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Tree vigour influences secondary growth but not responsiveness to climatic variability in Holm oak

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ABSTRACT

Many tree species from Mediterranean regions have started to show increased rates of crown defoliation, reduced growth, and dieback associated with the increase in temperatures and changes in the frequency and intensity of drought events experienced during the last decades. In this regard, *Quercus ilex* L. *subsp. ballota* [Desf.] (Holm oak), despite being a drought-tolerant species widely distributed in the Mediterranean basin, it has recently started to show acute signs of decline, extended areas from Spain being affected. However, few studies have assessed the role of climatic variability (i.e., temperature, precipitation, and drought) on the decline and resilience of Holm oak. Here, we measured secondary growth of seventy Holm oaks from a coppice stand located in central Spain. Sampled trees had different stages of decline, so they were classified into four vigour groups considering their crown foliar lost: healthy (0%), low defoliated (< 25%), highly defoliated (25 to 70%), and dying (70 to 100%). Our results showed that during the study period (1980 - 2009) the highly defoliated and dying Holm oaks grew significantly less than their healthy and low defoliated neighbours, suggesting permanent growth reduction in the less vigorous individuals. Despite these differences, all four vigour groups showed similar responses to climatic variations, especially during winter and late spring – early summer seasons, and similar resilience after severe drought events, managing to significantly recover to pre-drought growth rates after only two years. Our findings, hence, illustrate that tree vigour influences secondary growth but not responsiveness to climatic variability in Holm oak. Still, as reduced growth rates are frequently associated with the process of tree mortality, we conclude that the less vigorous

Holm oaks might not be able to cope with future water stress conditions, leading to increased mortality rates among this emblematic Mediterranean species.

KEYWORDS

Holm oak; drought; tree-rings; coppice; defoliation.

INTRODUCTION

Tree decline is currently one of the main worrisome and studied issues in forest ecology worldwide (Allen et al., 2010; Carnicer et al., 2011), being mainly associated with increasing temperatures and changes in precipitation intensity and frequency (IPCC, 2014). In the last decades this phenomenon has affected all major forest biome types, and thus many conifer and broadleaf species, both evergreen and deciduous, independent of their sensitivity or tolerance to stressful climatic conditions (e.g., droughts) (see Allen et al., 2010). Tree decline leads to low ecosystem productivity, changes in species distribution, and altered forest succession, finally affecting all forest ecosystem services (Anderegg et al., 2013a). Thus, to minimize and prevent such changes, identifying the causes that underlie forest vulnerability and decline (e.g., defoliation, growth reduction, dieback), and how these ecosystems respond to changes in climatic conditions, have become of upmost importance.

Tree rings have been recognized as good predictors of increased vulnerability, decline, and stress-induced mortality events. For instance, studies like Hereş et al. (2012) or Cailleret et al. (2017) have identified that long-term decreases in radial growth rates precede tree mortality events. However, in Cailleret et al. (2017) the authors also highlighted that mortality can be preceded by quick growth declines, or even by increased growth rates, with different patterns varying among tree species and drought tolerance-strategies. As a consequence, species-specific studies are needed to better identify the causes that underlie forest vulnerability and decline.

Mediterranean regions, where water availability is the main limiting factor for plant growth (Cherubini et al., 2003; Martínez-Vilalta et al., 2008), are considered to be especially vulnerable to increased temperature and changes in the frequency and intensity of drought events (Giorgi and Lionello, 2008; IPCC, 2014). In the Iberian Peninsula, where predicted climatic conditions are already felt (Kovats et al., 2014), many tree species have started to show alarming signs of decline and dieback in the last decades (Peñuelas et al., 2000; Martínez-Vilalta and Piñol, 2002; Camarero et al., 2015a; Hereş et al., 2012; Natalini et al., 2016). Affected tree species include those that reach their southernmost distribution limits in the Iberian Peninsula (e.g., *Pinus sylvestris* L.), and that are considered to be particularly vulnerable to conditions induced by climate change (e.g., droughts), but also species well adapted to dry conditions and widely distributed in the Iberian Peninsula such as the Holm oak (*Quercus ilex* L. *subsp. ballota* [Desf.]).

Holm oak is an evergreen tree species, usually retaining its leaves up to three years (Montserrat-Martí et al., 2009). Its distribution covers western Iberia and North Africa (Rodá et al., 1999), dominating areas with continental Mediterranean conditions (Blanco et al., 1997). Almost 60% of all Holm oak areas are located in Spain (Corcuera et al., 2004), where this species forms natural forests or dehesa ecosystems, playing thus an important role from an environmental and socio-economic point of view (Patón et al., 2009). From all areas covered by Holm oak in Spain, it is estimated that almost 44% of them are coppice stands (see Corcuera et al., 2004 and references therein). Holm oaks tolerate thermal stress and precipitation variability (Gratani, 1996), conditions that are characteristic for the continental Mediterranean climate, being considered a species that can endure both winter frost and summer drought (Terradas and Savé, 1992; Martínez-Vilalta et al., 2002; Montserrat-Martí et al., 2009). Despite the drought-tolerant strategy provided by evergreenness and narrow vessels in the diffuse-to semi-ring-porous wood (Corcuera et al., 2004), this species has recently started to show acute signs of decline (i.e., wilting of leaves, defoliation, growth reduction, dieback, etc.), with extensive affected areas (Brasier, 1996; Gea-Izquierdo et al., 2011; Navarro, 2011; Natalini et al., 2016). Climatic stress (e.g., drought) plays an important role in the decline of this tree species (Gea-Izquierdo et al., 2011; Granda et al., 2013; Camarero et al., 2015b; Camarero et al., 2016; Natalini et al., 2016), as well as other factors such as the pathogenic oomycete *Phytophthora cinnamomi*, and intense management practices (see Natalini et al., 2016 and references therein).

