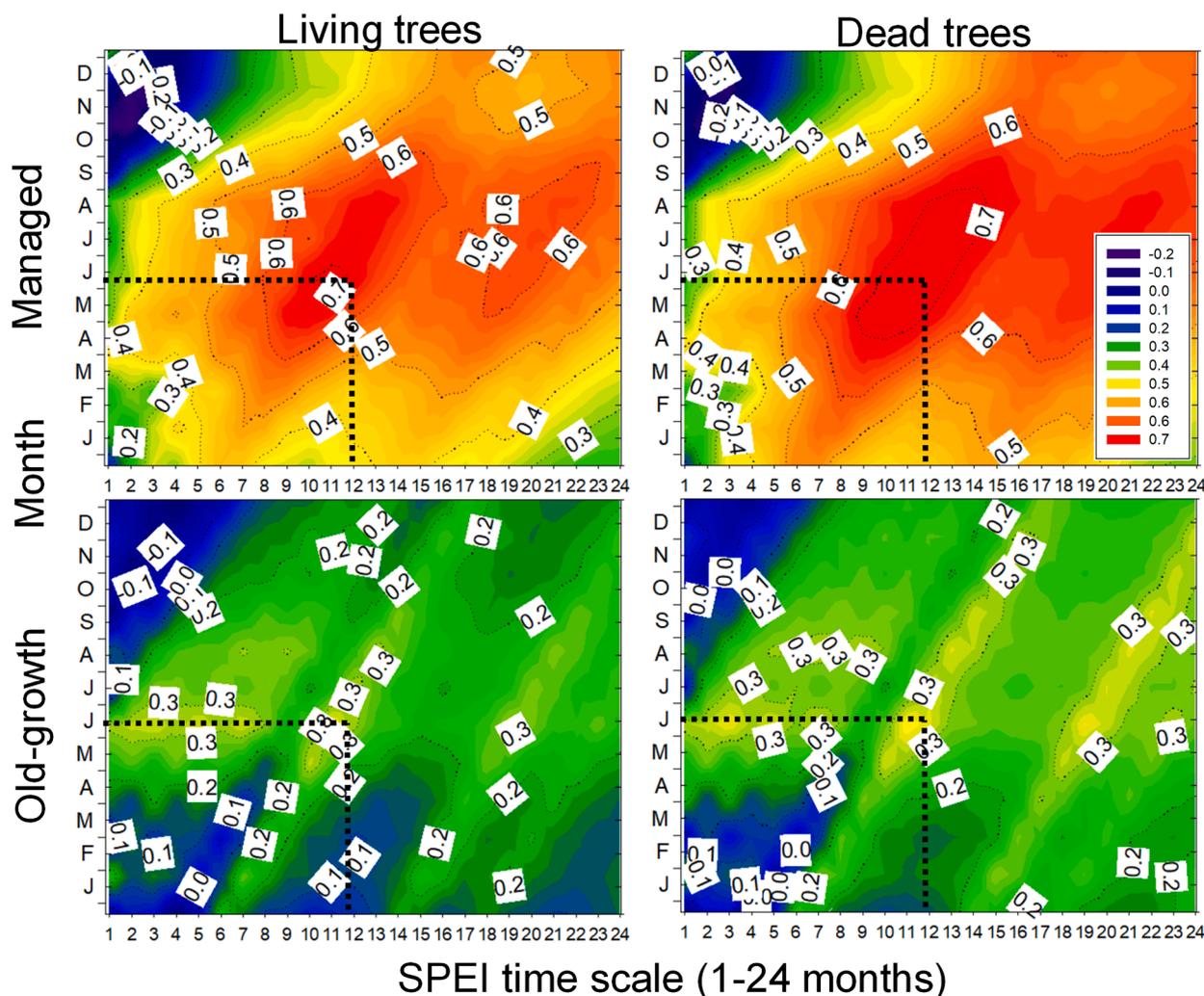


Fig. 2. Standardized Basal Area increment (BAI) responses of the Managed and Old-growth forests to drought. The color scale shows the correlations (Pearson coefficients) calculated between standardized BAI and the SPEI drought index obtained for 1- to 24-month-long scales (x-axes) for living (left column) and dead (right column) trees. The correlations were calculated for the common and best-replicated period 1950–2013 and considering the months of the current growth year (y axes). Correlation values above +0.25 and below -0.25 are significant at the $P < 0.05$ level. The dashed black lines indicate the SPEI temporal scale (x-axes) and month (y-axes) when the maximum BAI-SPEI correlation was obtained.

