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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Growth and carbon isotopes of Mediterranean trees reveal contrasting responses to increased carbon dioxide and drought

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Abstract Forest dynamics will depend upon the physiological performance of individual tree species under more stressful conditions caused by climate change. In order to compare the idiosyncratic responses of Mediterranean tree species (*Quercus faginea, Pinus nigra, Juniperus thurifera*) coexisting in forests of central Spain, we evaluated the temporal changes in secondary growth (basal area increment; BAI) and intrinsic water-use efficiency (iWUE) during the last four decades, determined how coexisting species are responding to increases in atmospheric CO_2 concentrations (C_a) and drought stress, and assessed the relationship among iWUE and growth during climatically contrasting years. All species increased their iWUE (ca. +15 to +21 %) between the 1970s and the 2000s. This increase was positively related to C_a for *J. thurifera* and to higher C_a and drought for *Q. faginea* and *P. nigra*. During climatically favourable years the study species either increased or maintained their growth at rising iWUE, suggesting a higher CO_2 uptake. However, during unfavourable climatic years *Q. faginea* and especially *P. nigra* showed sharp declines in growth at enhanced iWUE, likely caused by a reduced stomatal conductance to save water under stressful dry conditions. In contrast, *J. thurifera* showed enhanced growth also during unfavourable years at increased iWUE, denoting a beneficial effect of C_a even under climatically harsh conditions. Our results reveal significant inter-specific differences in growth driven by alternative physiological responses to increasing drought stress. Thus, forest composition in the Mediterranean region might be altered due to contrasting capacities of coexisting tree species to withstand increasingly stressful conditions.

Keywords Climate change · Intrinsic water-use efficiency · Tree rings · Physiological responses · Atmospheric carbon dioxide

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Introduction

The current rise in the atmospheric CO_2 concentration (C_a) is a central driver of climate change, leading to substantial increases in temperature and to an altered annual distribution of rainfall (Robertson et al. 2001). The occurrence of increased C_a in drought-prone environments such as Mediterranean forest ecosystems is expected to drastically affect gas exchange, water use and secondary growth of tree species (Ehleringer and Cerling 1995; Huang et al. 2007). Therefore, it is crucial to study how the new climatic and environmental conditions are already affecting secondary growth through changes in physiological responses of trees growing under natural conditions (Huang et al. 2007) to detect potential impacts on forest composition.

Global vegetation models expect photosynthesis to be enhanced due to a higher C_a uptake, which in turn would lead to a higher synthesis of carbohydrates, further allocated to plant tissues (Norby et al. 1999; Beedlow et al. 2004; Morgan et al. 2004). As a consequence, intrinsic water use efficiency (iWUE; i.e. the ratio of net assimilation to water conductance) and growth are expected to increase (Farquhar et al. 1989; Feng 1999). iWUE can be estimated by measuring stable C isotopes in tree-ring wood or cellulose (McCarroll and Loader 2004). However, very few studies integrate long-term iWUE, climate, C_a and growth records (but see Linares et al. 2009; Silva et al. 2010; Maseyk et al. 2011; Linares and Camarero 2012). Indeed, Peñuelas et al. (2011) compiled 47 studies related to changes in tree-ring iWUE and/or growth from tropical, arid, Mediterranean, wet temperate and boreal regions, and only seven of them had analysed iWUE and growth together. Peñuelas et al. (2011) concluded that the observed increases in C_a and iWUE do not suffice to increase growth, probably because additional factors such as drought stress also underlie the observed growth patterns.

The effects of drought stress on tree physiology and growth are likely to be exacerbated in Mediterranean forests (Lavorel et al. 1998; Lindner et al. 2010; Sarris et al. 2011). These ecosystems are experiencing strong drought events due to temperature increases and altered precipitation during the growing season (Christensen et al. 2007). Predictions suggest that the future climate will be characterized by even greater rises in spring temperatures. This, coupled with decreased rainfall, will induce severe drought stress on tree species, particularly during seasons in which they become very active, acquiring resources for growth and reproduction (Durante et al. 2009).

Contrasting inter-specific growth responses to climate change are often found in Mediterranean forests. A few studies point to enhanced growth as a response to increased C_a (Rathgeber et al. 2000; Koutavas 2008), while others show declining growth trends at increasing C_a or iWUE (Tognetti et al. 2000; Maseyk et al. 2011). These discrepancies may be caused by particular species' strategies in terms of iWUE and growth adjustments, linked to long-term acclimation to either elevated C_a or additional contingent factors (e.g. drought stress) limiting the expected CO_2-induced growth enhancement (Huang et al. 2007; Andreu-Hayles et al. 2011; Levanic et al. 2011; Linares and Camarero 2012). Thus, the impact of climate change on Mediterranean forest composition will be strongly determined by the extent of acclimation responses of each species (Pias et al. 2010). As a result, further studies are needed to provide additional information about the inter-specific ecophysiological responses regulating iWUE and growth at increasingly higher CO_2 levels and at climatically contrasting years in drought-prone ecosystems.

