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Intensity and timing of warming and drought differentially affect growth patterns of co-occurring Mediterranean tree species

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Abstract Climate change involves warmer temperatures, altered precipitation patterns, increased climatic variability and, in Mediterranean regions, increased frequency and severity of droughts. Tree species may show different growth responses to these components of climatic change, which may trigger changes in forest composition and dominance. We assessed the influence of recent climatic changes on secondary growth of mature trees from four species co-occurring in a Mediterranean continental forest: *Quercus ilex*, *Quercus faginea*, *Pinus nigra* and *Juniperus thurifera*. We used dendrochronology to relate radial-growth variables [earlywood and latewood widths, basal area increment (BAI)] to annual and seasonal climatic variables for the period 1977–2007. Our results showed that *Q. faginea* BAI has declined, whereas *J. thurifera* BAI has increased over time while *Q. ilex* and *P. nigra* have maintained their growth rates. Growth was mainly favored

by higher precipitations and tree size for all species. Reduced growth during extremely dry years was observed for all study species, but all of them except *Q. faginea* recovered their growth levels 2 years after drought. Our findings illustrate how the effects of climatic changes on growth should include analyses of seasonal climatic trends and extreme events such as severe droughts. We conclude that the seasonal timing of warming and precipitation alterations leading to drought events caused contrasting effects on growth of co-occurring Mediterranean tree species, compromising their future coexistence.

Keywords Climate change · Coexistence · Mediterranean forests · Dendroecology · Drought · Radial growth

Introduction

Forests worldwide are recently experiencing modifications in their productivity and dynamics due to climate change. In fact, changes in intensity, duration and frequency of droughts are responsible for many observed shifts on vegetation and forest dieback, even in forests not

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considered to be water limited (Allen et al. 2010). Prolonged water deficits and extreme events are related to forest growth declines, but while in the former case, acclimation may occur, in the latter one, the acclimation capacity of tree species might be surpassed by the intensity of the unusual and severe events (Gutschick and BassiriRad 2003). Extreme warming-related droughts have been shown to not only affect at the species level but also at the population, community and ecosystem levels (Bredá and Badeau 2008). However, species and communities might strongly differ in their responses with situations of stability and lack of abrupt vegetation shifts despite the occurrence of such extreme climatic events (Lloret et al. 2012).

In drought-prone Mediterranean forests, the occurrence of intense and prolonged warming-linked drought episodes has been highlighted to be critical for tree species growth, composition and abundance, potentially compromising species coexistence (Terradas and Savé 1992; West et al. 2008; Peñuelas et al. 2011). In fact, several studies have found evidence of a negative impact of increasing drought stress on growth and resilience of many woody species like *Pinus nigra* (Martín-Benito et al. 2010), *Pinus brutia* (Sarris et al. 2007), *Pinus halepensis* (Linares et al. 2011; Pasho et al. 2012) and *Abies pinsapo* (Linares et al. 2011). However, species present differential sensitivities to drought stress and to competition for space, water and light (Bolte et al. 2010; see discussion in Lloret et al. 2012). Under a warmer and drier climatic scenario, the chances of colonization by more drought-vulnerable species are expected to decrease, favoring competitive exclusion and the expansion of the more drought-resistant species (Cotillas et al. 2009; Montserrat-Martí et al. 2009) although demographic and evolutionary mechanisms could counteract individual vulnerabilities (Lloret et al. 2012).

Most climatic models project temperature rises at a mean rate of +1.2 °C during winter and +2 °C during summer for the forthcoming 30 years in the Western Mediterranean Basin (A2 scenario, Christensen et al. 2007). Total annual precipitation is expected to decrease in the same area according to most climatic models, although discrepancies exist among models regarding the extent of the reduction. Interestingly, the timing of the occurrence of increased temperature and decreased precipitation can be equally or even more important for plant performance than mean annual climatic values (Menzel et al. 2006). However, the impact of this timing has received still little attention, despite the fact that aridification is expected to aggravate during spring, a critical season for the vegetative activity of most Mediterranean trees (Mitrakos 1980; de Castro et al. 2005).

Dendrochronology allows quantifying and comparing growth responses to drought through time in tree species, which could be cross-dated with yearly resolution (Fritts 1976). Trees and other woody species reduce their radial

growth in response to water-deficit depending on the species sensitivity to drought stress and also as a function of the seasonal occurrence of the drought, which may affect differently earlywood and latewood formation. For instance, spring droughts reduced more the earlywood than the latewood width in the Mediterranean conifer *P. halepensis* (Pasho et al. 2012). Comparing growth responses to extreme droughts of coexisting tree species is crucial for understanding future forest dynamics under more arid conditions. However, most of the comparative studies in the Mediterranean Basin are based on only one or two species (but see Rozas et al. 2009) and are usually focused on whole tree-ring width. In contrast, studies distinguishing earlywood and latewood widths allow better understanding on how tree growth is differently affected by seasonal water shortage, since xylogenesis and the formation of both earlywood and latewood are influenced by distinct climatic factors (Pasho et al. 2012).

We have studied the dominant tree species in a Mediterranean continental area (*Quercus ilex*, *Q. faginea*, *Pinus nigra*, *Juniperus thurifera*) to (1) quantify radial-growth variability across time among coexisting species with contrasting leaf habits and wood types; (2) assess how the changes in earlywood, latewood and tree-ring widths of the different species have responded to seasonal climatic variables during the last three decades; and (3) evaluate how radial growth is affected by severe drought events, comparing species' recovery capacity after drought occurrence. We hypothesized that the responsiveness to severe droughts would vary among species according to their wood anatomy and leaf habit. We expect *Q. faginea*, a deciduous species with ring-porous wood, to be more negatively affected by the observed increases in temperature and drought episodes than the evergreens, as growth and carbon gain are limited to spring and autumn in this species (Montserrat-Martí et al. 2009). In contrast, we expect evergreens to better tolerate water deficit than the deciduous species (Cherubini et al. 2003), but such tolerance will also depend on wood and conduit anatomy. Vessels of the diffuse—to semi-ring-porous wood type of *Q. ilex* have higher conductivity but are also more vulnerable to embolism than tracheids (Hacke and Sperry 2001). Thus, we expected that the narrow tracheids of the two conifers would allow them to be less vulnerable to the loss of hydraulic conductivity caused by drought-induced embolism, particularly in the case of *J. thurifera* which forms the narrowest conduits of all study species. We expect *P. nigra*, the species with highest growth rates, to exhibit the strongest growth reduction (particularly in earlywood production), if drought severity increases over spring when radial-growth peaks. We discuss the implications of the different growth patterns and of the potential trade-offs within the context of coexisting tree species under warming climate scenarios where extreme drought events are expected to become more frequent.

