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Long-term impacts of drought on growth and forest dynamics in a temperate beech-oak-birch forest

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Abstract

The role of climatic extremes on forest dynamics is still not fully understood. This is the case for droughts in temperate forests where growth of tree species is more driven by tree-to-tree competition than by climate. In this study we examine whether droughts shape growth trends and forest dynamics in a temperate forest of beech, oak and birch located in the “Picos de Europa” National Park in northern Spain. We used a dendroecological approach to quantify climate-growth associations and to evaluate growth resilience after droughts. We detected growth releases and quantified the increase in the number of trees established following each drought. Beech was the dominant tree species. Tree growth was only weakly related to climate variables in the three species studied. Oak was more resistant to drought than the other two species in terms of growth, with beech displaying higher vulnerability to drought. A significant association is displayed by all three species among droughts, growth releases and tree establishment pulses. After 1923 and following the dry 1940s, beech presented a peak of growth releases, whereas growth releases in oak and birch were concentrated in the 1960s and 1990s, respectively. Drought-induced growth releases probably reflect gap formation, these gaps being filled by recruitment of the three species.

Keywords: *Betula pubescens*, dendroecology, *Fagus sylvatica*, gap dynamics, growth releases, *Quercus petraea*.

1 Introduction

Droughts may trigger disturbances and drive forest dynamics (Shuman et al., 2009). Rapid climate change may increase the frequency of severe droughts, challenging the ability of tree species which usually have long lifespans and slow evolution rates, to locally adapt to the new climate conditions (Alberto et al., 2013). In drought-prone forests, climate is one of the main factors that determine their dynamics. Tree mortality caused by dry spells generates gaps and patches which are filled by tree regeneration during cool-wet periods (Villalba and Veblen, 1997). In this way, drought removes old or less vigorous individuals and favors the establishment of regeneration of the same tree species or even of different species with contrasting requirements (Brown and Wu, 2005).

In contrast, in temperate forests, tree mortality and gaps are often considered stochastic processes, not necessarily generated by climatic extremes such as droughts (McCarthy, 2001). Gap dynamics in these forests are characterized by small-scale disturbances in the mature forest canopy, where a single or a small group of trees dies, creating a “hole” in the canopy that is occupied by released regeneration (Runkle, 1985). Tree death can be related with multiple biotic (stem size, stand conditions, tree species and pathogens) and abiotic factors (storms, precipitation, topographic features, edaphic conditions and disturbance history) and is usually due to stem breakage or uprooting caused by wind-throw or standing death caused by root and butt diseases (McCarthy, 2001). The generation of gaps is a continuous process which may dominate the disturbance regime in these forests (Lewis and Lindgren, 2000). Furthermore, in contrast to drought-prone conifer forests, the impact of pests and fires on broadleaf temperate forests is typically limited and spatially heterogeneous, without large-scale dieback (Man, 2012; McEwan, et al., 2007; Parshall and Foster, 2002).

The influence of climatic extremes on temperate-forest dynamics is poorly understood due to the difficulty involved in separating anthropogenic or natural disturbance-induced successional changes from climate-related alterations (Prentice, 1992). Furthermore, in the case of temperate forests climate-growth associations are usually less relevant than in dry or cold forest biomes, and competition often becomes the most important driver of radial growth (Fernández-de-Uña et al., 2016; Lebourgeois et al., 2005; Sangüesa-Barreda et al., 2015). However, exceptionally dry years can lead to abrupt growth declines, even in temperate forests (Gazol et al., 2017; Stahle et al., 2000; Zang et al., 2014). Recent evidence indicates that droughts may be key to understanding the dynamics of humid broadleaf-dominated forests; synchronizing growth declines, large-scale disturbances and post-drought recruitment pulses (Pederson et al., 2014). In addition, growth decline and tree mortality in these temperate forests may be amplified under warmer and drier climate conditions (Bréda et al., 2006).

In Western Europe, mixed broadleaf forests dominate temperate oceanic regions which are predicted to experience more severe droughts and warmer conditions during the 21st century (Jacob et al., 2014). Most importantly, the frequency and magnitude of extreme climatic events, such as dry spells, will also increase under predicted climatic scenarios (EEA, 2004). These extreme events are particularly important to understanding forest dynamics (Jentsch et al., 2007). Some of the temperate forests in Spain constitute the southernmost distribution limits of important tree species such as European beech (*Fagus sylvatica* L.) or the sessile oak (*Quercus petraea* Liebl.). These populations are situated in areas with a Mediterranean influence, characterized by warmer and drier conditions during the growing season, particularly in summer (Giorgi and Lionello, 2008). Therefore, droughts and warmer conditions may contribute to the substitution of the dominant tree species in these southern temperate forests.

In this study we reconstruct forest disturbances by studying the abrupt and sustained increase in radial growth in trees with improved growing conditions (e.g., more light availability) following the death of neighboring trees. This sudden increase in wood production corresponds to a growth release (Altman et al., 2014). We reconstruct radial growth dynamics and associated tree recruitment pulses in a temperate forest situated in the “Picos de Europa” National Park in Northern Spain, close to the limit of the southern range of European beech and sessile oak. No logging has taken place in this well-preserved forest over the past century, enabling us to characterize the effects of climate on growth and to infer past gap dynamics. We aim to answer the following questions: (i) what is the climatic sensitivity of the tree species? (ii) is climate the driver of growth releases in the study area and do these releases underlie an increase in tree establishment? (iii) what factors influence growth releases?

