Trees
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Effect of ecological factors on intra-annual stem girth increment of holm oak

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Abstract

Key message **The intra-annual stem girth increment of *Quercus ilex* is mainly driven by water availability and secondly by temperature. Tree size and competition modulate the growth response to climate.**

Abstract Holm oak (*Quercus ilex* ssp. *ballota* [Desf.] Samp.) is the most widespread species in the Iberian peninsula, being one of the most representative trees in forests and open woodlands. The analysis of stem girth increment of holm oak may provide valuable information about how Mediterranean ecosystems will respond to the forecasted climate changes. However, due to the variability of the Mediterranean climate, the knowledge of intra-annual patterns of growth is needed for a better understanding of the influence of the climatic variables at this scale. To this end, we used band dendrometers to measure monthly stem girth increments of 96 holm oak trees from 2003 to 2010, located in open woodlands and dense Mediterranean forests in southwestern Spain. We assessed the effects of climate, competition, topography, and initial stem diameter on stem girth increment. The major stem increment periods were in spring and autumn whereas increment rates were very low or even negative in winter and summer. Spring was not every year the season with the higher stem increments, but autumn when spring was very dry. Higher precipitation, soil moisture, and relative humidity had significant positive effects on stem increment, whereas higher temperature, reference evapotranspiration, and solar radiation had significant negative effects. Initial tree diameter and competition from nearby trees partly explained significant differences in stem increment of individual trees. Therefore, the forecasted climatic changes, in which decreased rainfall in spring and increased summer drought are expected in the Mediterranean region, may be a significant threat to the *Q. ilex* ecosystems.

Keywords Ecological modeling · *Quercus ilex* · Stem growth · Climate · Competition

Introduction

Holm oak (*Quercus ilex* L.) is the most widespread *Quercus* species in the Iberian Peninsula where it covers an area of about 3 million ha (Bravo et al. 2008). It occurs in different ecosystems, from sea level up to 2,000 m, in limestone to siliceous rock systems, and it is able to withstand the high temperatures and summer droughts of the Mediterranean region (Rodà et al. 1999). Forests of holm oak and cork oak (*Quercus suber* L.) in the western Iberian Peninsula have been transformed into open woodlands with densities of 20–100 trees ha^{-1} and canopy covers of 10–50 %, with an understory of croplands, grasslands, and shrublands where cattle, sheep, pigs, and goats are raised (San Miguel 1994). These systems have been harvested (fuelwood, acorns, grasses, livestock) for more than 4,500 years (Stevenson and Harrison 1992) and even nowadays have an important role in local economies. Open woodlands of *Quercus* in southwestern Spain are also highly diverse ecosystems, create unique landscapes and constitute a refuge for many endangered species, including the Spanish imperial eagle *Aquila adalberti*, the cinereous

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vulture *Aegypius monachus*, and the Iberian lynx *Lynx pardinus* (Carrete and Doñázar 2005).

Forestry studies have traditionally measured tree growth as the main indicator of yield. However, measurements of tree growth also provide information about health and vigor of the forests, phenological processes, the influence of management systems, or resource competition (Gea-Izquierdo et al. 2009). In a time when climate change is affecting the dynamics of different ecosystems, the analysis of stem growth in a species such as holm oak may provide valuable information about how these ecosystems will respond to forecasted climate changes, where temperature will increase and precipitation will decrease (IPCC 2007). Hence, measurements of tree growth and its ecological determinants are essential for planning sustainable management of these Mediterranean ecosystems.

Some previous studies have examined *Quercus ilex* growth patterns, but many of them have been focused on *Quercus ilex* ssp. *ilex*, which is ecologically and genetically distinct and has a different and more limited geographical distribution than *Quercus ilex* ssp. *ballota* (Lumaret et al. 2002). Previous studies have employed dendrochronological techniques (e.g., Zhang and Romane 1991; Cherubini et al. 2003; Gea-Izquierdo et al. 2009, 2011; Campelo et al. 2010) for annual measurements of growth. However, monthly measurement of stem growth is needed to provide valuable information on growth during different seasons in a Mediterranean area where climate changes among and within years, and regarding the trade-offs of growth with other phenological processes such as acorn production (Mund et al. 2010). The analysis of the relationship of climatic variables with intra-annual stem growth of *Q. ilex* will provide a more complete understanding of the influence of climate on growth (Campelo et al. 2007; Gutiérrez et al. 2011) and of the possible effects of climatic change on phenology, structure, and even geographic distribution of this species.

Band dendrometers provide accurate measurements of stem girth increment at different temporal scales and are especially useful for intra-annual studies. These devices measure the increment of the entire cross-section of a tree. Therefore, they are more accurate than techniques that sample one or two points of the stem only (e.g., analysis of cores or microcores, electronic point dendrometers), which can be affected by local changes in the xylem or bark (Gutiérrez et al. 2011). It is especially important to measure the entire cross-section in anatomically complex trees such as *Q. ilex* (Gea-Izquierdo et al. 2011), which has frequent medullar rays, false rings and growth eccentricity (Cherubini et al. 2003; Campelo et al. 2007). Nevertheless, band dendrometers also register expansions and contractions of the stem due to changes in hydration (Gutiérrez et al. 2011), so their use might be combined with other techniques, such as ecosystem net carbon and water vapor flux measurements with eddy covariance system (Mund et al. 2010) to determine accurately the timing of growth cycles. In addition, band dendrometers can also be useful to assess remote sensing data at monthly scale (e.g., NDVI values) and they have also been used in ecological studies and dendrochronology (Gea-Izquierdo et al. 2011).

In harsh environmental conditions, such as the Mediterranean ones, resource competition (especially for water) can reduce the growth rates of trees. If forest managers understand how trees respond to competition, they can adjust stand density according to the climatic conditions and thereby improve the response to drought (Moreno and Cubera 2008). Moreover, *Q. ilex* trees in hydrologically favorable locations will respond differently to climatic factors such as drought (Miller et al. 2001). Nevertheless, no studies have yet employed intra-annual measurements of tree growth to assess the importance of competition and microtopography in forest stands.

The main questions that we wanted to answer in this study were:

(a) How is the intra-annual stem girth increment pattern of holm oak (*Quercus ilex* ssp. *ballota* [Desf.] Samp.) in open woodlands and forests of southwestern Spain?
(b) Are there differences in intra-annual stem increment among plots? Do trees within each plot have similar increment rates?
(c) How does climate drive intra-annual stem increment?
(d) Do the competition, topography and stem size have a significant influence on intra-annual stem increment?

