

Sex and tree rings: Females neither grow less nor are less water-use efficient than males in four dioecious tree species

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ABSTRACT

Females of woody dioecious species usually expend more resources on reproduction than males. Therefore, it is expected that females incur greater costs of reproduction than males, and, as a result, trade-offs between reproduction and growth should emerge. The aim of this study is to test those hypotheses by analyzing the differences between genders regarding radial growth (basal area increment) and wood carbon isotope composition ($\delta^{13}\text{C}$), a proxy of water-use efficiency. We compared these two variables in males and females of four dioecious tree species inhabiting drought-prone Mediterranean sites in Spain (*Pistacia terebinthus*, *Ilex aquifolium*, *Juniperus thurifera* and *Ailanthus altissima*). We analyzed the influence of sex on the radial growth patterns throughout the tree life considering the growth stage of individuals, the differences in the response of genders to climate variables (air temperature, precipitation and drought severity), and the $\delta^{13}\text{C}$ during a severe drought period. One site was studied for each species and 21–33 trees per species were sampled in each site. No differences in growth were found between genders for any of the four species throughout their life span. No significant interactions between gender and precipitation were found, although *A. altissima* males were more responsive to summer (June–July) temperature. No differences in $\delta^{13}\text{C}$ were found between genders excepting for *P. terebinthus*, indicating that the males of this species show a less efficient water use during drought events than the females. These results do not support the broad assumption that females of woody dioecious plants show lower growth and are less water-use efficient than males or that they respond differently to precipitation variability, except for *P. terebinthus* during drought events. Further analyses could be performed in other dioecious species inhabiting seasonally dry regions to confirm or reject our conclusions.

1. Introduction

Dioecious species represent about 6% of the plants in the world (Renner and Ricklefs, 1995). Dioecious plants provide an opportunity for investigating the costs of reproduction and the trade-offs between reproduction and other life-history traits such as growth, maintenance or investments in defense (Cepeda-Cornejo and Dirzo, 2010; Dawson and Geber, 1999). Females of woody dioecious species usually expend more resources on reproduction than males (Delph, 1990; Nicotra, 1999; Obeso, 2002). Differences in growth or performance between genders

can be linked to the seasonal patterns of resources uptake versus investment in reproduction. In this sense, males tend to expend more in flowering –which usually happens early in the growing season– while females expend more in reproductive structures and fruit development –which happens later in the growing season and usually requires a more prolonged investment period (Delph, 1990; Juvany and Munné-Bosch, 2015; Obeso, 2002).

The direct (short-term) cost of reproduction involves the allocation of carbon and nutrients at the time of reproduction. However, field studies do not always detect short-term effects of reproduction on

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growth (Juvany and Munné-Bosch, 2015). Reproducing plants may increase their resource intake and develop other compensatory mechanisms such as photosynthesis of reproductive structures, increase in vegetative meristems or nutrient resorption from senescent structures; and thus in some cases the reproduction cost is only detected in the branches bearing the reproductive structures (Delph, 1990; Obeso, 2002).

On the other hand, the indirect and long-term costs of reproduction include lower rates of vegetative growth, lower performance under stress conditions or increased mortality (Juvany and Munné-Bosch, 2015; Obeso, 2002). At the whole-plant level, the effect of reproduction on the long-term growth of trees may be estimated through measuring tree-ring width, which can be interpreted as a proxy of investment in vegetative growth (Xu et al., 2017). Dendrochronology has been used to analyze indirect costs of reproduction, but also to explore how these costs are influenced by the interaction between sex and climate constraints (Cattaneo et al., 2013; Montesinos et al., 2006; Rovere et al., 2003; Rozas et al., 2019). Females tend to show higher resource acquisition capacity, while males frequently exhibit higher resource use efficiency, which allows them to survive in more stressful periods (Dawson and Geber, 1999; Hultine et al., 2013; Tognetti, 2012). Tree-ring C and O isotope analysis can complement the dendrochronological approach, since water stress influences stomata conductance and photosynthetic rates, thus affecting isotopic fractionation (Battipaglia et al., 2010; Granda et al., 2014). Yet, in some woody dioecious plants a cost of reproduction is detected at lower modular levels, i.e. branches, while not being found at higher modular levels (Bañuelos and Obeso, 2004; Juvany and Munné-Bosch, 2015; Obeso, 2002). It has been proposed that this is related to species-specific degrees of integration at the modular level (i.e. the degree of branch autonomy).

In the Mediterranean region, the information about the effect of sex on growth dynamics of woody species is scarce, despite the fact that woody dioecious are relatively abundant in this region where seasonal water shortage is a major growth constraint (Aronne and Wilcock, 1996). The studies on species such as junipers (e.g., *Juniperus thurifera* L., *Juniperus communis* L.), the common holly (*Ilex aquifolium* L.) and lentisk (*Pistacia lentiscus* L.) hint at either reduced radial growth of females or at higher sensitivity of females to water shortage (Correia and Diaz-Barradas, 2000; Iszkulo et al., 2011; Iszkulo and Boratyński, 2011; Montesinos et al., 2006; Obeso and Retuerto, 2002; Retuerto et al., 2000). However, on *J. thurifera*, *I. aquifolium* and *P. lentiscus* it was also hinted that these effects are context-dependent and contingent on site conditions (Correia and Diaz-Barradas, 2000; Desoto et al., 2016; Iszkulo et al., 2011; Obeso and Retuerto, 2002). Such context-dependent sexually dimorphic growth rates were also observed for other dioecious tree species in Mediterranean areas of South America (Rozas et al., 2019). Mediterranean climate is characterized by the irregularity of precipitation distribution, and summer drought is considered the main constraint to plant development (Cowling et al., 2005; Mitrakos, 1980). This is likely to play a relevant role in the ecology of dioecious trees, since they tend to show gender-specific responses to water shortage, with males generally showing a more conservative water use during drought events (Hultine et al., 2016; Tognetti, 2012). Added to this is the fact that, in many Mediterranean plants, fruits develop during the dry summer, probably incurring more costs on the plant water pools than on carbon reserves (Aronne and Wilcock, 1997; Herrera, 1986).