Since the species studied in this case are close to the limit of their southern range, we hypothesize that climate has an important influence on growth and that extreme climatic events drive the growth releases and the establishment of recruitment in this temperate forest.

2 Materials and methods

2.1 Study area

The study area comprises mixed, uneven-aged forest of European beech (*Fagus sylvatica* L., hereafter beech), sessile oak (*Quercus petraea* (Matt.) Liebl., hereafter oak) and birch (*Betula pubescens* Ehrh., hereafter birch). The three species are deciduous and form conspicuous growth rings. Oak forms ring-porous wood, but beech and birch form diffuse-porous wood. Birch is an early-successional, shade-intolerant species whereas European beech is a late-successional, shade-tolerant species and

sessile oak has intermediate characteristics (Frelich et al., 2015). Where European beech and sessile oak coexist, beech displaces oak due to its greater competitiveness and higher canopy cover (von Lüpke, 1998; Petritan et al., 2013). The site is located in León (northwestern Spain) at one of the southernmost distribution limits of beech and oak in Europe (**Appendix A**). Beech is the most abundant and widespread species throughout the studied forest. Oaks are more sparsely distributed, whilst birch appears at higher altitudes and on peatlands. The study area has undergone little human disturbance over the last century apart from cattle grazing and firewood collection. No logging has taken place over this period. There is a temperate oceanic climate with average temperatures of 8° C and annual precipitation of 1250 mm (data from Riaño station, ©AEMET, 42° 58' N, 05° 01' W, 1048 m a.s.l.; located at 20 km from the study site; see **Fig. 1**). The soils are Mollic Leptosols (FAO, 2015).

2.2 Field sampling

We conducted a field survey consisting of 103 sampling points systematically distributed on a square grid of 250 m x 250 m, occupying an area of 800 ha between coordinates 43° 8' 59'' – 43° 10' 29'' N, 4° 58' 48'' – 5° 2' 40'' W. The altitude ranges from 900 to 1600 m a.s.l. with a mean elevation of the sampling of 1283 m. The sampling was carried out during 2014 and 2015. At each sampling point, a pair of stereoscopic hemispherical images was captured using ForeStereo (patent MU2005-01738 of the Spanish Forest Research Centre) to characterize the neighborhood and estimate stand basal area, tree density and diameter at breast height (DBH_{stand}) (Herrera et al., 2009; Rodríguez-García et al., 2014; Sánchez-González et al., 2016). In addition, one dominant tree of each species was randomly selected at each sampling point and its diameter at breast height (DBH) was measured. Two cores were extracted using a

Pressler increment borer at breast height. These cores were always extracted perpendicular to the maximum slope. In total we cored 92 beech trees, 34 oaks and 11 birches. Topographical variables (altitude, slope and aspect) for each point were obtained from a Digital Terrain Model (PNOA®, © Instituto Geográfico Nacional, Spain) with a spatial resolution of 25 m.

2.3 Climatic data

Due to the lack of long, complete series of local meteorological data from stations situated in the study area, we used monthly data for precipitation, mean temperature and cloud cover from the 0.5°-gridded Climatic Research Unit (CRU) dataset (Harris et al., 2014) for all the analyses. CRU climatic data are considered to be homogeneous and are available from 1900 onwards with the exception of cloud cover data, which is available from 1950 onwards. We obtained the CRU climatic data for the period 1900-2014 from the 0.5° grid with coordinates 42.5°-43.0° N and 5.0°-5.5° W.

In addition, we used the reconstructed spring precipitation data in Pauling et al. (2006) and the self-calibrating Palmer Drought Severity Index (scPDSI) of the Old World Drought Atlas (Cook et al., 2015). Monthly potential evapotranspiration (PET) was estimated empirically using the method described in Willmott et al. (1985) from CRU temperature data. To show the long-term climate trends we fitted piecewise regressions to the data using the *segmented* package (Muggeo, 2008) in R statistical software (R Core Team, 2016).

2.4 Dendrochronological analyses

Cores were mounted on wooden supports and carefully sanded until the tree rings were clearly visible. The ring widths were then measured to the nearest 0.01 mm using the

semi-automatic Lintab device with the TSAP-Win software (Rinntech, Heidelberg, Germany). Tree rings were visually cross-dated and measured, and cross-dating was further verified using the COFECHA program (Holmes, 1997).

We calculated the mean growth series for each individual and species using the *dplR* package in R (Bunn et al., 2016). Subsequently, these growths were transformed into basal area increments (BAI) as this variable is preferable to tree-ring width data for analyzing growth trends (Biondi and Qeadan, 2008). The BAI was calculated as follows:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t and r_{t-1} are the stem radius at the end and the beginning of a given annual ring increment corresponding to rings formed in t and $t-1$ years, respectively.

The age was estimated for the sampled dominant trees according to Rozas (2003b). This method is explained in **Appendix B**.