Materials and methods

Field plots

This study was performed in three experimental plots in the Huelva province of southwestern Spain (Table 1). The Huerto Ramirez (HR) plot is in open woodland of *Q. ilex* with soils characterized as acrisols, alisols and lixisols, or less developed as regosols and cambisols (IUSS Working Group 2007); a sparse understory of mainly *Cistus ladanifer* and *Cistus crispus*, and an abundant herbaceous layer of mainly grasses. The San Bartolomé (SB) plot is in an open woodland of *Q. ilex* that is characterized by soils that are endoleptic regosols (episkeletic) or deeper profiles as endoleptic luvisols (dystric) in depositional or concave areas (IUSS Working Group 2007); a very scarce understory due to frequent tillage, and an abundant herbaceous layer of mainly grasses. The Hinojos (HI) plot is in a

Table 1 General and dendrometric characteristics of study plots

Plot	Coordinates (UTM, Zone 29)	Area (ha)	Density (trees ha^{-1})	Mean diameter ± SD(cm)	Mean height ± SD (m)	Sample size (trees)	Species
Huerto Ramírez	X:644288 m Y:4161376 m	2.94	73.0	30.02 ± 7.68	6.58 ± 1.58	55	*Q. ilex*
San Bartolomé	X:669638 m Y:4145966 m	2.70	36.0	35.40 ± 7.23	6.54 ± 1.08	32	*Q. ilex*
Hinojos	X:728082 m	1.78	17.3	24.34 ± 9.11	7.20 ± 1.90	9	*Q. ilex*
	Y:4133575 m		84.4	28.39 ± 8.39	8.11 ± 1.93	n.a.	*Q. suber*

SD standard deviation, *Q. ilex Quercus ilex*, *Q. suber Quercus suber*, *n.a.* not applicable

Quercus suber stand that has some scattered *Q. ilex* trees and is characterized by soils with complex profiles classified as haplic regosol (dystric) over stagnic regosol (dystric) (IUSS Working Group 2007), and an understory that consists of a dense layer of *Cistus salvifolius* and *Halimium halimifolium* with scattered individuals of *Pistacia lentiscus*, *Phillyrea angustifolia* and *Chamaerops humilis*.

The climate of all three plots is Mediterranean, with highly variable temperature and rainfall within and among years. The nearby ocean modulates temperature and increases the precipitation with respect to more continental areas. There were no large monthly variations in temperature during the study period (2003–2010), but there were large monthly and annual changes in precipitation (Figs. 1, 2; Table 2). In particular, the annual precipitation in HI was only 274 mm (156 mm in autumn) during 2005, but was 1,011 mm in 2010. The year 2009 was also remarkable: in HI (651 mm total rain) more than 50 % of the rain was in December and only 36 mm was in the spring.

Measurement of stem girth increment

A total of 96 aluminum band dendrometers (system developed by the University of Huelva) were installed at breast height (1.30 m), with care taken to avoid stem deformities. Details of band dendrometers' theory and construction are available in Keeland and Young (2014). Trees were selected within plots using stratified sampling so that different diametric classes were considered. There were 55 trees in HR, 32 trees in SB, and 9 trees in HI (which only had scattered *Q. ilex* trees) (Table 1). Measurements were recorded each month with a digital caliper (0.01 mm accuracy) in SB and HI from 2003–2010, and in HR from 2006–2010. Because there were differences in measurement dates and in the number of days per month, average daily increments for each tree between the first day and the last day of each month were calculated. Girth increment data were not transformed into diameter increment because *Q. ilex* is a species with high within-tree variability in girth stem growth and then the stems were not enough cylindrical to assume diameter transformation. Hence, girth increment data of entire cross-sections were used instead of diameter increment.

Dendrometry, hydrological parameters and competition indexes

Stem diameter at breast height, tree height (using a Vertex III, Haglöf Sweden AB), and topographic location (using a topographical total station Sokkia 3B) were measured for all 96 trees. Based on topographic location and a digital elevation model (Junta de Andalucía 2005), three hydrological parameters were calculated for each tree: flow length (FL), specific catchment area (SCA), and wetness index (WI) (Barling et al. 1994). Based on the location and size of each tree, 725 distance-dependent competition indexes were calculated in four groups, as described by Vázquez-Piqué and Pereira (2004): Area Overlapping Indexes (AOI), Distance-weighted Ratio (DR), Punctual Density (PD), and Area Potentially Available (APA). Hydrological parameters were calculated with ArcGIS ver. 9.2 (ESRI) and competition indexes with INCO ver. 1.0 (Vázquez-Piqué et al. 2001).

Climatic parameters and soil moisture

Two meteorological stations (HOBOH21-001) were installed in HR and HI for recording of temperature and relative humidity (Onset sensor S-THB-M002), precipitation (Onset rain gauge S-RGB-M002), wind speed and direction (Onset sensor S-WCA-M003), and photosynthetically active radiation (PAR, Onset silicon pyranometer S-LIB-M003) every 15 min. Reference evapotranspiration (ET_0) was calculated by the FAO Penman–Monteith method (Allen et al. 1998). Climatic data for SB were from the nearby Gibraleón meteorological station (37°24′49″N; 7°03′31″W; 169 m.a.s.l., Agroclimatic Information Network, Junta de Andalucía, available at http://www.