In this study, we aimed to analyze the effect of sex on the radial growth of four dioecious trees living in Mediterranean Spain: the exotic broadleaf deciduous *Ailanthus altissima* (Mill.) Swingle, the native broadleaf deciduous *Pistacia terebinthus* L., the native broadleaf evergreen *I. aquifolium*, and the native conifer evergreen *J. thurifera*. We also aimed to analyze the differences in the response of genders to climatic factors, particularly to drought stress. For each species, we evaluated: (i) the influence of sex on the radial growth pattern throughout the tree life, (ii) the influence of the interaction between sex and climatic factors on the radial growth pattern throughout the tree life, (iii) the gender-

specific differences on the wood carbon isotope ratio during a severe drought period, and (iv) the gender-specific differences on the correlation between radial growth and drought severity. We hypothesized that females would show lower radial growth, higher responsiveness to variability in precipitation and drought severity, and lower water-use efficiency (lower $\delta^{13}\text{C}$ values).

2. Materials and methods

2.1. Study area and climate data

The study was conducted on four dioecious tree species inhabiting northeastern Spain: the broadleaf deciduous *A. altissima* and *P. terebinthus*, the conifer evergreen *J. thurifera* and the broadleaf evergreen *I. aquifolium* (see Table S1 for their reproductive phenology). We studied one site for species: an *A. altissima* site in Fitero (upper Ebro Depression in Navarra region, 42.1° N, 1.9° W, 450 m a.s.l.), a *J. thurifera* site in Corbalán (southern Iberian System in Teruel province, 40.4° N, 1.0° W, 1300 m a.s.l.), *P. terebinthus* in the Congosto del Entremón site (Pre-Pyrenees in Huesca province, 42.3° N, 0.2° E, 500 m a.s.l.), and *I. aquifolium* in the Garagüeta site (northern Iberian System in Soria province, 42.0° N, 2.5° W, 1500 m a.s.l.) (Fig. 1). The climate of the sites is continental Mediterranean in all cases, with the *A. altissima* and *J. thurifera* sites being much drier than the *I. aquifolium* and *P. terebinthus* sites, and the *A. altissima* and *P. terebinthus* sites being much warmer than the *I. aquifolium* and *J. thurifera* sites (Table 1, Fig. S1). *Ailanthus altissima* grows spontaneously in Spain as an invasive species, whereas the remaining three species are native and their sites are situated within the core area of each species in Spain (Castroviejo, 2012).

Monthly values of mean minimum temperature, mean maximum temperature and precipitation for each study site were retrieved at 0.25° (ca. 27.5 km) spatial resolution from the gridded E-OBS dataset v. 17 for the 1950–2015 period (Haylock et al., 2008). Values of the Standardized Precipitation and Evapotranspiration Index (SPEI) were used as an estimate of drought severity (Vicente-Serrano et al., 2010). Taking into account that summer is the most limiting period for plant growth in the Mediterranean region, we retrieved the 3-, 6-, 9- and 12-month long August SPEI indices (the 3-month long SPEI encompassing the June–August period, and the 12-month long SPEI encompassing the September–August period) from a 1.1 km²-gridded Spanish dataset for the 1961–2020 (Vicente-Serrano et al., 2017b).

2.2. Dendrochronological methods and analysis

For each site, we selected 21–33 adult, healthy individuals of the target species (Table 1). The gender of each tree was ascertained by closely inspecting the inflorescence structures during the fruiting peak in late summer and early autumn. The trees were sampled through taking wood discs (*P. terebinthus*, *I. aquifolium*) or cores (*A. altissima*, *J. thurifera*) sampled at 0.7–1.3 m using hand saw or 5-mm increment borers, respectively. Wood samples were sanded until tree rings were clearly visible and then visually cross-dated (Fritts, 2001). Once dated, tree-ring widths were measured to the nearest 0.01 mm along two radii per tree using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). The accuracy of visual cross-dating was checked with the program COFECHA (Holmes, 1983). The annual radial growth of an individual was expressed as the basal area increment (BAI, i.e. annual tree-ring area), calculated from annual tree-ring widths from pith to bark using the *bai.in* function of the package dplR (Bunn et al., 2020) in the R environment (R Core Team, 2020). The age of each tree ring was expressed as its cambial age (number of growth rings from the pith). For each tree ring, the basal area of the tree prior to the ring growth (BA), i.e. the cross-sectional area of the tree stem before its annual growth, was also calculated. Tree age and BA were used as proxies for the growth stage or ontogeny of the individual in the statistical analysis.