The main objective of this study was to assess the role of climatic variability (i.e., temperature, precipitation, and drought) on the decline and resilience of Holm oak trees growing in a coppice stand located in central Spain. We used tree-ring chronologies that provide retrospective precise temporal insights into the climate-growth relationships of woody plants (Fritts, 1976), and allow comparison on long-term growth rates between trees at different stages of decline. Specifically, we studied Holm oak trees growing in a coppice stand that were classified into four vigour groups depending on their level of defoliation (% of crown foliar lost; used here as a proxy to define the level of decline of the studied trees), with the aim to: *i*) study potential differences in historical growth rates between trees of contrasting defoliation levels; ii) assess whether early signs of growth decline or abrupt growth changes may be identified in less vigorous trees; *iii*) analyse the annual and seasonal climatic influence on the growth of these Holm oaks growing in a coppice stand; and *iv*) evaluate the response of these trees during and after severe drought events.

MATERIALS and METHODS

Study area

The study area hosts Holm oaks at varying stages of defoliation (between 0 and 100% of crown foliar lost). Tree-ring samples and site data were collected from two coppice stands separated by <5 km, situated between two localities from the centre of the Iberian Peninsula (Spain, Community of Madrid): Chapinería (40°23'03.4"N 4°11'37.8"W, ≈ 650 m a.s.l.) and Navas del Rey (40°23'55.80"N 4°14'26.70"W, ≈ 675 m a.s.l.). Holm oaks from Chapinería and Navas del Rey were treated as a single database as the two coppice stands are close, have similar abiotic and stand conditions, and no significant growth differences were found between the trees sampled in each of them (W = 1330, p = 0.433). The study area is characterized by a low tree density (≈180 trees ha^{-1}; Rodríguez et al., 2016). The overstory is dominated by Holm oak trees, with scarce *Juniperus oxycedrus* (Sibth. and Sm) present, while the understory is represented by shrubs (*Retama* sp., *Lavandula* sp., etc.) and herbaceous species (*Vulpia* sp., *Bromus* sp., *Xolantha* sp., etc.) (Rodríguez et al., 2016). The study area has been traditionally used for pasturage, hunting and logging, although in the last decades human use has been considerably reduced, and no signs of recent logging are observed. The soils have a pH of 6, are sandy upon fractured bedrock mainly formed by biotite granites (8% of estimated superficial stoniness) (García-Angulo et al., unpublished data), and belong to the Cambisols type group (Monturiol Rodríguez and Alcalá del Olmo Bobadilla, 1990). The steepness of the terrain is low, with an estimated slope average of 8%. The climate of the study area is continental Mediterranean, characterized by hot and dry summers and cold winters (Cuatro Vientos meteorological station; Spanish State Agency of Meteorology).

Field sampling and tree ring analysis

Tree-ring widths were used to reconstruct past growth rates (Fritts, 1976) of adult Holm oak trees showing variable rates of crown defoliation. Seventy Holm oak trees of similar age (years) (Table 1), with no signs of attack by biotic factors (e.g., insects, fungi), were selected and classified into four vigour groups, according to their crown foliar percentage lost: healthy (0% of defoliation), low defoliated (< 25% of defoliation), highly defoliated (25 to 70% of defoliation), and dying (70 to 100% defoliation). To do so, four 300 m long transects (two in Chapinería and two in Navas del Rey), placed 50 m away from each other (i.e., within the same coppice stand), were established. Holm oaks were sampled within 10 m of the central transect line, trying to balance the number of trees for each vigour group, and their distribution within the study area. To monitor the vigour condition of the seventy selected Holm oaks, the visual estimation of their crown foliar percentage lost was recorded in October 2010 (our reference date; see below), and again within the next two following years (i.e., May 2011, April 2012, and October 2012). Crown foliar percentage lost was evaluated at the whole tree level, and was always estimated by the same observer for consistency. To estimate crown foliar percentage lost, every sampled tree was compared to a reference tree with no defoliation. The four vigour groups differed in their diameter at breast height (DBH) given that a uniform selection during sampling was not possible (Table 1). Field sampling was conducted in October 2010 and consisted of extracting at breast height (standard 1.3 m above from soil) at least two radial wood cores from the largest stem of each of the seventy Holm oaks, using increment borers (5 mm diameter; Haglöf, Sweden). As the outermost tree ring (i.e., 2010, the year of sampling) was not completely formed, tree-ring chronologies ended in 2009. To avoid the juvenile effect that is characterized by irregular tree rings in the first years of tree growth (Richter, 2015), and to have sufficient sample depth per year for all Holm oak groups, we only considered 1980-2009 for analyses (see below).