Materials and methods

Study site and species

The study area is located in Alto Tajo Natural Park, in Central Spain (Guadalajara, Castilla-La Mancha). The climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual precipitation is 499 mm, with August being the driest month (25.6 mm) and May the rainiest one (66.1 mm). Mean annual temperature is 10.2 °C, with January being the coldest month (2.4 °C) and July the warmest one (19.5 °C), according to climatic data of the closest meteorological station, located at ca. 35 km from the sampling sites (Molina de Aragón: 40° 50' 40" N, 1° 53' 07" W, 1,063 m a.s.l., 1951–2007 period, data provided by the Spanish Agencia Estatal de Meteorología). The soils are calcareous, poorly developed and formed mainly from Cretaceous and Jurassic limestone.

We selected four representative and dominant tree species of the Mediterranean ecosystems in continental areas: two Fagaceae species including an evergreen oak with diffuse—to semi-ring-porous wood—*Quercus ilex* subsp.

ballota (Desf) Samp—and a deciduous oak with ring-porous wood—*Quercus faginea* Lam.—and two conifers of the Pinaceae [*Pinus nigra* J.F. Arnold subsp. *salzmannii* (Dunal) Franco] and Cupressaceae (*Juniperus thurifera* L.) families (Fig. 1). Within the study area, we randomly selected seven sites (Table 1), which have remained unmanaged, at least, for the last three decades. Between January and May 2008, we randomly selected 15–17 single-stemmed dominant trees per species at each site that had similar DBH (diameter at breast height, 1.3 m of height) and showed no symptoms of decline or pathogenic infection (see Table 2 for details on DHB, age, tree-ring width and number of sampled trees and radii). Trees were tagged, mapped and measured for DBH. Tree density was obtained from 100-m² plots at each site. While not all the species were present in all sites, the whole range of local climate where each of these species is present in the study area was covered.

Climatic data

Long-term regional climate records (mean monthly temperature and rainfall for each year between 1950 and 2007)

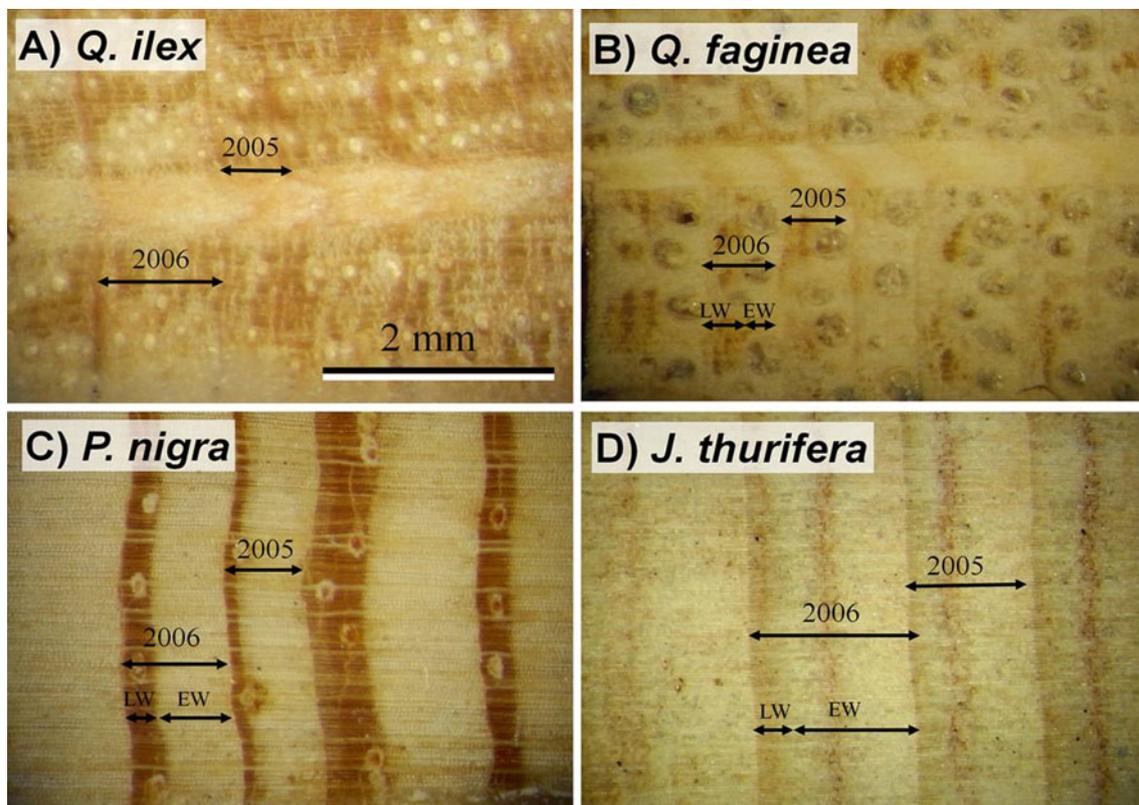


Fig. 1 Growth rings of the four study tree species found in Mediterranean forests: **a** *Quercus ilex* (diffuse- to semi-ring-porous wood), **b** *Quercus faginea* (ring-porous wood), **c** *Pinus nigra* (conifer wood), **d** *Juniperus thurifera* (conifer wood). The narrow tree ring

formed in 2005 corresponds to an extreme dry year. The distinctions between earlywood (EW) and latewood (LW) within a growth ring are also shown in the tree ring formed in 2006