2.5 Climate-growth relationships

To determine the main environmental drivers of tree growth, we first removed biological trends in growth by calculating the residual ring-width chronologies for each species using the *dplR* package in R (Bunn et al., 2016). We used a double detrending procedure to remove long-term growth trends. We fitted a negative exponential curve to raw ring-width data, and then fitted a 32-year long cubic smoothing spline. The autocorrelation of the resulting residuals was removed using first-order autoregressive models. Pearson correlation coefficients were then calculated between the residual chronologies (mean series of the residual ring-width indices calculated for each species) and monthly mean temperature and precipitation. Correlation coefficients were calculated from October of the previous year to November of the growth year

considering that: (i) climate during the previous year affects growth during the following year (Camarero et al., 2015; Rozas, 2001), and (ii) growth can occur until November (Pérez-de-Lis et al., 2017). We split the data into three sub-periods (1911–1944, 1945–1979 and 1980–2013) to analyze changes in the relationships between climate and ring-width indices over time separately. We chose these three sub-periods of similar length due to the contrasting climatic characteristics of each, according to previous studies carried out in the Iberian Peninsula (García-Cervigón et al., 2012; Herguido et al., 2016). We did not analyze the first period in the case of birch due to the abundance of missing rings in the 1940s. The evolution over time of the Pearson correlations calculated between climatic variables and residual chronologies was analyzed for the best-replicated period, 1950–2014, using 20-year moving averages. Given the potentially long growing season in the temperate study zone (Pérez-de-Lis et al., 2017), we grouped the monthly climatic data into seasons to better reflect the changes in the climate-growth relationships.

2.6 Impact of droughts on tree growth

Due to the lack of reliable climatic data before 1900, we analyzed the most important reductions in BAI during the 20th century. Negative pointer years were determined as those years in which at least 60% of the BAI series of one species showed a BAI decrease of at least 60% relative to the average BAI in the 4 preceding years (relative growth change method; Schweingruber et al., 1990). We used these percentages to find the years with the greatest decrease in growth.

To characterize the climatic conditions linked to those negative pointer years we calculated the ratio between the climate values of these years and the average values for the 1900–2014 period, using monthly and grouped CRU climatic data. We identified the

greatest differences and, furthermore, calculated the monthly climate variables with significantly ($p < 0.05$) different means between negative pointer years and the rest of the years. As all variables are homoscedastic and as temperature shows normal distributions while precipitation does not, we used a t -test for independent samples with temperature and Mann-Whitney U tests for precipitation data. We considered temperature and precipitation from October of the previous year up to November of the growth year.

To check the discriminatory power of climate variables to predict abrupt decreases in growth, we calculated a logistic model in which the predicted variable takes a value of 0 for the negative pointer years and 1 for the rest of the years. The predictor variables were standardized to facilitate the interpretation of the coefficients. The existence of multicollinearity among explanatory variables was evaluated and avoided by calculating the variance inflation factor (VIF) and removing variables with $VIF > 10$ (Dormann et al., 2013). We used the same variables as in the comparison of means and also tested different grouped variables such as mean temperatures from March to April (spring) and from October to November (late autumn).

The growth response to unfavorable years and the ability to recover pre-disturbance growth levels after the disturbance were estimated for the different increment series through the resistance (R_t) and resilience (R_s) indices (Lloret et al., 2011):

$$R_t = BAI_i / BAI_{i-4} \quad (2)$$

$$R_s = BAI_{i+4} / BAI_{i-4} \quad (3)$$

These indices were calculated from BAI data and 4-year long pre- (i-4) and post- (i+4) disturbance periods were used. To calculate pointer years and resilience indices we used the *pointRes* package in R (van der Maaten-Theunissen et al., 2015). To compare the

indices between the three species we used the Kruskal-Wallis test with Bonferroni *post-hoc*.

2.7 Reconstructing forest growth dynamics

To reconstruct forest disturbances, growth releases were detected through a quantification study of abrupt growth increments using the *TRADER* package in R (Altman et al., 2014). For beech and oak we employed the method proposed by Splechtna et al., (2005), which reduces the numbers of false releases (Altman et al., 2014). This method comprises two steps. Firstly, the average radial growth over the preceding 10-year period and the average radial growth over the subsequent 10-year period are calculated for each year of the growth series of each tree and the percentage growth change is obtained (Nowacki and Abrams, 1997). A release candidate is only considered if the growth pulse exceeds a 50% growth change threshold. Secondly, the boundary-line method (Black and Abrams, 2003), which standardizes the percentage growth change, is applied to the release candidates to remove the influence of age, size and other variables on growth (Black and Abrams, 2004). We followed Black and Abrams (2003), who defined moderate and major releases as those falling within 20–49.9%, and 50–100% of the boundary-line, respectively. Since the boundary-line method requires a large data set for calculating the boundary function (Black et al., 2009), it was only calculated for beech. In the case of oak we used the function proposed by Altman et al. (2013) for this species. There is no boundary function available for birch, hence we used the percentage growth change directly (Nowacki and Abrams 1997) to define the growth releases, taking into account that these would be overestimated (Altman et al., 2014). The boundary-line functions used for beech and oak are shown in **Appendix C**.

To analyze the relationship between the pointer years and the growth releases, we applied the modification of Ripley's $K(t)$ statistic (Ripley, 1976) for one-dimensional, bivariate data (see for instance Bigler et al. 2007). We transformed the $K(t)$ into the $L(t)$ function which does not show an increasing trend. This function is interpreted as positive associations (temporal coupling) between drought and growth release when the $L(t)$ values are positive. To assess the significance of the calculated $L(t)$ values confidence envelopes were constructed based on 999 simulations calculated using the “circular” method (Wiegand and Moloney, 2004). We calculated the $L(t)$ function for time lags varying from 0 to 14 years.