1–12 months long time scales in both sites, corresponding to short dry periods occurring at a high frequency (Fig. 2). The highest correlations with spring-summer SPEI calculated from 6 to 24 month-scale were found in managed forests for dead trees ($r = 0.76$, SPEI 12 months). In dead trees from old-growth forests, high correlations ($r = 0.39$) were also observed with late spring-early summer SPEI and considering 12-month scale (Figs. 2 and 3).

Growth responded negatively to warm late spring and early summer, regardless of forest type (Fig. 3); whereas negative associations for old-growth forests during previous August and September was significantly higher in dead trees. However, the growth of dead trees was significantly ($P < 0.05$) more sensitive to high April and summer maximum and mean temperatures in both forests but particularly in managed forests (Figs. 3 and S4). In managed forests, living trees were more sensitive to wet spring and summer conditions, whereas in old-growth forests the dead trees were more sensitive than the living one for previous August and current June and February precipitation (Fig. 3). Current wet autumn conditions were negatively associated to growth on both dead and living trees in managed and old-growth forests.

Moving correlations between BAI and the significant climate variables showed a noticeable shift in the 1990s, with changes from positive to negative correlations in maximum temperatures in old-growth forest.

In contrast, higher sensitivity to June (after 1990s) and August (after 1980s) precipitation increased, in old-growth and managed forests, respectively. Slightly higher correlations in dead than in living trees were observed in old-growth forest (Fig. 4). Similarly, the positive correlation with summer SPEI at 12-month scale increased since 1970s in managed forest and changed from negative to positive in 1990s for old-growth forest, with stronger signal in dead than in living trees in both sites (Fig. 4).

3.3. Long-term growth trends and climate influence on dieback process

The GAMMs models showed that calendar year and DBH have significant effects on BAI in both forests, whereas tree age affects BAI only in living trees from old-growth forests (Table 3). BAI of both dead and living trees in managed forests increased from the 1920s to late 1960s, with slight reductions in the early 1940s, stronger reductions during 1970s and growth shift between dead and living trees after early 1980s (Fig. 5). In contrast, BAI in old-growth forests increased from the 1940s to late 1960s and only in living trees after 1980s (Fig. 5). BAI started diverging between living and dead trees after relative cold summer conditions in 1970s and continued with dry 1980s, although this divergence became significant in the mid-1980s when severe hotter