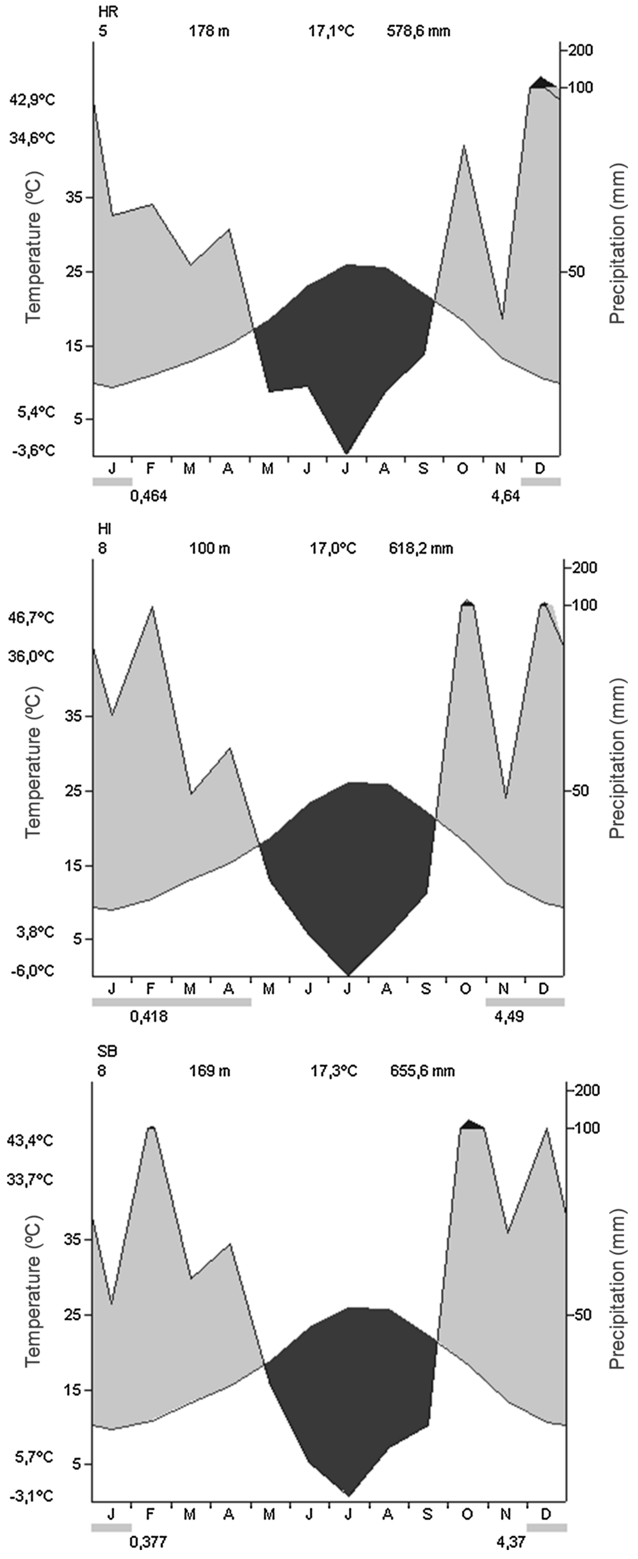


Fig. 1 Walter–Lieth climate diagrams of plots in Huerto Ramírez (HR), Hinojos (HI) and San Bartolomé (SB) during the study period

juntadeandalucia.es/agriculturaypesca/ifapa/ria/servlet/FrontController?action=Static&url=coordenadas.jsp&c_provincia=21&c_estacion=3), which provided temperature, precipitation, relative humidity (daily average, maximum, and minimum), wind speed and direction, PAR, and ET_0.

For analysis of soil moisture, 9 moisture sensors (ECH2O-20, Decagon Devices Inc.) were placed at 4 locations in the HR plot at depths of 5–25 cm, at 3 locations (matching the locations above) at depths of 25–45 cm, and at one location in SB at depths of 5–25 and 25–45 cm. Data were registered every 30 min. Calibration curves were performed in laboratory (eight calibration points per sensor) as described by Cobos (2010) to obtain percent soil moisture from measured voltage. The regression r^2 values of calibration ranged from 0.92 to 0.99. At HI, two capacitance sensors (C-Probe Corp.) were placed at depths of 10 and 30 cm at the same locations, and soil moisture was measured every 15 min. Relative Extractable Water (REW) (Granier 1987) was calculated between 5–25, 25–45, and 5–45 cm depths as:

$$\mathrm{REW} = \frac{\mathrm{WC} - \mathrm{WC}_{\mathrm{min}}}{\mathrm{WC}_{\mathrm{FC}} - \mathrm{WC}_{\mathrm{min}}} \qquad (1)$$

where WC is the water content (mm), $\mathrm{WC}_{\mathrm{min}}$ is the minimum water content (mm) registered during the study period, and $\mathrm{WC}_{\mathrm{FC}}$ is the water content at field capacity (mm), i.e., the registered water content 48 h after an intense rainfall event that saturated the soil. Soil temperature at 10 cm depth was measured simultaneously in all plots.

Data analysis

A linear mixed model with the following initial structure was used for data analysis:

$$y_{ijlm} = \mu + b_{i(j)} + \alpha_j + \gamma_l + \tau_m + (\alpha|\gamma|\tau)_{jlm} + e_{ijlm} \qquad (2)$$

where y_{ijlm} is the girth increase of tree i at plot j in the month l of year m (mm day^{-1}); μ is the general mean; $b_{i(j)}$ is a tree random effect within each plot with $i = 1, 2,\ldots, 0.55$ and $j = 1, 2, 3$ under the hypothesis $b_{i(j)} \sim N(0, \mathbf{G})$; α_j is a plot fixed-effect with $j = 1, 2, 3$; γ_l is a month fixed-effect with $l = 1, 2,\ldots, 12$; τ_m is a year fixed-effect with $m = 2003, 2004,\ldots, 2010$; $(\alpha|\gamma|\tau)_{jlm}$ is all possible double and triple interactions between fixed effects; and e_{ijlm} is residual error under the hypothesis $e_{ijlm} \sim N(0, \mathbf{R})$. The initial hypothesis of the independence of observations is not logical because spatial correlations can occur in the growth of trees from the same plot and temporal correlations can occur because observations in consecutive months have more similar growth values than those from non-consecutive months.

The following procedure was used to select the best model structure:

1. The model was adjusted by consideration of tree random effect, the presence of temporal correlations

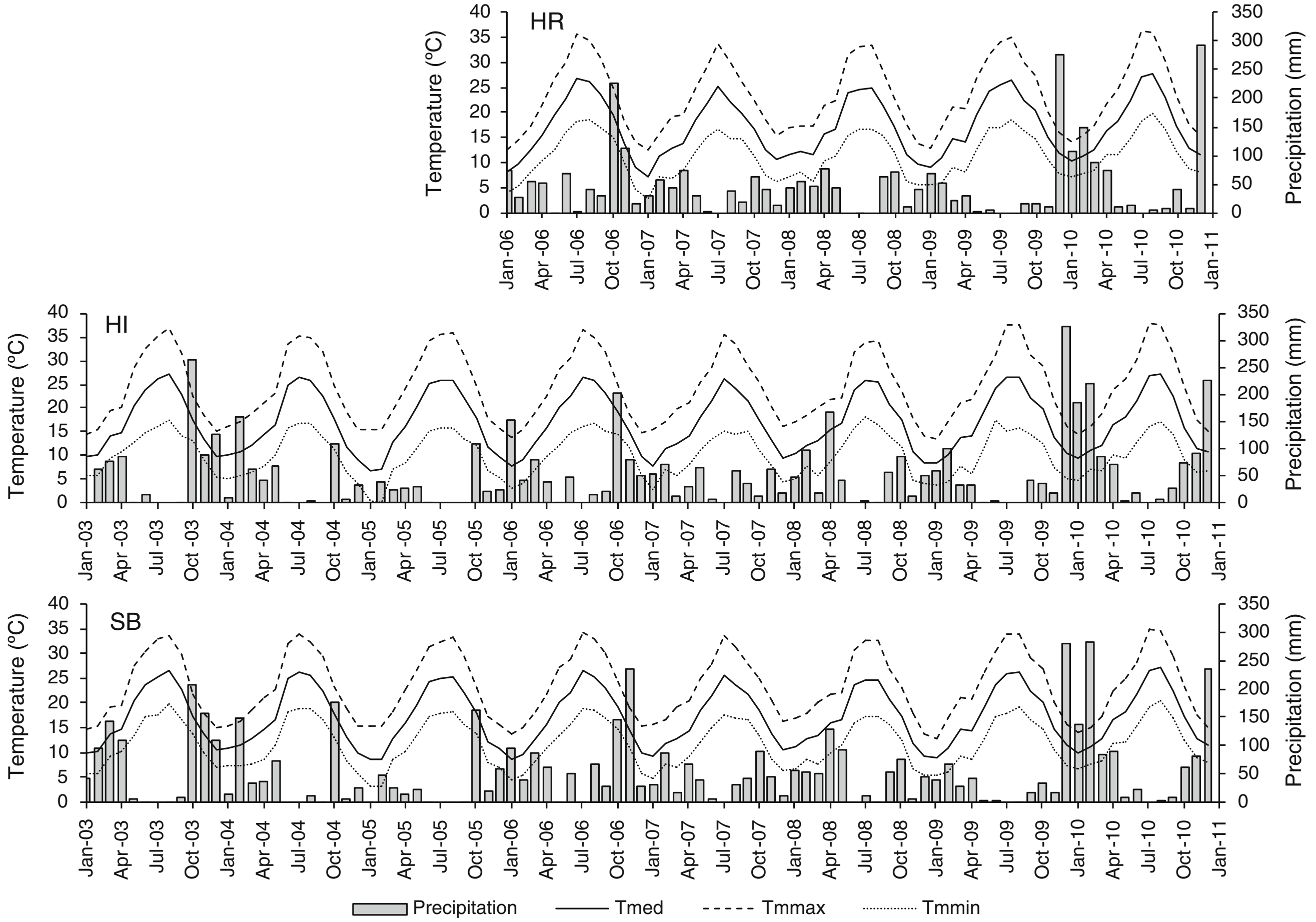


Fig. 2 Monthly precipitation and temperatures of plots in Huerto Ramírez (HR), Hinojos (HI) and San Bartolomé (SB) during the study period. *Tmed* mean temperature; *Tmmax* mean of the maximum daily temperature, *Tmmin* mean of the minimum daily temperature

Table 2 Precipitation and temperature of the three plots during the study period

Year	Precipitation (mm)						Temperature (°C)								
	HI		SB		HR		HI			SB			HR		
	P	P_{mn}	P	P_{mn}	P	P_{mn}	T_M	T_m	T	T_M	T_m	T	T_M	T_m	T
2003	780	534	884	634			36.9	5.8	17.5	33.8	5.8	17.5			
2004	495	293	536	343			35.3	4.0	16.9	33.9	6.0	17.4			
2005	274	212	362	251			35.9	0.0	16.8	33.3	3.2	17.1			
2006	734	487	850	684	713	592	36.5	3.0	17.3	34.4	4.5	17.4	35.6	4.2	17.4
2007	424	280	473	341	421	318	35.7	2.5	16.5	33.8	4.9	17.0	33.9	2.8	16.1
2008	577	381	584	424	458	315	34.4	3.9	16.7	32.7	5.7	17.0	33.4	5.5	16.8
2009	651	166	538	150	502	108	37.6	3.6	17.5	34.1	5.7	17.9	35.0	5.7	18.0
2010	1011	378	1019	362	799	252	38.0	4.7	16.9	34.9	6.7	17.5	36.3	7.1	17.6

P annual precipitation, P_{mn} precipitation from March to November, T_M mean of the maximum temperatures of the hottest month, T_m mean of the minimum temperatures of the coldest month, *T* mean annual temperature

between observations of different months for each tree and year, and the presence of heterogeneous variances in different months of the year. Hence, **G** was initially considered as a diagonal matrix and **R** as a block diagonal matrix, with each block corresponding to a 12 × 12 submatrix of observations taken in one year in each tree. We considered the following alternatives for the structure of blocks in the **R** matrix: autoregressive order 1, autoregressive heterogeneous, Toeplitz up to 5 bands, heterogeneous Toeplitz up to 5 bands, unstructured up to 5 bands, Huynh–Feldt, compound symmetry, compound symmetry heterogeneous, dependent covariance, and first-order factor analytic (Littell et al. 2006). Variance components for each structure were estimated by restricted maximum likelihood (REML) (Patterson and Thompson 1971) and model selection was based on the Akaike information criterion (AIC, Akaike 1974).

2. The significance of the tree random effect was determined by a likelihood ratio test, as the reduction of the statistic $-2 \times \log$ likelihood (-2LL), after introducing the tree random effect follows χ^2 distribution with 1° of freedom. An α value of 0.05 was considered an indication of improvement in the covariance structure.
3. If the tree random effect was significant, the presence of spatial correlation was determined. In particular, the following isotropic exponential covariance model was used:

   $$\operatorname{cov}\left(b_{i(j)}, b_{i'(j)}\right) = \sigma_b^2 \rho^{dii'} \tag{3}$$

   where $d_{ii'}$ is the distance between trees i and i' in location j; σ_b^2 is the variance component at tree level; and ρ is a parameter to be estimated with $|\rho| < 1$. Spatial covariance between observations of different locations was considered zero.
4. After selection of the best variance–covariance structure, the fixed effects were estimated by generalized least squares (GLS) (Searle 1971) and the significance of each effect was determined with an F test. Only significant effects ($\alpha = 0.05$) were retained in the model. Comparisons among levels of significant effects were determined by the Scheffé test.
5. If there was a significant tree effect, then tree diameter at breast height, hydrological parameters, and competition indexes were introduced to the model as covariates as additive linear effects and each significance was assessed with an F test. To analyze the significance of covariates, variance components were estimated by maximum likelihood (ML).
6. If there was a significant year × month, plot × month, or plot × year × month interaction, climatic and soil moisture data were added to the model as covariates at each of the significance levels to explain the categorical effects. Climatic variables at the month, year, or plot level were not introduced due to the small degrees of freedom at those levels. The covariates were introduced as additive linear effects after deleting the fixed categorical interaction at that level. All statistical analysis was performed with SAS/ETS (ver. 9.2).

Table 3 Significant fixed effects in the final model

Effect	F	$P_r > F$
Month	145.74	<0.0001
Year	58.07	<0.0001
Year × month	48.17	<0.0001
Plot	30.66	<0.0001
Plot × year × month	14.82	<0.0001
Plot × month	14.53	<0.0001
Plot × year	8.29	<0.0001

F *F*-statistic

Table 4 Variance components in the final model and percentage of variance accounted for by tree effect

Month	Variance components			% of variance absorbed by tree effect
	Tree	Month	Total	
Jan	0.017	0.244	0.261	6.52
Feb		0.444	0.461	3.69
Mar		0.676	0.693	2.45
Apr		0.846	0.863	1.97
May		0.623	0.640	2.66
Jun		0.426	0.442	3.84
Jul		0.243	0.260	6.53
Aug		0.132	0.149	11.43
Sep		0.311	0.328	5.18
Oct		0.361	0.378	4.49
Nov		0.352	0.369	4.60
Dec		0.154	0.171	9.95

Results

Pattern of stem girth increment

We ultimately selected a mixed model with a significant tree random effect, significant plot, year, and month fixed effects, and significant plot × month, year × month, plot × year, and plot × year × month interactions. The structure of the variance–covariance matrix for the 12 × 12 blocks of the **R** matrix is unstructured with 4 bands. This indicates that the variance of observations was different for different months (heterogeneous structure) and that there was a temporal correlation for groups of four consecutive months. Structures of heterogeneous variances had smaller AIC than structures of homogeneous, indicating clear heteroscedasticity of stem increment. All fixed effects and their interactions were highly significant ($p < 0.0001$) (Table 3). Tree random effect was also significant ($p < 0.0001$), but spatial covariance was not ($p = 0.934$). In other words, the significant stem increment