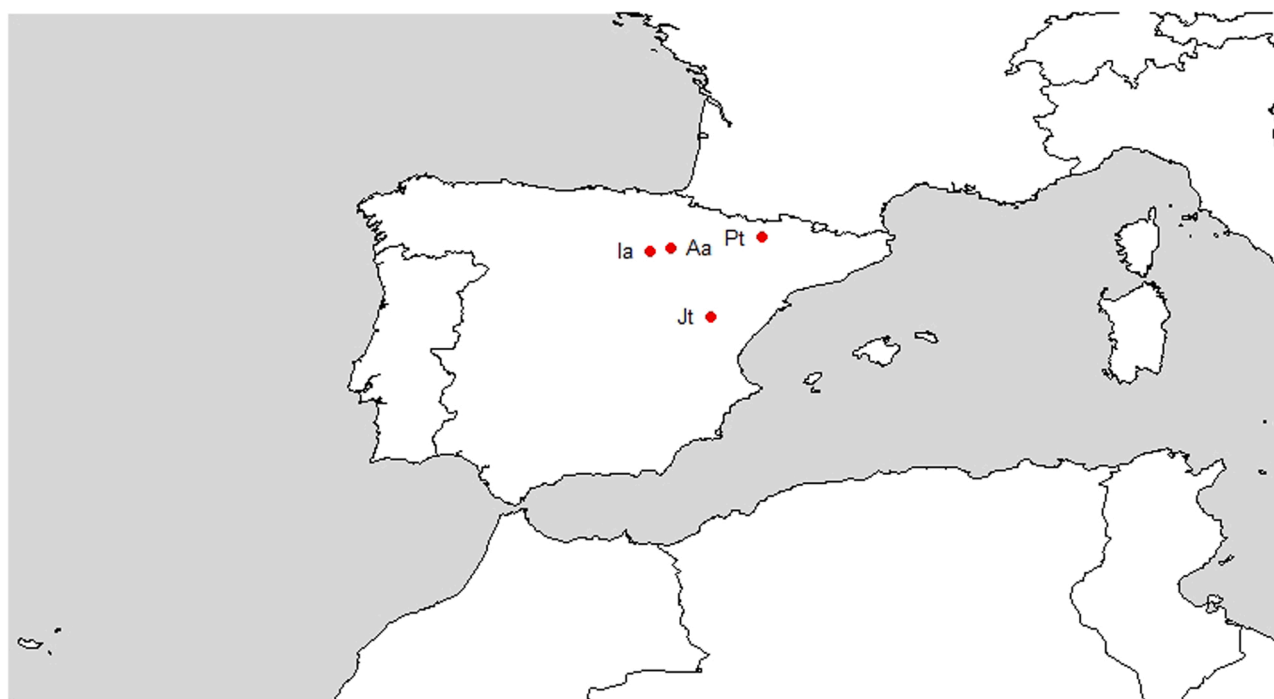


Fig. 1. Geographical distribution of the studied sites in Spain (Aa: *Ailanthus altissima*, Jt: *Juniperus thurifera*, Pt: *Pistacia terebinthus*, Ia: *Ilex aquifolium*).

Table 1

Geographical characteristics and dendrochronological statistics of the studied stands. For tree-ring width, annual average value and standard deviation are shown.

Species	<i>A. altissima</i>	<i>J. thurifera</i>	<i>P. terebinthus</i>	<i>I. aquifolium</i>
Mean annual temperature (°C)	13.4	10.6	13.6	8.2
Mean annual rainfall (mm)	385	416	1045	837
No female individuals (No radii)	11 (22)	17 (34)	15 (30)	16 (32)
No male individuals (No radii)	10 (20)	16 (32)	7 (14)	17 (34)
Timespan	1966–2013	1938–2015	1948–2006	1896–1997
Best-replicated timespan	1997–2013	1968–2015	1985–2006	1955–1997
Basal area at sampling (cm ²)				
Females	26–603	51–262	6–116	42–554
Males	58–401	60–211	9–106	18–569
Age at sampling ^a (years)				
Females	7–48	44–71	9–59	41–91
Males	7–47	34–78	13–58	39–102
Tree-ring width (mm)	3.55 (2.55)	1.07 (0.66)	1.14 (0.96)	1.00 (0.75)
Mean correlation with site series	0.32	0.54	0.53	0.50
Expressed Population Signal of the best-replicated timespan	0.76	0.95	0.93	0.91

^a Cambial age at a height of 1.3 m

We performed Pearson correlations between radial growth and climatic variables to discern the most relevant climatic factors. For each species and gender, the individual ring-width or BAI series were standardized and detrended by applying a cubic-smoothing spline curve, with the detrend function of the R package dplR. Then, the individual

detrended series were averaged for each site and gender using bi-weight robust means to obtain mean series of detrended BAI or ring-width indices (Fritts, 2001). Mean series of detrended BAI or tree-ring width indices were correlated against monthly values of mean minimum and maximum temperatures and precipitation, using Pearson correlation coefficients on a 14-month window from September of the year before tree growth until October of the year of tree-ring formation.

2.3. Isotope analysis

The 2002–2006 period was selected for isotope analysis, because during these years northeastern Spain was affected by a major drought (the mean 12-month August SPEI in 2002–2006 was -0.68 , with a minimum value of -1.66 in 2005). Due to the lack of tree-ring samples of *I. aquifolium* for the 2002–2006 period, for this species the 1992–1996 period was selected instead (the mean 12-month August SPEI value was -0.17 ; with a minimum value of -1.08 in 1994). These droughts negatively impacted tree growth in that region (Gazol et al., 2018).

