



Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Drought constrains acorn production and tree growth in the Mediterranean holm oak and triggers weak legacy effects

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ARTICLE INFO

Keywords:

Drought
Legacy
Acorn production
Radial growth
Quercus ilex
Masting

ABSTRACT

Droughts are becoming more frequent in the Mediterranean basin due to warmer conditions. Droughts negatively impact forests growth for several years, often generating negative legacies or carryover effects. However, these legacies differ among tree species, sites and drought characteristics and have been mainly studied considering tree growth or canopy greenness, but ignoring reproductive phenomena. Here, we compare the legacy effects of drought on acorn and male inflorescence production and radial growth by using a 19-year series of 150 *Quercus ilex* individuals in three stands located in north-eastern Spain. We evaluate the relationships between monthly climate variables, tree-ring width, acorn production and male inflorescence production. For the two driest years considered (2005 and 2012), when very few acorns were produced, we did not find negative legacy effects on acorn production in the three years following droughts. The production of male inflorescences did not show any significant legacy after drought, although its annual variation was related to the climatic conditions of the year before acorn ripening. Acorn production was higher than expected for some of these years, apparently following the pattern of tree growth recovery with a certain lag. This compensatory response of acorn production differed between the two analysed droughts, in accordance with different conditions of drought timing and post-drought climate conditions. Even though few negative legacy effects of growth and acorn production were found, we confirmed the negative effect of drought stress on tree growth and acorn production, linked to dry winter conditions. Our findings confirm that drought features (timing, duration, intensity) and post-drought climate conditions influence tree growth and reproduction legacies.

1. Introduction

Droughts are becoming more frequent and severe in climate hotspot regions such as the Mediterranean basin (Spinoni et al., 2018; Vicens-Serrano et al., 2014). This could drastically alter forest function, productivity and ecosystem services (Bréda et al., 2006; Huang et al., 2017; Ivits et al., 2014; Schwalm et al., 2012). Droughts are complex phenomena provoking stress due to both water scarcity and evaporative demand, and they can have different impacts on trees depending on the seasonality, duration and severity of the drought (Anderegg et al., 2013; Bose et al., 2021; Camarero et al., 2015; Gao et al., 2018). These conditions decrease leaf gas exchange, water potential and hydraulic conductivity in trees, thus reducing growth or increasing mortality rates (Corcuera et al., 2004; Damesin and Rambal, 1995; Forner et al., 2018; Pasho et al., 2011). Besides these immediate effects, droughts can have

legacy effects on forests by altering their post-drought growth rates and depleting the tree carbon and nutrient reserves (Anderegg et al., 2015; Galiano et al., 2012; González de Andrés et al., 2022; Orwig and Abrams, 1997). However, this legacy appears to be different among tree species, sites, drought characteristics and stand density (Anderegg et al., 2015; Bose et al., 2021; Camarero et al., 2018; Huang et al., 2018).

The legacies of drought on forest growth have been thoroughly investigated in recent years, due to its potential consequences on forests resilience in response to climate warming projections (Anderegg et al., 2015; Huang et al., 2018). However, no studies have focused on the possible legacy effects on reproduction processes, to the best of our knowledge, possibly due to the scarcity of long-term databases for forest seed production (Clark et al., 2016). The dynamics of seed production in forest trees is a central question in forest ecology, with a key role in regeneration, forest composition and wildlife populations (Bogdziewicz

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Received 26 September 2022; Received in revised form 17 March 2023; Accepted 20 March 2023

Available online 22 March 2023

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et al., 2020; Pearse et al., 2016). Previous research has shown that water availability affects seed production in Mediterranean forests, although with species-specific effects of climate factors that frequently match with key reproductive phenological events (García-Barreda et al., 2021; Ogaya and Peñuelas, 2007; Pérez-Ramos et al., 2010).

The evergreen holm oak (*Quercus ilex* L.) is a keystone tree species in many forested areas of the western Mediterranean basin (Barbero et al., 1992). Previous research suggests an important role of climate control over fruiting in these seasonally dry forests (Espelta et al., 2008; Fernández-Martínez et al., 2015; Pérez-Ramos et al., 2010). A positive association of acorn production with wet winter conditions has been reported, as envisaged by the resource-matching hypothesis (García-Barreda et al., 2021), but also a direct effect of spring climatic conditions, linked to flowering and fertilization, and of summer conditions, linked to acorn development (Bogdziewicz et al., 2017; Le Roncé et al., 2021; Montserrat-Martí et al., 2009; Pérez-Ramos et al., 2010). However, no information is available on the post-drought recovery of *Q. ilex* acorn production. Andereg et al. (2015) reported that radial growth in *Quercus* species was more resilient after drought than in *Pinus* species, with *Quercus* in dry sites tending to show post-drought compensatory growth, i.e., positive legacies. Likewise, Gazol et al. (2020) analysed 15 *Q. ilex* stands in Spain and only found negative drought legacies in radial growth for 14% of them during the first year, and for 7% the following years. Ogaya et al. (2014) and Camarero et al. (2015) found that *Q. ilex* was able to recover its leaf production one year after a drought event, but the recovery of radial growth and leaf production were uncoupled.