In the present study we used tree-ring width and stable C isotope analysis to evaluate the effects of C_a and drought stress on growth and iWUE for three coexisting tree species (*Quercus faginea*, *Pinus nigra* subsp. *salzmannii* and *Juniperus thurifera*) in continental Mediterranean forests of central Spain. To emphasize the inter-annual changes, we selected contrasting years characterized by climatically favourable and unfavourable conditions for growth during four decades (from the 1970s to 2000s). Our specific goals were (1) to compare temporal changes in secondary growth and iWUE of coexisting tree species during the last four decades, (2) to determine whether and how growth and iWUE of coexisting species are responding to increases in C_a and drought stress, and (3) to assess the relationship among iWUE and growth during climatically contrasting years. To fulfil these aims we have taken into account the interacting effects of the main factors that are causing the observed growth trends, to shed light on the potential underlying physiology related to changes in iWUE. Finally, we discuss the idiosyncratic growth responses of coexisting tree species to climate change and potential future dynamics in Mediterranean forests.

Materials and methods

Study area, climatic data and species

The study area is located in Alto Tajo Natural Park, central Spain (Guadalajara, Castilla-La Mancha). The climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual rainfall is 499 mm and mean annual temperature is 10.2 °C. Climate data (mean monthly temperature and accumulated precipitation for each year) were obtained from the closest station, Molina de Aragón (40°50′40″N, 1°53′07″W, 1,063 m a.s.l., for the 1951–2007 period, data were provided by the Spanish Agencia Estatal de Meteorología), located at ca. 36 km from the study area

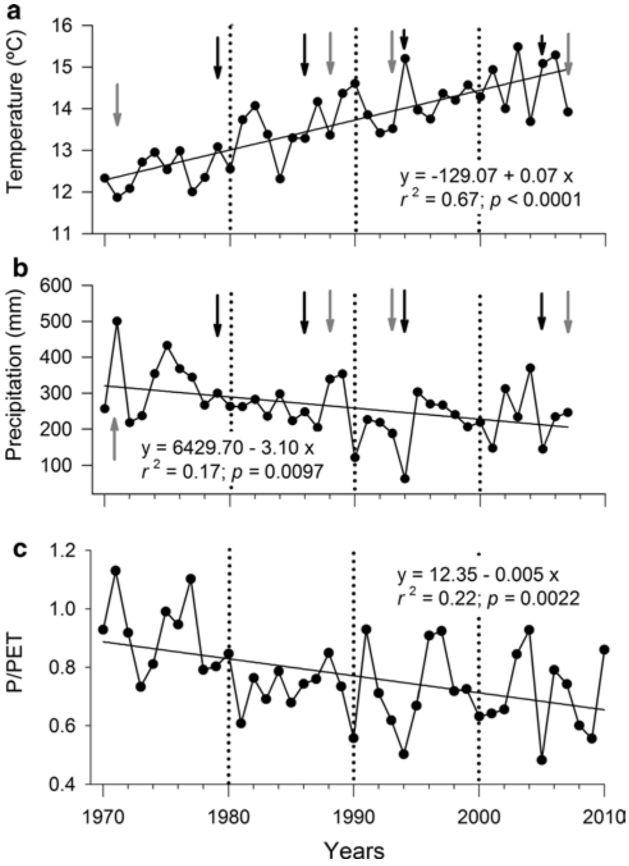

Fig. 1 Temporal evolution during the growing period (spring and summer) of **a** mean temperature (°C), **b** accumulated precipitation (*P*; mm), and **c** drought index [P divided by annual potential evapotranspiration (PET); *P/PET*], used to select climatically contrasting years within each period. *Black arrows* represent the selected climatically unfavourable years and *grey arrows* the selected favourable ones. *Vertical dotted lines* separate each decade. Climate data were obtained from the closest meteorological station, located at ca. 36 km from the study area (Molina de Aragón, 40º50′40″N, 1º53′07″W, 1,063 m a.s.l., 1951–2007 period, data provided by the Spanish Agencia Estatal de Meteorología)

(Fig. 1). A drought index was calculated as precipitation (P) divided by potential evapotranspiration (PET) (P/PET) (following Thornthwaite and Mather 1957) for the study years, where lower values correspond to higher drought stress.

Within the study area, we sampled trees at six sites differing in orientation and elevation to encompass the natural range of microclimatic conditions of continental Mediterranean ecosystems. At each site we randomly chose and sampled mature trees of similar diameter at breast height (DBH; 1.3 m) and age corresponding to the local dominant species: *Quercus faginea* Lam., *Pinus nigra* J.F. Arnold subsp. *salzmannii* (Dunal) Franco and/or *Juniperus thurifera* L. Tree density was obtained from 100-m^2 plots situated at each site [see Electronic supplementary material (ESM), Table S1].

Sampling and dendrochronological procedures

Dendrochronological methods were used to assess changes in stem radial growth. Between January and May 2008 we sampled 15 dominant trees per species and site that showed no symptoms of decline or pathogenic infection. These were tagged, mapped and their DBH was measured. Selected trees were bored at breast height (1.3 m) using a Pressler increment borer. Three complete radii were extracted from each tree and the pith was reached in most of the cores. Two of the radii were used for assessing changes in growth following dendrochronological protocols. These cores were air dried, glued onto wooden mounts and polished using sandpaper of progressively finer grain until tree rings were clearly visible under a binocular microscope. Then, the wood samples were visually cross-dated to check for missing and false rings using the identification of signature years (Stokes and Smiley 1968). Ring widths were measured on a LINTAB measuring device (Rinntech, Heidelberg, Germany) with resolution up to 0.001 mm. Tree-ring cross-dating was checked using the program COFECHA (Holmes 1983). For each tree, measurements from the two cores were averaged as they were considered as replicates. The trend of decreasing ring width with increasing tree size was removed by converting radial increment into basal area increment (BAI) using the formula:

$$\mathrm{BAI} = \pi\left(r_{\mathrm{t}}^{2} - r_{\mathrm{t}-1}^{2}\right), \tag{1}$$

where *r* is the tree radius and *t* is the year of tree-ring formation. The third sampled radius was used for isotope analyses.

