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Research paper

Extreme droughts affecting Mediterranean tree species' growth and water-use efficiency: the importance of timing

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It has been known for a long time that drought intensity is a critical variable in determining water stress of Mediterranean tree species. However, not as much attention has been paid to other drought characteristics, for example the timing of the dry periods. We investigated the impact of the timing and intensity of extreme droughts on growing season length, growth and water-use efficiency of three tree species, *Pinus nigra* ssp. *Salzmannii* J.F. Arnold, *Quercus ilex* ssp. *ballota* (Desf.) Samp. and *Quercus faginea* Lam. coexisting in a continental Mediterranean ecosystem. Over the study period (2009–13), intense droughts were observed at annual and seasonal scales, particularly during 2011 and 2012. In 2012, an atypically dry winter and spring was followed by an intense summer drought. *Quercus faginea* growth was affected more by drought timing than by drought intensity, probably because of its winter-deciduous leaf habit. *Pinus nigra* showed a lower decrease in secondary growth than observed in the two *Quercus* species in extremely dry years. Resilience to extreme droughts was different among species, with *Q. faginea* showing poorer recovery of growth after very dry years. The highest intra- and inter-annual plasticity in water-use efficiency was observed in *P. nigra*, which maintained a more water-saving strategy. Our results revealed that the timing of extreme drought events can affect tree function to a larger extent than drought intensity, especially in deciduous species. Legacy effects of drought over months and years significantly strengthened the impact of drought timing and intensity on tree function.

Keywords: carbon isotope composition, extreme drought, *Pinus nigra*, *Quercus faginea*, *Quercus ilex*, water-use efficiency.

Introduction

Drought intensity has been widely recognized as a factor determining the extent of drought effects on tree species (McDowell 2011). Effects of extreme droughts in Mediterranean forests are difficult to predict due to the non-linear relationship between climatic perturbations and tree growth (Anderegg et al. 2015, Cavin and Jump 2017), and the synergetic effects of different climate drivers on growth (Lloyd et al. 2013, Vicente-Serrano et al. 2015). Many previous studies have shown that severe drought reduce significantly growth, leaf gas exchange, water potential

and hydraulic conductance in Mediterranean tree species (see for example Damesin and Rambal 1995, Corcuera et al. 2004a, Martín-Gómez et al. 2017). Mediterranean tree species have developed a variety of mechanisms to tolerate, resist or avoid these effects during strong water stress periods (Baldocchi et al. 2010), and a high capacity for physiological and morphological plasticity and acclimation (Ogaya and Peñuelas 2003a, Flexas et al. 2014, Matesanz and Valladares 2014). Mediterranean tree species are able to adjust their growing season length to climatic conditions and some species can advance leaf emergence

when exposed to increasing temperatures (Gordo and Sanz 2009, Morin et al. 2010), despite the risk of late frosts, while other species delay foliar development (Adams et al. 2015). Moreover, some species are able to have significant growth during hot and dry summers, e.g., *Pinus halepensis* (Maseyk et al. 2008). Therefore, tree growth may have a wide range of threshold responses to drought, which is also related to other processes, such as tree transpiration or resource-use efficiency (e.g., water-use efficiency, WUE). For example, dry conditions have been observed to enhance WUE (Granda et al. 2014, Vicente-Serrano et al. 2015). However, increased WUE does not always imply increased growth, neither at mesic nor at xeric sites (Peñuelas et al. 2008, Levesque et al. 2014). In fact, growth reductions in Mediterranean forests under drought have been pointed out in parallel with increases in WUE (Sarris et al. 2007, Barbeta et al. 2013). The relationship between growth and WUE is quite complex, being species-specific and non-linear (Camarero et al. 2015b).

The impact of drought intensity is the basis of many ecophysiological studies in environments prone to dry periods. However, not much is known about the impact of drought timing on plant function (see Granda et al. 2013, Camarero et al. 2015a). Drought stress can affect species during different key growth phases, and it can critically affect trees during resumption of cambial activity in temperate biomes (Camarero et al. 2010, Rozas et al. 2011). Therefore, effects of annual, seasonal or monthly dry periods on growth phases of the species can severely affect relevant aspects of species functioning. In particular, spring and autumn could be of special relevance for overall growth in Mediterranean environments (Gil-Pelegrín et al. 2017).

Decreases in net primary production due to drought throughout the growing season can be compensated by longer growing periods if species take advantage of mild conditions before or after the drought periods, and during short but intense rain events occurring during these periods (Vicente-Serrano et al. 2010b). Dendrochronology studies have shown that short- or long-term drought stress not only reduces growth on the current year, but can also impact growth on the following growing season (Badeau et al. 1996, Linares et al. 2010, Bauerle et al. 2012). The recovery after these carry over effects of drought on growth relies upon the specific strategy followed by each tree species according to its resistance and resilience (McDowell et al. 2013, Roman et al. 2015).

The main objective of this study was to identify how timing, length and intensity of extreme droughts impact growth and WUE of three coexisting Mediterranean tree species. We hypothesized that timing of extreme dry periods can affect tree functioning in a different way than drought intensity, depending on the leaf habit and drought sensitivity of each species. Second, we hypothesized that the coupling between growth and WUE during extremely dry conditions varies depending on

species. In order to assess these hypotheses, we have measured growth and WUE in adult trees of three coexisting Mediterranean species continuously for 3 years.

Materials and methods

Study site

The study was conducted at the Alto Tajo Natural Park, Guadalajara (central Spain). Soils are calcisols from Cretaceous and Jurassic limestone that rendered shallow and poorly developed soil (Ferrero et al. 2006) with a mean depth of 48.7 cm. The climate is continental Mediterranean with hot and dry summers and cold winters (mean temperature and mean precipitation: 18.5 °C and 20.7 mm in summer; 2.9 °C and 38.5 mm in winter). Mean annual temperature and precipitation is 10.3 °C and 490.5 mm, respectively (Molina de Aragón, 40°50'40"N, 1°53'07"W, 1951–2013 period; data provided by the Spanish Meteorological Agency, AEMET).