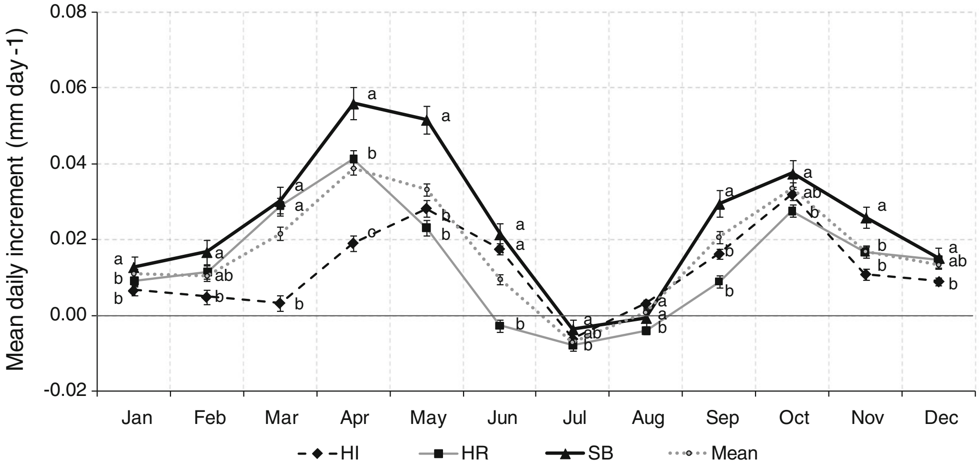
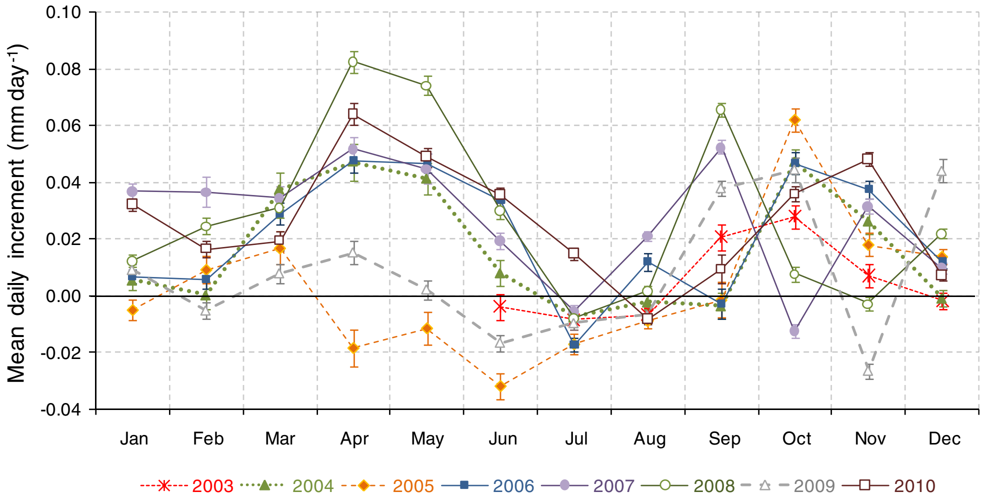


Fig. 3 Least squares means of daily girth increment rate (mm day^{-1} ± standard error) of holm oak trees in the study plots during different months of the study period (2003–2010). *Different letters* indicate significant differences between plots in a month ($p < 0.05$)

Fig. 4 Least squares means of daily girth increment rate (mm day^{-1} ± standard error) of holm oak trees in different months during each year of the study period



differences among trees cannot be explained by their relative positions within the plots.

Monthly variance was higher in the spring (March, April, and May), when most stem increment occurred (Table 4). In August, when the stem increment rate was very low, variability among trees was smaller. In September, October, and November, variability among trees increased, although it was less than during the spring. The fixed effects that accounted for most of the variance were month and the interaction of year × month. These two factors accounted for 31.5 and 43.6 % of the total variance, respectively. The estimated correlations among months within a tree were greater for consecutive months during the spring (April and May, $\rho = 0.62$). The correlations between non-consecutive months were more irregular and not dependent on proximity (data not shown).

Stem girth increment varied significantly throughout the year, with peaks in all plots during the spring and autumn, but with some differences in the timing among the three plots (Fig. 3) and in different years (Fig. 4). In all plots and years, there was little increment or even stem contraction during the summer. The stem increment during the spring was typically greater and lasted longer than that during the autumn (Figs. 3, 4). However, in 2005, spring increment was about 0.02 mm day^{-1}, stem contraction occurred from April to September, increment was about 0.062 mm day^{-1} in October, and then it declined until December. The same trend, but not so strong, occurred in 2009. In 2005 and 2009, most of the annual stem increment was in the autumn, with 78 and 69 %, respectively, contrary to common years where spring growth accounted for 66–75 % of annual stem increment.

Comparison of the three plots indicated that stem increment started in February in SB and HR (Fig. 3) and reached a maximum in April. In contrast, stem increment in HI was very small until April, and reached a peak in May.