We obtained wood samples from five mature individuals of each gender with similar ages, except in the case of *A. altissima* for which only three samples per gender were available. For each tree, the rings of all the years of the studied dry period were pooled. Wood samples were carefully homogenized and milled to a fine powder using a ball mixer mill (Retsch MM301, Haan, Germany). Wood samples were used for $\delta^{13}\text{C}$ analyses as studies comparing whole wood and cellulose show similar water-use efficiency trends (Saurer et al., 2004). Wood aliquots (0.001 g) were weighed on a microbalance (AX205 Mettler Toledo, OH, USA) into tin foil capsules and combusted to CO_2 using a Flash EA-1112 elemental analyser interfaced with a Finnigan MAT Delta C isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., MA, USA). Isotope analyses were conducted at the Stable Isotope Facility of the University of California at Davis (USA). Stable isotope ratios were expressed as per mil deviations using the δ notation relative to Vienna Pee Dee Belemnite (VPDB). The standard deviation for repeated analyses was better than 0.1‰.

The gender-specific differences in $\delta^{13}\text{C}$ were assessed with an analysis of variance. The assumptions of normal distribution and constant variance were tested, and a Kruskal-Wallis test was used instead when

the normality assumption was not met. The correlations between radial growth and SPEI indices were explored for each species and gender, using the mean series of detrended BAI at the site and sex level. Mean series of detrended BAI were correlated against several SPEI indices using Pearson correlation coefficients.

2.4. Generalised additive mixed models (GAMMs)

GAMMs were used to compare radial growth (BAI) in male and female individuals throughout the tree life, including a random effect for the “tree” variable to model tree-specific intercepts. Firstly, we assessed which was the best proxy for the growth stage or ontogeny of individuals: (i) cambial age of the growth ring, or (ii) tree basal area (BA). Two GAMMs were built and the one with the lowest Akaike information criterion (AIC) was selected. A third GAMM using the calendar year of the radial growth as a predictor was also built as a reference base, but it did not yield the lowest AIC in any case. Then at a second step, we included an autoregressive moving-average (ARMA) correlation structure for the random effect. In such models the notation ARMA(p , q) describes a model with p autoregressive terms and q moving-average terms. We assessed which correlation structure best accounted for the auto-correlation and partial auto-correlation of the radial growth with the plots of auto-correlation function (ACF) and partial autocorrelation function (PACF) of the GAMM residuals. Finally, the most relevant climatic factors were included in the GAMM. These were selected based on exploratory correlation analyses relating climatic variables with detrended BAI (Fig. S2) and ring-width indices (Fig. S3). Both the interaction between gender and the proxy for the growth stage (i.e. cambial age or BA) and the interaction between gender and climatic factors were included in the model (with cubic regression splines), to evaluate whether females and males behave differently. All the models were evaluated using the AIC criterion, selecting the best model for each species/site. The assumptions of normal distribution, constant variance and temporal independence were tested in the final model, and the presence of concurvity was examined. In the four species/sites, the BAI was arcsine-transformed to meet the model assumptions. In assessing the effect of BA/age on radial growth, only the BA/age range for which at least three individuals are available is presented, to avoid misleading extrapolations. The analysis was conducted with the package mgcv in R (Wood, 2011), using a 0.05 threshold for statistical significance.

3. Results

For the *A. altissima* stand, the BAI of the individuals was significantly affected by their age, both for females and males (Table 2). The individual BAI of both genders rapidly increased to reach its maximum at cambial age 7–8, and then slightly declined (Fig. 2b). The GAMM did not show significant differences in annual BAI between genders throughout the shared cambial age range (0–26 years old). Among the analyzed climatic factors, only the mean maximum temperature of June–July decreased the AIC (Figs. S2–S3, Table S2). This variable did not show any significant relationship with the BAI of female individuals, but it showed a significant and negative relationship with the BAI of male individuals for the 24–28 °C range (Table 2, Fig. 2c). The GAMMs met the assumptions of constant residual variance (Fig. S4a), normal distribution (Fig. S4b–c) and temporal independence (Fig. S4d). The predictors showed worst-case concurvities between 0.67 and 0.77, with all the pairwise values of worst-case concurvity being lower than 0.60 (Table S3).

For the *J. thurifera* stand, the BAI of the individuals was significantly affected by their BA, both for females and males (Table 2). The individual BAI of both genders rapidly increased up to BA values of 60 cm². From that moment, the individual BAI of both genders remained relatively stable with slight oscillations (Fig. 2e). The GAMM did not show significant differences in annual BAI between genders throughout the shared BA range (0–116 cm²). Among the analyzed climatic factors,

Table 2

Summary of the best-fitted Generalised additive mixed models (GAMMs) on annual BAI of female and male individuals in the four analyzed stands. The correlation structure that best accounted for the auto-correlation and partial auto-correlation of the radial growth was ARMA(2, 1) for *A. altissima*, ARMA(1, 1) for *J. thurifera* and *P. terebinthus*, and ARMA(3, 1) for *I. aquifolium*. WSE: within-subject effect, edf: estimated degrees of freedom.