We selected a plot (1 ha) at the Armallones site (40°46'37" N, 2°19'42" W, 1079 m a.s.l.), where the three main woody species studied have similar importance in terms of basal area: *Quercus faginea* Lam. (38.7%), *Pinus nigra* ssp. *Salzmannii* J.F. Arnold (35.1%) and *Quercus ilex* ssp. *ballota* (Desf.) Samp. (25.8%). It has a western orientation with a 48% slope and a total basal area of 13.7 m² ha⁻¹. We randomly selected healthy and fully sun-exposed representative trees with similar diameter at breast height (i.e., at 1.3 m height) of Portuguese oak, *Q. faginea* ($n = 5$), black pine, *P. nigra* subsp. *salzmannii* ($n = 4$) and Holm oak, *Q. ilex* subsp. *ballota* ($n = 3$). *Quercus faginea*, *P. nigra* and *Q. ilex* mean diameters of selected trees were in the range of 25.5 ± 3.0 cm, 23.5 ± 2.5 cm and 21.4 ± 1.5 cm, respectively. The low density of the plot allowed selecting scattered trees with well sun-exposed crowns, and with a low interference with neighbor trees. Mean leaf area index (LAI) of the study site is 1.9 ± 0.3 m² m⁻².

Microclimatic conditions were recorded continuously from 2010 to 2013 at the study site using an automatic weather station (HOBO[®], Onset Computer Co., Bourne, MA, USA). It was composed of a rain gauge (RGA-MoXX), temperature and relative air humidity (12-Bit Temperature/RH Smart Sensor), solar radiation (S-Lib-MOO3) and wind speed (Wind Speed Smart Sensor, S-WA-MOO3) sensors. Readings of each sensor were recorded every 30 min with a data logger (HOBO[®] H21-001; Onset Computer Co.).

Drought intensity and timing

Drought intensity and duration was assessed using two drought indexes: the water stress index I_s and the standardized precipitation-evapotranspiration index (SPEI). I_s considers a longer dataset while SPEI can be calculated at different time scales (Vicente-Serrano et al. 2010a). Calculation of both drought indexes allowed comparisons with other studies and a

more accurate description of drought intensity at both the regional and local scales.

Regional climatic data for the long-term series (1951–2013) were obtained from the closest weather station (at ~36 km from the study site), Molina de Aragón (1063 m a.s.l.), from AEMET (Spanish Meteorological Agency). Cross-correlation between the annual series calculated with AEMET data and microclimatic data were calculated to assess the representativeness of regional data for the local climate. The high and significant correlation ($R^2 = 0.910$, $P < 0.001$) between precipitation/potential evapotranspiration (P/PET) calculated from both climatic data sets (AEMET and microclimatic station at our site) reinforces the validity of the drought intensity results (I_s) obtained from the long time series for making inferences at our study site. Moreover, this consistency allowed the generalization at a regional scale of the results obtained at our study site regarding the effects of drought in the studied species.

I_s was calculated annually from 1961 to 2013 by running the BILJOU© water balance model (Granier et al. 1999) with measurements of daily rainfall, air temperature, relative humidity, global radiation and wind speed from the Molina de Aragón meteorological station. BILJOU© also uses the leaf area index (LAI), dates of bud burst and leaf fall for deciduous species and soil properties. Leaf area index was estimated with a LAI 2000 Plant Canopy Analyzer (PCA, LI-COR, Lincoln, NE, USA) in 2012 (data provided by M. Pollastrini). Leaf area index was kept constant to detect changes in climatic conditions independently of the LAI effect on drought intensity variation. The relative extractable water (REW) was calculated at a daily time scale as the ratio of available soil water to maximum extractable water. The REW ranges from 1.0 (field capacity) to 0.0 (permanent wilting point). In addition, REW_c was defined as the REW below a threshold of 0.4. This threshold is considered the point below which water stress reaches levels at which water is limiting tree transpiration, and causing stomatal closure for most forest tree species (Granier et al. 1999). The water stress index I_s (unitless) used as surrogate of drought intensity was calculated for a given period as the sum of the daily differences between REW and REW_c and divided by 0.4, with higher values corresponding to higher water stress. I_s was calculated annually starting in 1961 due to the lack of temperature and wind speed data between 1951 and 1961. The beginning date (BS) and duration (DS) of water stress, i.e., when $REW < 0.4$, were extracted from REW simulations to study the importance of drought timing, i.e., how the duration and the starting date of the drought matters to tree functioning. Moreover, both BS and DS complement the analysis of the temporal evolution of water stress over a half century. The timing effect on tree functioning was also addressed to identify possible carry over effects.

The SPEI is a multi-scalar drought index which considers precipitation and PET (Vicente-Serrano et al. 2010a, Beguería et al. 2014). Lower SPEI values indicate drier conditions. The SPEI data were obtained from the SPEIbase using Armallones coordinates

(Beguería et al. 2010) (available at: <http://sac.csic.es/spei/database.html>). This dataset considers the Penman–Monteith's method to calculate PET values. We used 3-month SPEI to obtain seasonal SPEI (December–February for winter, March–May for spring, June–August for summer and September–November values for autumn), 6-month SPEI to obtain the SPEI for the growing season (May–November) and 12-month SPEI to obtain the annual SPEI (January–December), from 1961 to 2013. We used those SPEI data to explore the correlations between drought and growth variables.