In this study, we examined the influence of climate conditions on growth and fruit production of three *Q. ilex* stands located in north-eastern Spain, as well as their response to drought. First, we evaluated the relationships between climatic factors, radial growth, acorn production and male inflorescence production. We implemented statistical models for these relationships at the individual level. Then, we quantified how much radial growth, acorn production and male inflorescence production departed, during the years following the severe droughts of 2005 and 2012, from the expected values according to the implemented models. Additionally, we characterized the performance of the tree individuals regarding inter-individual synchrony and stability of individual rankings from year to year. The production of male inflorescence was included in the study because previous research showed a positive correlation of acorn production with pollen abundance (García-Mozo et al., 2007), although another study showed a more important correlation with flowering synchrony (Bogdziewicz et al., 2017). We hypothesized that in this drought-prone *Q. ilex* forest tree growth and acorn production would be negatively affected by dry conditions in summer and during the preceding winter and spring, as shown in previous studies (Corcuera et al., 2004; García-Barreda et al., 2021; Pérez-Ramos et al., 2010). We also hypothesized that this would be related to negative legacy effects on tree growth and acorn production after severe droughts, in accordance with previous studies pointing to a uncoupling of leaf production and radial growth in *Q. ilex* after drought events (Camarero et al., 2015; Ogaya et al., 2014).

2. Material and methods

2.1. Study area, climate data and target tree species

The study was conducted in a *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. site situated in Arascués (Sierra de Guara, Huesca province), in north-eastern Spain (42° 14' N, 0° 27' W, 650 m a.s.l., Fig. S1). The climate is continental Mediterranean, with a mean annual rainfall of 505 mm and a mean annual temperature of 13.1° C (Fig. S2). The site is relatively flat and soils are shallow (mean depth ca. 50 cm), calcareous, rocky and rich in clay (Camarero et al., 2015). The forest is dominated by coppice *Q. ilex* individuals forming a closed canopy cover with mean diameter at breast height (1.3 m) of 8.4 cm (Camarero et al., 2010).

Quercus ilex is an evergreen oak, forming diffuse to semi-ring porous

wood, mainly present in dry areas of western Mediterranean basin (Fig. S1). It is a monoecious species with wind pollinated, unisexual flowers. It usually flowers in April–May, with female (pistillate) flowers maturing a few days after male (staminate) flowers, which grow in inflorescences called catkins (Gómez-Casero et al., 2007; Le Roncé et al., 2021). The fertilization and fruit initiation happens in June – July and the acorn ripening ends in October – November (Gómez-Casero et al., 2007; Le Roncé et al., 2021). Thus, the period in which acorns more rapidly enlarge and gain weight is late summer, when cumulative water deficit peaks in the Mediterranean region (S.M. Vicente-Serrano et al., 2017). Regarding the initiation of the buds containing flower primordia, it was generally accepted that it happened in February–April of the year of acorn ripening, although recently it has been hinted that for male flowers it could happen in the summer of the year before acorn ripening, and thus could be affected by climatic conditions of that year (Gómez-Casero et al., 2007; Le Roncé et al., 2021). Radial growth in this species usually peaks in late spring to summer (May–July), and a second autumn (October) peak is usually observed, particularly in sites with mild autumn–winter conditions located near the coast (Camarero et al., 2021; Gutiérrez et al., 2011).

2.2. Climate data

Monthly values of mean minimum temperature, mean maximum temperature and precipitation for the study site were retrieved at 0.25° (ca. 27.5 km) spatial resolution from the gridded E-OBS dataset for the 1950 – 2021 period (Haylock et al., 2008). The monthly climatic water balance was calculated as precipitation minus potential evapotranspiration (P – PET). The data of potential evapotranspiration was directly retrieved from Laboratorio de Climatología y Servicios Climáticos of IPE – CSIC (LCSC) webpage (<https://lcsc.csic.es/>) and calculated with Monteith – Penman method (Sergio M Vicente-Serrano et al., 2017). To examine the effect of droughts we also explored associations with the SPEI (Standardized Precipitation Evapotranspiration Index) drought index, which was retrieved from LCSC webpage (Vicente-Serrano et al., 2010).

2.3. Acorn and male inflorescence production

In the study site, we selected three stands of around 3–4 ha located at least 500 m apart. In each stand 50 trees were randomly selected and tagged in 2003. Sampled trees were at least 20 m apart. For each tree, acorn crop was estimated each year in late October using a semi-quantitative scale from 0 to 4 (category 0: no acorns, category 1: less than 25% of tree branches with acorns, category 2: 25 – 50% of tree branches with acorns, category 3: 50 – 90% of tree branches with acorns, category 4: more than 90% of tree branches with acorns). Similarly, for each tree the production of male inflorescences was estimated each year in late May (category 0: no catkins, category 1: less than 25% of tree branches with catkins, category 2: 25 – 50% of tree branches with catkins, category 3: 50 – 90% of tree branches with catkins, category 4: more than 90% of tree branches with catkins). The male inflorescence production was recorded for the 2003 – 2018 period, with data missing for 2015, and the acorn production was recorded for the 2003 – 2021 period, although in the last year only the 39 trees sampled for tree ring width were recorded (Fig. S3).