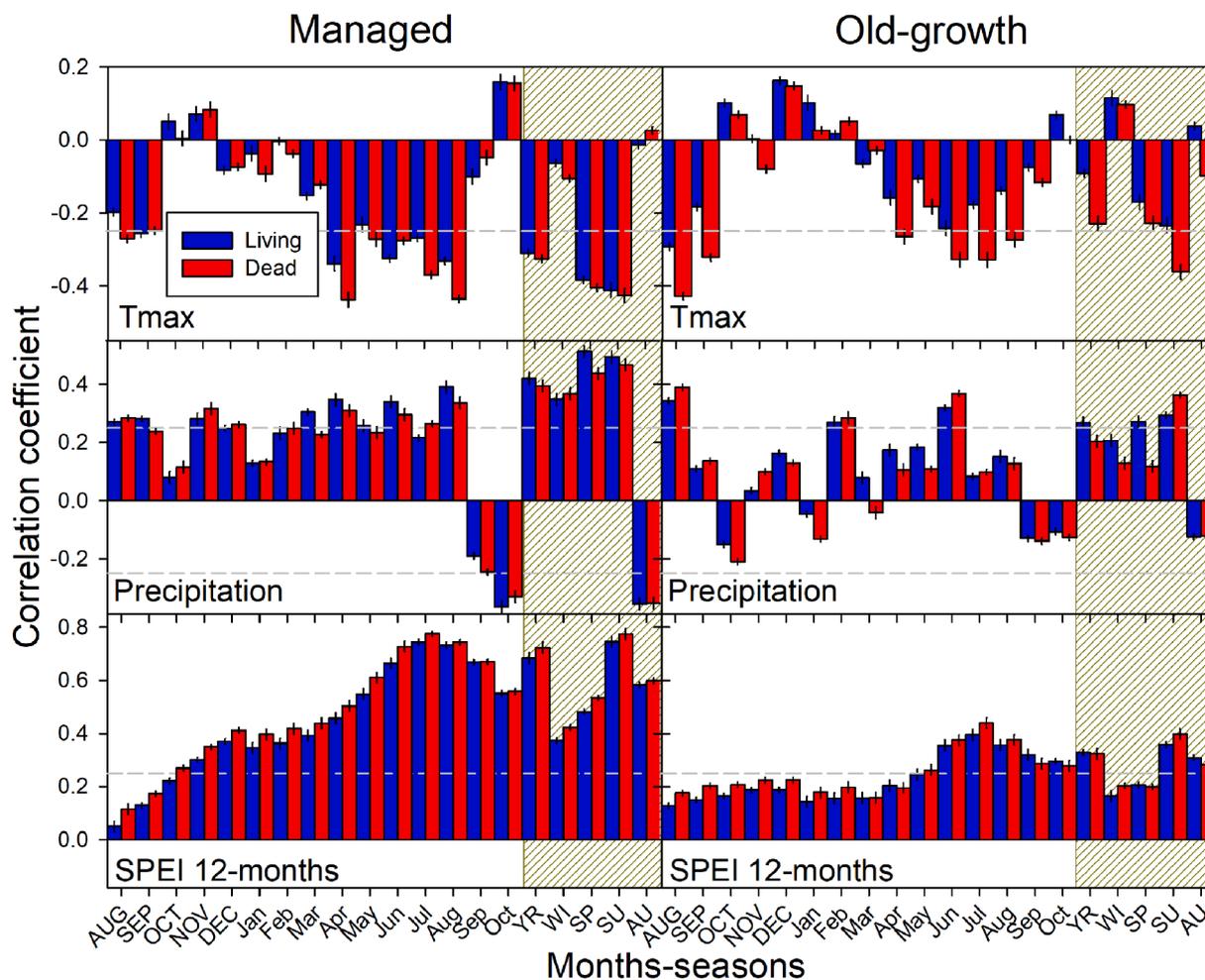


Fig. 3. Individual Pearson correlation coefficients calculated between *Q. petraea* radial growth for living and dead trees (BAI) and the monthly maximum temperature (upper plot), precipitation (middle) and SPEI 12-month scale (lower plot) for the 1950–2013 period in the managed (left) and old-growth (right) forests. Growth is related with climate data from the previous (months abbreviated by uppercase letters) and current months (lowercase letters) and current seasons (YR, annual; WI, winter; SP, spring; SU, summer, AU, autumn) years; being the current year that of tree-ring formation. The significance levels of correlation coefficients are indicated by dashed grey lines ($P < 0.05$).

droughts occurred in both forests (Fig. 5).

The GLMM models showed that the most significant drivers of BAI were DBH (size-competition), summer SPEI (wet and cool summer conditions enhance growth) and summer (June, July and August) maximum temperatures and precipitation (warm and dry summer conditions reduce growth) (Tables 4 and S2). BAI was also positively affected by February precipitation in old-growth forests. At both study sites, BAI was negatively affected by the competition (higher DBH implies less competition), regardless the declining status (Table 4). The models including competition and climate variables explained better the differences in growth between living and dead trees at the old-growth site than in the managed forests (Tables 4 and S2).

4. Discussion

Increasing warming-enhanced drought stress in recent decades is likely linked to ongoing oaks dieback in central Europe (Lindner et al., 2010; Neumann et al., 2017). The shifts in mean temperature after 1980s (see Reid et al., 2016) is the longest warmer and dry period detected in central Europe since 1900s (Ionita et al., 2016, 2017), although precipitation did not present clear trends in the study sites (Figs. 1 and S3). These long-term changes in the climatic conditions concur with increases in the intensity, severity and the frequency of recent extreme heat waves and drought events since 1980s in central

Europe: 1987, 1993, 2000–2001, 2003, 2011, 2015, 2018 (Buras et al., 2020; Ionita et al., 2016, 2017). Overall, our results suggest that managed oak population showed higher sensitivity to warming-related drought events than nearby old-growth (unmanaged) population (Mausolf et al., 2018).