Growth and growing season length

Plant growth was continuously monitored from 2010 to 2013 by measuring stem circumference changes at breast height of the selected trees using automatic band dendrometers (DRL26, Environmental Measuring Systems (EMS), Brno, Czech Republic). Data were stored in a data logger (EdgeBox V12, EMS) every 10 min as a mean of the 10 previous measurements recorded every minute. All data were thoroughly revised for possible abrupt or unusual jumps due to freezing events or resin, which can impede tap movement. Unusual jumps (>0.1 mm between two records) were erased from the data. Basal area increment (BAI, cm^2) was calculated to obtain the stem increment and calculate relative growth rates according to $\text{BAI} = \pi(r_t^2 - r_{t-1}^2)$ and relative growth rate ($\text{RGR} = (\ln r_t^2 - \ln r_{t-1}^2)/t$, where r is the tree radius and t is the time interval considered (Hoffmann and Poorter 2002, Jump et al. 2006). The whole growing season BAI (BAI_{gs}) was calculated as the difference between BAI at the beginning (spring) and end of the growing season (autumn). The whole growing period was divided in two parts, spring and autumn, in order to quantify the relevance of growth in both seasons. We considered the beginning of spring growth to be when BAI was higher than the culmination point of the previous year over seven consecutive days (according to Zweifel et al. 2010 approach and Lempereur et al. 2015). We considered autumn growth to begin when BAI was higher than the point where spring growth ended over seven consecutive days. The spring and autumn growth was considered to be over when BAI was null or negative over seven consecutive days. Therefore, BAI and RGR estimated in spring (BAI_{sp} and RGR_{sp}) and autumn (BAI_{au} and RGR_{au}) were calculated using r_t and r_{t-1} , with r representing the mean of tree radius 7 days before and after the beginning and the end of the considered growing period. The beginning and length of the growth during spring and autumn were determined for each tree considering BAI evolution over time for the four study years (2010–13) and following the method described before. The effect of the trunk refilling during spring and autumn rainfall on the growth calculation was removed by subtracting the diameter decrease produced during the previous summer and winter. We assumed that during spring and autumn, trees achieved the maximum replenishment of internal water capacitances, so a diameter decrease during

drought was only due to water loss (Betsch et al. 2011). Therefore, diameter increases after drought events were due to water recovery and to reactivation of secondary growth.

Water-use

Tree water-use was inferred from sap flow measurement as a surrogate of tree transpiration. This approach has been proved to be useful in integrating overall tree water consumption, scaling water used by individual trees to the stand level (Granier et al. 1996, 2000, Poyatos et al. 2008). It represents an interface between the leaf scale studies (Ogaya and Peñuelas 2003b, Roman et al. 2015) and those using eddy-covariance that allow making inferences on carbon and water fluxes at the ecosystem level. Sap flow density measurements were continuously monitored from 2010 to 2013 in selected trees (see S1 available as Supplementary Data at *Tree Physiology* Online), using sap flow sensors (EMS 51, EMS) as in previous studies (Čermák et al. 2004, Forner et al. 2014).

Tree-level water-use efficiency Tree-level WUE ($\text{cm}^2 \text{BAI m}^{-3} \text{H}_2\text{O}$) was calculated for each individual dividing the tree growth by the tree transpiration per unit crown area for the same period. We used BAI measurements as surrogate of tree growth, and the sum of sap flow (dm^3) divided by the crown projected area (m^2) as tree transpiration per unit crown area (E , mm). Values were calculated for the whole growing season (WUE_{gs}), spring (WUE_{sp}) and autumn (WUE_{au}).

Leaf-level water-use efficiency Carbon isotope composition in leaves ($\delta^{13}\text{C}$) is a proxy of the intrinsic water-use efficiency (iWUE) integrated over time of plant growth (Dawson et al. 2002, McCarrroll and Loader 2004) and calculated through the equations of Farquhar (Farquhar et al. 1982, 1989) (see S1 available as Supplementary Data at *Tree Physiology* Online). Moreover, $\delta^{13}\text{C}$ has been used as an indicator of intensity of drought exposure in plants (O'Leary 1995, Saurer et al. 1995), and to establish ecological strategies with regard to water-use from single individuals to population and species (Aranda et al. 2010, de Miguel et al. 2012, Lázaro-Nogal et al. 2015).

Five individuals per species were selected to collect two healthy, fully-expanded and sunny leaves per individual both in spring and summer in the years 2011–13. Two (*Q. ilex*) or four (*P. nigra* and *Q. faginea*) of the selected individuals were equipped with dendrometers and sap flow sensors. Leaf samples were oven-dried at 65 °C for 48 h and finely ground (MM300, Retsch Haan, Germany). Between 1 and 2 mg of the powdered leaf material from each tree was weighed (Radwag XA 52/2x Semi-Micro Balance, Nevada Weighing, Las Vegas, NV, USA) and placed into tin capsules (Sn 98 capsules, Lüdswiss, Flawil, Switzerland) for carbon isotope composition analysis ($\delta^{13}\text{C}$, ‰). Analyses were carried out at the Technical Platform of Functional Ecology (OC081) at the INRA Forest

Ecology and Ecophysiology Unit, using an EA-GC/IRMS (Delta S, Finnigan MAT, Bremen, Germany; $\pm 0.2\%$).

Statistical analysis

Percentiles (5%, 50% and 95%) for the water stress index I_s and beginning date (BS) and duration (DS) of water stress were calculated annually for the time series 1961–2013 to identify extreme events, and unusual drought periods during 5 years (2009–13) at a regional scale. Further, we tested the correlation between P/PET calculated using the AEMET climatic dataset and P/PET calculated using the climatic data obtained from the study site using Spearman's rank correlation coefficients.