The dated tree ring width measurements were used to fit a diameter-age potential model per species and to estimate the age of the all trees retrieved from the ForeStereo data. Hurdle regression models, using the *pscl* package in R (Zeileis et al., 2008), were fitted for each species and pointer year to identify differences in the number of trees per 10 year age class (response variable) between those plots where growth release was detected during the 11 years following a pointer year in any of the species (predictor variable = 1) and plots with no growth release in the same pointer year (predictor variable = 0). The hurdle regression is a two-component model: a truncated count component is employed for positive counts, and a hurdle component models zero vs. larger counts. A negative binomial and a binomial distribution were employed for the count and hurdle components respectively.

The influence of topographical and tree factors over the intensity of the growth releases was also evaluated. This was done by calculating stepwise linear regressions between the response variables (the maximum value of the boundary-line, or the percentage growth change for birch, in the subsequent 10-years for each pointer year, BL_{max}) and the predictor variables (DBH and age of the cored tree when the drought

occurred, altitude, aspect and slope). Response variables were normalized through the inverse transformation $1/(BL_{\max}+1)$. We only calculated regressions for the pointer years followed by more pronounced growth releases for each species. We checked the model assumptions and the absence of multicollinearity.

3 Results

3.1 Climate trends and drought events

In our study area, local and CRU climate data showed a gradual increase in temperatures and potential evapotranspiration together with a decrease in precipitation over recent decades (**Fig. 1a**). Reconstructed climatic data indicate that the 1940s were dry years and drought frequency has increased since 1990 (**Figs. 1b, c**). In addition, the period from 1990 to 2013 was the driest since 1800.

3.2 Stand structure and growth sensitivity to climate

The sampled plots had an average basal area of $49.8 \text{ m}^2 \text{ ha}^{-1}$ and a mean density of $526 \text{ trees ha}^{-1}$. Beech, oak and birch were the more abundant species with mean basal areas (taking into account only those plots where the tree species appear) of 38, 25 and $21 \text{ m}^2 \text{ ha}^{-1}$ respectively (see **Table D.1** in appendices). The cored oaks were larger and older than the beeches or birches (**Table 1**). BAI was higher for oak than for the other two species (**Fig. 2**). The mean sensitivity of tree-ring width was lower in oak and higher in birch (see **Table 1**), whilst correlations of the individual growth series with the master series of each species were high for beech and birch, but low for oak, suggesting a higher growth coherence in beech than in oak. Abrupt BAI reductions in all species were noticeable in 1945 and 1995. Both birch and beech showed a high frequency of

missing rings in the 1940s and 1990s indicating growth limiting conditions (**Appendix E**).

Figure 1. Climatic trends (annual mean temperature and total precipitation) and potential evapotranspiration (PET) in the study area (a) calculated using annual gridded (CRU data, empty symbols) and local climatic data (Riaño station, data with gaps). The coefficients of simple regressions fitted to CRU temperature and precipitation are shown. Reconstructed spring precipitation was taken from Pauling et al. (2006) (b) and the self-calibrating Palmer Drought Severity Index of the Old World Drought Atlas (Cook et al. 2015) (c) are also presented to highlight the 1940s dry period (positive and negative values of the scPDSI correspond to wet and dry periods, respectively). PET is calculated from February to November following Pérez-de-Lis et al. (2017). The slope of the simple and piecewise regressions fitted to CRU temperature and precipitation, PET, reconstructed spring precipitation and scPDSI charts are shown. Vertical dashed lines show the break points of the piecewise regressions.

Table 1. Description of structural and dendrochronological variables of cored trees.

	Beech	Oak	Birch
Number of cored trees	92	34	11
Number of sampled cores	184	68	22
Mean diameter at breast height (cm)	38.0	61.9	27.1
Mean / maximum length of series (years)	119 / 314	153 / 441	106 / 200
Mean / maximum age (years)	141 / 342	197 / 487	130/218
Mean tree-ring width (mm)	1.28	1.30	0.70
Mean basal area increment (cm ²)	9.8	16.8	4.4
Mean correlation with master series	0.56	0.34	0.47
Mean sensitivity	0.37	0.28	0.49
Expressed Population Signal	0.94	0.69	0.68
Expressed Population Signal since 1900	0.98	0.85	0.79

Figure 2. Growth trends (basal area increment, lines with symbols) for the three studied species (beech, oak and birch) since 1900 and number of cored trees (right y axis). Growth value area means $\pm$ SE. Different symbols and lines correspond to each species.

Tree growth was only weakly related to climate variables in the three species studied (**Fig. 3**). The correlations are in general low and not consistent across time periods. They only reach significance in a few instances. Climate-growth correlations

were stronger in oak than in beech, particularly up to 1979, and very low in birch. In general, cool (and also wet in the case of oak) conditions from February to April and wet spring conditions enhanced growth in oak and beech. Birch growth displays a similar relationship with climate although correlations do not reach a level of significance in these periods.

Figure 3. Climate-growth relationships based on Pearson coefficients, calculated by relating ring-width indices to monthly mean temperature, total precipitation and cloud cover. Correlations were calculated for three periods (1911-1944, white bars; 1945-1979, grey bars; 1980-2013, black bars) from the previous October through to November of the growth year considered (months with lowercase letters correspond to

the previous year). Dashed and solid horizontal lines indicate significant correlations ($p < 0.05$ and $p < 0.01$, respectively).