Tree species	Source of variation	edf	F	P	R ²
<i>A. altissima</i>	Age (females)	8.4	8.4	< 0.001	0.598
	Age (males)	7.2	6.3	< 0.001	
	Max. temp. June–July (females)	0.1	0.1	0.54	
	Max. temp. June–July (males)	2.2	1.2	< 0.001	
	Tree (WSE)	1.6	4.1	< 0.001	
<i>J. thurifera</i>	BA (females)	5.9	24.6	< 0.001	0.547
	BA (males)	5.2	14.2	< 0.001	
	Min. temp. February (females)	3.9	5.2	< 0.001	
	Min. temp. February (males)	4.1	4.7	< 0.001	
	Precipitation May–July (females)	2.5	3.4	< 0.001	
	Precipitation May–July (males)	1.3	1.0	< 0.001	
	Tree (WSE)	18.3	1.2	< 0.001	
	Tree (WSE)	18.3	1.2	< 0.001	
<i>P. terebinthus</i>	BA (females)	11.3	17.5	< 0.001	0.767
	BA (males)	7.6	6.6	< 0.001	
	Min. temp. January–June (females)	2.4	0.9	0.004	
	Min. temp. January–June (males)	2.5	1.4	< 0.001	
	Precipitation April–June (females)	3.9	4.1	< 0.001	
	Precipitation April–June (males)	1.6	2.7	< 0.001	
	Tree (WSE)	10.5	1.0	0.008	
<i>I. aquifolium</i>	BA (females)	10.1	5.1	< 0.001	0.646
	BA (males)	9.5	10.2	< 0.001	
	Tree (WSE)	16.5	0.9	0.005	

both the mean minimum temperature of February and May–July precipitation decreased the AIC (Figs. S2–S3, Table S4). Both variables showed a significant and positive relationship with the annual BAI of female and male individuals (Table 2, Fig. 2f–g). The GAMM did not show significant differences between genders in the relationship between climatic factors and BAI (Fig. 2f–g). The GAMM met the assumptions of constant residual variance (Fig. S5a), normal distribution (Fig. S5b–c) and temporal independence (Fig. S5d). The predictors showed worst-case concurvities between 0.53 and 0.60, with all the pairwise values of worst-case concurvity being lower than 0.57 (Table S5).

For the *P. terebinthus* stand, the BAI of the individuals was significantly affected by their BA, both for females and males (Table 2). The individual BAI of both genders steadily increased throughout the analyzed range of BA (Fig. 2i). The GAMM did not show significant differences in BAI between genders throughout the shared BA range (0–81 cm²). Among the analyzed climatic factors, both the mean minimum temperature of January–June and April–June precipitation decreased the AIC (Figs. S2–S3, Table S6). Both climatic variables showed a significant and positive relationship with female and male individuals, restricted to the 3.5–5.5 °C range in the case of January–June temperature (Table 2, Fig. 2j–k). The GAMM did not show significant differences between genders in the relationship between climatic factors and BAI (Fig. 2j–k). The GAMM met the assumptions of constant residual variance (Fig. S6a), normal distribution (Fig. S6b–c) and temporal independence (Fig. S6d). The predictors showed worst-case concurvities between 0.64 and 0.74, with all the pairwise values of worst-case