Linear mixed-effects models (LMMs) were used to assess the effect of year, species, season and their interactions (fixed factors) on BAI, RGR, E , WUE and $\delta^{13}\text{C}$ (Zuur et al. 2007). The study of the specific effect of each season (spring and autumn, or summer in the case of $\delta^{13}\text{C}$) was assessed with LMMs considering as fixed factors year and species. Individual trees were considered as random effects. Models were fitted based on a restricted maximum-likelihood method using the nlme package from R statistical software (Pinheiro et al. 2007). Tukey post hoc analysis was applied to significant results using the package lsmeans (Russell and Maxime 2015). The non-parametric Kruskal–Wallis test was used to identify individually the effect of year, species and their interaction on the beginning and length of plant growth in both spring (Beg_{sp} and Len_{sp} , respectively) and autumn (Beg_{au} and Len_{au} , respectively).

A relationship between carbon isotope composition in summer ($\delta^{13}\text{C}_{\text{su}}$) and integrated WUE in the growing season (WUE_{gs}) considering all species was established by fitting linear model. Regression was performed using SigmaPlot version 11, from Systat Software, Inc., San Jose, CA, USA. Adjusted R -squared (R^2) was indicated.

Further, relationships between growth and climatic variables were assessed for each species using Spearman's rank correlation coefficients to analyze the effect of drought stress on growth. Results were shown using correlograms which were performed using the package corrplot from R statistical software (Wei and Simko 2016). These analyses were carried out using the R statistical software (version R3.3.3; R Development Core Team 2017).

Results

Extreme drought events occurring at different time scales

Three of the five study years (2009, 2011 and 2012) showed higher values of water stress index (I_s) than average for the time series 1961–2013 (Figure 1a). The year 2011 was also the most stressful year over 52 years at our study site, showing not only extremely high I_s but also unusually high duration (DS) (higher values than the 95% percentile of the time series 1961–2013). Despite 2011 being around 1.7 times more

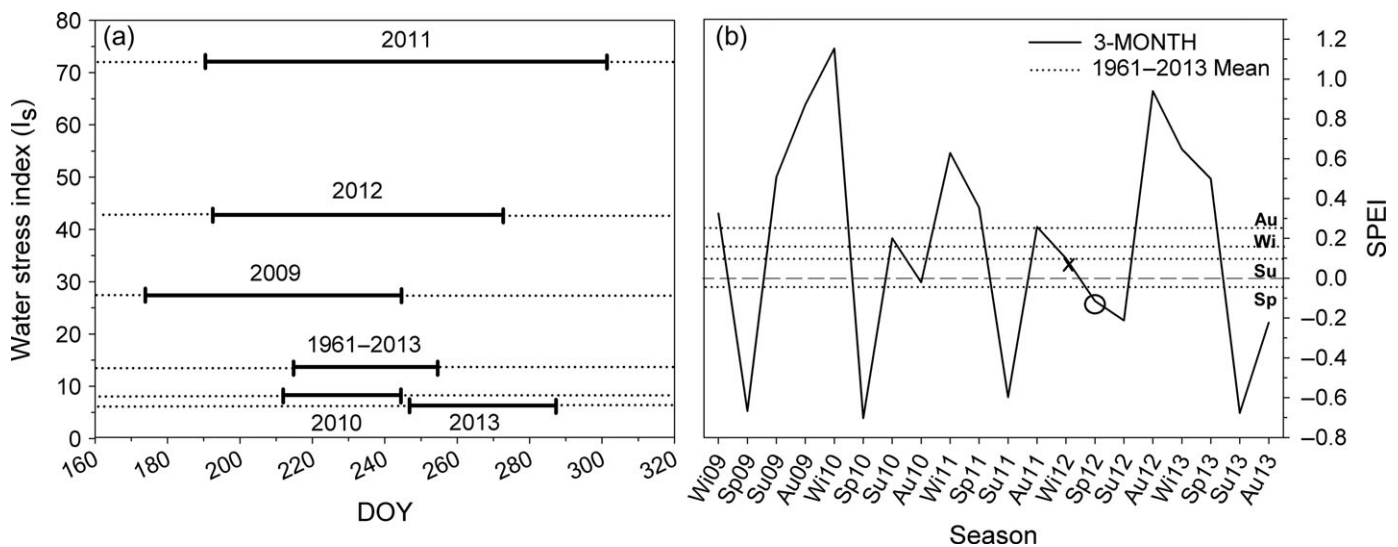


Figure 1. (a) Annual water stress index (I_s) for the years 2009–13 and the mean for the period 1961–2013 (y-axis). Higher values of the index indicate more water stress. The beginning and length of the line indicates the day of the year (DOY) when the drought began and ended in the corresponding year (x-axis). (b) Time evolution of the seasonal (3-month) SPEI at the study site for the years 2009–13 (solid line) and the seasonal mean for the period 1961–2013 (dotted line). Cross and circle mark winter and spring of 2012, respectively. Lower SPEI values indicate drier conditions.

stressful than 2012, water stress of the latter was also very high (value equal to the percentile 95%) in comparison with 2010 and 2013 (Figure 1a). Moreover, the beginning of water stress (BS) was similar and later than the median of the long-term time series in 2010 and 2013, respectively. However, BS was earlier than the long-term value in 2011 and 2012. The year preceding the study period, i.e., 2009, was also very dry, which could potentially influence drought responses during the study period.

Drought periods were observed during all seasonal periods (Figure 1b; see Table S1 available as Supplementary Data at *Tree Physiology Online*). Only winter 2012 was drier compared with the rest of the winters in the study period or compared with the 1961–2013 seasonal mean. Winter 2012 was also followed by a drier than average spring, although springs in 2009 and 2010 showed even lower SPEI values. Three consecutive summers (2011, 2012 and 2013) were drier than average, with 2011 and 2013 reaching similarly low SPEI values. The occurrence of consecutive seasons with lower than average SPEI was observed only for winter–spring 2012 and summer–autumn 2013, although the drought was more intense in the latter case.