2.4. Dendrochronological methods

We randomly selected 39 of the 150 trees among the dominant trees of the site, which resulted in 17 trees from stand 1, 9 from stand 2 and 13 from stand 3 being sampled for dendrochronological analyses. Two cores from each tree were extracted at height 1.3 m using Pressler increment borers. 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 each individual was expressed as the basal area increment (BAI, i.e. annual increment in 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, 2022). The age of each tree ring was expressed as its cambial age (number of growth rings from the pith).

2.5. Statistical analysis

Generalised additive mixed models (GAMMs) were used to assess, at tree level, the relationship of climatic variables with BAI, acorn production and male inflorescence production. We included a random effect for the “tree” variable to model tree-specific intercepts. We used the cambial age of the tree to assess the existence of time trends in these tree variables. A normal (Gaussian) error distribution was used for BAI, whereas a Poisson error distribution was used for acorn and male inflorescence production. The Akaike information criterion (AIC) was used to select the final GAMM by tentatively including and excluding the most relevant variables according to previous research (Corcuera et al., 2004; Garcia-Barreda et al., 2021; García-Mozo et al., 2007; Gutiérrez et al., 2011; Montserrat-Martí et al., 2009; Pérez-Ramos et al., 2010). We also included an autoregressive moving-average (ARMA) correlation structure for the random effect (tree) in order to account for auto-correlation in response variables. In such models the notation $ARMA(p, q)$ describes a model with p autoregressive terms and q moving-average terms. The assumptions for normal distribution, constant variance and temporal independence were tested in the final BAI model, and thus BAI was log-transformed to meet these assumptions. The fit of the chosen distribution for the acorn and male inflorescence models was assessed through overdispersion, (with the ratio residual deviance to residual degrees of freedom) whereas the temporal independence assumption was assessed with the plots of auto-correlation function (ACF) and partial auto-correlation function (PACF). In all models, the presence of concurvity (a generalization of collinearity to the GAM setting) was examined. The analyses were conducted with the package *mgcv* in R (Wood, 2011), using a 0.05 threshold for statistical significance.

Secondly, we examined the inter-individual synchrony and the stability of ranking of individual trees in the studied tree population. The inter-individual synchrony (i.e. the concordance among trees throughout a determined time period) was assessed with the Kendall's W . This statistic was calculated for the BAI, the acorn index and the male inflorescence index. According to García-Crespo et al. (2010), when W is around 0.7, it indicates as a strong consensus; when W is around 0.5, it can be interpreted as a moderate consensus; and when W is lower than 0.3, it indicates weak consensus. For the variables showing moderate or strong inter-individual synchrony, the relationships with climatic factors were also analysed at the population level, in order to assess its consistency with the same relationships at the individual tree level. For this, the mean detrended acorn series were correlated against monthly climatic variables using Spearman correlation coefficients and testing statistical significance at $\alpha = 0.05$ level. Detrended values were used because the acorn index showed a significant relationship with BAI.

The stability of ranking of individual trees from year to year (i.e. the correlation between the ranking of one individual in year i and its ranking in another year) was assessed with the Kendall's tau (τ), testing statistical significance at $\alpha = 0.05$ level.

Finally, the legacy effects of severe droughts on BAI, acorn production and male inflorescence production was analysed. Legacy effects were quantified as the difference between the observed and the predicted values of the response variable (BAI, acorn index or male inflorescence index) according to the corresponding GAMM. These values were calculated for the four years following the analysed drought

events. For this, the dry 2005 and 2012 years were selected. In the study site, year 2005 presents the lowest SPEI-12 value for August and September in the 1962 – 2021 series, according to the LCSC database (Vicente-Serrano et al., 2010); whereas 2012 presents the second lowest SPEI-12 value for June and July, only surpassed in year 1989. Both drought events were characterised by a previous dry winter (January – March) and dry conditions in late summer (August – September), with the 2005 drought being also intense in late spring – early summer (May – July) (Fig. S4).

3. Results

The BAI of the individuals was positively correlated to their cambial age, with a steady increase up to age 40 and then remaining relatively stable up to age 80 (Table 1, Fig. 1a). The BAI was also positively correlated with the climatic water balance from the prior December to the current February and from current May to July (Table 1, Fig. 1d, g). Finally, the BAI was significantly correlated with the mean maximum temperature of the current May – July, with an optimum in the 24 – 27°C range (Table 1, Fig. 1j). The GAMM analysing the BAI behaved well with regard to the assumptions of constant residual variance, normal distribution and temporal independence (Fig. S5). The predictor variables showed worst-case concurvities between 0.31 – 0.78, with all the

Table 1

Summary of the best-fitted generalised additive mixed models (GAMMs) analysing the basal area increment (BAI, $n = 2643$), acorn index ($n = 484$) and male inflorescence index ($n = 484$). For the BAI model, the correlation structure that best accounted for the auto-correlation and partial auto-correlation of the radial growth was $ARMA(1,1)$, whereas for the acorn and male inflorescence models no serious auto-correlation problems were found. Edf: estimated degrees of freedom. WSE: within-subject effect. Min. temp.: mean minimum temperature. Max. temp.: mean maximum temperature. P – PET: climatic water balance.