Tree-ring isotopes: tree-ring selection, cellulose extraction and isotope analysis

Stable C isotopes in tree rings provide useful estimates of long-term changes in iWUE (McCarroll and Loader 2004). The two stable C isotopes present in the biosphere (^{12}C and ^{13}C) are incorporated in C_3 plants in varying amounts depending on the ratio between the intercellular C (C_i) and the atmospheric C concentrations (C_a). For example, if a drought event occurs, stomatal conductance will decrease relative to the rate of photosynthesis, and the diminished C_i will cause less discrimination against ^{13}C (Farquhar et al. 1989).

For isotope analyses we selected five trees of each species at each site with similar growth trends in the selected years. Within each decade (between the 1970s and the 2000s), we selected two climatically contrasting years using mean temperature and accumulated precipitation during the growing period (spring and summer; Fig. 1): one favourable year (i.e. year within a decade with a combination of high precipitation and low temperatures) and one unfavourable year (i.e. year within a decade with a combination of low precipitation and high temperatures). The selected climatically favourable years corresponded to 1971, 1988, 1993 and 2007; while the unfavourable years were 1979, 1986, 1994 and 2005 (Fig. 1). Tree rings (including earlywood and latewood) were separated manually from the cores using a scalpel under a stereomicroscope. We then proceeded to extract cellulose from 1 mg of wood per individual ring. Cellulose extraction was performed to obtain purified α-cellulose based on a modification of the method of Leavitt and Danzer (1993) for the removal of extractives and lignin, as detailed in Ferrio and Voltas (2005).

Oven-dried α-cellulose was weighed (0.10–0.20 mg) into tin foil capsules and combusted using a Flash EA-1112 elemental analyser interfaced with a Finnigan MAT Delta C isotope ratio mass spectrometer at the Stable Isotope Facility (University of California, Davis, USA). The isotope signature is expressed in the delta notation (δ; C isotope composition) relative to the standard Vienna Pee Dee belemnite (VPDB) (IAEA 1995).

$$\delta^{13}C\ (‰) = \left[\left(\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{standard}}\right) - 1\right] \times 1{,}000, \quad (2)$$

in which R_{sample} and R_{standard} represent the $^{13}C/^{12}C$ ratios of the sample and the VPDB international standard, respectively (Farquhar et al. 1982).

Water-use efficiency

Following Farquhar et al. (1982) we estimated iWUE using the equation:

$$\mathrm{iWUE} = A/g = \mathrm{C_a}\,[1 - (\mathrm{C_i}/\mathrm{C_a})]\ 0.625, \quad (3)$$

where A is the rate of net photosynthesis, g is stomatal conductance to H_2O, C_i is intercellular CO_2 concentration, C_a is the ambient air CO_2 concentration, and 0.625 is the relation among the conductance of H_2O compared to the conductance of CO_2 due to the higher molecular weight of the latter ($0.625\ g_{H_2O} = g_{CO_2}$). To determine C_i, we used the following equation proposed by Francey and Farquhar (1982):

$$C_i = C_a[(\delta^{13}C_{plant} - \delta^{13}C_{atm} + 1)/(b - a)], \quad (4)$$

where $\delta^{13}C_{\mathrm{plant}}$ and $\delta^{13}C_{\mathrm{atm}}$ are the plant and atmospheric C isotope compositions, respectively, a is the diffusion fractionation across the boundary layer and the stomata (+4.4 ‰), and b is the Rubisco enzymatic biologic fractionation (+27.0 ‰). The long-term C_a and atmospheric $\delta^{13}C$ from 1971 to 1994 were obtained from McCarroll and Loader (2004). Additional data (2005 and 2007) for C_a and $\delta^{13}C$ were taken from the Earth System Research Laboratory website (http://www.esrl.noaa.gov/gmd/about/aboutgmd.html).

Statistical analyses

To understand how co-occurring species respond to the observed atmospheric and environmental changes, all the analyses were performed for each separate species (number of tree-ring $\delta^{13}C$ records are $n = 80$ for *Q. faginea*, $n = 155$ for *P. nigra* and $n = 75$ for *J. thurifera*). For BAI, the analyses were performed on log-transformed values to normalize the variable. Linear mixed-effects models (LMMs) were used following Zuur et al. (2007) to assess the influence of model 1) tree size (DBH), tree density, drought stress (P/PET), C_a and their interactions (fixed factors) on growth (BAI) and on iWUE, and model 2) tree size (DBH), year type (climatically favourable or unfavourable), iWUE and their interactions (fixed factors) on BAI (see correlations among variables in ESM, Table S2). The random effects were the individual trees sampled at each site. We built a set of models per species and the model with the best subset of predictors was selected using the Akaike information criterion (AIC) (Burnham and Anderson 2002). Models were fitted based on a restricted maximum likelihood method and these analyses were performed using the nlme package (Pinheiro et al. 2000) in R software (version R2.14.1; R Development Core Team 2011, Vienna).