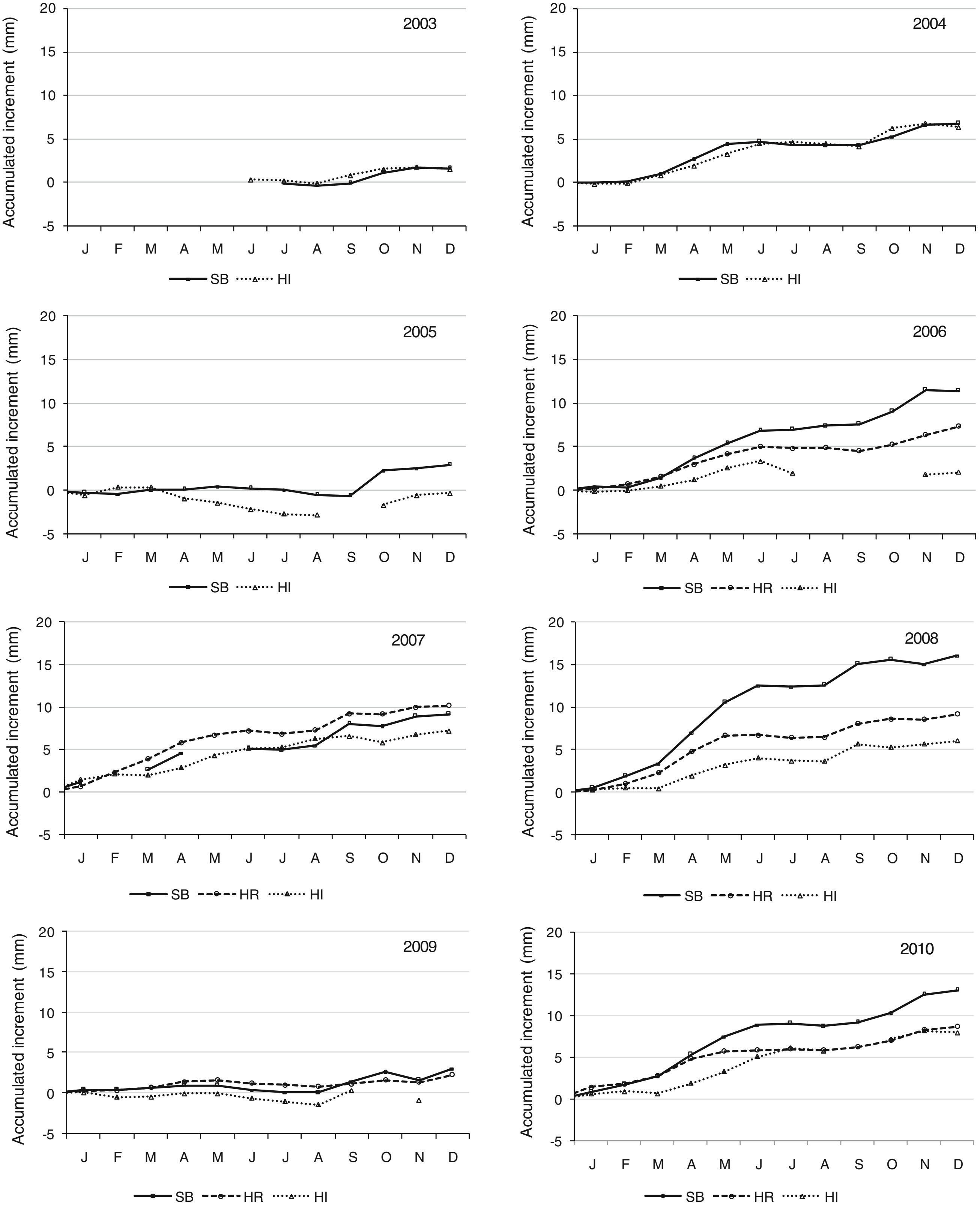


Fig. 5 Least squares means of accumulated monthly change in girth (mm) of holm oak trees in each plot during each year of the study period

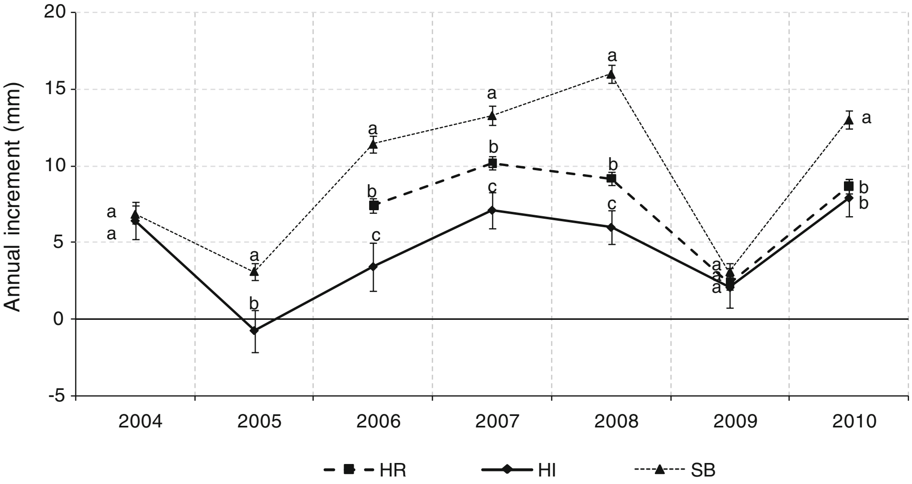


Fig. 6 Least squares means of annual girth increment rate (mm year^{-1} ± standard error) of holm oak trees from 2004 to 2010 in the three different plots. *Different letters* indicate significant differences between plots in a year ($p < 0.05$)

Trees stopped growing in June in HR and in July in SB and HI. Larger stem contractions always occurred in July. Stem increment increased during September and October in all plots, and then decreased until December, with similar growth rates in SB and HR, and slightly smaller growth rates in HI. The average annual estimated increment of stem girth for the three plots was 8.98 ± 0.34 mm year^{-1} in SB, 5.18 ± 0.30 mm year^{-1} in HR, and 4.43 ± 0.65 mm year^{-1} in HI. All differences at the plot level were significant ($p < 0.0001$).

The stem increment differences between plots varied in different years. For example, in 2008 growth in SB was much larger than in HR and HI; but in years with small average growth (e.g., 2009), these differences were smaller (Fig. 6). The smallest average annual increment in all plots occurred during 2005 and 2009. In 2005, annual stem contraction exceeded annual stem increment in HI (Figs. 5, 6).

Effect of climatic parameters and soil moisture

Table 5 shows the climatic parameters that explain the plot × year × month interaction. The results indicate that high precipitation and relative humidity were correlated to higher stem increment and that high air and soil temperature and high solar radiation were correlated with lower increment. At the year × month interaction level (Table 5; Fig. 4), the same results occurred, but soil moisture and relative extractable water at every soil layer were also significant. This indicates a positive association of soil moisture and stem increment. ET_0 was also significant at this level, and higher values correlated with lower increment. The climatic and soil parameters that explained the plot × month interaction (Table 5; Fig. 3) were similar to those that explained the year × month interaction, but ET_0 and the temperature (mean, minimum, mean of the maximum, and soil temperature) had an effect opposite to that of the year × month interaction, in that higher ET_0 and temperature were correlated with greater stem increment. Figure 7 shows that the response of stem increment to precipitation was positive and rapid, except during December and February.

Effect of initial diameter, hydrological parameters and competition

Initial tree diameter was a significant covariate ($p = 0.0038$, coefficient = 0.056), and explained 12 % of the variance at the tree level. This indicates that thicker trees have greater stem increment. None of the hydrological parameters were significant (FL: $p = 0.54$, coefficient = −0.019, SCA: $p = 0.11$, coefficient = −0.004, WI: $p = 0.989$, coefficient = −0.0038).

Five of the 725 competition indexes used in our model were significant, with each accounting for 12–25 % of the total variance at the tree level (Table 6). The APA index, with weight factor $k = 4$ (the highest value that we tested), was the most significant. An APA index with $k = 0$ was also significant, but model convergence was not possible with $k = 1$, 2, or 3. The positive values of the APA coefficients show that as the potentially available area is larger, tree stem increment is greater. Three Distance-weighted ratio (DR) indexes were also significant and they use the basal area factor (BAF) as the criterion to select competitors. We tested four values of BAF (1, 2, 3 and 4 m^2 ha^{-1}) and the only significant indexes occurred with BAF = 1, that is the lowest we tested. A lower BAF is associated with a selection of more competitors for a tree, suggesting large competition zones in our plots. The negative coefficients of all three DR indexes indicate that higher competition is associated with less stem increment.