Table 1 Characteristics of the study sites

Site code	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Aspect	Dominant tree species	Tree density (trees/ha)	Total annual precipitation (mm)	Mean annual (minimum–maximum) temperatures (°C)	Annual AET (mm)	Annual WA (mm)
HP	40° 47' 38"	2° 17' 09"	848	NE	PN, QF	900	598.7	11.7 (5.5–18)	506.2	92.5
RS	40° 51' 10"	2° 18' 02"	953	SE	JT	1400	603.0	11.5 (5.3–17.8)	508.9	94.1
TI	40° 48' 16"	2° 13' 58"	981	S	PN, QI	2500	639.2	11.5 (5.3–17.8)	516.8	122.4
BF	40° 49' 02"	2° 12' 55"	1220	NW	JT	1200	611.9	10.5 (4.2–16.8)	489.5	122.4
TA	40° 49' 01"	2° 12' 36"	1233	NE	PN, QI, JT	2000	620.3	10.5 (4.2–17.6)	488.7	131.6
QU	40° 47' 26"	2° 17' 57"	884	N-NW	PN	2100	653.1	12.0 (5.9–18.3)	502.8	150.3
AR	40° 46' 40"	2° 19' 36"	1060	NW	PN, QF, QI	2400	796.2	11.5 (5.2–17.7)	530.3	265.9

Climatic variables for the period 1951–1999 were obtained from Ninyerola et al. (2005). Dominant tree species: QI, *Quercus ilex*; QF, *Q. faginea*; PN, *Pinus nigra*; JT, *Juniperus thurifera*; AET, actual evapotranspiration; WA, water availability (WA = P–AET)

Table 2 Characteristics of the study species and sites

Species	Site	DBH (cm)	Age (years)	TRW (mm)	No. trees	No. radii
<i>Q. ilex</i>	TI	13.6 ± 0.6	70 ± 2	0.6 ± 0.4	17	30
	TA	17.7 ± 0.5	62 ± 2	1.0 ± 0.5	12	21
	AR	13.9 ± 0.7	41 ± 4	1.1 ± 0.6	12	24
	Mean	15.1 ± 0.6	58 ± 3	0.9 ± 0.5		
<i>Q. faginea</i>	HP	17.7 ± 1.0	47 ± 1	1.4 ± 0.7	16	29
	AR	17.9 ± 0.7	46 ± 2	1.4 ± 0.8	14	28
	Mean	17.8 ± 0.8	47 ± 1	1.4 ± 0.7		
<i>P. nigra</i>	HP	28.8 ± 1.6	51 ± 5	2.0 ± 0.8	15	30
	TI	29.9 ± 1.5	48 ± 1	2.3 ± 1.2	17	30
	TA	28.6 ± 1.0	42 ± 3	2.6 ± 1.2	15	30
	AR	24.8 ± 1.1	62 ± 8	1.5 ± 0.8	16	31
	QU	31.2 ± 2.0	44 ± 2	2.4 ± 0.9	15	29
	Mean	28.7 ± 1.2	49 ± 2	2.2 ± 1.0		
<i>J. thurifera</i>	RS	19.5 ± 0.6	44 ± 3	1.9 ± 0.6	14	27
	BF	17.7 ± 1.6	42 ± 3	1.8 ± 0.7	14	18
	TA	16.5 ± 1.3	43 ± 3	1.5 ± 0.7	14	27
	Mean	17.9 ± 1.2	42 ± 2	1.7 ± 0.7		

DBH Diameter at breast height (mean ± SE), Age Age estimated at 1.3 m (mean ± SE), TRW tree-ring width (mean ± SD)

were obtained from the “Molina de Aragón” meteorological station. We estimated water availability as precipitation minus actual evapotranspiration (WA = P–AET, Fig. 2b), where AET was calculated following a modified Thornthwaite method (see Willmott et al. 1985), with a software developed by Daniel G. Gavin (<http://geography.uoregon.edu/envchange/pbl/software.html>). Mean and total annual precipitations were calculated from September of the previous year to August of the current year following Camarero et al. (2010). Linear regressions were conducted to test the climatic trends (temperature, precipitation and WA) for different periods (Supporting material, Table S1). To estimate local climate at each site (an average value for

the period 1951–1999; Table 1), we used the Digital Climatic Atlas of the Iberian Peninsula (DCAIP). The DCAIP is a set of digital climate maps of air temperature (minimum, mean and maximum), precipitation and solar radiation for the whole Iberian Peninsula, with monthly and annual temporal resolutions and a spatial resolution of 200 m (Ninyerola et al. 2005). These maps are obtained using data for the climatic variables from meteorological stations and data for geographic variables (altitude, latitude, continentality, solar radiation and the geomorphology of the terrain).

Sampling and dendrochronological procedures

Trees selected in the field were cored at 1.3 m height using a Pressler increment borer. Two complete radii were extracted from each tree. The cores were air-dried, glued onto wooden mounts and polished. Then, the wood samples were visually cross-dated (Stokes and Smiley 1968, Fig. 1). Earlywood, latewood and tree-ring widths were measured on a LINTAB measuring device (Rinntech, Heidelberg, Germany) with a resolution of 0.001 mm. Earlywood and latewood were measured for all the species at each site except for *Q. ilex* because the diffuse—to semi-ring wood of this species did not allow distinguishing the two types of wood (Fig. 1). We distinguished earlywood and latewood based on the cross-sectional area of vessels and tracheid lumens and the thickness of tracheid double cell walls in the case of conifers (see also Corcuera et al. 2004a; Camarero et al. 2010; Pasho et al. 2012). The visual cross-dating was statistically checked using the program COFECHA (Holmes 1983). For each tree, measurements from the two cores were averaged. The trend of decreasing ring width with increasing tree size was removed by converting radial increment into basal area increment (BAI) using the formula: $BAI = \pi (r_t^2 - r_{t-1}^2)$; where r is the tree radius and t is the year of tree-ring formation. In the case of