Results

Changes in climate, BAI and iWUE

Our results indicate a warming trend in the study area for the period 1970–2007 during the growing season (spring–summer), coupled with reduced precipitation in more recent years and, therefore, increased frequency and intensity of dry seasons (Fig. 1). During the whole study period, *P. nigra* showed the highest growth (mean BAI ± SE = 7.17 ± 0.41 $cm^2\ year^{-1}$), while *Q. faginea* presented the lowest BAI values (2.72 ± 0.22 $cm^2\ year^{-1}$) and *J. thurifera* displayed intermediate ones (4.20 ± 0.30 $cm^2\ year^{-1}$; Table 1; Fig. 2). The percentage of change between the 1970 and the 2000s (considering mean values of all years for each decade) for growth of *Q. faginea* was −6.32 %, but BAI increased (+28.9 %) during favourable years and decreased (−27.0 %) during unfavourable ones (Table 1; Fig. 2). In contrast, *P. nigra* showed a slight increase (+8.10 % from the 1970s until the 2000s; Table 1) but, as occurred with *Q. faginea*, growth increased (+80.2 %) during favourable years and decreased during unfavourable ones (−48 %). Growth of *J. thurifera* increased consistently since the 1970s (+57.18 %; Table 1; Fig. 2) both during favourable and unfavourable years (+50.1 and +72.1 %, respectively). The highest values of iWUE were found

Table 1 Mean values (±SE) of basal area increment (*BAI*) and intrinsic water-use efficiency (*iWUE*) for favourable years (1971, 1988, 1993 and 2007), unfavourable years (1979, 1986, 1994 and 2005) and decades (1970s–2000s) for each study species. The percentages of change between extreme decades for the indicated period are also shown for both variables

Type of year	Year	BAI (cm^2 $year^{-1}$)			iWUE (μmol mol^{-1})		
		Quercus faginea	*Pinus nigra*	*Juniperus thurifera*	*Q. faginea*	*P. nigra*	*J. thurifera*
Favourable	1971	2.77 ± 0.41	4.94 ± 0.84	3.73 ± 0.32	83.55 ± 1.49	101.06 ± 1.78	118.39 ± 2.72
	1988	2.89 ± 0.50	9.65 ± 1.13	5.82 ± 0.90	85.33 ± 2.10	108.78 ± 1.87	127.23 ± 1.25
	1993	3.04 ± 0.54	8.02 ± 0.81	5.39 ± 0.69	90.14 ± 1.75	109.68 ± 1.78	132.57 ± 2.59
	2007	3.57 ± 0.60	8.90 ± 1.03	5.60 ± 0.96	99.07 ± 1.79	123.59 ± 2.42	142.04 ± 1.51
	1971–2007	28.9 %	80.2 %	50.1 %	18.6 %	22.3 %	20 %
Unfavourable	1979	2.78 ± 0.21	7.62 ± 0.90	2.09 ± 0.46	86.88 ± 2.07	104.85 ± 1.76	125.75 ± 1.95
	1986	2.51 ± 0.41	6.38 ± 0.71	2.95 ± 0.41	88.11 ± 2.69	112.79 ± 1.60	128.87 ± 1.78
	1994	2.28 ± 0.32	7.58 ± 0.82	4.20 ± 0.51	92.42 ± 1.92	115.08 ± 1.99	133.89 ± 1.79
	2005	2.03 ± 0.31	3.93 ± 0.54	3.61 ± 0.38	103.04 ± 2.21	126.43 ± 2.03	141.50 ± 2.06
	1979–2005	−27 %	−48 %	72 %	19 %	21 %	13 %
Decade	1970s	2.79 ± 0.11	6.76 ± 0.37	2.76 ± 0.14	85.22 ± 1.30	103.06 ± 1.27	123.30 ± 1.79
	2000s	2.61 ± 0.14	7.31 ± 0.34	4.35 ± 0.24	101.05 ± 1.46	125.05 ± 1.56	141.77 ± 1.25
	1970s–2000s	−6.32 %	8.10 %	57.18 %	18.6 %	21.3 %	15 %