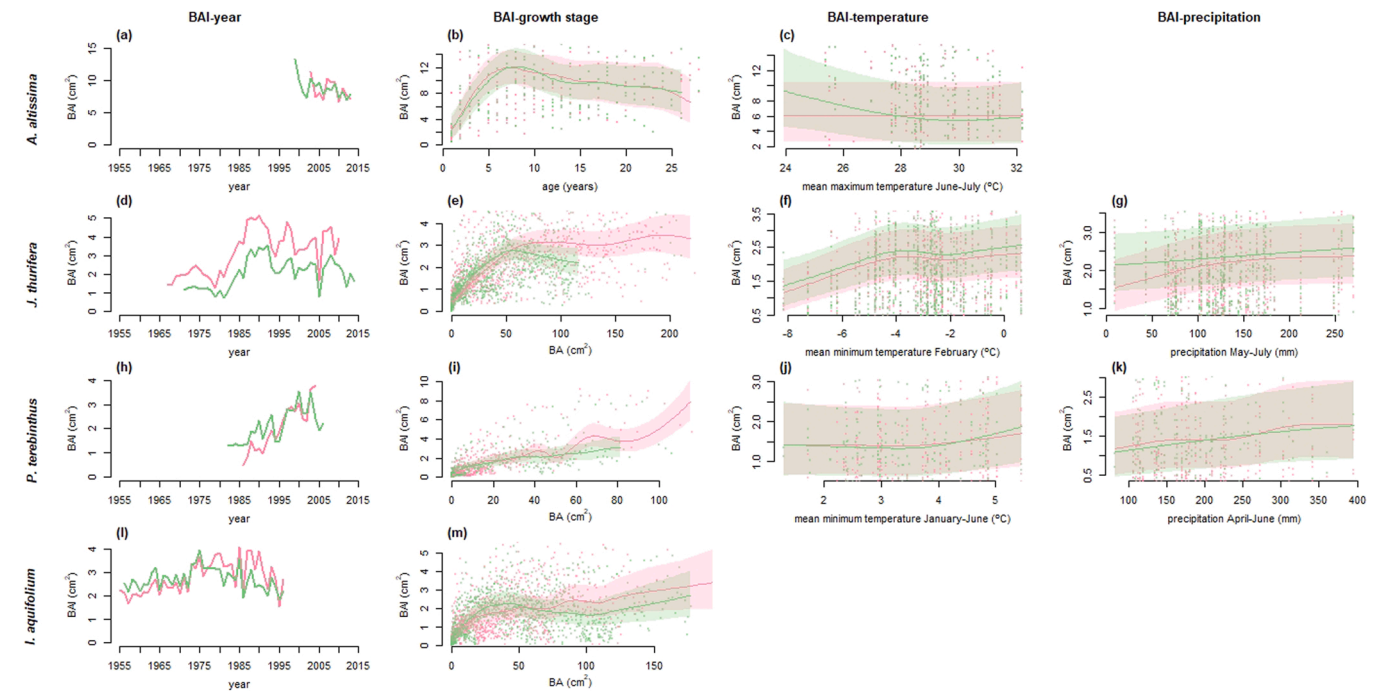


Fig. 2. Basal area increment (BAI) of female (pink lines and symbols) and male (green lines and symbols) trees of *A. altissima* (a-c), *J. thurifera* (d-g), *P. terebinthus* (h-k) and *I. aquifolium* (l-m) in the four study sites. Mean annual BAI for female and male trees during the corresponding study periods (a, d, h, l). Relationship of the BAI with the basal area prior to ring growth (BA) (with the cambial age in the case of *A. altissima*) (b, e, i, m) as predicted by the GAMMs summarized in Table 2 (fitted relationship and 95% confidence band, with points depicting raw observations). Relationships of the BAI with climatic variables (c, f, g, j, k) as predicted by the GAMMs.

concurrency being lower than 0.67 (Table S7).

For the *I. aquifolium* stand, the BAI of the trees was significantly affected by their BA, both for females and males (Table 2). The BAI of both genders rapidly increased up to BA values of 40 cm². From that moment, the individual BAI of both genders remained stable or slightly increasing (Fig. 2 m). The GAMM did not show significant differences in BAI between genders for the shared BA range (0–177 cm²). None of the tested climatic factors decreased the AIC, despite the fact that some of these factors showed a significant correlation with the stand-level BAI and ring-width indices (e.g. mean minimum temperatures of previous October, mean maximum temperature of current April, precipitation of current June-July, Figs. S2-S3, Table S8). Again, the GAMM met the assumptions of constant residual variance (Fig. S7a), normal distribution (Fig. S7b-c) and temporal independence (Fig. S7d). The predictors showed worst-case concurrencies between 0.44 and 0.54, with all the pairwise values of worst-case concurrency being lower than 0.50 (Table S9).

The wood $\delta^{13}\text{C}$ values for the selected dry period did not show significant differences between genders for *A. altissima*, *J. thurifera* or *I. aquifolium*. For *P. terebinthus*, the $\delta^{13}\text{C}$ values of wood were significantly lower for males than for females (Table 3).

Table 3
Values and statistics (*F*, *P*) of analyses of variance on $\delta^{13}\text{C}$ values (in ‰) for female and male individuals in the four analyzed stands and species. Mean values and standard deviations in parentheses (n = 10 individuals for *I. aquifolium*, *J. thurifera* and *P. terebinthus*, n = 6 individuals for *A. altissima*).

Species	Period	Females	Males	F	P
<i>A. altissima</i>	2002–2006	-24.7 (0.1)	-25.3 (1.3)	0.8	0.42
<i>J. thurifera</i>	2002–2006	-23.7 (0.4)	-23.5 (0.4)	1.3 ^a	0.25
<i>P. terebinthus</i>	2002–2006	-25.5 (1.0)	-28.4 (2.0)	8.7	0.02
<i>I. aquifolium</i>	1992–1996	-25.5 (1.3)	-25.1 (0.5)	0.4	0.55

^a In this case the Kruskal-Wallis test was used instead of an ANOVA due to non-normality. The chi-square instead of the *F* value is presented.

Detrended values of BAI at the site level positively and significantly correlated with some of the calculated August SPEI drought indices of males and females of *J. thurifera*, *P. terebinthus* and *I. aquifolium*. In the case of *J. thurifera* and *P. terebinthus*, the highest correlation was found with the 12-month long SPEI (i.e. SPEI for the September-August period) for both genders. In the case of *I. aquifolium*, the highest correlation was found with the 6-month long SPEI (i.e. SPEI for the March-August period) for both genders. By contrast, *A. altissima* showed contrasting gender patterns: while male BAI showed a significant and positive correlation with 9- and 12-month long SPEI, females did not show any significant correlation (Fig. 3).

4. Discussion

Our findings did not support the hypothesis that females show lower radial growth than males for any of the study species and sites. No differences were found for any moment through tree life. The hypothesis that females would show higher responsiveness to variability in precipitation and drought severity was not supported either. Finally, the hypothesis that females would show a less conservative water use during droughts was neither supported. In fact, we found significant differences for *P. terebinthus*, but were opposed to expectations since they indicated lower water-use efficiency in males. Physiological differences between genders are usually magnified under stressful conditions, with males generally being more drought-tolerant and showing higher water-use efficiency (Chen et al., 2010; Dawson and Ehleringer, 1993; Xu et al., 2008). Yet, in our study, three out of the four species did not show differences in isotope ratios during the drought period, and the differences between *P. terebinthus* females and males did not translate into significant radial growth differences. Our results for *P. terebinthus* agree with those of Correia and Diaz-Barradas (2000) for *P. lentiscus* indicating that females had a higher water-use efficiency under water stress conditions, but are not in line with those of Zahoueh (1991) showing that females suffer more stress than males from lower water availability.