Response variable	Predictor variables	Edf	F value ^a	P value	R ²
BAI ^b	Age ^c	6.7	99.1	< 0.001	0.474
	P – PET December – February ^c	2.4	21.5	< 0.001	
	P – PET May – July ^c	1.1	7.9	< 0.001	
	Max. temp. May – July ^c	5.4	15.0	< 0.001	
	Tree (WSE)	2.4	0.1	0.36	
Acorn index	BAI	1	4.3	< 0.001	0.418
	Male inflorescence index	1	4.6	< 0.001	
	Min. temp. prior August ^c	2.5	69.3	< 0.001	
	P – PET July ^c	3.8	23.0	< 0.001	
	Tree (WSE)	17.4	32.0	0.001	
Male inflorescence index	Min. temp. prior January	1	3.1	0.002	0.361
	Max. temp. prior June	1	–3.7	< 0.001	
	P – PET prior August	1	–2.8	0.006	
	Min. temp. prior October	1	–3.5	< 0.001	
	Age ^c	1.9		0.37	
Tree (WSE)	13.9		0.013		

^a F-value for the BAI model (normal distribution), Z-value for non-smooth terms of the acorn and male inflorescence models (Poisson distribution), chi-square for smooth and random terms in acorn and male inflorescence models.

^b Variable log-transformed.

^c Smoothed terms.

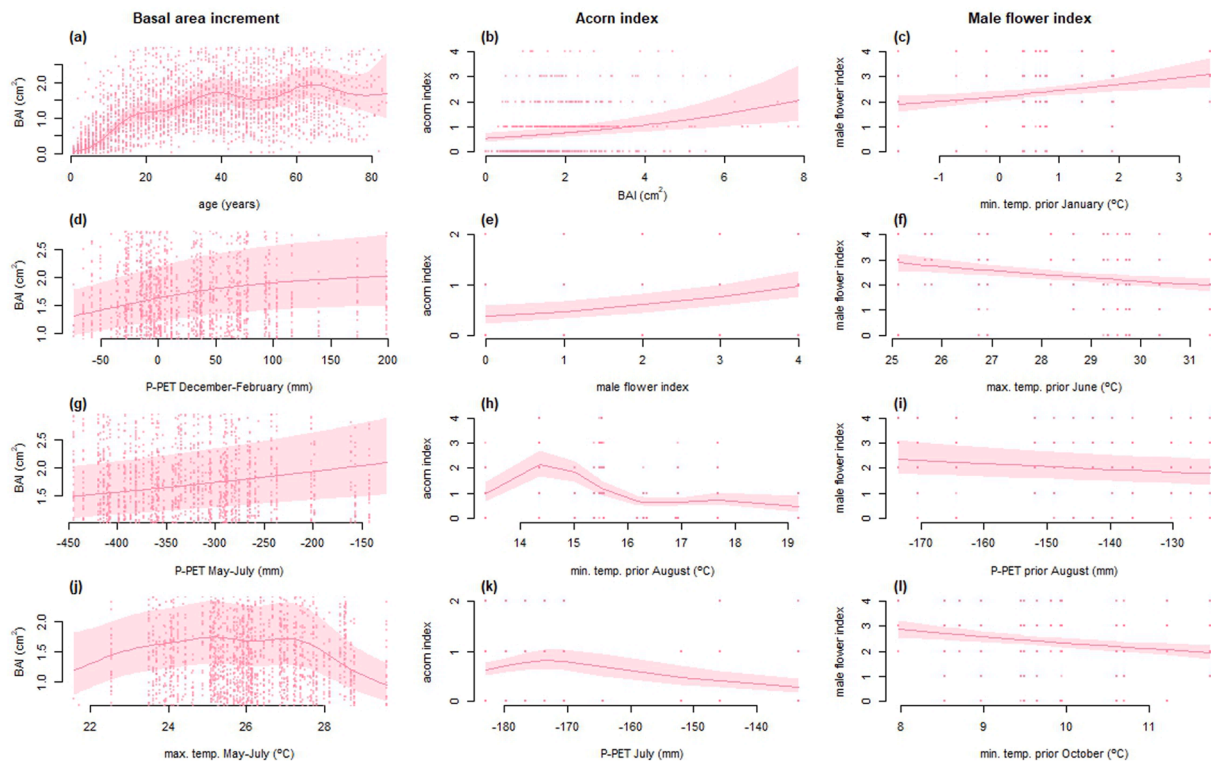


Fig. 1. Predicted relationships (mean and 95% confidence bands) of basal area increment (BAI) (a, d, g, j), acorn index (b, e, h, k) and male inflorescence index (c, f, i, l) with the significant predictors according to the corresponding GAMM (Table 1). Points depict raw observations.

pairwise values of worst-case concurrency being lower than 0.75, which indicates limited concurrency problems (Table S1).