Figure 4. Moving averages of climate variables (dashed lines, right y axes) and moving climate-growth correlations (continuous lines with circles, left x axes) in beech, oak and birch. Pearson correlations were calculated for the 1950–2014 period using 20-year long intervals, relating ring-width indices and grouped monthly climate variables (mean temperature and total precipitation of grouped months). Significant ($p < 0.05$) climate-growth correlations are indicated by horizontal lines. Only the variables with the greatest changes over time are shown.

The warmer and drier conditions observed in the study area over the last half century corresponded to an increment in the negative associations between winter temperatures and oak growth and in the positive associations between growing-season precipitation (from April to June) and beech growth as conditions became drier, particularly from the 1980s onwards (**Figs. 1 and 4**). In the case of birch, associations between temperatures from March to May and growth became negative as climate warmed.

3.3 Climate extremes and negative pointer years

The negative pointer years were 1923, 1945 and 1995 in beech and 1923, 1945, 1947, 1962, 1995, 1997 and 2006 in birch, whereas no negative pointer years were observed in the case of oak. These years coincided with extreme climate events (see **Figs. 1 and 2**) and were characterized by warm spring-summer (March, April and July) and autumn (October and November) conditions and to a lesser degree, by low spring (April) precipitations (**Table 3**). The logistic model efficiently discriminated these negative pointer years with the exception of 1923 and 1962, which were characterized by cold early springs and unusually dry summers (**Table 2**). The accumulated precipitation from February to June in 1945 was half that of the long-term mean. In fact, the 1945 rings revealed the lowest average growth for the whole of the 20th century in the three species.

Table 2. Climatic characterization of negative pointer years observed in the three study species. Average values were calculated for the 1900-2014 period using CRU climatic data.

Year	Variable	Ratio (value /average value)
1923	Precipitation from previous October to previous December	0.6
	June precipitation	0.2
	April temperature	0.8
1945	Precipitation from February to June	0.5
	April temperature	1.4
1947	April precipitation	0.3
	July precipitation	0.3
	April temperature	1.3
1962	Precipitation from May to September	0.4
	March temperature	0.8
1995	Precipitation from March to April	0.4
	June precipitation	0.4
	Temperature from January to February	1.4
1997	Precipitation from February to April	0.2
	September precipitation	0.2
	Temperature from February to March	1.6
2006	Precipitation from May to June	0.5
	Temperature form October to November	1.3

Table 3. Variables with significantly ($p < 0.05$) different means between negative pointer years and the rest of the years (left) and slope coefficients of the logistic regression (right) relating pointer years to climate variables. P is precipitation and T is mean temperatures. The “•” symbol indicates interaction between considered variables.

Climate variables	p	Logistic model	Coefficients
P _{April}	0.04	Intercept	4.63
T _{March}	0.04	T _{March-April}	0.08
T _{April}	0.001	T _{October-November}	-0.68
T _{July}	0.03	(T _{March-April})•(T _{October-November})	-1.49
T _{October}	0.001		
T _{November}	0.05		

3.4 Growth responses to droughts

Extreme climate conditions were usually characterized by severe droughts, leading to a high abundance of missing rings in beech and birch (**Appendix E**). There were abundant missing rings in 1923, 1945, 1947, 1995, and 1997 and also, to a lesser degree, in 2006. In the case of beech, one third of the sampled trees lacked a complete ring in 1995 and 1997, and one fourth had missing rings in 1923 and 1945. In birch, the number of missing rings was greater, with more than 50% of the samples lacking a complete ring in 1947, 1995 and 2006, and all samples lacked the 1945 ring.

The three species showed similar responses for the selected negative pointer years considering the resistance and resilience indices (**Fig. 5**). Oak was the species least affected by droughts and showed significantly higher resistance indices than beech and birch ($p < 0.001$ in both). Birch showed the greatest growth reduction.

Figure 5. Resistance and resilience indices for oak (dark-grey box-plots), beech (grey box-plots) and birch (white box-plots) considering all the negative pointer years. Significant differences ($p < 0.05$) are marked with an asterisk.

3.5 Effects of drought events on forest dynamics

Most major releases in beech were observed in the late 1940s followed by the early 1930s, whilst in oak and birch releases were most frequent in the 1960s and 1990s, respectively (**Fig. 6**). After the 1995 and 1997 negative pointer years, the percentage of beech and oak trees showing releases was small when compared with previous droughts. The distribution of releases across the sampled plots was widespread and showed no spatial pattern (*results not shown*). In **Appendix F** we provide, as an illustrative example, a growth release over time of a selected beech after the 1945 severe drought.

Figure 6. Major and moderate growth releases detected in beech, oak and birch during the 20th century. The negative pointer years 1923, 1945, 1962 and 1995 are highlighted with dashed vertical lines.

Pointer years related to droughts resulted in significantly ($p < 0.05$) increased growth releases 6-11 years, 7 years and 0-7 years later in beech, oak and birch, respectively (Fig. 7).

Figure 7. Bivariate event date analysis for growth release and drought. The $L(t)$ function is shown for lags of 0 to 14 years. Dashed and dotted lines display the confidence envelopes (95% and 99% CE).

The analysis of the age distribution from the ForeStereo data shows a greater number of trees in age classes just established around the pointer years in the plots where growth releases were detected for the three species (**Fig. 8**). In the plots with growth release there are significantly more beeches and oaks established around the pointer years of 1923 and 1945/1947 and there are significantly more birches established around the pointer year of 1962. Due to the error in the age estimation we analyzed the differences in a window of 30 years, centered on the decade of each pointer year and considering years prior to the 1990s.