The warmer climate conditions have been shown to cause a reduction in growth in other deciduous oak species growing at central Europe (e.g., Cufar et al., 2014). In the present study, dead and living trees did not show significant differences ($P < 0.05$) in growth rates before 1980s both in managed and old-growth forests (Fig. 5). Only during early stage of growth dead trees showed higher BAI values than living trees in managed forests (Fig. 5). The increasing hotter-drought events after 1980s and warmer temperatures triggered recent dieback episodes in both forests (Fig. 5) (Allen et al., 2015). The dead trees in both sites showed lower growth rates than living trees after 1980s, in agreement with previous studies indicating lower growth rates preceding tree death (Cailleret et al., 2017). Recent studies have also suggested that this feature is related directly to drought-induced mortality (Berdanier and Clark, 2016). Our findings also confirm that oaks dieback and death can be a long-lasting process with lagged effect of drought by several years (Colangelo et al., 2018; Sohar et al., 2014). In addition, our results seem to indicate a growth constraint after the climate shift and match with previous studies in oak species showing a growth decline after cold 1970s and dry 1980s with dieback symptoms characterized by shoot and

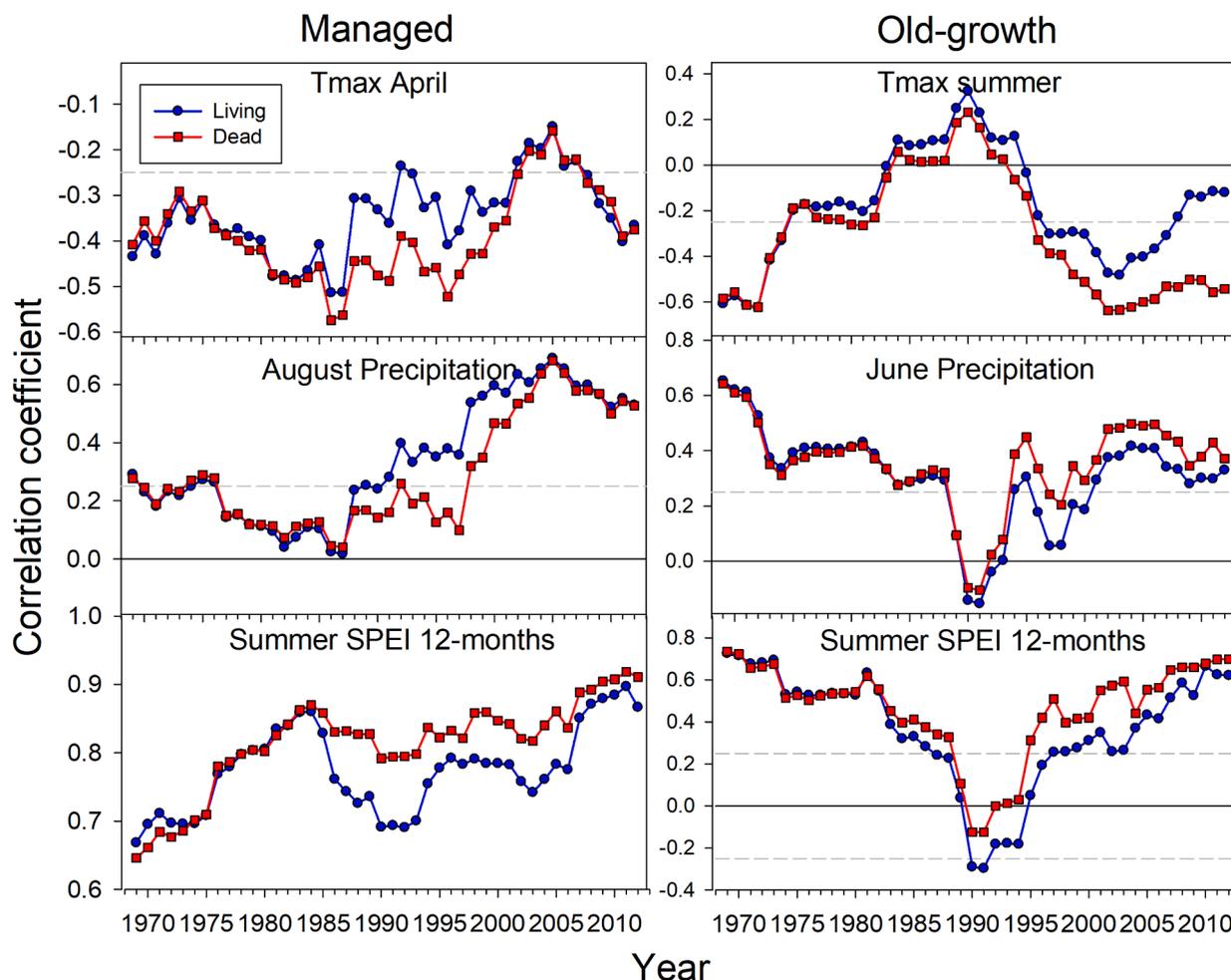


Fig. 4. Temporal changes in moving correlation coefficients using 20-year long intervals shifted by one year for the period 1950–2013 (values are arranged for the last year of each 20-year long interval). The included climate variables were the best correlated with BAIi (see Fig. 3). Dashed horizontal lines indicate statistically significant correlation coefficients ($P < 0.05$) in Managed and Old-growth forests for living (blue) and dead (red) trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Influences of calendar year (Year), cambial age (Age), and tree diameter (DBH) on basal area increment (BAI) of *Q. petraea* at the two study sites (old-growth vs. managed) and considering Living and Dead trees according to the best-fit GAMMs. The influence of the covariates affecting BAI is indicated by the F statistic and its associated probability (P). In addition, the estimated degrees of freedom (edf) for each variable are shown. The amount of variance explained by each model (R^2) is indicated in the last row.