Following field sampling, cores were air-dried, glued and polished using a series of sand-paper grits so tree-ring boundaries were clearly visible. Cores were first visually cross-dated using wide and narrow pointer years (Stokes and Smiley, 1968) and then measured to the nearest 0.01 mm using a LINTAB digital positioner and the TSAP-Win^{TM} software (Rinn, 2004). Cross-dating accuracy was repeatedly checked using COFECHA (Holmes, 1983). In total 112 series from 70 trees were cross-dated, with an inter-series correlation of 0.67 and an average mean sensitivity of 0.43. Our intention was to analyse two radii per tree, but for 31 trees we could only cross-date one radius: the second radius of 7 of them had branch scars or breaks that made them not datable, while the second radius of the other 24 could not be dated due to difficulties in distinguishing the ring boundaries, a common challenge for Holm oak cross-dating (Gea-Izquierdo et al., 2009 and references therein) given its diffuse-to semi-ring-porous wood with multiseriate rays (Schweingruber, 1990; Supplementary Fig. 1). Of the 31 trees with one cross-dated radius, the cross-dated radius was longer than the non-cross-dated one for 23 of the trees. We decided to use only one cross-dated radius for all 70 Holm oaks, selecting for all of them the core with the longer radius. To understand the potential bias introduced by analysing growth from the longer radius only, we compared the average growth from the two radii to the growth of the longer and found that the longer radii overestimated radial growth by 4%, and this pattern was consistent across tree diameters (linear regression $\text{Radius}_{\text{longer}}$ (mm) = 1.04*$\text{Radius}_{\text{average}}$ (mm) + 2.54; $R^2 = 0.95$). The inter-series correlation for the final selected 70 cores was 0.66 and the average mean sensitivity had a value of 0.44. Our final chronology correlated well with a Holm oak chronology obtained from individuals growing in a dehesa ecosystems situated in the Central Mountain Range in Spain ($R^2 = 0.52$, $p < 0.001$) (Gea-Izquierdo et al., 2009).

To remove the trend of decreasing ring width with increasing stem size and tree age over time, and to have a better estimate of overall tree growth (Biondi and Qeadan, 2008), measured tree-ring widths were transformed into basal area increment (BAI) using the dplR R package (Bunn, 2008; Bunn et al., 2016). In addition, tree-ring widths were transformed into dimensionless ring width indices (RWI; needed for the superposed epoch analyses (SEA), see below) with both age-related growth trends and lower-frequency variation removed from the time series (Fritts, 1976; Cook and Kairiukstis, 1990). For this, raw ring width data were double detrended: first, a negative exponential curve or linear regression was fitted, and then a cubic smoothing spline with a 50% frequency (Cook and Peters, 1981). These latter analyses were done using the ARSTAN software (Cook and Holmes, 1986).

Climatic data

Mean monthly temperature (T, ºC) and accumulated precipitation (P, mm) data for the 1973 - 2009 period were available from the Cuatro Vientos meteorological station situated at ca. 36 km from the study area (data provided by the Spanish State Agency of Meteorology). Average annual precipitation is 435 mm, with August being the driest month (12.3 mm) and October the rainiest (56.1 mm) (Supplementary Fig. 2a). Annual mean temperature is 14.7ºC, with January the coldest month (6.0ºC) and July the warmest (25.2ºC) (Supplementary Fig. 2a). The summer dry period may last approximately from June to September (Supplementary Fig. 2a). Additionally, standardized precipitation-evapotranspiration index (SPEI) values were downloaded for the same time period from the Global SPEI database webpage (Vicente-Serrano et al., 2010a, 2010b; http://sac.csic.es/spei/index.html). SPEI is a multi-scalar drought index that accounts for both temperature and evapotranspiration effects on the water balance. SPEI may take negative and positive values, indicating dry and wet periods, respectively (Vicente-Serrano et al., 2010a, 2010b).

Data analyses

To test for age differences among the four vigour groups we performed one-way ANOVA analyses followed by a Tukey's Honest Significant Difference (HSD) *post hoc* test. BAI and DBH differences between vigour groups were checked through Kruskal Wallis analyses followed by a pairwise Wilcoxon test with a Bonferroni correction.

Temporal trends (1980 - 2009) of annual climatic variables (T and P) and mean growth rates (BAI) for each of the four Holm oak vigour groups were assessed by means of linear regressions. Furthermore, to detect possible points in time at which the statistical properties of the growth trends (BAI) of Holm oak vigour groups experienced a significant change in mean, we run Changepoint analyses using the "cpt.mean" function from the changepoint R package (Killick and Eckley, 2014). The algorithm used in these analyses was the pruned exact linear time (PELT), which allows for an optimal detection of the location of the changepoints of a time series through an accurate segmentation (Killick et al., 2012a).