Figure 8. Relative density of the age class origin shown for each species, according to plots with growth release in each pointer year (R) and plots without growth release (Not R). The relative density (%) was calculated for each plot and species and then was averaged for the whole study area. Asterisks (*) indicates significant differences ($p < 0.05$) in the count component of the hurdle regression, symbols (X) indicates significant differences ($p < 0.05$) in the hurdle component (zero vs. larger counts) and crosses (+) indicate differences that could not be analyzed with the model since all the values were zero in one of the groups.

Due to the inverse transformation of BL_{max} , the relationships between the maximum value of the boundary line and the coefficients in **Table 4** are reversed. We only performed regressions for the pointer years with the greatest growth releases for each species, i.e. 1923 and 1945/1947 in beech, 1945/1947 and 1962 in oak and all pointer years in birch. No significant relationships were obtained for birch. One regression for each pointer year was calculated in beech due to the different relationships obtained in each one. According to the models, beech growth release increases with small diameter and younger age and in the case of the pointer year of 1923, growth release increases at high altitudes. Oak growth release increases with younger age and at lower altitudes.

Table 4. Regression coefficients (standard errors in parentheses) and adjusted R^2 for the linear models of the transformed maximum value of the boundary-line ($1/(BL_{max}+1)$) for beech and oak. Significance levels: * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$, respectively. Variables were standardized prior to fitting the models.

Pointer year	Beech		Oak
	1923	1945/47	1945/47 and 1962
Intercept	0.782 (0.014) ***	0.803 (0.013) ***	0.835 (0.016) ***
DBH	0.031 (0.014) *	0.029 (0.014) *	
Altitude	-0.032 (0.014) *		0.049 (0.021) *
Age		0.037 (0.014) *	0.046 (0.021) *
Adjusted R^2	0.11	0.18	0.32

4 Discussion

The lack of recent, intensive silvicultural activity in the studied forest is corroborated by the mean ages of the dominant trees, which are 141 and 197 years old in the case of beech and oak, respectively, with a maximum age of 487 years (**Table 1**).

The correlations among individual ring-width series and the master series (**Table 1**) were within the range of values of the International Tree-Ring Data Bank (ITRDB) (Grissino-Mayer and Fritts, 1997) for beech. However oak and birch presented lower

correlations with masters than at other ITRDB sites because many birches and aged oaks presented suppressed growth, with low variability between years and low sensitivity to climate (*results not shown*), possibly due to the competition from beeches, which display greater competitiveness (Manso et al., 2015).

The negative correlation between growth and temperature from February to April and the positive response to June precipitation (**Fig. 3**) have been observed in different beech populations of Circum-Mediterranean regions (Biondi, 1993; Gutiérrez, 1988; Piutti and Cescatti, 1997). This indicates a higher sensitivity of beech growth to water availability during the growing season at the study site in comparison to other European populations subjected to mild or cool conditions (Eckstein and Frisse, 1982; Lebourgeois et al., 2005; Rozas, 2001). In addition, warmer, drier conditions from the 1980s onwards were more detrimental to growth in the three species (**Figs. 1 and 4**). The sensitivity of oak to winter temperatures may be related to its higher proportion of living parenchyma in sapwood and higher respiration values during the dormant period compared with beech (Rodríguez-Calcerrada et al., 2015). Warmer winter conditions are associated with an increased consumption of non-structural carbohydrates, reducing the amount of reserves for starting growth the following year (Bréda et al., 2006). In any case, a markedly poor climatic signal in the tree growth series was observed (**Fig. 3**), even though the study populations were located near the southernmost limits of the species' distribution areas (**Appendix A**). Such a weak climatic signal indicates that climate conditions were not limiting to growth, as occurs in humid zones (Rozas, 2001) or cool, high-elevation sites (Camarero et al., 2015; Lebourgeois et al., 2005). Although mean climatic conditions are loosely associated with growth variability, extreme climate events such as severe droughts might trigger abrupt growth reductions and changes in forest dynamics (Martín-Benito and Pederson, 2015; Pederson et al., 2014).

It is possible that only extreme climate events, such as dry spells, reveal the growth sensitivity of temperate tree species to climatic constraints. In fact, the years with the lowest growth rates were characterized by warm spring and autumn conditions, but also by scarce precipitation during the growing season and the previous autumn and winter (**Table 2**) (see also Tessier et al., 1994). The synergistic effect of high temperatures and low precipitation prior to the start of the growing season can cause growth decline or even trigger tree death (Bréda et al., 2006). The years 1923 and 1962, which were not correctly classified by the logistic model (**Table 3**), had short vegetative periods caused by spring frosts and a dry summer. Indeed, the growth releases in beech that occurred after 1923 were greater at higher altitudes (**Table 4**), where colder conditions prevail. Spring frosts combined with other stress factors such as drought, could lead to canopy dieback and increase mortality rates because frost fatigue (a decrease in cavitation resistance caused by freeze-thaw cycles) can predispose to xylem embolism and damage the expanding shoots and leaves (Hacke and Sauter, 1996; Thomas et al., 2002).