The acorn index of the individuals was positively correlated with the BAI and the male inflorescence index of the same year (Table 1, Figs. 1b, e). The acorn index was negatively correlated with the mean minimum temperature of the prior August and the climatic water balance of the current July (Table 1, Figs. 1h, k). The GAMM analysing the acorn index behaved well with regard to the assumption of overdispersion (index: 1.27) and temporal independence (Fig. S6). The two smooth predictor variables showed a pairwise value of worst-case concurrency of 0.63.

The male inflorescence index of the individuals was positively correlated with the mean minimum temperature of the prior January and negatively correlated with the mean maximum temperature of the prior June, the climatic water balance of the prior August and the mean minimum temperature of the prior October (Table 1, Figs. 1c, f, i, l). The GAMM analysing the acorn index behaved well with regard to the assumption of overdispersion (index: 1.07) and temporal independence (Fig. S7).

Regarding inter-individual synchrony, the acorn index showed a Kendall's $W = 0.55$ ($p < 0.001$, $n = 150$, period 2003–2021), whereas the BAI showed $W = 0.22$ ($p < 0.001$, $n = 39$, period 1983–2011) and the male inflorescence index showed $W = 0.39$ ($p < 0.001$, $n = 150$, period 2004–2018). The W values for the 39-tree dataset were similar to those obtained for the larger sample of 150 trees ($W = 0.61$, $p < 0.001$, for the acorn index; and $W = 0.35$, $p < 0.001$, for the male inflorescence index).

The years showing lower diversity of the acorn index were 2005 and 2012 (severe droughts), in which the 99% of trees showed a value of zero (Fig. 2b, Fig. S8). Similarly, in years 2004, 2016, 2018 and 2019 the 99% of the trees showed an acorn index equal to zero or one (Fig. 2b, Fig. S8). In the case of the inflorescence index, all categories were present all the years, except for year 2017 (with no tree in category 0). In years 2009, 2011 and 2017 more than 96% of trees showed an inflorescence index equal to 2, 3 or 4, respectively (Fig. 2c, Fig. S9).

The moderately high W value for the acorn index, indicating a

moderate inter-individual synchrony, means that the analysis at tree level (Table 1, Fig. 1) might be well correlated with an analysis at the population level (mean series of the 39 tree individuals). Indeed, the population-level acorn index showed a negative correlation with the mean minimum temperatures of the prior August and September, as well as a positive correlation with the BAI of the same year (Figs. S10–S11). It also showed a positive correlation with the mean minimum temperatures of the current February and April (Fig. S10). Besides, the acorn index did not significantly correlate with any SPEI drought index of the year in which acorns are formed. However, the acorn index showed a negative correlation with the SPEI 12 and SPEI 48 of the prior September (Fig. S12).

Regarding the stability of ranking of individual trees from year to year, the BAI rankings were relatively stable for the 39 trees studied, with 90% trees showing significant Kendall's tau correlations with BAI of the previous four years, thus indicating that trees maintain consistent BAI rankings for this lag period (Fig. S13). On the contrary, the ranking of the individual trees according to the acorn index and the male inflorescence index were not stable from year to year (Fig. S14). Thus, trees with relatively high BAI in year i tended to maintain relatively high BAI in the following years, i.e. they were fast-growing trees, but this was not observed with the acorn and male inflorescence indices.

The analysis of drought legacies did not show any consistent pattern after the severe 2005 and 2012 droughts, either for BAI or acorn index. Two and three years after the 2005 drought the observed BAI was significantly higher than predicted by the GAMM, whereas for the 2012 drought it was significantly higher one year after the drought and significantly lower three years after the drought (Figs. 3a, d). The acorn index was significantly higher than predicted by the GAMM four years after the 2005 drought, but non-significantly different before. Meanwhile, after the 2012 drought, the acorn index was significantly higher than predicted the first two years, and significantly lower the fourth year (Figs. 3b, e). The observed male inflorescence index did not show significant differences with the predicted values (Figs. 3c, f).