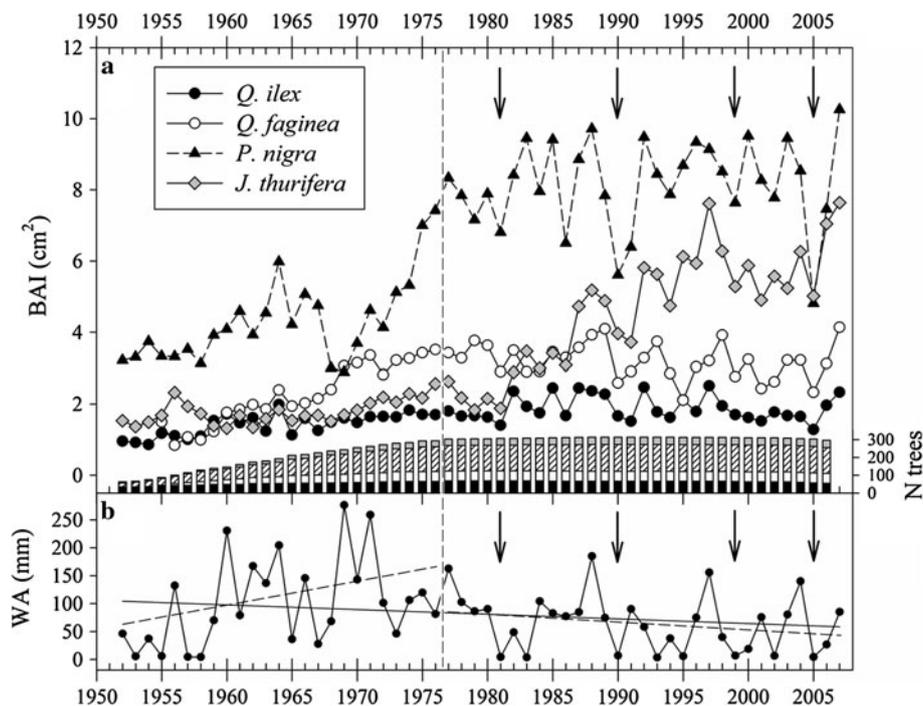


Fig. 2 Temporal evolution of mean basal area increment (BAI, lines) and number of measured trees (bars, right y-axis) per year for the four species (a; *Quercus ilex*, black bars and circles; *Quercus faginea*, white bars and circles; *Pinus nigra*, striped bars and black triangles; *Juniperus thurifera*, gray bars and diamonds) as compared with annual water availability (WA) during the period 1952–2007 (b).

Broken lines represent trends for two different sub-periods (1952–1976 and 1977–2007), while the continuous line shows the trend for the period 1952–2007. Regression coefficients for annual and seasonal temperature, precipitation and water availability are shown in Supporting material, Table S1. Arrows in graphs (a) and (b) point extreme drought years chosen for further analyses

cores without pith, we used a geometric method based on the curvature of the innermost tree-ring to estimate the number of missing rings up to the theoretical pith.

A local tree-ring-width chronology was established for each site and species. For each tree, its cross-dated ring-width series was detrended and standardized to remove age-related growth trends (Fritts 1976; Cook and Kairiukstis 1990). The series of raw data were processed with a double detrending. First, a negative linear or exponential function was fitted. Then, we used cubic smoothing splines with a 50 % frequency response cutoff of 30 years to keep the high-to-medium frequency response to climatic variability (Cook and Peters 1981). Autoregressive modeling was performed on each detrended ring-width series to remove most of the first-order autocorrelation, and the pre-whitened series were finally averaged using a biweight robust mean to obtain residual site chronologies (Monserud 1986). These analyses were done using the program ARSTAN (Cook 1985). We used site residual chronologies (Supporting material, Table S2) for assessing growth–climate relationships and also for calculating correlations between earlywood, latewood and ring-width indices (Supporting material, Tables S2 and S3). We used earlywood, latewood and ring-width indices for the period

1977–2007, which ensured us that most of the trees from the four species had reached a mature phase. Plus, since 1977 mean annual temperatures have increased at least +0.3 °C per decade in the Iberian Peninsula and also in the study area (de Castro et al. 2005; Gimeno et al. 2012).

Growth patterns in relation with tree density, annual and monthly climatic variables

A linear mixed-effects model was used following Zuur et al. (2007) to test the effect of tree size (DBH), time (year), tree density (trees/ha) and annual precipitation [$P_{\text{Sep–Aug}}$, from September of the year previous to growth ($t-1$) up to August of the year of growth (t)] on (log-transformed) BAI of each species. Thus, our response variable was BAI of each year for each tree, while DBH, year, tree density and annual precipitation were included in the model as fixed factors. The random components of the model were the individual trees at each site. We built a set of models per species, and the model with the best subset of predictors was selected comparing the Akaike Information Criterion (AIC; Burnham and Anderson 2002). These models were performed using growth data from the 12–17 trees per species and site (all years for the period

1977–2007). Analyses were performed using the *nlme* package in the R statistical software (Pinheiro et al. 2011, R Development Core Team 2011, Vienna, Austria).

To relate each species residual chronology (earlywood, latewood and tree-ring widths) to monthly climatic data (mean temperature and total precipitation derived from the “Molina de Aragón” meteorological station), we calculated Pearson correlation coefficients for the period 1977–2007, and response function coefficients to reduce the spurious effects on correlations caused by the collinearity among climatic variables. The significance and stability of the calculated regression coefficients were evaluated based on 1,000 bootstrap estimates obtained by random extraction with replacement from the initial data set (Guiot 1991). Growth–climate relationships were analyzed from September ($t-1$) up to August (t) for the whole ring width and also for earlywood and latewood widths separately. In the case of *Q. ilex*, only tree-ring width was considered. To calculate the correlation and response coefficients, we used the program Dendroclim2002 (Biondi and Waikul 2004).