Climate-growth relationships of healthy, low defoliated, highly defoliated, and dying Holm oak vigour groups were analysed using correlation functions implemented in the DendroClim 2002 software (Biondi and Waikul, 2004). For these analyses BAI values for each of the four vigour groups were analysed against monthly T, P, and SPEI data considering the following time span: January of the previous to growth year (t-1) to December of the current year of growth (t). Based on the obtained significant correlations (Fig. 2a, b, and c), various sets of T, P, and SPEI, covering different time intervals, were calculated and used in further analyses: (1) annual: (a) from July (previous to growth year, [t-1]) to August (current year of growth, [t]) for T and P (i.e., $T_{Jul(t-1)Aug(t)}$, $P_{Jul(t-1)Aug(t)}$), and (b) from August (previous to growth year, [t-1]) to June (current year of growth, [t]) for SPEI (i.e., $SPEI_{Aug(t-1)Jun(t)}$); and (2) seasonal: (a) from November (previous to growth year, [t-1]) to February (current year of growth, [t]) for T, P, and SPEI (i.e., $T_{Nov(t-1)Feb(t)}$, $P_{Nov(t-1)Feb(t)}$, $SPEI_{Nov(t-1)Feb(t)}$), and (b) from May to June (current year of growth, [t]) for T, P, and SPEI (i.e., $T_{May(t)Jun(t)}$, $P_{May(t)Jun(t)}$, $SPEI_{May(t)Jun(t)}$). Above mentioned annual and seasonal climatic variables were used to run linear mixed-effects models (see below). Additionally, $SPEI_{Aug(t-1)Jun(t)}$ was used to define severe drought events corresponding to the 1980 – 2009 study period. Those events were periods when $SPEI_{Aug(t-1)Jun(t)}$ dropped below the -0.3 value (i.e., -0.47, -0.59, -0.39, -0.36, -0.73, -0.50, and -0.32), and were associated to calendar years: 1983, 1986, 1989, 1992, 1995, 2005, and 2009, with 1995 being the driest year (Fig. 1 – right panel).

We used linear mixed-effects models (nlme R package; Pinheiro et al., 2016) to analyse the influence of the annual climatic variables (e.g. $T_{Jul(t-1)Aug(t)}$, $P_{Jul(t-1)Aug(t)}$, and $SPEI_{Aug(t-1)Jun(t)}$) on the growth (logBAI) of the four Holm oak vigour groups. The fixed part of the first model included the effect of the vigour group (healthy, low defoliated, highly defoliated, and dying), $T_{Jul(t-1)Aug(t)}$, $P_{Jul(t-1)Aug(t)}$, and the interactions vigour group x $T_{Jul(t-1)Aug(t)}$, vigour group x $P_{Jul(t-1)Aug(t)}$, and $T_{Jul(t-1)Aug(t)}$ x $P_{Jul(t-1)Aug(t)}$. The fixed part of the second model included the effect of the vigour group, $SPEI_{Aug(t-1)Jun(t)}$, and the interaction vigour group x $SPEI_{Aug(t-1)Jun(t)}$. Linear mixed-effects models were also used to account for the influence of the seasonal climatic variables ($T_{Nov(t-1)Feb(t)}$, $P_{Nov(t-1)Feb(t)}$, $SPEI_{Nov(t-1)Feb(t)}$, $T_{May(t)Jun(t)}$, $P_{May(t)Jun(t)}$, $SPEI_{May(t)Jun(t)}$) on the growth (logBAI) of the four Holm oak vigour groups. These six models (one per each seasonal climatic variable) had exactly the same structure as the previous two. For all eight models tree identification was introduced as a random effect and a first-order autoregressive covariance structure was used to account for temporal autocorrelation. To look for differences between vigour groups, the least-squares means were analysed applying a Tukey correction. The coefficients were estimated using the restricted maximum likelihood method (REML). The residuals of the models fulfilled the conditions of normality ($p > 0.05$). The selection of the final models was based on the Akaike's information criterion (AIC) (i.e. minimal models with the lowest AIC). In order to check if the multi-stem condition (i.e., the number of stems of each of the seventy Holm oaks; Table 1) influenced their response to climatic conditions, all saturated models included in the fixed part a multi-stem factor, but this explanatory variable was removed as it was always non-significant.

Superposed epoch analyses (SEA) (dplR R package; Bunn et al., 2016) were used to compare mean growth rates (RWI) between the four vigour groups during, before, and after severe drought events (Lough and Fritts, 1987). Specifically, SEA analyses were used to evaluate mean growth departures from selected severe drought events (i.e., 1983, 1986, 1989, 1992, 1995, and 2005) considering a temporal window of 2 years before (years -2, and -1), and after (years 1, and 2) these events (year 0). To estimate the confidence intervals ($p < 0.05$) of the plotted growth departures, 1000 sets of five years from each vigour group were randomly selected.

All variables were checked for normality (Shapiro-Wil test) and logarithm transformed if necessary (only in the case of BAI when used in linear mixed-effects models). When the normal distribution assumption was not met, nonparametric tests were used (e.g., DBH). Relationships for all statistical analyses were considered significant at $p < 0.05$. Statistical analyses, if not otherwise mentioned, were carried out with the R software (v. 3.3.1, 2016, The R Foundation for Statistical Computing).

RESULTS

Climate, crown, and growth temporal trends

Climate got drier between 1980 and 2009 in the study area, with temperature increasing significantly ($R^2 = 0.35$, $p < 0.001$) and precipitation not showing a significant temporal trend ($R^2 = 0.01$, $p = 0.538$) (Supplementary Fig. 2b).

The crown foliar percentage lost showed no important temporal changes. The values estimated in October 2010 (i.e., the year of sampling), were maintained within the next two years following sampling (May 2011, April 2012, and October 2012) (Fig. 1 – left panel).