Variables	Managed		Old-growth	
	Living	Dead	Living	Dead
Year				
edf	85.716	93.666	95.952	96.593
F	36.043	29.830	20.886	38.909
P	< 0.001	< 0.001	< 0.001	< 0.001
Age				
edf	2.250	1	3.358	2.712
F	1.142	1.306	2.287	2.024
P	0.239	0.253	0.038	0.068
DBH				
edf	1.552	1	1	1
F	49.890	36.888	327.413	106.626
P	< 0.001	< 0.001	< 0.001	< 0.001
R^2	0.54	0.41	0.56	0.42

leaf shedding, divergence in growth rates and high mortality rates (e.g., Andersson et al., 2011; Colangelo et al., 2017a, 2017b, 2018; Sohar et al., 2014).

In accordance, warmer spring and summer temperature increasing evapotranspiration rates (Figs. 1 and S3), were identified as main factors driving the observed recent growth decline in these forests (Figs. 2, 3 and 5), in agreement with previous studies across central European temperate species (e.g., Cufar et al., 2014; Mausolf et al., 2018; Popa et al., 2013; Zimmermann et al., 2015). Our results confirmed that growth in dead trees is strongly limited by spring-summer temperatures, more in managed than in old-growth forests (Fig. 4), constraining water availability during growing season (Doležal et al., 2010; Lebourgeois et al., 2004; Stojanović et al., 2017); thus, showing that growth in dead trees is significantly associated with the SPEI in managed forests (Fig. 2). Moreover, while the growth of living trees in managed forests are positively and significantly related to April, June and August precipitation, only the February and June precipitation significantly enhanced the growth of living trees growing in old-growth population (see Dobrovolný et al., 2016; Friedrichs et al., 2009). This positive influence of spring-early summer water availability on sessile oak growth has been reported in other oak species from France (Mérian et al., 2011), Germany (Friedrichs et al., 2009), Poland (Bronisz et al., 2012), Czech Republic (Dobrovolný et al., 2016; Stojanović et al., 2017) and Romania (Ciceu et al., 2020; Popa et al., 2013). It is noticeable that dead trees responded negatively to previous autumn temperatures, suggesting