Trends in growth and growing season length

Growth The BAI in both the whole growing season (BAI_{gs}) and in spring (BAI_{sp}) changed significantly between years and species in a similar manner, while no effect of both factors was observed in BAI_{au} (Table 1 and Figure 2). *Pinus nigra* showed significantly higher basal area increment than *Q. ilex* and *Q. faginea* in all seasons. The same patterns observed in BAI_{gs} and BAI_{sp} were explained by a high positive correlation between both variables in all species (see Figures S1–S3 available as Supplementary Data at *Tree Physiology Online*). In general, BAI_{sp} was higher than BAI_{au}

Table 1. Summary statistics for the linear mixed models (LMM) testing the effect of year, species and its interaction on the basal area increment and the relative growth rate in spring (BAI_{sp} and RGR_{sp} , respectively) and autumn (RGR_{au} and BAI_{au} , respectively) and the growing season for the former (BAI_{gs}). Kruskal-Wallis test (KWT) results are shown for the beginning and length of spring (Beg_{sp} and Len_{sp} , respectively) and autumn (Beg_{au} and Len_{au} , respectively). Bold numbers represent statistically significant results ($P < 0.05$).

	Statistical method	Intercept	Year	Species	Year x species
BAI_{gs}	LMM F	58.85	10.57	5.81	
	P	<0.0001	0.0001	0.0240	
BAI_{sp}	F	64.14	16.56	12.23	
	P	<0.0001	<0.0001	0.0027	
BAI_{au}	F	25.02			
	P	<0.0001			
RGR_{sp}	LMM F	8491.35	2.06	25.13	3.22
	P	<0.0001	0.1329	0.0002	0.0192
RGR_{au}	F	13,063.27	22.37	16.57	
	P	<0.0001	<0.0001	0.001	
Beg_{sp}	KWT χ^2		9.18	22.57	
	P		0.0269	<0.0001	
Beg_{au}	χ^2		35.25	2.96	
	P		<0.0001	0.2280	
Len_{sp}	χ^2		10.14	18.01	
	P		0.0063	0.0004	
Len_{au}	χ^2		0.46	27.40	
	P		0.7950	<0.0001	

for the three species. The year 2011 resulted in significantly more growth in spring than the other 3 years for all the species. The BAI_{sp} decreased in 2012 by 85%, 68% and 53% for *Q. ilex*, *Q. faginea* and *P. nigra*, respectively, concerning to the previous and extremely dry year 2011.

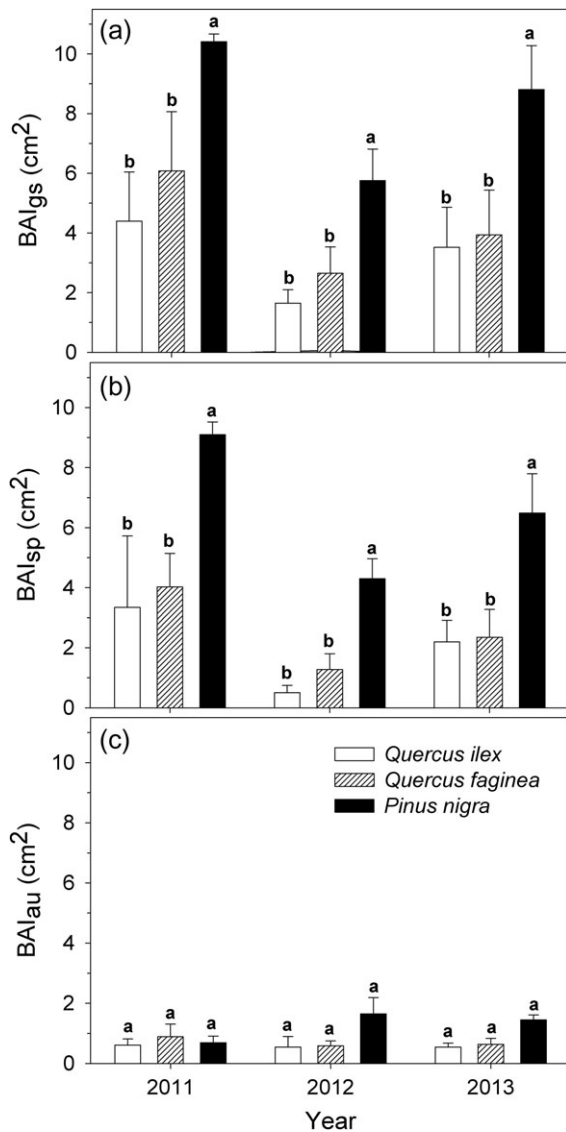


Figure 2. Mean basal area increment (cm^2) in the growing season (BAI_{gs} , a), spring (BAI_{sp} , b) and autumn (BAI_{au} , c) for each species and study period (2010–13). Different letters indicate significant differences between species for each year at $P \leq 0.05$.