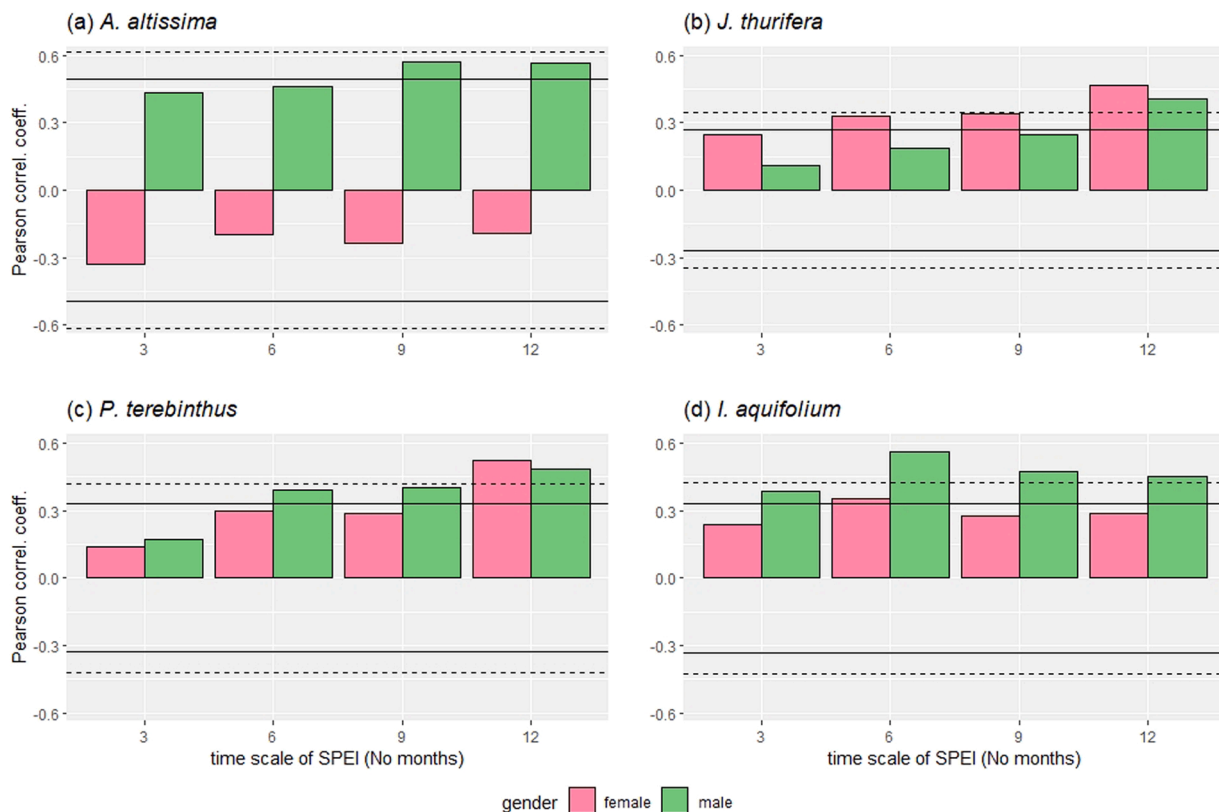


Fig. 3. Pearson correlation coefficients between detrended values of the basal area increment (BAI) calculated at the site and sex levels and August SPEI drought indices calculated for 3–12 month long periods (x axes), for the four studied sites ($n = 16$ years for *A. altissima*, $n = 54$ years for *J. thurifera*, $n = 36$ years for *P. terebinthus*, and $n = 35$ years for *I. aquifolium*). Horizontal solid lines represent $P = 0.05$ significance level, and dashed lines represent $P = 0.01$.

Perhaps, *P. lentiscus* males are more able to extract deep water sources and prevent water loss through stomata, whilst females show a more efficient water use to enlarge fruits during summer when drought stress peaks (Montserrat-Martí and Pérez-Rontomé, 2002). Albeit we did not find long-term differences in growth, mast years could lead to short-term differences in growth between males and females as suggested the higher coefficient of variation in BAI of females found in all species excepting *I. aquifolium* (results not presented).

In contrast to our results, other studies on woody dioecious species found that females have lower vegetative growth or increased susceptibility to water stress, and they linked differences with reproduction costs (Bañuelos and Obeso, 2004; Cedro and Iszkulo, 2011; Dawson et al., 2004; Gao et al., 2010; Rozas et al., 2019; Xu et al., 2008). Our results apparently contradict those previously reported for *I. aquifolium* and *J. thurifera*. For *I. aquifolium*, Retuerto et al. (2000) and Obeso and Retuerto (2002) reported that males showed higher water-use efficiency, with females showing higher radial growth in the pre-reproductive stage and males in adult trees. For *J. thurifera*, Montesinos-Torres (2006) reported that adult females had lower radial growth than males, whereas Rozas et al. (2009) hypothesized that females have lower water-use efficiency. In both species, as well as in *P. terebinthus*, females expend more resources in reproduction than males (Montesinos-Torres, 2007; Obeso and Retuerto, 2002; Zahoueh, 1991). A higher reproductive effort of females is expected to be associated with lower vegetative growth or less conservative water use (Juvany and Munné-Bosch, 2015). However, our results suggest that females are able to mitigate or compensate the negative effects of the reproduction costs throughout the growing season. For *I. aquifolium*, Obeso and Retuerto (2002) reported some compensatory mechanisms, such as increased photosynthesis in non-fruiting branches. They also found that branches have an important degree of autonomy for resource allocation, which may make it difficult to detect costs at the whole-plant level. For