Superposed epoch analysis (SEA)

The superposed epoch analysis (SEA) was used to quantify growth reductions during extreme drought events (Lough and Fritts 1987). SEA is a simple but powerful randomization test to evaluate growth departures from mean values for selected dry years, which has been previously used in dendroecology (Orwig and Abrams 1997; Martín-Benito et al. 2008; Pasho et al. 2012). We selected four extremely dry years for the period 1977–2007: 1981, 1990, 1999 and 2005, which mean water availability (WA) values were 4.23, 6.69, 6.74 and 4.17 mm, respectively, being the mean WA for the period 65.15 ± 9.16 mm. Mean indexed growth values of earlywood, latewood and ring width during these extreme drought years and also during 2 years before and after the drought year were considered within the temporal window of the analyses. We used the software Resampling Stats (Bruce 1991) to randomly select 10,000 sets of 5 years from each series and to estimate the confidence intervals ($P < 0.05$) for the plotted growth departures (cf. Haurwitz and Brier 1981).

Results

Climatic trends, tree characteristics and growth patterns

Our results support a seasonal warming trend in the study area since both spring and summer mean temperatures have risen significantly at a rate of +0.7 and +0.6 °C per decade

since the late 1970s, respectively ($R^2 = 0.42$ and 0.29 ; $P < 0.0001$ and $P < 0.001$; see Supporting material, Table S1). Contrastingly, winter and autumn temperatures and precipitation and water availability showed no significant trends (Fig. 2b, Supporting material, Table S1).

Mean growth rates were minimal for *Q. ilex* and maximal for *P. nigra*, with intermediate values for *Q. faginea* and *J. thurifera* (Fig. 2a; Table 2 and Supporting material, Table S2). All species showed significant positive temporal autocorrelation at a lag of 1 year in their BAI series at least in one site (Supporting material, Table S4). In the case of *J. thurifera*, this positive temporal autocorrelation was observed in all the sites, while for the other species, this was observed in the site with the highest water availability (AR, Table 1). Regarding the dendrochronological statistics, we found a strong common signal within each stand for most variables except in the case of earlywood width in *Q. faginea* and latewood width in *J. thurifera* (Supporting material, Table S2).

Linear mixed-effects models indicated that BAI has significantly declined through time for *Q. faginea* and increased for *J. thurifera* since the late 1970s (Fig. 2; Table 3), while *Q. ilex* and *P. nigra* maintained stable growth rates for the same period. Tree density at each site did not show significant effects on tree growth for any species, as indicated by the exclusion of such variable in the best model for each species (Table 3). Annual precipitation and tree size had a positive effect on BAI for all species.

Relationships between growth and seasonal climate

Quercus ilex growth was favored by warm temperatures during the previous autumn (November) and by warm conditions in February and mild and rainy conditions in April. The growth of this species was also enhanced whenever summers were wet and mild (Fig. 3a, b). Growth of *Q. faginea* was mainly favored by precipitation during winter (February) and spring (April, May), although temperatures also had an effect on earlywood (positive during the previous October and negative during the current July, Fig. 3c, d). Overall, the radial growth of *P. nigra* was not significantly correlated with temperatures. Instead, previous rainy autumns (September–November) and rainy springs (May) of the year of ring formation favored growth of this species (Fig. 3e, f). The growth of *J. thurifera* (Fig. 3g, h) was significantly and positively related to current April temperatures, but negatively to rainy conditions in March. Wet autumns during the previous year and rainy and mild summers (June and July) enhanced growth of this last species.

Table 3 Results from the linear mixed models of basal area increment for the period 1977–2007

Species	Factor	Estimate	SE	DF	<i>t</i> value	<i>P</i> value
<i>Q. ilex</i>	(Intercept)	−0.1223	0.0941	1041	−1.2996	0.194
	DBH	0.0290	0.0060	33	4.8145	<0.0001
	P _{Sep–Aug}	0.0002	0.0000	1041	6.9937	<0.0001
<i>Q. faginea</i>	(Intercept)	2.7741	0.6642	868	4.1767	<0.0001
	DBH	0.0275	0.0047	27	5.8249	<0.0001
	Time	−0.0014	0.0003	868	−4.2800	<0.0001
	P _{Sep–Aug}	0.0002	0.0000	868	6.8708	<0.0001
<i>P. nigra</i>	(Intercept)	0.1524	0.0631	2219	2.4138	0.0159
	DBH	0.0204	0.0021	73	9.6839	<0.0001
	P _{Sep–Aug}	0.0004	0.0000	2219	12.6944	<0.0001
<i>J. thurifera</i>	(Intercept)	−28.9458	0.8982	1181	−32.2247	<0.0001
	DBH	0.0286	0.0032	39	9.0281	<0.0001
	Time	0.0146	0.0004	1181	32.5194	<0.0001
	P _{Sep–Aug}	0.0002	0.0000	1181	5.3664	<0.0001

Only the fixed factors of the best model obtained by AIC selection criteria are shown

Fixed factors were *DBH* diameter at breast height, *Time* year (from 1977 to 2007), P_{Sep–Aug} annual precipitation (from September (*t*−1) to August (*t*) for the period 1977–2007) obtained from the meteorological station from “Molina de Aragón” and Tree density = trees/ha. Random factors were the trees at each site (SD for the random effects are 0.1, 0.09, 0.1 and 0.08 for *Q. ilex*, *Q. faginea*, *P. nigra* and *J. thurifera*, respectively