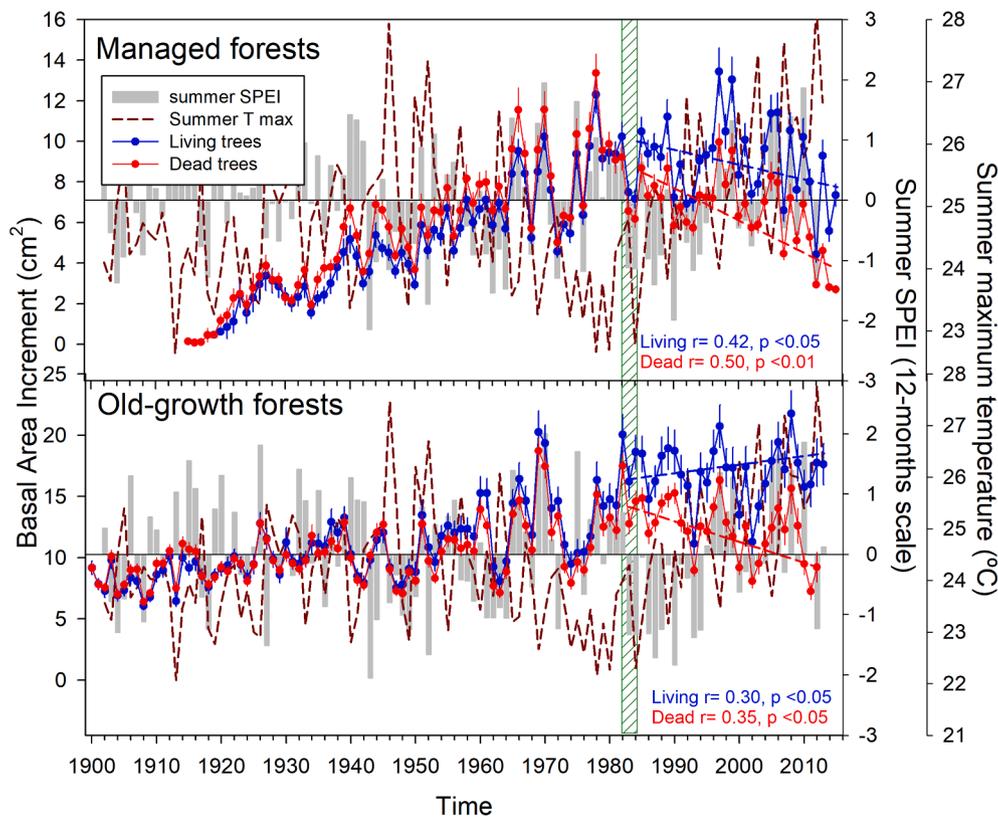


Fig. 5. Long-term changes in raw basal area increment (BAI), summer maximum temperature (Txs) and drought index (SPEI). The BAI was calculated for managed and old-growth *Q. petraea* considering living (blue) and dead (red) (values are means \pm SE). The right y-axis shows the cumulative SPEI (bars) from June to August calculated at 12-months scale. The right offset y-axis shows the summer maximum temperature. Pearson correlations (r) between BAI and the summer-SPEI and associated probability values (P) are show for L and D trees. Green area shows the growth divergence after cold 1970s and dry 1980s. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4

Best linear mixed-effects models of basal-area increment (BAI) of *Q. petraea* fitted to living and dead trees from the Managed and Old-growth forests as a function of climatic variables and the competition variables (DBH). A null model considering BAI as a constant was also included (see Table S2 for details). Tree age and the tree identity were used as random effects.

Foresttype	Tree type	n trees	Df	Best model	R ²
Managed	Living	52	3256	$-0.37 + 0.04DBH + 0.05SPEIs - 0.02Txs$	0.56
	Dead	54	3387	$0.07 + 0.02DBH + 0.02P8 + 0.04SPEIs - 0.02Txs$	0.57
Old-growth	Living	48	3007	$0.05 + 0.03DBH + 0.01SPEIs + 0.01P2 + 0.01P6 - 0.01Txs$	0.65
	Dead	48	3256	$0.05 + 0.02DBH + 0.02SPEIs + 0.01P2 + 0.02P6 - 0.02Txs$	0.66

*Variables abbreviations: DBH, diameter at breast height; SPEIs, summer SPEI at 12-month scale; Txs, summer maximum temperature; P2, February precipitation, P6, June precipitation; P8, August precipitation.

consumption of stored sugars due to cumulative drought stress during the production of new earlywood vessels in the current growing season (Barbaroux et al., 2003), whereas living trees growth responded more to wet early spring conditions when growth resumption occurs (Fig. 3) (Gricar et al., 2019). Interestingly, our findings also show that warming trends and drought sensitivity of *Q. petraea* strongly depends of the legacy of management history, being less sensitive to climate in the unmanaged old-growth forests (cf. Mausolf et al., 2018).

In contrast with Bennett et al. (2015), but in agreement with other studies about anisohydric oak species (e.g., Andersson et al., 2011; Colangelo et al., 2017a, 2017b, 2018), our results showed that living trees were significantly taller and thicker than dead trees (Table 2), maybe due to the rapid leaf loss associated with apical shoot dieback (Colangelo et al., 2017b), observed especially in the managed forest.