The four Holm oak vigour groups did not show any significant temporal growth trends (healthy, $R^2 = 0.04$, $p = 0.303$; low defoliated, $R^2 = 0.00$, $p = 0.805$; highly defoliated, $R^2 = 0.00$, $p = 0.926$; dying, $R^2 = 0.01$, $p = 0.584$) (Fig. 1 – right panel). Still, BAI showed temporal variability with high values coinciding with wet periods (i.e., 1988, 1997, 2007), and low values coinciding with severe drought events (low $SPEI_{Aug(t-}$

$_{1)Jun(t)}$; i.e., 1986, 1995, 2005, 2009) (Fig. 1 – right panel). According to the Changepoint analyses, BAI trends of healthy, low defoliated, and highly defoliated vigour groups showed the following significant changes in mean: during drought years (i.e., 1986, 1995) these Holm oaks significantly reduced their growth, but managed to significantly recover afterwards (i.e., 1987, 1996) (Supplementary Fig. 3). Although a similar temporal BAI variability was observed also for the dying vigour group, the changes in mean were not significant (Supplementary Fig. 3).

Growth differences between vigour groups

DBH differed significantly among the four vigour groups ($H(3) = 15.441$, $p < 0.01$). Highly defoliated trees had significantly lower DBH values than healthy and low defoliated ones ($p < 0.05$), while dying trees had significantly lower DBH values than healthy ones ($p < 0.05$) (Table 1). BAI values also differed significantly among the four vigour Holm oak groups ($H(3) = 123.65$, $p < 0.001$). BAI values of highly defoliated and dying trees were always lower than the BAI values of healthy and low defoliated ones ($p < 0.001$). No significant differences were found between the healthy and low defoliated trees, and between the highly defoliated and dying ones (Table 1; Fig. 1 – right panel).

Climate-growth relationships

Holm oak trees from the four vigour groups tended to respond similarly to climatic variability (T, P, and SPEI), BAI being significantly influenced by both previous (t-1) and current (t) year climatic conditions (Fig. 2a, b, and c). Overall, most of the significant correlations occurred during winter (November [t-1] to February [t]), and late spring – early summer (May [t] to June [t]). Specifically, BAI was positively influenced by winter T (November [t-]) to February [t]), and negatively by late spring – early summer T (May [t] to June [t]) and summer T of the previous to growth year (August [t-1]) (Fig. 2a). BAI was positively influenced by P, as it follows: during winter (November [t-1] to January [t]), spring (May [t]), and summer (July [t]) of the current year of growth, and during summer (July [t-1]) of the previous to growth year (Fig. 2b). SPEI generally had a positive influence on BAI during winter (November [t-1] to January [t]), late spring - early summer (May [t] to June [t]), and August (t-1) of the previous to growth year (Fig. 2c).

The results of linear mixed-effects models indicated that Holm oaks responded significantly and positively to annual climatic conditions, i.e. $T_{Jul(t-1)Aug(t)}$ ($p < 0.01$), and $P_{Jul(t-1)Aug(t)}$ ($p < 0.001$), and negatively to the $T_{Jul(t-1)Aug(t)}$ x $P_{Jul(t-1)Aug(t)}$ ($p < 0.001$) interaction (Table 2), regardless of the vigour group. The annual $SPEI_{Aug(t-1)Jun(t)}$ climatic variable also had a significant and positive effect on the growth of the studied Holm oaks ($p < 0.001$) (Table 3), regardless of the vigour group. For this latter model, the least-squares means were lower for the highly defoliated vigour group than for the other three vigour groups, but significant differences were found only between the highly and low defoliated Holm oaks ($p < 0.05$).

Linear mixed-effects models including seasonal data showed that winter (November [t-1]) to February [t]) T conditions promoted growth ($p < 0.001$), while late spring - early summer (May [t] to June [t]) T conditions limit it ($p < 0.001$) (Table 3). Precipitation conditions had an overall positive and significant effect on Holm oak growth both during winter (November [t-1]) to February [t]) and during spring - early summer (May [t] to June [t]) ($p < 0.001$) (Table 3). Regarding SPEI, this climatic variable influenced significantly and negatively the growth of the four Holm oak vigour groups during winter November [t-1]) to February [t]), and positively during spring - early summer (May [t] to June [t]) ($p < 0.001$) (Table 3). None of all these relationships depended on the vigour group. For the seasonal P and SPEI models, the least-squares means were always lower for the highly defoliated Holm oaks than for the other three vigour groups, but significant differences were found only between the highly and low defoliated ones ($p < 0.05$).

Growth response to severe drought events

SEA analyses revealed that all vigour groups responded similarly to severe drought events (Fig. 3). Specifically, each of the four vigour groups of Holm oaks showed a significant, sharp growth (RWI) reduction during severe drought events (year 0; $p < 0.05$): 58% for the healthy Holm oaks, and ca. 50% for the low defoliated, highly defoliated, and dying ones. Two years after the severe drought events, all vigour groups managed to significantly recover their growth rates ($p < 0.05$), registering similar to pre-drought RWI values (Fig. 3).