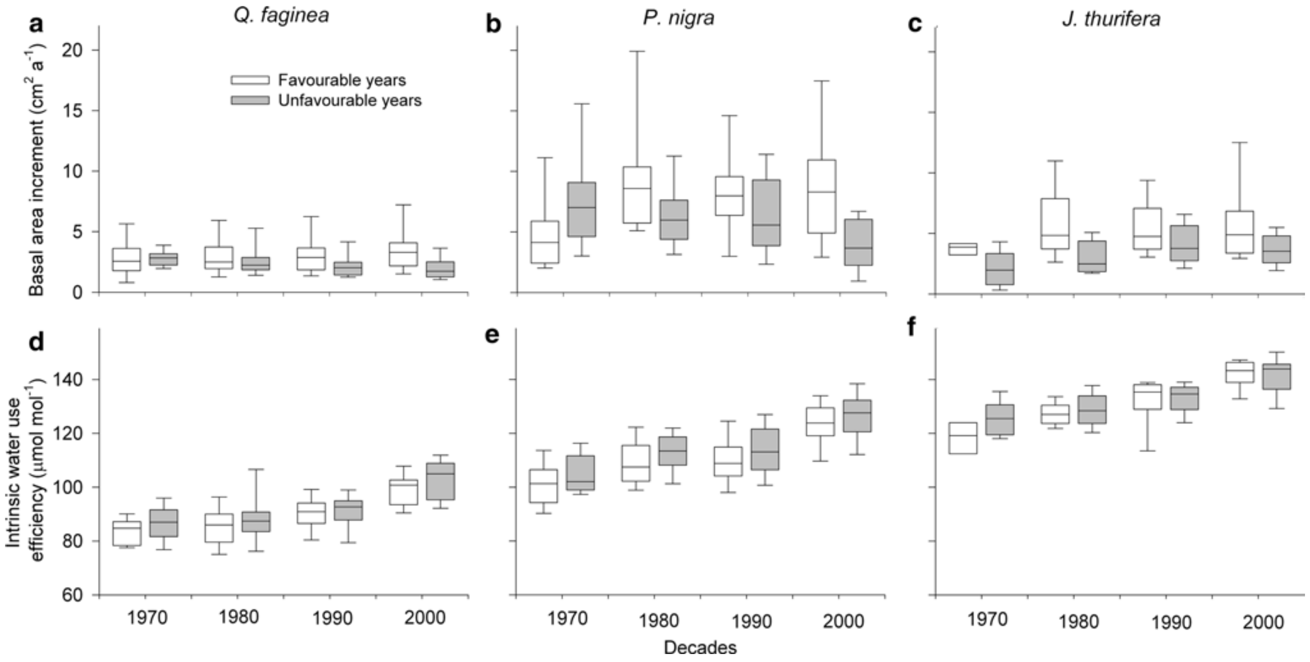

Fig. 2 Responses of basal area increment (BAI; **a–c**) and intrinsic water use efficiency (iWUE; **d–f**) of the study species **a**, **d** *Quercus faginea*, **b**, **e** *Pinus nigra*, and **c**, **f** *Juniperus thurifera* to climatically favourable (*white boxes*) and unfavourable (*grey boxe*s) years during the last four decades (1970s–2000s)

for *J. thurifera* (132.14 ± 1.04 μmol mol^{-1}, mean ± SE), followed by *P. nigra* (112.4 ± 0.91 μmol mol^{-1}) and *Q. faginea* (91.07 ± 0.99 μmol mol^{-1}). All species increased their iWUE from the 1970s to the 2000s (+15.0, +21.3 and +18.6 % for *J. thurifera, P. nigra* and *Q. faginea*, respectively), without strong differences among favourable and unfavourable years (Table 1; Fig. 2).

Effects of tree size, drought stress and C_a on BAI and iWUE

Growth (BAI) of all species significantly increased with tree size (DBH), while tree density had no effect on BAI (Table 2). For both *Q. faginea* and *P. nigra* a significant effect of the interaction among drought stress (P/PET) and

Table 2 Summary of the linear mixed-effects models (LMMs) fitted to explain changes in BAI (log-transformed values) and iWUE of the study species *Q. faginea, P. nigra* and *J. thurifera*

Species	ΔAIC	Fixed effects	Coefficients	SE	*df*	*t*-value	*p*-value
BAI							
Q. faginea	19.96	(Intercept)	2.028	0.777	67	2.609	0.011
		DBH	0.020	0.007	8	2.922	0.019
		P/PET	3.136	0.944	67	−3.322	0.002
		C_a	−0.006	0.002	67	−2.677	0.009
		P/PET × C_a	0.010	0.003	67	3.558	0.001
P. nigra	65.51	(Intercept)	7.202	0.955	132	7.539	<0.0001
		DBH	0.020	0.003	18	6.228	<0.0001
		P/PET	−9.361	1.176	132	−7.960	<0.0001
		C_a	−0.020	0.003	132	−7.417	<0.0001
		P/PET × C_a	0.027	0.003	132	7.983	<0.0001
J. thurifera	18.56	(Intercept)	−1.099	0.381	64	−2.882	0.005
		DBH	0.025	0.007	8	3.866	0.005
		C_a	0.004	0.001	64	3.660	0.001
iWUE							
Q. faginea	80.90	(Intercept)	−153.041	40.073	67	−3.819	<0.0001
		P/PET	185.369	49.310	67	3.759	<0.0001
		C_a	0.701	0.112	67	6.247	<0.0001
		P/PET × C_a	−0.546	0.142	67	−3.846	<0.0001
P. nigra	135.95	(Intercept)	−99.665	40.895	132	−2.437	0.016
		P/PET	90.828	50.647	132	1.793	0.075
		C_a	0.606	0.115	132	5.287	<0.0001
		P/PET × C_a	−0.271	0.146	132	−1.855	0.066
J. thurifera	79.56	(Intercept)	−7.192	11.227	64	−0.641	0.5241
		C_a	0.390	0.031	64	12.496	<0.0001