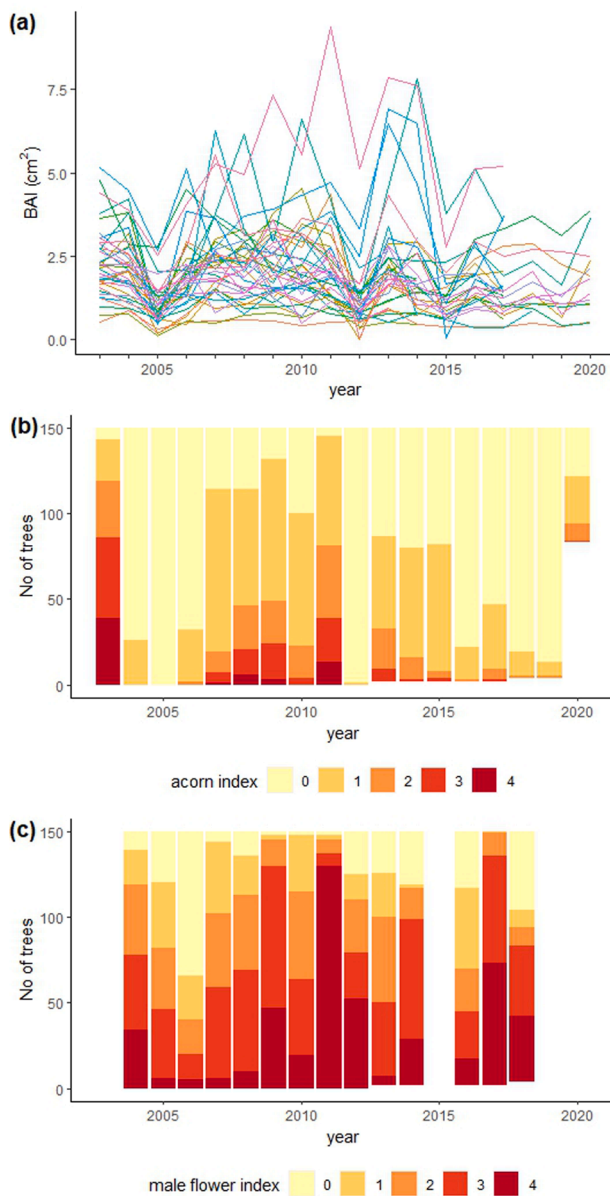


Fig. 2. Temporal variation (period 2003–2020) of individual-tree basal area increment (BAI) (a), frequency for acorn index (b) and frequency for male inflorescence index (c). Higher values of the indices indicate higher production of acorns and male inflorescences, respectively (0–4 scale). Category 0: no male catkins, category 1: less than 25% of tree branches with male catkins, category 2: 25–50% tree branches with male catkins, category 3: 50–90% of tree branches with male catkins, category 4: more than 90% of tree branches with male catkins.

4. Discussion

Our results did not show lower than expected acorn production in the three years following the 2005 and 2012 droughts. In fact, the model showed higher than expected acorn production for some of these years, apparently following the pattern of radial growth recovery but with a certain lag. For the 2005 drought, the model pointed to a higher-than-expected BAI for years 2–3 after drought and higher than expected acorn production for year 4. For the 2012 drought, *Q. ilex* showed higher than expected BAI for year 1 and higher than expected acorn production for years 1–2. Relatedly, for the 2012 drought *Q. ilex* showed lower than expected BAI for year 3 and lower than expected acorn production for year 4 (although with no acorn data for year 3). For some tree species, it

has been shown that warm, dry conditions can be beneficial during flower induction the year before seeds ripen (Clark et al., 2016; Houle, 1999). However, we did not find higher than expected male inflorescence production after an extreme drought. In short, our data suggest the existence of a compensatory response of *Q. ilex* acorn production after drought, with some relation to the compensatory response of tree growth but apparently not to male inflorescence production. Such compensatory effects could be also explained by wet climate conditions after some of the two considered droughts (Fig. S3).

The higher than expected recovery of *Q. ilex* growth after the 2005 (years 2–3) and 2012 droughts (year 1) was contrary to our expectations, but agrees with previous studies indicating that oaks frequently present positive drought legacy effects, probably linked to increased reserve amounts (Anderegg et al., 2015). Gazol et al. (2020) studied the legacy effects of drought on *Q. ilex* growth in Spain and only found negative legacies in 14% of the sites, pointing to the bimodal xylogenesis of *Q. ilex* as a compensation mechanism that facilitates a quick recovery after release from the drought stress, at least in sites with mild autumn conditions (Camarero et al., 2021; Gutiérrez et al., 2011). Besides, Ogaya et al. (2014) and Camarero et al. (2015) found that the post-drought recovery of radial growth and leaf production was uncoupled, and attributed the faster leaf production recovery to the presence of long-lived apical buds in *Q. ilex*, which improves its capacity to resprout from stem and branches (Alla et al., 2013). Rapid leaf production after drought could also play a role in the recovery of radial growth, although Camarero et al. (2010) and Martín et al. (2015) pointed out that in *Q. ilex* autumn growth may compete for resources with acorn production. However, acorn production did not lead to a decrease in non-structural carbohydrate concentrations at the shoot level (Alla et al., 2012).

In both analysed drought events *Q. ilex* showed some years with higher-than-expected recovery, although with some differences between 2005 and 2012. Tree growth and acorn production showed positive legacies one year after the 2012 drought, whereas in 2005 positive legacies were observed after 2–3 years (for tree growth) and after 4 years (for acorn production). These differences correspond with differences in annual climatic conditions. Both 2005 and 2012 included intense drought conditions during late summer and during the prior winter (Fig. S4). However, the 2012 drought implied less intense drought conditions during late spring and early summer, as well as much more positive water balances during the post-drought autumn (Fig. S4). This suggests that differences in drought timing and intensity, or in post-drought climatic conditions, influence the capacity of *Q. ilex* to recover from these extreme climate events (Camarero et al., 2015; Forner et al., 2018).