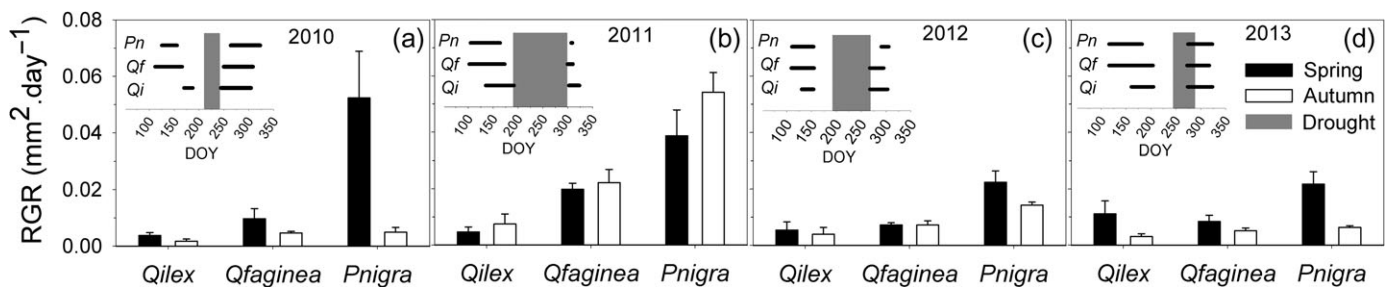


Figure 3. Mean relative growth rate ($\text{mm}^2 \text{day}^{-1}$) in spring (RGR_{sp}) and autumn (RGR_{au}) for each species and study period (2010–13, a–d). Small figures inside represent the beginning and length of growth (Julian days) in spring (Beg_{sp} and Len_{sp}) and autumn (Beg_{au} and Len_{au}) for each species (Pn: *Pinus nigra*; Qf: *Quercus faginea*; Qi: *Quercus ilex*) and year. Bars in gray represent the beginning and length of the drought for each year according to the water stress index (I_s).

The BAI_{sp} was correlated positively with the drought index SPEI_{sp} , and similarly with mean autumn temperature (T_{au}) in *Q. ilex*. However, BAI_{sp} depended on T_{wi} and not on drought indexes in *Q. faginea* and *P. nigra* (see Figures S1–S3 available as Supplementary Data at *Tree Physiology* Online).

Relative growth rate in spring (RGR_{sp}) varied significantly among species with a significant species per year interaction (Table 1). The RGR_{sp} and RGR_{au} were higher in *P. nigra* than in *Quercus* species, with slightly higher values in *Q. faginea* than in *Q. ilex* (Figure 3). *Pinus nigra* showed the highest values of RGR_{sp} in 2010, *Q. faginea* in 2011 and *Q. ilex* in 2013 (Figure 3). The highest RGR_{au} was found in *P. nigra* in 2011 (Figure 3b). In *Q. faginea* and *P. nigra* RGR_{au} was correlated positively and strongly with the number of days of water stress (DS), the drought indexes I_s and SPEI_{au} and the T_{sp} (for more correlations see Figures S1–S3 available as Supplementary Data at *Tree Physiology* Online).

Growing season length The beginning and length of spring growth (Beg_{sp} and Len_{sp} , respectively) varied among years and species (Table 1 and Figure 3). In the dry years (2011 and 2012), both *P. nigra* and *Q. ilex* advanced Beg_{sp} due to warmer spring temperatures, while *Q. faginea* did not change the beginning of growth significantly (Figure 3b and c). Beg_{sp} was more correlated with BS, I_s and T_{sp} in *Q. faginea* and DS and T_{gs} in *P. nigra* (for more correlations, see Figures S1–S3 available as Supplementary Data at *Tree Physiology* Online). Len_{sp} was positively and strongly correlated with SPEI_{sp} in the three species, and with T_{au} in *Q. ilex* and *P. nigra*. Moreover, Len_{sp} was correlated significantly with BAI_{gs} and BAI_{sp} in *Q. ilex*, and only with the latter in *Q. faginea*.

The beginning of autumn growth (Beg_{au}) depended on the year (Table 1), taking place later in 2011 (Figure 3b). The length of the autumn growth (Len_{au}) varied significantly among species but not among years (Table 1). Beg_{au} was positively correlated with DS and T_{au} in the three species (for more

correlations see Figures S1–S3 available as Supplementary Data at *Tree Physiology* Online). Len_{au} was negatively correlated with DS in the three species and with $SPEI_{au}$ and other temperature variables in *P. nigra* and *Q. faginea* (strong correlation with T_{sp} and T_{au} in *Q. faginea* and with T_{sp} in *P. nigra*). Moreover, Len_{au} was correlated significantly with BAI_{au} only in *P. nigra*.

Regulation of water-use efficiency across years and species

Water-use efficiency in spring (WUE_{sp}), autumn (WUE_{au}) and whole growing season (WUE_{gs}) depended on species (Table 2). Moreover, WUE_{au} was affected by year, and by the interaction year x species, while WUE_{sp} was not (Table 2). Significant differences among species were found in 2013 and 2012 for WUE_{au} . WUE was higher in *P. nigra* in the two seasons and for the whole growing period (WUE_{sp} , WUE_{au} and WUE_{gs}), followed by *Q. faginea* (Table 2).

Carbon isotope composition in spring ($\delta^{13}C_{sp}$) and summer ($\delta^{13}C_{su}$) showed significant differences among years and species (Table 2). $\delta^{13}C_{su}$ showed the highest differentiation among species across years, being significant in 2012 and 2013. *Pinus nigra* showed the highest $\delta^{13}C$ and WUE values regardless of the temporal period of integration. However, *Q. ilex* showed lower efficiencies than *Q. faginea* if we considered WUE but higher if $\delta^{13}C$ ($\delta^{13}C_{sp}$ or $\delta^{13}C_{su}$) was considered (Table 2). Species were more efficient in the use of water in 2012, with the lowest $\delta^{13}C$ values in the extremely dry year 2011. *Pinus nigra* showed higher $\delta^{13}C_{su}$ than both *Quercus* species regardless of the I_s , showing also higher variability among years. We observed a positive and significant relationship between $\delta^{13}C_{su}$ and WUE_{gs} (see Figure S5 available as Supplementary Data at *Tree Physiology* Online).