Fixed effects were diameter at breast height (*DBH*), tree density, drought index as precipitation divided by potential evapotranspiration (*P/PET*, lower values corresponding to more drought stress), atmospheric CO_2 concentration (C_a), and their interaction. Only those factors of the best model obtained by minimizing the Akaike information criterion (AIC) are shown. The ΔAIC (AIC_{null}–AIC_{best}) is shown for each model. Random factors were the trees at each site, being the residual variance for the growth models (logBAI), $\sigma^2 = 0.082$, $\sigma^2 = 0.140$, $\sigma^2 = 0.148$; and for the iWUE models, $\sigma^2 = 4.32$, $\sigma^2 = 6.00$, $\sigma^2 = 4.57$ for *Q. faginea*, *P. nigra* and *J. thurifera*, respectively. Note that a significant interaction reflects that the main effects are not constant but conditional for specific values of the interacting variable and thus, the understanding of the coefficient sign for main effects alone might be misinterpreted (Jaccard and Turrisi 2003); see Electronic supplementary material, Figs. S1, S2 for representation of the interacting effects, P/PET × C_a. For other abbreviations, see Table 1

C_a on growth was found (Table 2): *Q. faginea* growth was enhanced at higher P/PET values (wetter years) coupled with higher C_a, but at high drought stress (P/PET values lower than 0.7) growth was very low irrespective of the C_a (see ESM, Fig. S1a); *P. nigra* growth was maximum at the highest P/PET (lowest drought levels) and C_a, and minimal at high drought stress and C_a, showing intermediate growth values at low C_a irrespective of the drought stress (see ESM, Fig. S1b). *J. thurifera* presented significant increases in BAI at increasing C_a without any response to drought stress (Table 2). As expected, we found significant increases in iWUE at higher C_a for all species (Table 2). While *J. thurifera* iWUE did not respond to drought stress, the influence of the interaction between P/PET and C_a on iWUE was significant for *Q. faginea* and marginally significant ($p = 0.066$) for *P. nigra* (Table 2), iWUE being enhanced at higher C_a and lower P/PET (i.e. higher drought; see ESM, Fig. S2).

Relationships among iWUE and BAI during climatically favourable and unfavourable years

LMMs highlighted contrasting relationships during climatically favourable and unfavourable years among growth (BAI) and iWUE for all species (although marginally significant for *J. thurifera*, $p = 0.087$; Table 3). Models predicted slight increases or growth maintenance at increasing iWUE during favourable climatic years (Fig. 3a–c). In contrast, during unfavourable years *Q. faginea* (Fig. 3a) and especially *P. nigra* showed growth declines (Fig. 3b),

Table 3 Summary of the LMMs fitted to explain changes in log BAI

Species	ΔAIC	Fixed effects	Coefficients	SE	*df*	*t*-value	*p*-value
Q. faginea	20.45	(Intercept)	−0.131	0.2	67	−0.655	0.515
		DBH	0.019	0.007	8	2.826	0.022
		F-U	0.566	0.196	67	2.888	0.005
		iWUE	0.004	0.002	67	2.22	0.03
		F-U × iWUE	−0.007	0.002	67	−3.243	0.002
P. nigra	30.61	(Intercept)	−0.032	0.223	132	−0.145	0.885
		DBH	0.02	0.003	18	5.927	<0.0001
		F-U	0.749	0.261	132	2.867	0.005
		iWUE	0.003	0.002	132	1.911	0.058
		F-U × iWUE	−0.007	0.002	132	−3.133	0.002
J. thurifera	36.28	(Intercept)	0.13	0.336	62	0.389	0.699
		DBH	0.024	0.008	8	3.109	0.015
		F-U	−0.929	0.432	62	−2.152	0.035
		iWUE	0.001	0.002	62	0.658	0.513
		F-U × iWUE	0.006	0.003	62	1.739	0.087

Only those factors of the best model obtained by minimizing the AIC are shown [DBH, favourable and unfavourable years (*F-U*), iWUE]. The ΔAIC (AIC_{null}–AIC_{best}) is shown for each model. Random factors were the trees at each site, being the residual variance, $\sigma^2 = 0.082$, $\sigma^2 = 0.159$, $\sigma^2 = 0.124$ for *Q. faginea*, *P. nigra* and *J. thurifera*, respectively. Note that a significant interaction reflects that the main effects are not constant but conditional for specific values of the interacting variable and thus, the understanding of the coefficient sign for main effects alone might be misinterpreted (Jaccard and Turrisi 2003); see Fig. 3 for representation of the interacting effects, F-U × iWUE. For abbreviations, see Tables 1 and 2