DISCUSSION

Secondary growth of the drought-tolerant Holm oak varied between vigour groups but not its responsiveness to climatic variability, nor its resilience following severe drought events. Within the studied coppice stand, Holm oaks showing different stages of decline cope with the increased aridity caused by warming coupled with no parallel increases in rainfall (Supplementary Fig. 2b; Granda et al., 2013). As expected, although none of the four vigour groups showed significant temporal growth trends between 1980 and 2009, less vigorous Holm oaks (i.e., highly defoliated and dying) grew significantly less than the most vigorous ones (i.e., healthy and low defoliated). This pattern persisted during the whole study period.

Despite the lack of numeric records of Holm oak defoliation rates preceding the sampling date (i.e., October 2010), the fact that the studied trees maintained the same crown foliar percentage levels two years after, points out towards a synchrony between growth rates (low or high) and crown condition (less or more vigorous). Reduced growth rates systematically followed the severe drought events registered during the study period as droughts reduce carbon allocation to stem growth through stomatal closure, which eventually leads to crown defoliation, a common pattern found for both conifer and broadleaf species (Dobbertin, 2005). According to previous findings, crown defoliation following extreme droughts can prolong up to seven years after these events (Galiano et al., 2012), which suggests that the observed Holm oak defoliation could have occurred before 2010 given the repeated severe drought events registered. Actually, the 2005 severe drought event resulted in strong defoliation and mortality of Holm oaks in the studied coppice stand (Valladares F., personal observation), which supports our hypothesis about the presence of important defoliation rates before 2010.

Growth of Holm oak was similarly influenced by climatic variability regardless of the crown condition. According to other results from Mediterranean forests (Natalini et al., 2016) warmer winter temperatures enhanced growth of Holm oaks while high late spring – early summer temperatures impaired it. Contrary to our results, Granda et al. (2013) showed that Holm oak was favoured by high spring temperatures, although our study site is more arid than the one considered in that study. Interestingly, we did not find any significant climate-growth relationship for the early-spring (March-April, [t]), despite that Holm oak individuals usually register high growth rates during this period (Corcuera et al., 2004; Gea-Izquierdo et al., 2009; Granda et al., 2013; Natalini et al., 2016). This result could be explained by low early spring precipitation, especially compared to those in May that almost doubled March values (Supplementary Fig. 2a). On the other hand, higher precipitation and SPEI favoured Holm oak growth, an effect that was more evident during the winter and late spring – early summer periods. Spring and summer climatic conditions are expected to be the most important variables affecting tree growth in the Mediterranean region, characterized by hot and dry summers (Granda et al., 2013), as water availability is considered to be the main limiting factor for plant growth (Cherubini et al., 2003; Martínez-Vilalta et al., 2008). In fact, cambial activity is usually affected (i.e., reduced, or stopped) during the summer season in these regions (Cherubini et al., 2003). Nevertheless, Holm oak trees are able to maintain carbon gain during this period of the year (Corcuera et al., 2005). The capacity of Holm oak to tolerate the dry summer season is supported by our results that showed significant positive responses to late spring – early summer precipitation and SPEI, in accordance with previous studies (Corcuera et al., 2004; Gea-Izquierdo et al., 2011; Barbeta et al., 2013).

The climatic conditions during the winter period (i.e., usually cold) play an important role in Mediterranean regions, highlighting the influence of the timing of precipitation and temperature increases several months before growth resumption (Corcuera et al., 2004; Natalini et al., 2016). Winter climatic variables had a positive effect on the growth of all Holm oak trees, similar to the results reported by Granda et al. (2013). These results point out that this species largely depends on favourable winter climate conditions (Barbeta et al., 2013; Granda et al., 2013). For instance, enough precipitation assures the crucial replenishment of soil water reservoirs (Campelo et al., 2009; Gea-Izquierdo et al., 2011; Abrantes et al., 2013), and mild winter temperatures may allow for extended periods of photosynthesis (Granda et al., 2014). Winter photosynthesis and the associated carbon gain allow Holm oaks to recover carbon reserves (Gea-Izquierdo et al., 2011) and ensures the annual carbon balance needed to form wood during the following growing season (Savé et al., 1999), and to minimize drought-induced decline (Galiano et al., 2012; Rosas et al., 2013).

The severe drought events registered in the study area (1983, 1986, 1989, 1992, 1995, and 2005) acutely affected tree growth independently of their defoliation state. All Holm oak trees registered very low growth rates under these water stress conditions, a typical pattern for oaks experiencing drought (Corcuera et al., 2004; Di Filippo et al., 2010; Barbeta et al., 2013; Natalini et al., 2016). However, only two years after the severe drought events ceased, Holm oaks, independent of their crown condition, were able to recover to previous to drought growth rates, a pattern previously found for this species (Granda et al., 2013). Drought-induced defoliation rates in *Quercus ilex* are associated with low concentrations of stored non-structural carbohydrates that may impede trees to recover after drought events (Galiano et al., 2012; Rosas et al., 2013). We have no proof of such depletion in our study individuals, but given the resilience shown by all vigour groups, we suspect that Holm oaks studied here either do not have this limitation or are able to rapidly accumulate, mobilize and invert available carbohydrate reserves into growth when conditions become favourable (Sala et al., 2012). The observed post-drought rebound in Holm oak growth highlights the ability of this species to overcome stressful conditions (i.e., drought) independently of its growth and current defoliation rates. Nevertheless, despite the resilience shown by all vigour groups, the most defoliated trees showed persistent low growth. In fact, the growth rates registered by the dying individuals were so low that, despite recovery after the severe drought events, these changes were not detected through the Changepoint analyses. Hence, our results suggest that if drought events become more frequent and intense (IPCC, 2014), the time period needed for Holm oak reserves to recover may be too long, leading to a progressive loss of resilience (Galiano et al., 2012) and increased decline and/or mortality rates (Gea-Izquierdo et al., 2011; Granda et al., 2013; Camarero et al., 2015b; Camarero et al., 2016; Natalini et al., 2016).