Oaks have higher resistance values compared to beeches, which in turn have higher values than birches (**Fig. 5**). Oak did not present missing rings, whereas missing rings were frequent in beech and birch (**Appendix E**). In addition, oak displayed higher resilience than beech and/or birch in 1945, 1962 and 1995, and oak was the only species to recover its previous growth after all negative pointer years ($R_s \geq 1$). This agrees with ecophysiological findings which show that beech is more vulnerable to drought than sessile oak when they coexist and are subjected to certain drought stress during the growing season (Aranda et al., 2000, 2005). In fact, a recent tree-ring study suggests that oak adapts better than beech to Mediterranean climatic conditions, characterized by dry summers (Dorado-Liñán et al., 2017). Birch was the species most negatively

affected by drought, showing the greatest growth reductions although its resilience values were similar to those of beech.

In closed-canopy temperate forests, growth is often driven more by disturbances or biotic interactions (e.g., competition) than by climate (Cook, 1990; Fritts, 1962; Lebourgeois et al., 2005; Nowacki and Abrams, 1997). However angiosperms in temperate forests are vulnerable to hydraulic failure and tree mortality due to drought induced embolism (Choat et al., 2012). The warming-induced rise in tree respiration rates (Tjoelker et al., 2001), raising the consumption of carbohydrates and transpiration, could also increase the water requirements of these species making them more vulnerable to xylem embolism (McDowell et al., 2008). In our study, around 90% of the major releases detected took place during the ten years following each pointer year (taking into account all the pointer years for the three species: 1923, 1945, 1947, 1962, 1995, 1997 and 2006) (**Fig. 6**). There was a significant dependence between droughts and post-drought releases (**Fig. 7**), possibly caused by mortality of surrounding trees. As in other studies (Bigler et al., 2007), there were lags of 7 (for oak and birch) to 11 (for beech) years between the detected disturbance (e.g., a drought) and a growth release. Droughts can cause tree mortality both directly and indirectly, predisposing trees to insect or pathogen attacks (Bréda et al., 2006). In the latter case, the tree may die a few years after the drought and this would trigger a lagged growth release in neighboring trees (Bigler et al., 2007). The impact of releases on annual growth differs according to the canopy position (Vašíčková et al., 2016), the species considered and their shade tolerance (Rozas, 2001). A high proportion of oaks are larger in size than the other species (see **Table 1** and **Appendix D**). This could have reduced the amount of detected releases because it is probable that they were already dominant trees during the analyzed periods and therefore less sensitive to additional canopy gaps than codominant

or suppressed trees. However, previous studies also reported that mature dominant oaks tend to respond conservatively to canopy disturbances (Nowacki and Abrams, 1997; Petritan et al., 2017; Rozas, 2004), while beech shows a more pronounced response to disturbances (Peters and Poulson, 1994; Rozas, 2003a). The strongest release pulses took place after 1923 and 1945 in beech, after 1962 in oak and after 1995 in birch (**Fig. 6**). The largest growth releases were detected after the 1945 and subsequent droughts which characterized the dry period of the late 1940s (**Figs. 1 and 6**). This suggests that repeated drought may trigger growth releases due to tree mortality (McDowell et al., 2008; Pedersen, 1998; Villalba, 2002). Since 1980 there has been an increase in PET and temperatures and a decrease in precipitation (**Fig. 1**), with successive droughts affecting the study area. However, since 1990 few releases were identified in beech and oak, probably due to: (i) the maintenance of lower competition levels after the 1945 dry spell (reflected in the sustained growth increase in oak and beech; **Fig. 2**); and (ii) as trees grew and became dominant, growth responsiveness to disturbances was lost, depending on the shade tolerance of the species (Vašíčková et al., 2016). However, the increase in spring temperatures after the 1980s seems to have had an impact on birch growth (**Fig. 4**), which has shown an increasing rate of releases since 1990, although these results must be analyzed with caution given the absence of reference values for this species. The large percentage of birches with growth releases detected during that decade may be related to the use of the Nowacki and Abrams (1997) method without considering boundary-line standardization. In addition, the method used to detect releases does not allow for assessment after 2003, so the effects of the 1995 and 1997 droughts on growth releases may not be fully uncovered.

Due to the different drought tolerance levels of beech, oak and birch, we expected that the growth releases would result from the mortality of the less drought-

resistant beech and birch, thus benefitting oak. These releases seem to generate gaps of sufficient size to regenerate the three species (**Fig. 8**), not only the more shade-tolerant beech (Valladares et al., 2002).

Young or small oaks and beeches displayed greater growth increases after droughts (**Table 4**) due to their higher sensitivity to competition in comparison to older dominant trees (Schröder and Gadow, 1999; Maleki et al., 2015). The greater growth response of young and smaller trees to a decrease in competition allows the canopy ascension in these trees (Rentch et al., 2003). Altitude was found to have opposite effects on beech and oak growth. This might be explained by the fact that altitude is related to air temperature, with colder conditions at higher altitudes alleviating the negative effect of droughts on growth while also increasing the likelihood of spring frosts.

We expected a strong influence of climate on growth due to the location of the studied forest, close to the southern limit of the species distribution. However climate was not restrictive for growth, possibly because the mountainous relief creates favorable microclimate conditions and lessens the Mediterranean drought. In fact, the current distribution of beech in southern Europe does not match its climatic potential (Sánchez de Dios et al., 2016). Moreover, droughts become more limiting under high densities (Fernández-de-Uña et al., 2015) whereas our data indicate that moderate densities are maintained during the analyzed period, probably favored by cattle grazing. However, our results confirm that drought is the main driver of growth releases, adding further evidence of climate legacies in temperate forest dynamics (Pederson et al., 2014). Severe droughts, characterized by high temperatures and low precipitation during spring, summer and autumn, increase growth releases, possibly as a result of tree

mortality. Mortality would lead to the formation of canopy gaps, generating conditions favorable for the establishment of the three species.