No significant correlations were found between leaf $\delta^{13}C$ and BAI , neither between $\delta^{13}C$ nor tree transpiration (E) in the two *Quercus* species (data not shown). However, $\delta^{13}C_{su}$ in *P. nigra* was significantly correlated with BAI_{sp} ($r = -0.608$, $P = 0.0400$), BAI_{gs} ($r = -0.636$, $P = 0.0404$) and E_{sp} ($r = -0.721$, $P = 0.0242$), and marginally with E_{au} ($r = -0.714$, $P = 0.0881$). A marginally significant correlation was also found in *P. nigra* between $\delta^{13}C_{sp}$ and BAI_{au} ($r = 0.582$, $P = 0.0655$). *Pinus nigra* showed the highest sensitivity to drought in terms of inter-annual changes in $iWUE$ as it was able to increase the $\delta^{13}C_{su}$ in 2012 after the high drought observed in 2011, with reductions of the BAI_{gs} of 40% in 2012 comparing with growth recorded in 2011. However, the two *Quercus* species showed higher reductions in BAI_{gs} (43% and 50% for *Q. ilex* and *Q. faginea*, respectively) and lower increases in $\delta^{13}C_{su}$ than *P. nigra*.

Discussion

Effects of drought timing on species growth

Our results highlight the primary role of drought timing on growth responses relative to the intensity of the drought.

Table 2. Mean integrated water use efficiency (WUE , $cm^2\ BAI\ m^{-3}\ H_2O$) in the growing season (WUE_{gs}), spring (WUE_{sp}) and autumn (WUE_{au}) and carbon isotope composition in spring ($\delta^{13}C_{sp}$) and summer ($\delta^{13}C_{su}$). Moreover, summary statistics for the linear mixed models testing the effect of year, species and its interaction on those variables. Bold numbers represent statistically significant results ($P < 0.05$) comparing species in each year. Different letters indicate results of post hoc analysis done for each year and variable with significant differences between species. *Only calculable for one tree. na: not available data.

	Year			Q. ilex			Q. faginea			P. nigra			Intercept			Year			Species			Year x species		
	2011	2012	2013	2011	2012	2013	2011	2012	2013	na	2011	2012	2013	F	P	F	P	F	P	F	P	F	P	
WUE_{gs} ($cm^2\ m^{-3}$)	0.55 ± 0.20	0.40 ± 0.09	0.69 ± 0.24^a	2.01*	0.59 ± 0.07	1.14 ± 0.34^{ab}	3.23*	2.32 ± 0.50	2.31 ± 0.36^b	64.33	<0.0001	8.42	0.0087											
WUE_{sp} ($cm^2\ m^{-3}$)	0.43 ± 0.08	0.35 ± 0.11	0.43 ± 0.08	2.33 ± 0.23	2.43 ± 0.84	3.40 ± 0.53	3.90 ± 1.89	3.40 ± 0.53	225.78	<0.0001	0.10	0.9034	0.0153											
WUE_{au} ($cm^2\ m^{-3}$)	2.27 ± 1.06	4.10 ± 1.25	0.65 ± 0.16^a	8.14 ± 2.27	8.14 ± 2.27	1.37 ± 0.51^{ab}	na	9.28 ± 2.11^b	10.09	0.0112	12.31	0.0127	0.0009											
$\delta^{13}C_{sp}$ (‰)	-28.05 ± 0.50	-26.34 ± 0.41	0.56 ± 0.15^a	-27.84 ± 0.57	-27.09 ± 0.61	-27.18 ± 0.48	-26.87 ± 0.26	2.27 ± 0.08^b	9447.16	<0.0001	6.79	0.0031	0.0066											
$\delta^{13}C_{su}$ (‰)	-27.88 ± 0.57	-27.10 ± 0.30	-26.63 ± 0.21^{ab}	-27.97 ± 0.45	-27.18 ± 0.48	-27.97 ± 0.45	-26.44 ± 0.46	-26.44 ± 0.46	28,051.74	<0.0001	8.66	0.0008	0.0001											
	-27.26 ± 0.23 ^a	-27.26 ± 0.23 ^a	-27.52 ± 0.49^a	-27.52 ± 0.49 ^a	-27.52 ± 0.49 ^a	-27.52 ± 0.49 ^a	-24.05 ± 0.21 ^b	-25.29 ± 0.26 ^b																

Consecutive severe droughts occurring at different time scales (i.e., over whole seasons to a few weeks) produce legacy effects on growth, transpiration and WUE of trees in successive years. In addition, the impact of drought timing is highly dependent on species.

We observed that the time of year when drought occurs, in particular dry winters and springs, can impact tree growth equally or even more than drought intensity integrated over the year, as observed in 2012. Winter 2012 was drier than the historical mean (1961–2013) and was followed by a very dry spring. In spite of not having leaves in winter, winter-deciduous species like *Q. faginea* can be affected by dry winters since their cambial activity can be affected, and also the formation of the new functional ring porous xylem at the beginning of the growing season (Fernández-de-Uña et al. 2017). In fact, winter temperature can also affect species growth, as suggested by significant correlations with spring growth and the length of the spring growth in *Q. faginea* and *P. nigra*. Our results agree with other studies that show that dry winters impact gross and net primary production in evergreen species like *Q. ilex* (Allard et al. 2008) and *Quercus suber* (Costa-e-Silva et al. 2015). Summer and autumn droughts in 2011 affected growth in 2012. These carry over effects on tree functioning were produced by the long-lasting and intense summer drought that occurred in 2011, which delayed resumption and decreased autumn tree growth and transpiration. Moreover, the time of the season when water stress occurred determined the growth in *P. nigra* and *Q. faginea*, as proved by significant and strong correlations between the beginning of water stress and spring and autumn relative growth rate. This vulnerability of species to the beginning of water stress could depend not only on water soil availability but also on spring and autumn temperatures, to which *Q. ilex* was not as responsive as the other two species. Clearly, the effects of the drought's timing on tree growth were species-specific. Effects of drought length were also relevant, and strongest for *Quercus* species (see e.g., growth reductions in 2012 vs 2011, *Q. ilex* 63%, *Q. faginea* 56% and *P. nigra* 45%), which is consistent with previous studies (Forner et al. 2014, Sánchez-Costa et al. 2015). *Quercus faginea* growth was affected, not only reducing current-year growth, but also limiting its inter-annual recovery as observed in the dry year of 2012 vs the next wet year of 2013. *Pinus nigra* and *Q. ilex* advanced spring growth in warmer years, as has been observed in *Quercus* species under warming conditions (Morin et al. 2010). Lower flexibility of *Q. faginea* in adjustments to growing season length can be explained by the requirement of certain heat hours to break dormancy, and/or a control of leaf flushing by photoperiod length (Sanz-Pérez et al. 2009). This may result in limiting plastic response in initiation of secondary growth for *Q. faginea* (Lempereur et al. 2015).