Colangelo et al. (2018) tried to explain this predisposition of smaller oak dominant trees to dieback through a lower capacity to buffer the effects of water deficit by rise the hydraulic capacitance due to a possible shallower root systems and smaller stem sapwood water reserves (Zhang et al., 2009). The contrasting vulnerability of dead and living trees in both forests during the late 20th century might be interpreted as a higher sensitivity to evapotranspirative demand of dead trees during the early stage of tree-ring formation, constraining the wood formation by decreasing cell turgor in the xylem and the cambium, with differences since 1980s in dead and living trees (Cuny et al., 2012). This is also consistent with specific mobilization of carbon reserves during the growing season (Michelot et al., 2012), since the carbohydrates assimilated during previous summer is used for maintaining respiration, to protect the tree against stresses, and partially for wood and foliage resumption in the early spring (Laureano et al., 2013). This is in line with the fact that earlywood resumption in sessile oak starts several weeks before bud bursting, and therefore depends on carbon reserves assimilated in the previous year (Michelot et al., 2012). Our results suggest that lower radial growth rates could also differentially influence the sapwood conductive area between living and dead trees, thus leading to an irreversible reduction in carbon uptake and hydraulic conductivity (Poorter et al., 2018). Furthermore, oaks species show strong anisohydric character during drought periods and continue consuming the available nutrient and water resources. Moreover, they continue transpiring with poor control of their stomata, thus, resulting in a high sensitivity to extreme events which triggers leaf and roots losses, leading subsequently to growth reduction (Zweifel et al., 2009). In this sense, under warmer conditions, oaks aiming to keep stable ratio between crown (transpiring area) and xylem hydraulic conductance, and reduce the carbon gain with cascading effects, ultimately resulting in xylem hydraulic failure in dead trees (Peguero-Pina et al., 2016). In addition, site-specific soil conditions together with large belowground competition for water and nutrients between neighboring oaks with initial phenotypic differences could increase the vulnerability to hotter-

droughts, since oaks with deeper root systems are able to use different soil water sources under water stress (Ripullone et al., 2020). The growth enhancement during favorable climate conditions (due to higher sensitivity) of dead trees in managed forests (Figs. 3 and 5; Table 4) can additionally generate structural overshoot (Jump et al., 2017) that produces a temporal decouple between water supply (hydraulic system) and water demand during extreme hotter-drought conditions causing drought-induced growth decline (Mausolf et al., 2018).

Other factors such as past management (competition changes, see Table 4) could be responsible for the higher sensitivity of tree growth of sessile oak (Stojanović et al., 2017). Indeed, the thinning treatments may trigger rapid crown expansion and enhance growth of the remaining trees in temperate broadleaf species, changing the root to shoot ratio balance (e.g., Fichtner et al., 2013; Salomón et al., 2016; Vrška et al., 2016), rainfall interception and increasing extractable water during the growing season (see Bréda et al., 1995). Trees released from competition in managed oak stands have also to adjust their hydraulic system (wider vessels) to the development of their crown and the subsequent increase in evaporative demand of leaves, thus, increasing oak susceptibility to consecutive extreme drought conditions (Jump et al., 2017). This is also influenced by the past management history, therefore, coppice forests have higher root biomass per unit of leaf area, hence reserve stocks in roots could be used for aboveground biomass development, while unmanaged old-growth high stands have to invest more assimilates into belowground structures in order to secure soil water and nutrients uptakes during the initial phase of forest development (Thomas and Gausling, 2000). Other studies have also suggested ageing like a driver of mortality in old-growth forests, but positive growth trends showed by living trees (Fig. 5), despite the 184-year-old on average (Table 2), confirm that senescence is not the cause of sessile oak forest dieback. Then, the response to climate change and drought observed across individual trees and species could be also explained by its genetic adaptation (cf. Alberto et al., 2013). Further studies on sessile oak dieback could be gained by linking genetic, ecophysiology (stable isotopes, nutrients) and long-term monitoring of forest phenology, xylogenesis and growth including past releases information and resilience to extreme events (e.g., Ciceu et al., 2020; Colangelo et al., 2017b, 2018; Petritan et al., 2017).

The divergent growth pattern after 1980s of living and dead trees in both forests, as well the weaker sensitivity of the dead and living trees of old-growth forest compared with those from managed forests suggest that the management legacies, but probably also the regeneration type (generative or vegetative), are important factors driving the climate sensitivity of sessile oak. It was already shown that past management practices could influence the tree growth response to climate trough legacy effects on the stand structure and changes in stand microsite conditions (Camarero et al., 2011; Latif and BlackBurn, 2010; Rozas, 2015; Sánchez-Salguero et al., 2015). Stojanović et al. (2017) found also that coppiced sessile oak trees have a higher sensitivity to summer temperature and water balance of the current year than high forest trees, originated from seed, and came to the conclusion that coppice forest will be highly vulnerable to further warmer and drier conditions.