5 Conclusions

Our findings show that drought events influence growth and forest dynamics in a temperate, mixed forest. Severe droughts were key drivers of abrupt drops in tree growth during the 20th century. Beech and birch were the species which were most adversely affected by droughts in terms of growth loss, whereas oak was the most drought-resistant species. Droughts not only caused growth reductions, but were also linked to growth releases up to 11 years after drought occurrence. These releases are interpreted as reduced competition for resources due to increased tree mortality, which allows the establishment of recruitment of the three species.

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Appendix A

Figure A.1. Distribution of *Quercus petraea* (left) and *Fagus sylvatica* (right) in Europe (EUFORGEN, 2009a, 2009b). Black dots show the site location in northwestern Spain.

References for appendix A

EUFORGEN, 2009a. Distribution map of Beech (*Fagus sylvatica*).

<http://www.euforgen.org/>

EUFORGEN, 2009b. Distribution map of Sessile oak (*Quercus petraea*).

<http://www.euforgen.org/>

Appendix B

Age at 1.3 m was estimated as follows. In those cases where cores reached the pith, age was estimated through cross-dating and counting of the rings. In all other cases, we first estimated the missing length to the pith and then the number of innermost lost rings. In these partial cores we used the arc of the innermost rings to estimate the length of the missing radius using a graphical method based on the convergence of xylem rays at the pith. In partial cores without conspicuous arcs, the length of the missing radius was estimated as the distance to the geometric center of the tree, assuming concentric growth. In the latter case, estimation was made by subtracting the corresponding cored length to the measured radius in the field, previously subtracting an estimated width of the bark. Bark thickness was estimated based on the tree diameter using equations from the Second Spanish National Forest Inventory (DGCONA, 1998). Functions used to estimate the bark thickness of beech and oak are as follows:

$$C_F = -0.00001d^2 + 0.0284d + 0.3545 \quad (\text{B.1})$$

$$C_Q = 1.4407d^{0.4071} \quad (\text{B.2})$$

where C_F is the bark thickness of beech, and C_Q is bark thickness of oak, and d are tree diameters measured at 1.3 m. Bark thickness of birch was also estimated with **B.1** function due to the lack of data for this species.

In partial cores, the number of missing rings was estimated using an empirical model of initial radial growth, a function of both the distance from the pith, and the mean radial growth rate of the 5 rings adjacent to the largest arc visible on the core (Rozas, 2003). We used these equations:

$$NMR_F = 3.41 - 3.15MRG5 + 2.07d - 0.037d^2 + 0.0002d^3 \quad (\text{B.3})$$

$$NMR_Q = 3.37 - 2.26MRG5 + 1.22d - 0.022d^2 + 0.0001d^3 \quad (\text{B.4})$$

where NMR_F is the number of missing rings in beech, NMR_Q is the number of missing rings in oak, and $MRG5$ is the mean growth rate of the innermost 5 rings of the core and d is the tree diameter. The number of missing rings in birch was also estimated with **B.3** function due to the lack of a specific function.

References for appendix B

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Appendix C

The boundary-line function obtained for beech was the following:

$$y = -0.01825 + 5.28364e^{-0.83170x} \quad (\text{C.1})$$

and the boundary-line function used for oak was (Altman *et al.*, 2013):

$$y = 5.0067e^{-0.664x} \quad (\text{C.2})$$

where x are the 0.5 mm segments of growth (see Black and Abrams, 2004).

References for appendix C

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Appendix D

Table D.1. Summary of the forest inventory carried out at the study sites. The results are the average for the plots where tree species appear. Values in parentheses are the standard deviation.

	Beech	Oak	Birch
No. plots	92	34	11
No. monospecific plots	62	8	0
No. mixed plots with beech	-	23	8
No. mixed plots with oak	23	-	4
No. mixed plots with birch	8	4	-
Basal area (m ² ha ⁻¹)	38 (29)	25 (27)	21 (12)
Diameter at breast height, DBH (cm)	27.6 (9.4)	35.2 (23.6)	28.8 (12.0)
Density (No stems ha ⁻¹ , all stems)	460 (302)	193 (204)	339 (297)
Density (No stems ha ⁻¹ , stems with DBH < 32.5 cm)	286 (232)	81 (188)	228 (266)
Density (No stems ha ⁻¹ , stems with DBH > 32.5 cm)	141 (113)	87 (65)	111 (78)

Appendix E

Figure E.1. Missing rings observed in beech and birch tree-ring width series.

Appendix F

Figure F.1. Notable growth release of a beech observed in 1949 and possibly connected to the 1945 drought and the release of light and nutrients due to mortality in the neighborhood of the tree. The black line shows the ring width and the blue line is the boundary line calculated according to Splechtna *et al.* (2005). According to the boundary-line method, positive growth changes between 20% and 49.9% (right y axis, dotted horizontal lines) are considered moderate releases, whereas growth changes above 50% are considered major releases.

References for appendix F

Splechtna, B.E., Gratzner, G., Black, B.A., 2005. Disturbance history of a European old-growth mixed-species forest – a spatial dendro-ecological analysis. *J. Veg. Sci.* 16, 511–522. <https://doi.org/10.1111/j.1654-1103.2005.tb02391.x>