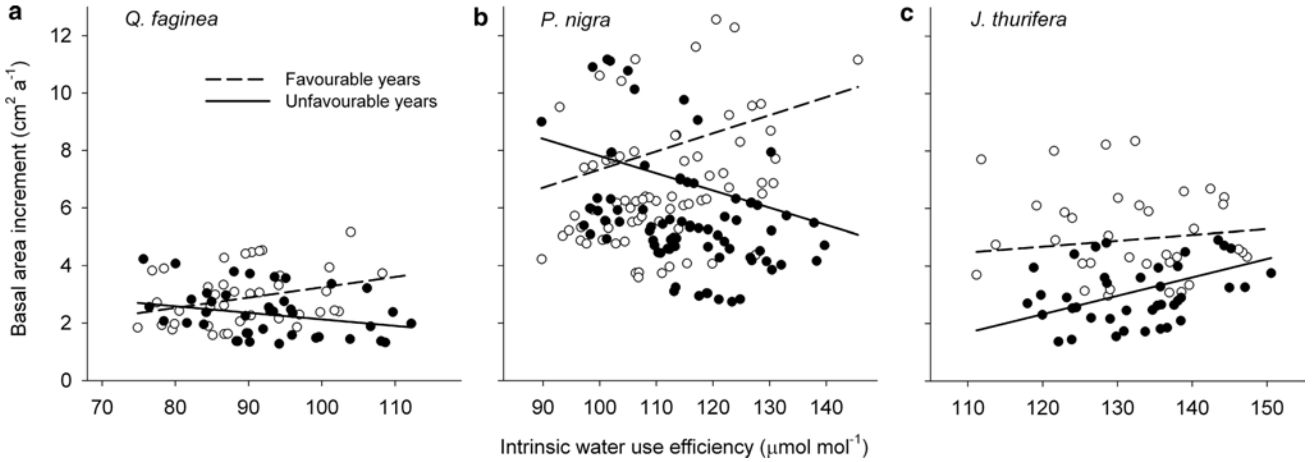

Fig. 3 Relationship between iWUE and growth (BAI) during climatically favourable (*open dots* and *dashed lines*) and unfavourable (*black dots* and *solid lines*) years predicted according to the linear mixed-effects models (reported in Table 3) for **a** *Q. faginea*, **b** *P. nigra* and **c** *J. thurifera*

while *J. thurifera* enhanced its growth (Fig. 3c) at increased iWUE.

Discussion

Contrasting growth and iWUE responses were found over time among the three coexisting species in Mediterranean forests of central Spain. As expected, during climatically favourable years all species increased their BAI (+28, +80 and +50 % for *Q. faginea, P. nigra* and *J. thurifera*, respectively, from the 1970s to the 2000s). In contrast, during unfavourable years *Q. faginea* and *P. nigra* showed sharp growth constraints (−27 % and −48 %, respectively), while *J. thurifera* exhibited an increase of 72 %. These contrasting growth responses suggest that the physiological mechanisms involved under atmospheric and climatic changes are indeed different among species. Moreover, stable C isotopes indicated that the Mediterranean tree species studied have been increasing their iWUE since the 1970s, with *J. thurifera* the species having the highest mean estimates over the study period, followed by *P. nigra* and *Q. faginea*. The high iWUE values for *J. thurifera* could be attributed to a greater overall assimilation capacity of this species, to a better stomatal control of water losses than the other two species, or to a combination of both factors. Although iWUE was higher for *J. thurifera*, the magnitude of the increase over time was slightly lower (+15 % from the 1970s until the 2000s) compared with that for the other two species (ca. +19, +21 % for *Q. faginea* and *P. nigra,* respectively). Since aridity has increased over time in the study area, our results suggest that *J. thurifera* is a more drought-tolerant species compared to *Q. faginea* and *P. nigra,* which showed larger growth reductions and iWUE increases under enhanced drought. Similarly, Ferrio et al. (2003) found that *Pinus halepensis* was more sensitive than *Quercus ilex* to water stress and exhibited faster increases in iWUE. Moreover, Liu et al. (2007) also reported species-specific responses in the long-term trends at semi-arid and arid sites to increased CO_2. In fact, we also need to account for the responses to C_a increases in our study, as they may greatly vary among species (see below).

Our results agree with most studies showing enhanced iWUE during the last decades, likely as a consequence of a physiological effect of increased C_a (Feng 1999; Peñuelas et al. 2008, 2011; Silva et al. 2010; Maseyk et al. 2011; Linares and Camarero 2012; Wang and Feng 2012). However, these studies usually indicate that even though the increase in C_a accounts for a high variation of the iWUE, additional environmental factors might be modulating the observed responses (Peñuelas et al. 2011). These environmental factors commonly include altitude (Peñuelas et al. 2008; Wang and Feng 2012), temperature (Wang and Feng 2012), precipitation (Maseyk et al. 2011) and/or drought (Linares and Camarero 2012). In this regard, our results demonstrate that the three coexisting species are distinctively responding to both C_a and environmental factors. While iWUE and BAI of *J. thurifera* were uniquely sensitive to the increase in C_a, *Q. faginea* and *P. nigra* also responded to drought stress. The latter two species showed the highest growth values at higher C_a and lower drought, while higher iWUE was found at elevated C_a coupled with higher drought. This result denotes that stomatal closure is plausibly being exacerbated by drought stress (Ferrio et al. 2003; Andreu-Hayles et al. 2011) in *Q. faginea* and *P. nigra* to minimize water loss. Further, growth was enhanced at increasing tree size for all species, while iWUE did not show any response to tree size, probably as ring width might be more affected by local factors, and C stable isotopes may contain a wider spatial climatic signal (Andreu et al. 2008). However, age and tree size differences have been also shown to affect $\delta^{13}C$ for some species (e.g. Nock et al. 2011).