Although Romanian forests were actively coppiced until the forest nationalization (1948), this silvicultural system was legally forbidden for sessile oak, and most of the former coppiced oak forests were being converted towards high forests (Nicolescu, 2010). This was the case of our study managed forest, which have been regenerated by coppice 85–90 years ago and showed neither higher growth rates in early stages nor along the whole life compared with seed origin trees growing in the old-growth forest (Fig. 5). Nevertheless, our results highlight that the theoretical better performance of coppices under limited water conditions due to a better root system (Stojanović et al., 2016), might not be an advantage to cope against drought-induced dieback processes in comparison with old-growth forests. In fact, managed forests show high sensitivity to climate warming and increasing drought stress with growth decline after 1980s, which should be expected to affect the

surviving trees in the near future (Camarero et al., 2011). Nonetheless, the main co-occurring species with same regeneration origin, *Q. cerris* in managed forests and *F. sylvatica* in old-growth forests, seems to be less affected by forest dieback (Bréda and Badeau, 2008; Petritan et al., 2017). Future works considering mixed oak forests across management gradients and taking into account the site characteristics and competition changes are needed to improve our understanding of the interactive effects of management legacies and drivers of global environmental change in forest dieback processes (Bottero et al., 2017; Sohn et al., 2016).

Regarding insight for forest management, converting coppices into high forests by thinning treatments, may be hindered by a progressive increase in root to shoot ratios, but it is further complicated by intense root sprouting and high economical costs (Vrška et al., 2016). However, the conversion by minimizing the root sprouting alongside, together with assisted natural seed regeneration of mixed structures of presented species, could improve the resilience and resistance of these managed forests to future climate scenarios (Rubio-Cuadrado et al., 2018). It is also suggested that a slight reduction of stand density opening gaps-based regeneration in old-growth forests will benefit the conservation as mixed sessile oak-beech forests, favoring the preservation of herbs, shrubs and understory vegetation to improve the capacity of water retention and reduce evapotranspiration, thus offering higher stability to increasing temperatures (Gentilesca et al., 2017; Jaloviar et al., 2020). However, the light demanding oaks (Bobic et al., 2011), although can regenerate in gaps of around 300 m² (von Lüpke, 1995), for further successful growth need larger gaps with at least 1000 m², being restricted its natural dynamics to large disturbance-related gaps (Petritan et al., 2013, 2017; Rubio-Cuadrado et al., 2018). Moreover, if advanced shade-tolerant species (e.g., beech, hornbeam, maple) are advanced regenerated, the oaks fail to regenerate also in such large gaps (Jaloviar et al., 2020). Without an active management by subsequent controlling of such competitive species the oak could be extinguished from these mixed stands (Petritan et al., 2014; Jaloviar et al., 2020). Anyhow, the anisohydric behavior of sessile oak under hotter-droughts could question the validity of thinning treatments in these drought-prone mixed *Q. petraea* forests (McDowell, 2011).

5. Conclusion

Our study provides novel results to understand the effect of management legacies on the sessile oak sensitivity to climate warming. We conclude that the temperature and evapotranspiration rise during growing seasons could explain the *Q. petraea* dieback and growth divergences between dead and living trees since the warm and dry 1980s. Our findings highlight that if heat waves and droughts become more severe and frequent as predicted in the central European temperate forests, hotter drought-induced tree mortality will be increasingly in sessile oak mixed forests. The understanding of the interaction between climate and stand historical management is therefore decisive for the future performance and persistence of sessile oak unique old-growth forests in central European climates.

CRedit authorship contribution statement

Any Mary Petritan: Conceptualization, Methodology, Resources, Data curation, Investigation, Writing - original draft, Project administration, Funding acquisition. **Ion Catalin Petritan:** Conceptualization, Methodology, Resources, Data curation, Investigation, Writing - review & editing. **Andrea Hevia:** Methodology, Software, Formal analysis, Investigation, Writing - review & editing. **Helge Walentowski:** Validation, Writing - review & editing, Funding acquisition. **Olivier Bouriaud:** Validation, Writing - review & editing. **Raúl Sánchez-Salguero:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Visualization, Supervision.

Declaration of Competing Interest

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

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The authors declare no conflicts of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119097>.

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