Drought effects on earlywood, latewood and tree-ring widths

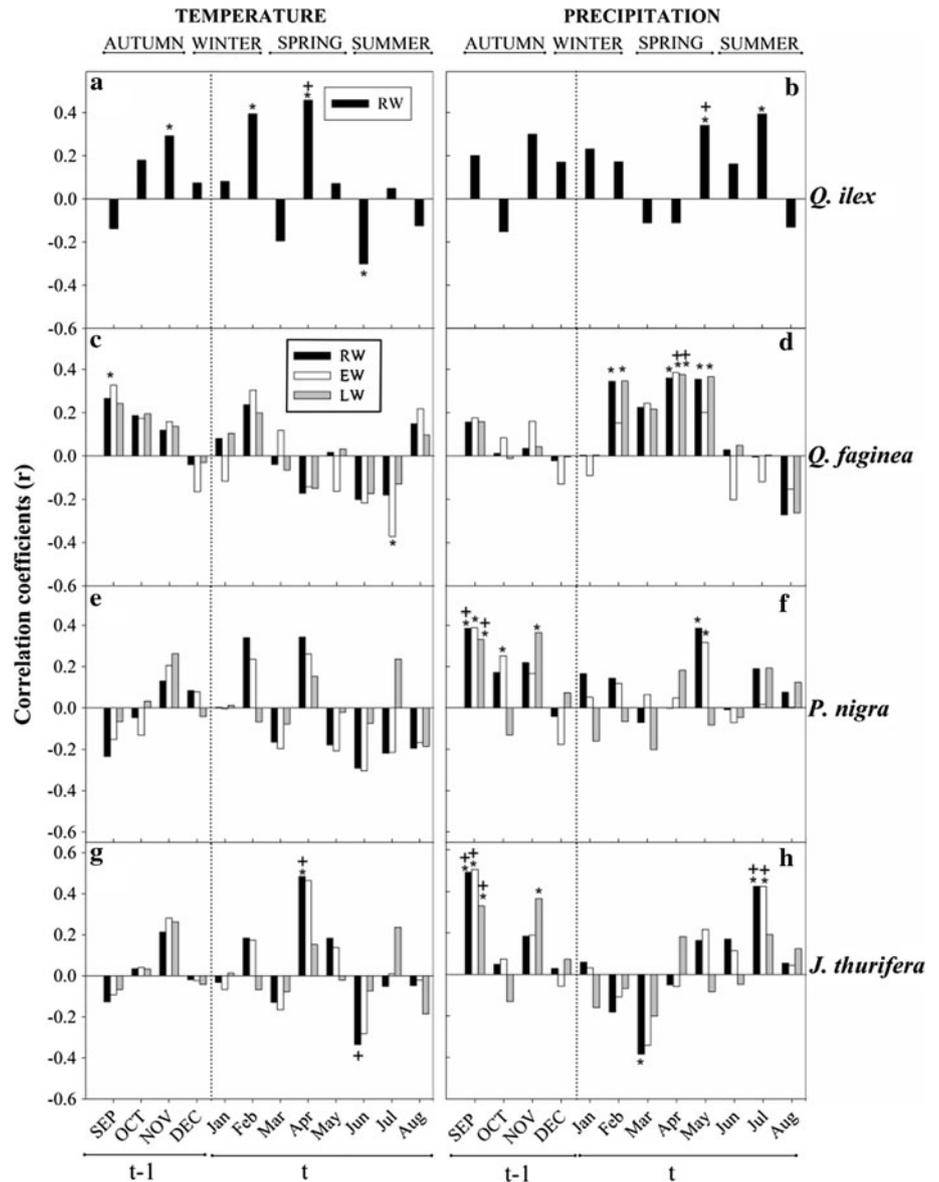
The analyses of the growth responses to selected droughts revealed that *P. nigra* was the species most affected by extreme drought events, showing sharp declines (ca. −40 %) in both earlywood and latewood widths (Fig. 4). Moreover, all the species showed significant growth reductions during the drought events in at least one site (Fig. 4). Two years after the drought events, most species recovered their growth rates at all the sites, being similar to those 2 years before the drought event or even showing higher growth rates (e.g., *P. nigra* in site TA). The evergreen *Q. ilex* only showed growth declines in AR (around 25 % reduction), and its growth recovered the following 2 years after the drought events. The deciduous *Q. faginea* showed the effects of drought only on latewood, and growth rates of this species had not completely recovered 2 years after drought occurrence. The conifers *P. nigra* and *J. thurifera* presented strong reductions of earlywood width (from −15 to −40 % depending on the site). However, their growth levels recovered 2 years after the drought, increasing the growth rates in some cases (Fig. 4). In the case of latewood, *P. nigra* showed the same pattern as earlywood, but in *J. thurifera*, it was barely affected being significant only in one of the sites (RS) with a 10 % mean reduction in width.

Discussion

Growth patterns across species and temporal growth trends

Very low growth rates were found in both *Quercus* species compared to the conifers, which may be a consequence of the higher density and construction costs of their wood and agrees well with previous reports for hardwoods versus softwoods (Hacke and Sperry 2001). While species with faster growth rates are considered to be more competitive than slow-growing ones under mesic conditions, there are many other factors that provide additional competitive advantage in drought-prone forests, favoring coexistence or unexpected displacement of co-occurring species. As an example, Camarero et al. (2010) recently discussed how plastic xylogenesis of *Juniperus thurifera* under distinct climatic conditions could provide an advantage against co-occurring *Pinus* species if water availability decreases. *Quercus faginea* showed a significant decline in basal area increment since the late 1970s, similar to other drought-sensitive tree species in Mediterranean ecosystems (Jump et al. 2006; Linares and Tiscar 2010). On the contrary, *J. thurifera* experienced an enhanced basal area increment through time. While CO₂ fertilization and warmer temperatures are supposed to enhance forest growth in temperate and cold areas, tree growth is expected to decline in