To conclude, our study shows that less vigorous Holm oaks (i.e., highly defoliated and dying) grow significantly less than their more vigorous neighbours (i.e., healthy and low defoliated). These patterns were persistent over the past three decades (1980-2009) and suggest permanent growth reduction for the less vigorous individuals. Reduced growth rates are frequently associated with the process of tree mortality (Cailleret et al., 2017). Therefore, our results support the use of growth data to detect early-warning signals of forest decline and swiftly design management plans to mitigate climate change effects. Despite these differences, all vigour groups responded similarly to climatic variability, with winter season having a strong effect on Holm oaks growing in this Mediterranean coppice stand, and contributing together with the spring and summer periods to the annual carbon budget and wood formation during subsequent seasons. Moreover, the high resilience that all Holm oak vigour groups have shown following severe drought events points out the efficiency of this evergreen species to overcome stressful conditions. Still, as reduced growth rates are frequently associated with the process of tree mortality, we think that the less vigorous Holm oaks might not be able to cope with future water stress conditions, leading to increased mortality rates among this emblematic Mediterranean species.

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Table 1 – Main characteristics of the four Holm oak vigour groups: healthy, low defoliated, highly defoliated, and dying. Age comparisons between the four vigour groups are based on one-way ANOVA analyses followed by a Tukey's Honest Significant Difference (HSD) *post hoc* test. BAI and DBH comparisons between vigour groups are based on Kruskal Wallis analyses followed by a pairwise Wilcoxon test with a Bonferroni correction.

Vigour group	**Defoliation (%)**	**No. of trees**	**Mean no. of stems per tree**	**Mean age (years)**	**Mean BAI (cm^2) 1980-2009**	**Mean DBH (cm)**
Healthy	0	14	5 (4.31)	44 (9.79)^a	8.23 (5.73)^a	22.61 (4.65)^a
Low defoliated	< 25	21	4 (4.12)	47 (11.08)^a	8.84 (7.78)^a	22.35 (6.32)^{ab}
Highly defoliated	25 – 70	19	4 (3.72)	40 (8.20)^a	5.41 (3.89)^b	17.30 (4.47)^c
Dying	70 - 100	16	3 (2.05)	39 (9.11)^a	5.59 (3.29)^b	17.84 (3.47)^{bc}

* Values in brackets represent standard deviations

* Different letters indicate significant differences between vigour groups

* *DBH*, diameter at breast height; *BAI*, basal area increment

Table 2 – Summary of the linear mixed-effects model (estimates ± SE) in which logBAI varied as a function of the vigour group (highly, low defoliated, highly defoliated, and dying), climatic variables ($T_{Jul(t-1)Aug(t)}$, and $P_{Jul(t-1)Aug(t)}$), and the interactions vigour group x climatic variables, and $T_{Jul(t-1)Aug(t)}$ x $P_{Jul(t-1)Aug(t)}$.

Model	**Estimates ± SE**
Intercept	**-3.845 ± 1.69***
Low defoliated	0.437 ± 1.23
Highly defoliated	-1.295 ± 1.26
Dying	0.183 ± 1.31
$T_{Jul(t-1)Aug(t)}$	**0.275 ± 0.10****
Low defoliated x $T_{Jul(t-1)Aug(t)}$	-0.017 ± 0.08
Highly defoliated x $T_{Jul(t-1)Aug(t)}$	0.063 ± 0.08
Dying x $T_{Jul(t-1)Aug(t)}$	-0.020 ± 0.08
$P_{Jul(t-1)Aug(t)}$	**0.020 ± 0.00*****
Low defoliated x $P_{Jul(t-1)Aug(t)}$	-0.000 ± 0.00
Highly defoliated x $P_{Jul(t-1)Aug(t)}$	-0.000 ± 0.00
Dying x $P_{Jul(t-1)Aug(t)}$	-0.000 ± 0.00
$T_{Jul(t-1)Aug(t)}$ x $P_{Jul(t-1)Aug(t)}$	**-0.001 ± 0.00*****

Significant relationships at 0.05, 0.01, and 0.001 probability levels are market with *, **, ***, and in bold. Abbreviations: *SE*, standard error; *(t-1)*, previous to growth year; *(t)*, current year of growth.

Table 3 – Summary of the linear mixed-effects models (estimates ± SE) in which logBAI varied as a function of the vigour group (highly, low defoliated, highly defoliated, and dying), climatic variables (SPEI$_{Aug(t-1)Jun(t)}$, T$_{Nov(t-1)Feb(t)}$, P$_{Nov(t-1)Feb(t)}$, SPEI$_{Nov(t-1)Feb(t)}$, T$_{May(t)Jun(t)}$, P$_{May(t)Jun(t)}$, and SPEI$_{May(t)Jun(t)}$), and the interactions vigour group x climatic variables.