Specifically, we found that the study species increased or maintained their BAI values at rising iWUE levels during climatically favourable years. These findings are consistent with an expected growth increase under elevated C_a in the absence of climatic stress, since photosynthesis is stimulated, thus leading to an enhanced CO_2 uptake (Beedlow et al. 2004; Norby et al. 2005). Remarkably, during climatically unfavourable years, *Q. faginea* and especially *P. nigra* exhibited growth declines as iWUE rose. These negative trends in growth are likely caused by a reduced stomatal conductance driven by highly stressful conditions. When stomata close, C gain may be reduced in spite of increasing C_a, dropping the internal concentration of CO_2 and reducing the discrimination against ^{13}C during C fixation (Farquhar et al. 1989). Many studies show similar patterns (Peñuelas et al. 2011): while photosynthetic rates are expected to increase in response to rising C_a, no overall increases in tree growth are usually observed. Possible explanations of such an uncoupling between C_a and growth involve higher drought stress caused by climate change, as shown by our results. But there may be additional factors at play, including nutrient limitation, acclimation to elevated CO_2 and reallocation of carbohydrates to other tissues with higher priority as C sinks than the xylem (Beedlow et al. 2004; Peñuelas et al. 2011). However, our results support the climatic stress hypothesis based on the negative influence of drought on the growth of *P. nigra* and *Q. faginea* and the observed positive effect of drought on iWUE coupled with increased C_a.

In contrast, *J. thurifera* showed enhanced BAI during unfavourable years as iWUE increased. This positive relationship among iWUE and growth under climatically harsh conditions might be attributed to a higher drought tolerance of this species. Certainly, *J. thurifera* may benefit from a CO_2-induced growth enhancement, as has been already reported for other species in the Iberian Peninsula (Martínez-Vilalta et al. 2008), if it maintains or increases its assimilation capacity, tightly regulating water loss through stomata under unfavourable climatic conditions (Gimeno et al. 2012). It is also possible that this species is able to adjust its physiological performance at gradually increasing CO_2, but further research is necessary to support this conclusion. Increased growth at higher iWUE under stressful conditions is rarely shown in the literature because, under these circumstances, increases in iWUE are usually attributed to stomatal closure. Gedalof and Berg (2010) analysed a global tree-ring record to find out if increasing trends in radial growth could be attributed to rising CO_2 concentrations in the atmosphere or to other causes (N deposition, elevation or latitude), and found that 20 % of the sites showed trends that concurred with a stimulation of photosynthesis rates due to rising CO_2.

Collectively, all these results indicate that forest species will show contrasting responses in a climate-change scenario depending on their particular physiological strategies to cope with the increased frequency and intensity of droughts. In accordance with the results here presented, the overall growth of *Q. faginea* and *P. nigra* might be compromised in response to drought stress if the frequency of climatically unfavourable years keeps increasing. Similar responses have been already reported by other authors for these species (Corcuera et al. 2004; Linares and Tíscar 2010) and other Mediterranean *Quercus* and *Pinus* spp. (Gea-Izquierdo et al. 2011; Sarris et al. 2011). However, these results should be interpreted with caution because reduced growth, despite being a reliable proxy for C uptake (McCarroll and Loader 2004), might not imply higher vulnerability. Instead, C may be allocated to root growth or canopy development (Brueggemann et al. 2011) and the species might exhibit ecophysiological adjustments to the new environmental conditions (Klein et al. 2013) if changes in climate are not extremely abrupt (Lloret et al. 2012).

Along with the potential effects of increasing C_a on tree growth and physiological performance, Mediterranean forests are likely to be strongly influenced by interspecies variability in response to both long-term trends in precipitation and temperature and inter- and intra-annual climatic variation (e.g. increased frequency and intensity of extreme events during particular seasons). Our study indicates that the combined analysis of iWUE (inferred from stable C isotope ratios), growth trends (derived from tree-ring records of BAI), C_a and drought impact over time is a powerful approach to disentangle species-specific responses to long-term environmental changes. Nevertheless, this work should be completed with further studies to analyse the differences in growth and iWUE trends among earlywood and latewood, as the factors acting at seasonal scales may vary from those acting at longer timescales (Maseyk et al. 2011; Sarris et al. 2013; Voltas et al. 2013). Moreover, it is interesting to note that the responses of two phylogenetically distant species such as *Q. faginea* and *P. nigra*, corresponding to different functional types (a deciduous broadleaved and a conifer evergreen species), were more similar than the responses of the two conifer species. As a result, xylem anatomy and/or canopy structure did not seem to be determinant for the observed responses. Instead, other physiological traits seem to be involved in such responses, and further studies comparing several coexisting species in a community subjected to similar stresses will enable researchers to test species-specific physiological responses.

Conclusion

Collectively, our results suggest that more frequent events of climatic stress (e.g. drought), despite being coupled with CO_2 increases, will have an overall negative impact on the performance of species like *Q. faginea* and *P. nigra,* which are already experiencing drought-induced growth declines due to, at least to some extent, a reduction of stomatal conductance to prevent water losses. However, other species such as *J. thurifera* may benefit from the rises in CO_2 concentrations due to their capacity to increase C assimilation in spite of intensifying aridity. Moreover, species-specific responses should be taken into account when predicting future forest dynamics under changing climatic conditions. Our results suggest that forest composition in the Mediterranean region might be altered due to both differential physiological responses to climatic changes and contrasting capacities to withstand stressful conditions among coexisting tree species.

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