Table 5 Climatic covariates that are significant at the plot × year × month, year × month and plot × month level

Level	Parameter	F value	$P_r > F$	Coefficient
Plot × year × month	P	59.51	<0.0001	0.1329
	T_{sm}	57.05	<0.0001	−4.0409
	$\mathrm{RH}_{\mathrm{mmax}}$	38.07	<0.0001	1.1180
	T_{mmin}	36.78	<0.0001	−4.5827
	T_{m}	36.24	<0.0001	−5.3178
	R_{m}	13.35	0.0003	−1.1286
	T_{max}	11.79	0.0006	−1.7911
	T_{mmax}	11.27	0.0008	−2.6691
Year × month	$\mathrm{RH}_{\mathrm{mmin}}$	410.48	<0.0001	0.9424
	RH_{m}	319.01	<0.0001	0.9947
	P	314.60	<0.0001	0.0976
	T_{mmax}	262.70	<0.0001	−3.2221
	R_{m}	260.55	<0.0001	−3.5810
	$\mathrm{RH}_{\mathrm{mmax}}$	251.45	<0.0001	1.5560
	$\mathrm{REWT}_{\mathrm{m}}$	237.41	<0.0001	38.6659
	$\mathrm{SM1}_{\mathrm{m}}$	200.92	<0.0001	0.4733
	$\mathrm{SMT}_{\mathrm{m}}$	199.42	<0.0001	0.2158
	$\mathrm{REW1}_{\mathrm{m}}$	198.89	<0.0001	31.6205
	ET_0	169.37	<0.0001	−12.8304
	T_{max}	158.4	<0.0001	−1.8464
	$\mathrm{REW2}_{\mathrm{m}}$	143.45	<0.0001	33.5260
	T_{m}	105.08	<0.0001	−2.5767
	$\mathrm{SM2}_{\mathrm{m}}$	103.42	<0.0001	0.2660
	T_{min}	91.85	<0.0001	−1.5855
	T_{sm}	24.87	<0.0001	−0.8929
Plot × month	$\mathrm{RH}_{\mathrm{mmin}}$	35.36	<0.0001	0.3463
	$\mathrm{REW1}_{\mathrm{m}}$	32.99	<0.0001	23.8818
	$\mathrm{REW2}_{\mathrm{m}}$	22.55	<0.0001	24.2224
	RH_{m}	20.36	<0.0001	0.4844
	T_{m}	19.66	<0.0001	6.4210
	$\mathrm{RH}_{\mathrm{mmax}}$	18.74	<0.0001	1.4202
	$\mathrm{SM2}_{\mathrm{m}}$	17.83	<0.0001	0.2706
	$\mathrm{REWT}_{\mathrm{m}}$	15.98	<0.0001	20.1011
	T_{min}	11.86	0.0006	1.3414
	ET_0	10.45	0.0012	5.8344
	T_{sm}	8.65	0.0033	0.5022
	$\mathrm{SMT}_{\mathrm{m}}$	8.55	0.0035	0.1095
	$\mathrm{SM1}_{\mathrm{m}}$	5.91	0.0151	0.2874
	P	5.29	0.0215	0.0661
	T_{mmax}	5.04	0.0248	1.4479

P precipitation, T_{sm} mean soil temperature, RH_{mmax} mean of the daily maximum relative humidity, T_{mmin} mean of the minimum daily temperature, T_m mean temperature, R_m mean solar radiation, T_{max} maximum temperature, T_{mmax} mean of the maximum daily temperature, RH_{mmin} mean of the minimum relative humidity, RH_m mean relative humidity, $REWT_m$ mean relative extractable water at 5–45 cm, $SM1_m$: mean soil moisture at 5–25 cm, SMT_m mean soil moisture at 5–45 cm, $REW1_m$ mean relative extractable water at 5–25 cm, ET_0 reference evapotranspiration, $REW2_m$ mean relative extractable water at 25–45 cm, $SM2_m$ mean soil moisture at 25–45 cm, T_{min} minimum temperature

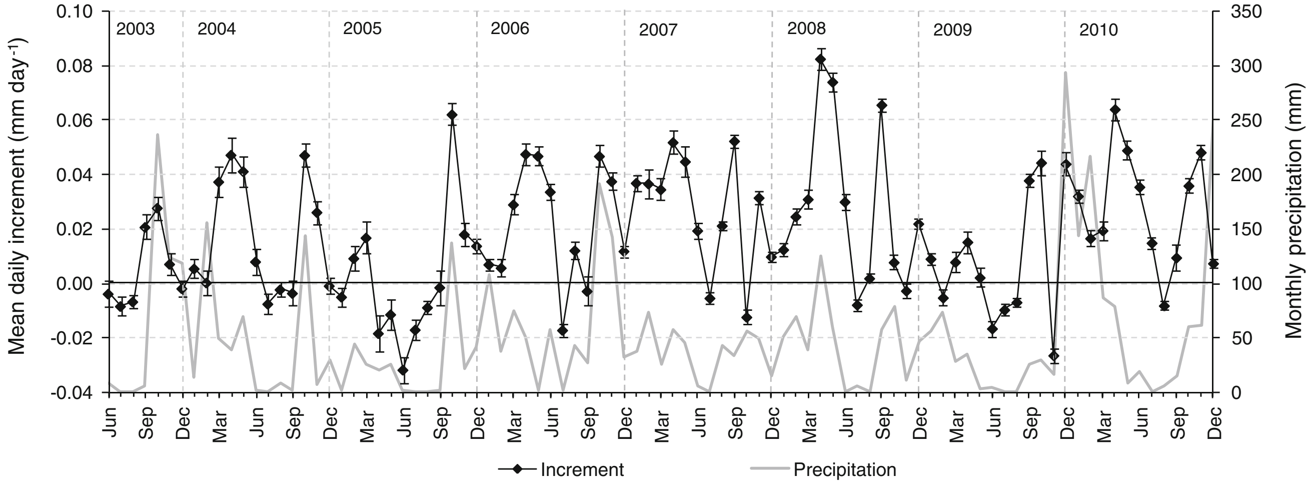


Fig. 7 Least squares means of daily girth increment rate (mm day^{-1} ± standard error) of holm oak trees and monthly precipitation (mm) during the study period

Table 6 Significant competition indexes from the final model

Competition index	*k*	BAF	Distance function	Laterality	*F* value	$P_r > F$	Coefficient
Area potentially available	4	n.a.	n.a.	n.a.	8.53	0.004	0.0099
Area potentially available	0	n.a.	n.a.	n.a.	5.22	0.022	0.021
Distance-weighted ratio	1	1	$1/\text{dist}_{ij}$	Bilateral	4.29	0.038	−65.513
Distance-weighted ratio	1	1	$1/\text{dist}_{ij}$	Unilateral	4.29	0.039	−46.758
Distance-weighted ratio	2	1	$1/\text{dist}_{ij}$	Unilateral	4.23	0.040	−29.877

Unilateral indexes do not consider trees smaller in diameter at breast height as competitors for a subject tree

k weighting factor, *BAF* basal area factor (m^2 ha^{-1}), *n.a.* not applicable

Discussion

Patterns of stem girth increment

In this study, we observed that *Q. ilex* had a bimodal stem increment pattern with maximum stem increment rates during the spring and a lesser peak during autumn, as also reported in other studies (Campelo et al. 2007; Gutiérrez et al. 2011). Thus, the maximum vegetative activity is synchronized with the most favorable conditions for growth, when water is available and temperatures are moderate (Pinto et al. 2011). However, in years with a dry spring (e.g., 2005; 2009), this pattern changed and the second period accounted for most of the total annual increment. This finding does not agree with former studies (Campelo et al. 2007; Gutiérrez et al. 2011) probably because our study sites were in drier and warmer locations.