Model (Climatic variable)	**Intercept**	**Low defoliated**	**Highly defoliated**	**Dying**	**Climatic variable**	**Low defoliated x Climatic variable**	**Highly defoliated x Climatic variable**	**Dying x Climatic variable**
SPEI$_{Aug(t-1)Jun(t)}$	**1.889 ± 0.13*****	0.021 ± 0.16	**-0.411 ± 0.17***	-0.318 ± 0.17	**0.803 ± 0.06*****	-0.137 ± 0.08	-0.145 ± 0.08	-0.114 ± 0.09
T$_{Nov(t-1)Feb(t)}$	0.009 ± 0.25	0.161 ± 0.33	-0.439 ± 0.33	0.138 ± 0.35	**0.244 ± 0.03*****	-0.017 ± 0.04	0.005 ± 0.04	-0.060 ± 0.04
P$_{Nov(t-1)Feb(t)}$	**1.471 ± 0.13*****	0.115 ± 0.17	**-0.391 ± 0.18***	-0.262 ± 0.19	**0.002 ± 0.00*****	-0.001 ± 0.00	-0.000 ± 0.00	-0.000 ± 0.00
SPEI$_{Nov(t-1)Feb(t)}$	**1.835 ± 0.13*****	0.028 ± 0.16	**-0.400 ± 0.17***	-0.308 ± 0.17	**-0.190 ± 0.04*****	0.007 ± 0.05	0.024 ± 0.05	0.037 ± 0.05
T$_{May(t)Jun(t)}$	**4.885 ± 0.35*****	-0.021 ± 0.46	-0.683 ± 0.47	-0.622 ± 0.49	**-0.158 ± 0.02*****	0.003 ± 0.02	0.015 ± 0.02	0.016 ± 0.02
P$_{May(t)Jun(t)}$	**1.578 ± 0.13*****	0.031 ± 0.17	**-0.377 ± 0.18***	-0.246 ± 0.18	**0.004 ± 0.00*****	-0.000 ± 0.00	-0.000 ± 0.00	-0.001 ± 0.00
SPEI$_{May(t)Jun(t)}$	**1.851 ± 0.13*****	0.029 ± 0.16	**-0.403 ± 0.17***	-0.313 ± 0.17	**0.253 ± 0.03*****	-0.014 ± 0.03	-0.038 ± 0.03	-0.061 ± 0.04

Significant relationships at 0.05, 0.01, and 0.001 probability levels are market with *, **, ***, and in bold. Abbreviations: *SE*, standard error; *(t-1)*, previous to growth year; *(t)*, current year of growth.

FIGURE CAPTIONS

Fig. 1 – Holm oak defoliation (%) during the year of sampling (October 2010; marked with a solid black arrow), and in the following two years (May 2011, April 2012, and October 2012) (left panel). Temporal (1980 – 2009) basal area increment (BAI) trends of healthy, low defoliated, highly defoliated, and dying Holm oak trees, and of the $\mathrm{SPEI}_{\mathrm{Aug(t-1)Jun(t)}}$ (standardized precipitation-evapotranspiration index) (right panel); *error bars* show standard errors.

Fig. 2 – Climate-growth relationships of healthy, low defoliated, highly defoliated, and dying vigour groups, based on the correlation functions implemented in the DendroClim 2002 software (Biondi and Waikul 2004). Monthly climatic data are represented by temperature (T°C; a), precipitation (P mm; b), and standardized precipitation-evapotranspiration index (SPEI; c). Time interval covers months from previous to growth year (January [t-1] to December [t-1]; left panels) and current year of growth (January [t] to December [t]; right panels). The vertical solid line separates between previous to growth year (t-1) and current year of growth (t) periods. All given relationships are significant ($p < 0.05$).

Fig. 3 – Superposed epoch analyses showing growth (RWI, ring width indices) departures from mean values given a set of key (severe drought events; year 0 on the x axis), and lagged events: two years before (-2, and -1 on the x axis) and two after the severe drought events (2, and 1 on the x axis). Values were calculated considering the severe drought events, i.e. 1983, 1986, 1989, 1992, 1995, and 2005 (see Materials and Methods), registered within the 1980 – 2009 study period. Black and grey columns indicate significant ($p < 0.05$) and no significant ($p > 0.05$), respectively, growth departures from year 0, considering random simulations.

Supplementary Fig. 1 – *Quercus ilex* L. *subsp. ballota* [Desf.] (Holm oak) wood core showing this species' diffuse-to semi-ring-porous wood with multiseriate rays, and tree-rings.

Supplementary Fig. 2 – Gaussian diagram (1973 – 2009) (a), and temporal (1980 – 2009) trends of temperature (T, °C) and precipitation (P, mm) (b). All climatic data were available from the Cuatro Vientos meteorological station.

Supplementary Fig. 3 – Basal area increment (BAI) changes in mean values for healthy, low defoliated, highly defoliated, and dying Holm oak trees, according to Changepoint analyses results for the 1980 – 2009 period. Horizontal solid black lines mark the fitted mean as it follows: if broken, then significant changes in mean are present (e.g., healthy, low defoliated, and highly defoliated vigour groups); if continuous, then no significant changes in mean are present (e.g., dying vigour group).