Even though in our study the drought legacy effects were mostly non-significant or positive, our data also show the negative impact of water deficit on acorn production and radial growth. In years 2005 and 2012, with severe droughts, *Q. ilex* barely produced acorns and radial growth was low (Fig. 2). The GAMMs showed a positive relationship of acorn production and tree growth, which had been previously attributed to wet winters favouring both growth and reproduction (García-Barreda et al., 2021). Our results agree with this view, with climatic water balance in winter being positively related to tree growth and this to acorn production. This relationship has been previously linked to climatic conditions in periods when trees accumulate resources (García-Barreda et al., 2021). Overall, a reduction in the rainfall amount reduces the reproductive ability of *Q. ilex* (Sánchez-Humanes and Espelta, 2011), which can have long-term consequences on the regeneration of this oak species (Pulido and Díaz, 2005).

The effect of summer conditions in our study site is less straightforward. The climatic water balance in late spring–early summer was positively related with BAI and this with acorn production. However, at the same time our model also showed a negative relation between the climatic water balance of July and acorn production for water balance values higher than -170 mm. This could be related to the fact that the

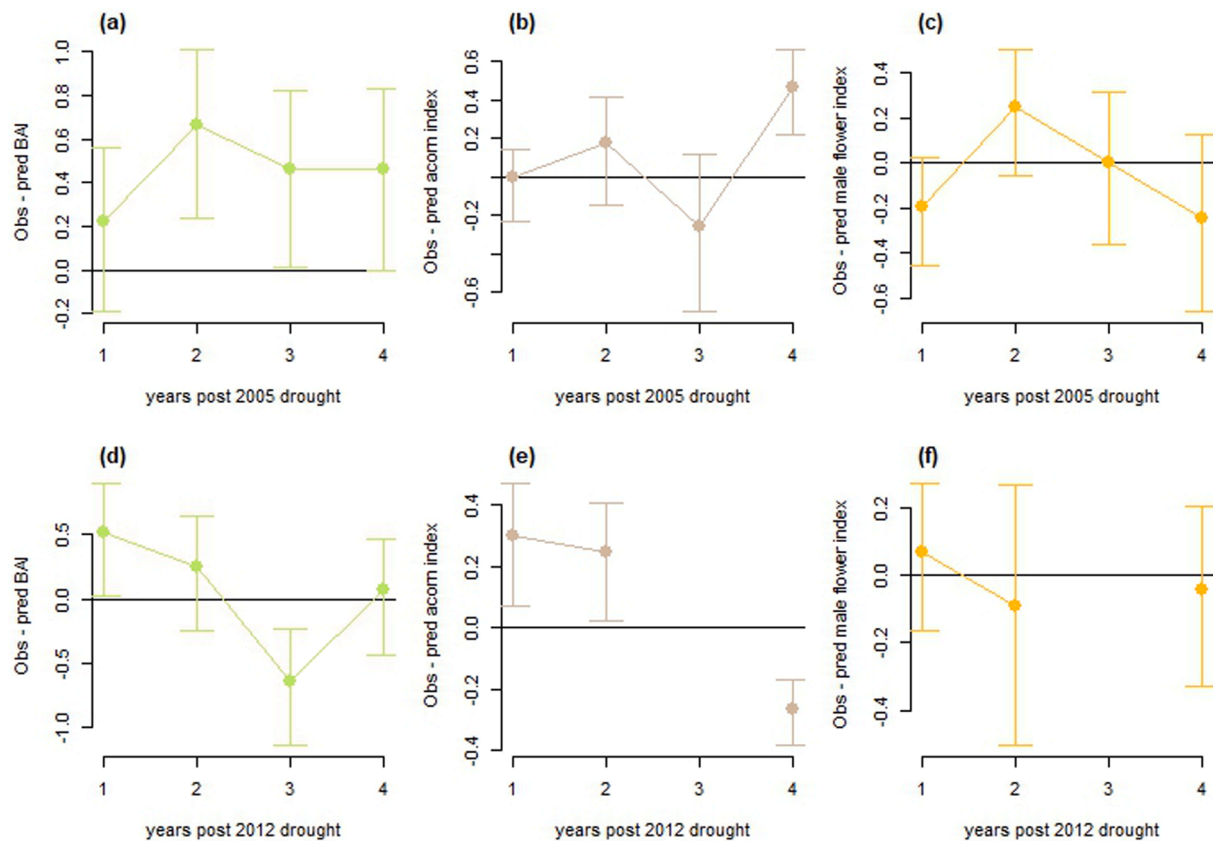


Fig. 3. Legacy effects of the 2005 (a – c) and 2012 (d – f) droughts on basal area increment (BAI, a and d plots), acorn index (b and e plots) and male inflorescence index (c and f plots), quantified as the difference between observed and predicted values of these variables (in cm^2 for BAI, unitless index for acorn and male inflorescence) according to the corresponding GAMMs. Year 3 is not available in (e – f) due to the lack of male inflorescence data for 2015. Values are means \pm 95% confidence intervals.

effect of early summer water balance was already accounted for in the model by BAI. In rainfall exclusion experiments, it has been shown that summer – autumn water stress reduced acorn production due to acorn abortion (Le Roncé et al., 2021; Pérez-Ramos et al., 2010). On the other hand, the typically-Mediterranean intense summer storms can provoke the premature abscission of acorns (Pérez-Ramos et al., 2010). In any case, it seems that longer and more detailed datasets would be needed to resolve the role of summer storms, soil water content and air humidity on acorn production and the possible interactions with other ecological factors.