Fig. 3 Relationships between monthly climatic variables (mean temperature, precipitation) and tree-ring (RW, black bars), earlywood (EW, white bars) and latewood (LW, gray bars) width indices for the four species. Pearson correlation coefficients were calculated between the residual chronologies and temperature or precipitation [*Q. ilex* (a, b); *Q. faginea* (c, d); *P. nigra* (e, f); *J. thurifera* (g, h)]. Significant correlation and response function coefficients ($P < 0.05$) are indicated with asterisks and crosses, respectively. Months abbreviated by capital and lower case letters correspond, respectively, to the years before (year $t-1$) and during tree-ring formation (year t)



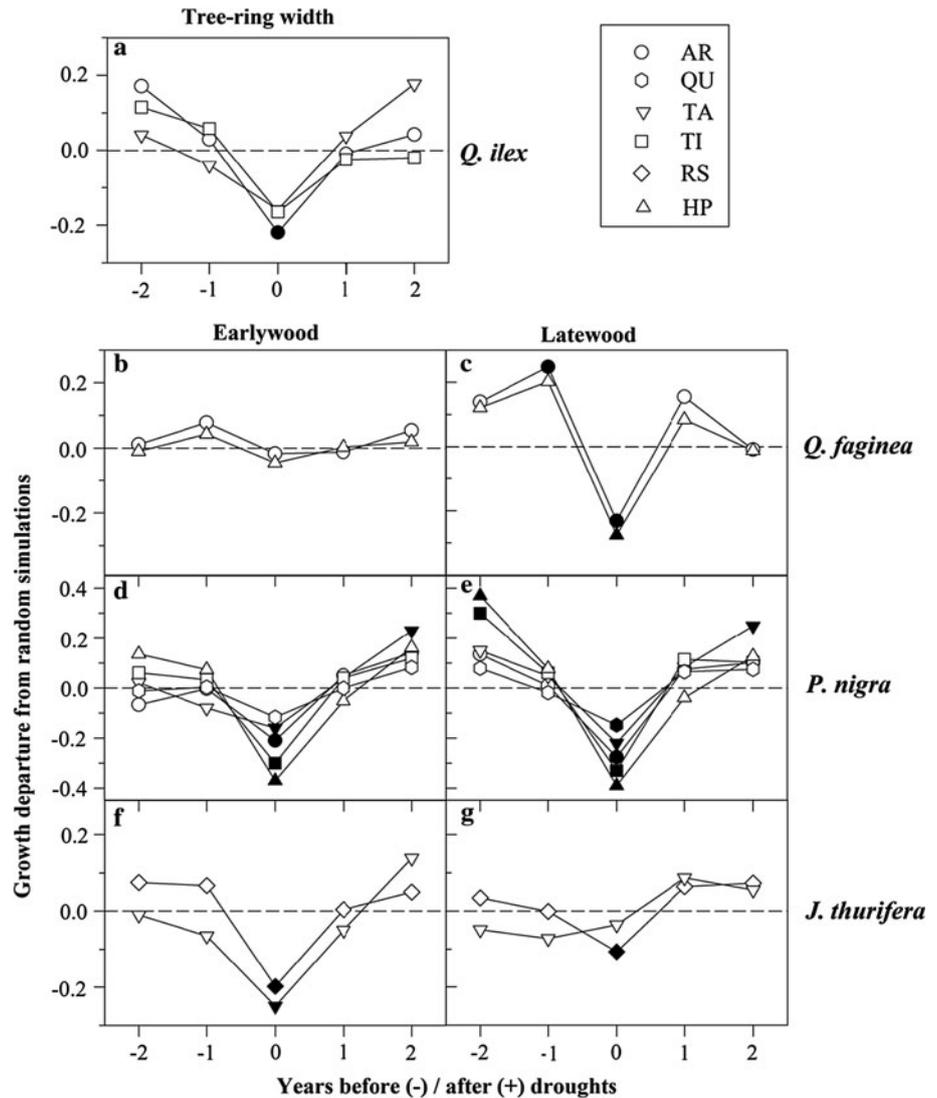
Mediterranean regions due to a lack of compensation between carbon fertilization and drought increase (Linares et al. 2009; Lindner et al. 2010). It is not easy to disentangle climatic from CO₂ fertilization effects on growth. However, positive effects of increasing atmospheric CO₂ concentrations on tree growth have been regarded as a potential driver explaining the rising growth trends in mesic Scots pine forests from north-eastern Spain (Martínez-Vilalta et al. 2008). In our case, the observed increase in growth rates of *J. thurifera* is most likely a joint effect of both the CO₂ fertilization effect (Granda et al. 2013, in press) and warmer temperatures (Gimeno et al. 2012), which matches well with the drought tolerant strategy of *Juniperus* species (Martínez-Ferri et al. 2000). As expected, tree size influenced growth responses (Gómez-Aparicio et al. 2011), but contrary to expectations (Linares et al.

2010; Gómez-Aparicio et al. 2011) competition was not an important factor affecting the growth of the trees studied.

Warm temperatures and changing precipitation: timing matters

The abrupt warming identified since mid 1970s has no precedents and it is mainly due to rises in spring and summer temperatures (Brunet et al. 2009). Our site, located in a Mediterranean continental area, also showed clear signs of warming since 1952, but this was particularly evident for the period 1977–2007. Despite precipitation showing no significant temporal trend, aridity as perceived by trees must have increased due to warming. Furthermore, our results show how all species were positively responding to high precipitations, but species-specific growth was

Fig. 4 Superposed epoch analyses showing positive and negative growth departures for the drought year (year 0) and 2 years before (years -1 and -2) and after the drought (years +1 and +2). The analyses corresponded to ring-width indices in the case of *Q. ilex* (a) and to earlywood and latewood width indices for the rest of species (*Q. faginea*, b and c; *P. nigra*, d and e; *J. thurifera*, f and g). Different symbols indicate different sites (see sampled sites in Table 1). Values were calculated considering four extreme drought years (1981, 1990, 1999, 2005). The black filling denotes a significant ($P < 0.05$) growth departure from random simulations



highly dependent on the timing, that is the month or season when temperature rise and precipitation decrease occur. Our results highlight the different responses of tree growth of coexisting species to seasonal and even monthly climatic oscillations (Sass-Klaassen et al. 2008; Rozas et al. 2009; Linares and Tíscar 2010).