J. thurifera, Montesinos-Torres (2007) indicated that during non-masting years, females showed higher photosynthetic rates than males. Finally, context-dependent sexually dimorphic growth rates could be an additional non-controlled variable that adds complexity to this question and could explain the lack of differences in growth between genders in some cases. These responses would be contingent on site conditions and occur if females outperform males under favorable (e.g., wet years or sites) conditions, whereas males outperform females under unfavorable (e.g., dry years or sites) conditions (Nuñez et al., 2008). In this sense, Desoto et al. (2016) found a better performance of *J. thurifera* females in terms of earlywood growth and starch accumulation under favorable conditions. In other species forming distinguishable earlywood and latewood such as *A. altissima*, *P. terebinthus*, *P. lentiscus* or *J. thurifera* it would be interesting to measure the two wood types separately considering the different timings of reproductive events in males and females.

Previous studies in Mediterranean forests and woodlands revealed significant interactions of sex with environmental factors such as light, water, slope aspect or the presence of an overstory (Iszkulo et al., 2011; Obeso and Retuerto, 2002; Retuerto et al., 2000). These studies suggested that males of *I. aquifolium* and *J. thurifera* are more efficient in water use only under stressful conditions. For *Austrocedrus chilensis* (D. Don) Pic. Ser. et Bizzarri in Argentina, site differences provoked gender-specific differences in radial growth, with males growing more in drier sites with higher radiation levels while in mesic sites both genders presented similar growth rates (Nuñez et al., 2008; Rovere et al., 2003). In our study, the environmental conditions do not seem especially stressful for any of the species. For the three native species, the location of the study site is far away from the xeric limit of distribution of the species, whereas in the case of *A. altissima*, this species is broadly naturalized throughout almost all Spain (Castroviejo, 2012). Our results suggest that gender-specific differences in tree growth are not

generalized in drought-prone Mediterranean species. However, in the Mediterranean region, the climatic and topographic heterogeneity generates important differences in habitat conditions for plants both at regional and local scales (Cantón et al., 2004; Pausas et al., 2003; Peñuelas et al., 1999). We cannot rule out the possibility that these differences would appear near the xeric or equatorward limits of the species, or under poor habitat conditions, or when individuals live in the forest understory under strong competition for light and water (Iszkulo et al., 2011).

Some authors highlight that the timing of investment in reproduction differs between genders, with males investing more during flowering and females investing more during fruit development (Delph, 1990; Juvany and Munné-Bosch, 2015; Obeso, 2002). This could help females compensate their higher reproductive costs, if fruit development happened in a period with higher resources availability. In our study species, the flowering happens during spring, whereas the main fruit growth occurs during summer except for *J. thurifera* which has a two-year period of cone growth (Montesinos-Torres, 2007; Montserrat-Martí and Pérez-Rontomé, 2002; Obeso, 1996; Sanz-Elorza et al., 2004). In the Mediterranean climate, summers are characterized by warm temperatures and low precipitation. If females expend more resources on reproduction than males during this stressful period, this may be more detrimental to their performance in comparison with the investment in inflorescences for males in spring (Juvany and Munné-Bosch, 2015). Alternatively, females may be more efficient by uptaking more carbon and storing more non-structural carbohydrates, nutrients and water used to develop fruits (Tognetti, 2012). Another possibility is that growth is reduced in mast years as observed in *Araucaria araucana* (Molina) K. Koch females during the year of seed maturation (Hadad et al., 2021).

Although the dendrochronological analyses did not find any interaction between sex and precipitation, for *A. altissima* it was found that males were more responsive than females to variability in temperature and drought intensity. Interestingly, this agrees with Liu et al. (2020) results for *Populus cathayana* Rehd. indicating that males response to summer weather was mainly related to temperature, while females response was mainly related to soil moisture. This gender-specific response to climate factors could also explain the higher water-use efficiency of *P. terebinthus* females.

To conclude, we did not find differences between females and males of *A. altissima*, *P. terebinthus*, *J. thurifera* or *I. aquifolium* regarding radial growth rates or growth responses to precipitation variability. This is particularly noteworthy because our study involves long-term time frames and takes into account the effects of tree size and age, with the species being studied in their natural habitats (except in the case of *A. altissima*, which is naturalized). We only found differences regarding water-use efficiency during droughts for one of the species, *P. terebinthus*, whose males showed a less conservative water use. It would be interesting to investigate whether gender-specific differences in growth or physiological parameters could be detected for these species in rear-edge or xeric populations or under poor habitat conditions, and in core populations what are the compensatory mechanisms for reproductive costs in females. Tognetti (2012) and Hultine et al. (2016) warned that gender-specific differences could make dioecious plants particularly vulnerable to the effects of global warming if one gender is more sensitive to the changing climatic factors than the other. Populations that show these differences could be at higher risk of local extinction. In Mediterranean Spain, the summer is characterized by warm, dry conditions; exacerbated in recent decades by a regional increase in spring temperatures, atmospheric evaporative demand and drought severity (Vicente-Serrano et al., 2017a). This suggests that females may be more vulnerable than males to regional climatic trends. However, for habitats where soil moisture is not limiting, males response may be more linked to increasing temperatures, but this should be further investigated.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2022.125944.

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