To advance knowledge in this area, it would be interesting to monitor in natural forests the effect of climate conditions on other phenological stages of *Q. ilex* reproduction such as production of female flowers or acorn abortion rates during summer, to confirm previous findings of rainfall exclusion experiments (Le Roncé et al., 2021; Pérez-Ramos et al., 2010). Droughts are complex phenomena that can have different features (timing, duration and intensity) and stress plants through soil water scarcity, atmospheric vapor pressure deficit and/or leaf and acorn heating (Anderegg et al., 2013; Gao et al., 2018). This is further complicated by the variability of Mediterranean climate, in which droughts can happen at any time of the year and last different periods (Gouveia et al., 2017). We used a visual rating of acorn production, similar to those used for evaluating phenological phases, which may allow to identify patterns but limits the quantification of the relationships, thus making it difficult to resolve questions such as non-linear responses of acorn production to severe water deficit. For instance, acorn production was almost null during the driest years 2005 and 2012, suggesting threshold responses. This limitation could be alleviated by using seed traps, although this would surely require a coordinated community effort due to the resources and commitment

necessary to generate a long-term record of seed production at a stand level. We also acknowledge that weak signals are a limitation of the study and the available data may not yet be sufficient to resolve some questions.

In any case, our data showed a positive relationship of acorn production and male inflorescence production, suggesting a relevant role of pollen limitation in the acorn production of the study site and showing that factors other than tree growth or accumulated resources are important to acorn production (García-Mozo et al., 2007; Koenig et al., 2013). This could be further explored by analysing regional networks of pollen and acorn production in oak species (e.g., Anderegg et al., 2021). These studies could fill the gap left by our study limitations.

Even though acorn production and male inflorescence production are correlated, the latter showed much a lower value of inter-individual synchrony, in relation with the presence of all male inflorescence categories in almost all years (Fig. 2c). Previous studies found that pollen production and male inflorescence production were relatively constant among years in comparison to acorn production, concluding that high inter-annual variation in acorn production was determined by the success in acorn development rather than by the flowering effort (Bogdziewicz et al., 2017; Gavinet et al., 2019; Pérez-Izquierdo and Pulido, 2013; Pérez-Ramos et al., 2010). Interestingly, in our study site the ranking stability of individuals was low for both acorn and male inflorescence, indicating that individual trees which showed a relatively high production (with respect to the rest of the sampled population) in a given year did not maintain it in the following one. This could be better refined by using quantitative scales of acorn and male inflorescence production.

Male inflorescence production is considered scarcely responsive to droughts (Gavinet et al., 2019; Pérez-Ramos et al., 2010), although in

rainfall exclusion experiments it was found that the production of viable pollen grains of these inflorescences could be negatively affected (Bykova et al., 2018). In our study, the lack of legacy effects on male inflorescence production contrasts with its responsiveness to annual climatic conditions. We found a negative relation of male inflorescence with June temperature and August water balance of the year before acorn ripening. Clark et al. (2016) pointed that dry conditions during the year before seed ripening could improve flower induction. Besides, we found that male inflorescence production was significantly related with the climatic conditions of the year before acorn ripening, but not with conditions in the year of acorn ripening. Recently, Le Roncé et al. (2021) posed that male flower induction could happen in the summer of the year before acorn ripening. This could explain the response we found for male flowering to climate.

5. Conclusions

We analysed the legacy effects of 2005 and 2012 droughts on the acorn production of *Q. ilex* and we did not find negative effects in the three years following these droughts. In both droughts, we found higher than expected acorn production for some of the post-drought years, apparently following the pattern of growth recovery with a certain lag but without any apparent relation to the response of male inflorescence production. The compensatory response of acorn production was delayed in 2005 compared with 2012, in agreement with the longer conditions of intense drought and the less favourable post-drought climatic conditions of 2005. Even though few negative legacy effects were found, we confirmed the negative effect of drought stress on tree growth and acorn production, linked to dry winter conditions. Dry conditions in early summer were detrimental to tree growth, although we could not find such a straightforward relation with acorn production. Besides, we found a positive relationship of acorn production with male inflorescence production, although the latter showed a lower value of inter-individual synchrony. Male inflorescence production did not show any significant legacy after drought, but its annual variation was responsive to climatic conditions during the year before acorn ripening.

Declaration of Competing Interest

J.J. Camarero reports financial support was provided by Spanish Ministry of Science, Innovation and Universities.

Data availability

Data will be made available on request.

Acknowledgments

This research was funded by Spanish Ministry of Science, Innovation and Universities, grant number FORMAL (RTI2018-096884-B-C31) to J.J.C. We acknowledge the E-OBS dataset from the EU-FP6 project UERRA (<http://www.uerra.eu>) and the Copernicus Climate Change Service, and the data providers in the ECA&D project (<https://www.ecad.eu>). We also thank Gabriel Montserrat Martí, Gabriel Sangüesa Barreda, Michele Colangelo, José Manuel Altarriba and Pedro Sánchez for their help in the field.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2023.109435](https://doi.org/10.1016/j.agrformet.2023.109435).

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