Spring and summer climatic variables are expected to be the most important factors affecting growth in Mediterranean forests. This was true for all species, but we found different species-specific responses. Our results point out that warmer temperatures during spring and an extended growing season due to climate change could enhance growth of the species that were favored by high spring temperatures, namely *Q. ilex* and *J. thurifera* in our study case (see also Corcuera et al. 2004b). Rain during March produced narrow rings in *J. thurifera*, which may be caused by the negative influence of cloud cover on tree growth on this species as shown by Gimeno et al. (2012). Instead, *P.*

nigra and *Q. faginea* positively responded to wet springs but not to warm temperatures. The second species was the one that responded earlier to spring precipitations (April). This is because, as a deciduous species with ring-porous wood, it needs to form a new ring of functional xylem before budburst in order to match its high spring water requirements (Corcuera et al. 2006; Sanz-Pérez et al. 2009). During summer, cambial activity is mainly arrested in most Mediterranean tree species (Cherubini et al. 2003; Camarero et al. 2010). However, species which are able to maintain carbon gain under harsh climatic conditions, such as *Q. ilex* and *J. thurifera* (Salleo and Lo Gullo 1990; Corcuera et al. 2005; Gimeno et al. 2012), may also be able to grow during summer, and thus, may be more affected by climatic conditions during this season. The negative effect of high summer temperatures on earlywood for *Q. faginea* indicates that when summers are very hot, earlywood formation is restricted to a few weeks in spring. Warmer

summers may lead to the formation of a low amount of wide earlywood vessels and, as a result, the risk of drought-induced xylem embolism may diminish (Tyree et al. 1994).

In Mediterranean areas, the timing of precipitation and temperature increase is not only important during the growing season, in fact, winter precipitation had a great positive effect on the growth of the deciduous oak *Q. faginea*, similar to what Corcuera et al. (2004a) found. Surprisingly, it was the latewood, which is mostly formed during summer and autumn, the wood section most sensitive to the amount of late-winter and late-spring precipitation. This finding could be explained by the water uptake from deeper soil layers thanks to the deep roots of this species (Corcuera et al. 2004a), or because of wet winter, and spring conditions enhanced earlywood production, indirectly improving latewood production (Pasho et al. 2012). Besides precipitation, low winter temperatures may cause freezing-induced xylem embolism and reduce hydraulic conductivity then decreasing growth in spring (Sperry et al. 1994; Tyree et al. 1994). We found that the evergreen oak *Q. ilex* was the species most influenced by winter warm temperatures, revealing that the synthesis of photosynthates during winter is important in this species probably to form wood during the following spring as discussed elsewhere (Savé et al. 1999).

The timing of certain climatic episodes does not only refer to seasons within a year, but also to specific years within a decade. Tree-ring formation may be very dependent on the water supply, temperatures and photosynthetic activity in the previous autumn as shown by our results. This relationship was particularly evident in *J. thurifera*, in which the latewood width of the previous year and the tree-ring width of the current one were highly correlated at all sites. As a result, this species might be able to store carbohydrates that can be used to grow the following year, as has been evidenced in other conifers (Kagawa et al. 2006). The other study species showed marked temporal autocorrelation only in the stand with greater water availability, meaning that the influence of previous year growth on the following year is dependent on site conditions. Such site-dependent carryover effect may be a valuable aim for further research because ongoing climate change might be uncoupling these temporal autocorrelations.

Responses to extreme drought events

Our results confirm that severe droughts affect tree growth, but also, and more importantly, that not all species were equally affected and not all of them presented the same recovery rates. The species showing the highest growth rates (*P. nigra*) showed the sharpest growth decline during drought events. Other studies have also revealed this species to be drought sensitive (Martín-Benito et al. 2008;

Linares and Tíscar 2010). However, growth rates recovered 2 years after the drought suggesting that drought-induced growth declines may be rapidly counterbalanced in *P. nigra*. Nevertheless, such recovery capacity could also be severely compromised under a drier scenario with more frequent and severe droughts (Allen et al. 2010). Overall, the latewood growth of *Q. faginea* (highly correlated to tree-ring width) was not completely recovered 2 years after drought. These results agree with other studies on oak species from temperate forests (Orwig and Abrams 1997). Reduced latewood production has very severe consequences for species with ring-porous wood. First, this partially constrains earlywood formation during the following year due to lower stem increment, and, second, it turns them more vulnerable to drought- and frost-induced cavitation, since narrow latewood vessels are responsible for water conductivity when the wider earlywood vessels cavitate (Corcuera et al. 2006).

Therefore, more frequent and severe droughts can have serious consequences for certain Mediterranean tree species, particularly ring-porous species, whose dominance might be reduced and might be eventually replaced by other co-occurring species that recover better after severe drought events. In addition, our results indicate that site differences also play an important role on individual responses to drought. As an example, *Q. ilex* showed a sharp growth decline during drought only in the stand with higher water availability, suggesting that trees may be more vulnerable to drought events when acclimated to humid environments (Martínez-Vilalta et al. 2012).

Conclusions

All dominant tree species in a Mediterranean continental forest (*Quercus ilex*, *Quercus faginea*, *Pinus nigra* and *Juniperus thurifera*) were affected by extreme droughts, being *P. nigra* the species that showed the strongest growth reduction. However, this species was able to recover its growth rates after these events, while the deciduous *Q. faginea*, less affected by extreme droughts, was not able to fully recover after 2 years. Thus, we claim that *Q. faginea*, particularly vulnerable to extreme drought events, will be the most affected by the expected increase in the frequency of intense drought. Not only tree size but also annual precipitation influenced growth of the four co-occurring species, but timing along the year of increased temperature and precipitation had important and contrasting effects on the study species.

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