We also observed a species-specific pattern in the impact of dry springs, which intensified the negative impact of the summer

drought, and limited growth recover in autumn. Autumn growth in *Q. ilex* was similar (2012) or even higher (2010) to the one recorded in spring for those years with a very dry spring. In those dry years, late season growth observed in *Q. ilex* can be considered as a way to resume growth and compensate the low spring growth (Campelo et al. 2007). This resumption of growth in autumn has been observed in other evergreen species such as *P. halepensis* or *Juniperus thurifera* in xeric sites (Camarero et al. 2010). This is less common in deciduous species or Eurosiberian pines (Zweifel et al. 2007, Camarero et al. 2010, Fernández-de-Uña et al. 2017). The length of growth in autumn for *Q. faginea* could not last as long as in *Q. ilex* due to premature leaf withering in *Q. faginea* that occurs during extreme dry summers, which limits carbon assimilation during autumn conditions (Pataki and Oren 2003). Early leaf senescence would be a mechanism for protecting the stem from full xylem cavitation, as observed in other *Quercus* species (Peguero-Pina et al. 2015). Winter-deciduous species such as *Q. faginea* can show a similar annual integrated carbon gain at the leaf level to that of evergreen species such as *Q. ilex* (Mediavilla and Escudero 2003, Escudero et al. 2017), but for these species early falling or a steep drop in the photosynthetic capacity could have a high penalty on current year growth. These results should be validated with other methods, such as for example with the study of species xylogenesis inferred from microcores (Camarero et al. 2010, Fernández-de-Uña et al. 2017), which increases the analytical resolution of growth study at times of low absolute growth of trees as in autumn. After a previous extremely dry year, *Q. faginea* showed lower resilience (like in 2013). Total annual growth recovery was higher for *Q. ilex* and *P. nigra* (68% and 66%, respectively) than for *Q. faginea* (37%), which is in agreement with other studies (Corcuera et al. 2004a, 2004b, Granda et al. 2013). Accordingly, this could reduce growth of *Q. faginea* in the long term if recurrence of dry springs is intensified, as chronic water stress reduces growth and the role of carbon sink of deciduous hardwood forests (Brzostek et al. 2014). These results confirm the higher dependence of growth on a good water availability for winter-deciduous oaks vs evergreen species not only in current years (reviewed recently by Gil-Pelegrián et al. 2017), but also in subsequent years (Granda et al. 2013).

Species water-use efficiency under extreme droughts

Our results showed differences between *P. nigra* and *Quercus* species in terms of WUE. *Pinus nigra* had the capacity to increase WUE, to mitigate drought effects affecting water consumption more than current-year growth. We observed in 2012 and 2013 that neither *Quercus* species increased iWUE between late-spring and summer as much as *P. nigra*. That plasticity of *P. nigra* in WUE could be due to a more water-saving strategy linked to a high control of water losses at the full tree level during dry periods (Forner et al. 2014). A similar trend was also observed for

interspecific differences in $\delta^{13}\text{C}$ for inter-annual variation, being *P. nigra* more plastic than *Quercus* species: species mean variations in $\delta^{13}\text{C}_{\text{su}}$ between the dry year of 2012 and the wet year of 2013 were 1.24‰ in *P. nigra*, 0.63‰ in *Q. ilex* and 0.18‰ in *Q. faginea*.

The general pattern of WUE was in agreement with the WUE from leaf $\delta^{13}\text{C}$ across species. However, although there was an overall significant relationship between both WUE proxies, results from each proxy revealed different patterns among years and species. In general, *P. nigra* had higher WUE than oaks independently of the year or the variable used as a proxy of WUE. There were different trends between growth and iWUE inferred from leaf $\delta^{13}\text{C}$ or calculated from tree transpiration and BAI. This agrees with Camarero et al. (2015b), who found that the relationship between iWUE and growth was species-specific. Also, it was consistent with the fact that an increase in WUE due to drier conditions does not keep pace with growth, as observed in long-term studies (Levesque et al. 2014), different forest biome types (Peñuelas et al. 2011) and short-term Mediterranean studies (Olano et al. 2014, Vicente-Serrano et al. 2015). The observed differences in the relationship between WUE and growth among species can be important for local stand dynamics at least at short-term: *P. nigra* modulated its WUE more than the other coexisting species (*Quercus* species), but without a penalty on secondary growth, as expected from the impact of drought in water-use alone.

Conclusions

Timing of extreme drought events can affect tree functioning to a larger extent than drought intensity, and this effect is species-specific. Contrary to expectations, growth resilience to extreme droughts seemed to be better in *P. nigra* and worse in *Q. faginea*. Control of water loss over growth was optimized in *P. nigra* more than in the two *Quercus* species. *Pinus nigra* restarted growth after atypical dry years even under early drought in winter and spring. Water-use efficiency and growth of the species were decoupled and not influenced by timing and intensity of the drought in the same way in the three species. This reinforces the need to ascertain not only growth but also the water-use strategy at different time scales, and from the leaf level to the overall tree. Water-use efficiency calculated from growth and transpiration can be used as a realistic integrative view of both the effects of drought stress, and the efficiency of the strategies followed by each species in optimizing carbon uptake under extreme water limitations.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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