The stem increment of holm oak begins to increase at the end of the winter and increases more significantly during the spring, in parallel with the significant increase in photosynthetic activity (Corcuera et al. 2005) and the formation of large xylem vessels (Campelo et al. 2010). The spring stem increment rates in our plots were higher than those reported by other authors for this species (e.g., Campelo et al. 2007; Gutiérrez et al. 2011). As summer comes, the stem increment rates decrease because of water stress, and xylem vessels become narrower (Corcuera et al. 2004; Nijland et al. 2011) and there is apparently a cessation of vegetative growth. As suggested by Cherubini et al. (2003), this should be considered as a “resting period” due to water stress rather than actual vegetative inactivity. Nevertheless, when stem contractions by water stress occur, we cannot determine with band dendrometers whether cambial activity stopped completely. Our results indicate that the duration of this summer rest period had a strong inter-annual variability and was strongly dependent on the length of the drought. This period can start as early as the beginning of spring and can last until the end of the summer, as occurred in 2005 and 2009. In 2005, only February and March accounted for the first stem increment period and stem contraction lasted until October because of scarce precipitation in spring and summer.

At the end of summer and matching with the first rains, the water status of *Q. ilex* improves, as reported by

Corcuera et al. (2004). Rapid stem increments detected were probably because of stem hydration. However, after that phenomenon, the stems' diameter was stabilized and increments occurred throughout the autumn, with a maximum accumulated stem increments at the end of each year higher than the previous spring maximum. It suggests that, despite water stem expansion occurred, there were a true second growth period, also reported by Campelo et al. (2007) and Gutiérrez et al. (2011). The results of these authors and Cherubini et al. (2003), who studied *Q. ilex* trees in central Italy, suggest that there is a relationship between this second growth period and the appearance of intra-annual density fluctuations in the wood and/or the existence of double rings, especially when there is a severe summer drought followed by high precipitation events at the end of summer and the start of autumn. Similar results for *Arbutus unedo* and *Erica arborea* in other Mediterranean regions have been reported by Battipaglia et al. (2010, 2014).

The stem increment rates slowed down at the end of autumn and the start of winter, with low values from December to February. Nevertheless, there was not a complete cessation of growth in the winters of 2006, 2007, 2008, and 2010. These results do not agree with other works of holm oak in colder and more continental areas (e.g., Gutiérrez et al. 2011; Nijland et al. 2011).

Effect of climate and soil moisture on stem increment

Stem increment of holm oak is strongly influenced by precipitation, especially in the spring. The amount of precipitation was significant in the three levels of the model in which this variable was tested, especially in the year × month interaction. Similar results have been reported in other Mediterranean regions in the south of France (Nijland et al. 2011), central Italy (Cherubini et al. 2003), and the Iberian Peninsula (Campelo et al. 2007; Gea-Izquierdo et al. 2011). Hence, an increase in the frequency and intensity of a spring drought could have a significant negative impact on holm oak, as suggested by Rodríguez-Calcerrada et al. (2011). We also found a significant and positive effect of soil moisture on stem girth increment indicating the importance of water availability. Soil moisture variables did not explain the plot × year × month interaction; however, this interaction accounted for more variability in autumn and winter months, when water availability was not limited for growth.

Holm oak has a high capacity for physiological recovery following summer drought, and the stem increment rate increased significantly in subsequent precipitation events. Corcuera et al. (2004) indicated that this species can maintain a relatively high hydraulic conductivity with very low xylem water potential (50 % of hydraulic conductivity at −5.6 MPa). Holm oak xylem contains a combination of large conductive vessels, which efficiently transport water but are vulnerable to cavitation, and small vessels, which are less efficient in water transport but less vulnerable to cavitation (Davis et al. 1999). Nevertheless, water stress can still lead to the loss of cambial cell turgor and low cellular division rates (Wimmer et al. 2000). The loss of cambial cell turgor may be an important cause of the stem contraction that we observed during certain dry periods. After the summer drought, precipitation seems to be the main factor responsible for stem increment, as suggested by Campelo et al. (2007). Nevertheless, the influence of precipitation in this period apparently does not occur in colder and more continental areas (e.g., Zhang and Romane 1991; Nijland et al. 2011). We also found a significant and positive effect of relative humidity on stem increment. This effect may be due to a positive correlation of relative humidity and precipitation, or because leaf stomata close during drought to avoid water loss, leading to a reduction of photosynthesis and growth.

The mean daily temperature, maximum daily temperature, mean of the maximum daily temperature, and soil temperature, all had negative effects on stem increment at the plot × year × month and year × month levels. This could be explained because there was a stronger negative effect of high temperature during dry springs and summers than positive effect during autumn and winter. Campelo et al. (2009) reported that low precipitation is associated with higher temperatures in May, increased evapotranspiration, and the formation of narrow rings. Campelo et al. (2007) and Gutiérrez et al. (2011) reported similar results regarding the influence of high summer temperatures on growth of holm oak in the Iberian Peninsula. Nevertheless, the minimum daily temperature and the mean of the minimum temperature also had a negative effect at year × month and plot × year × month levels, respectively. This could be because temperatures were never very low in our study area, with the exception of occasional events during the winter (Fig. 2; Table 2). Cavender-Bares et al. (2005) reported that *Q. ilex* can maintain most of its hydraulic conductivity at a temperature of −5 °C. We recorded temperatures below 5 °C only on a few days in the HI plot, so our trees were probably not affected by embolisms. The maintenance of photosynthetic and vascular function during the winter gives evergreens as holm oaks a competitive advantage over deciduous ones (Cavender-Bares et al. 2005).

The reference evapotranspiration (ET_0) negatively influenced stem increment at the year × month level. This negative relationship can be considered a combined effect of temperature and radiation, because the highest values of both occur in the middle of the summer, when water availability limits growth. The negative effect of solar radiation on stem increment may be explained by the induction of phototoxic reactions due to excessive radiation. However, we believe a more plausible explanation is that high radiation leads to increased evapotranspiration. On the contrary, ET_0 and the temperature had positive effects on stem increment at the plot × month level. This may be because the plot × month level interactions account for more variability during March, when there is a higher temperature (and hence higher ET_0) and readily available water.

Effect of initial diameter, hydrological parameters and competition

We were not able to attribute the significant stem increment differences of trees to spatial processes or hydrological parameters, suggesting that all locations in our plots were about equally favorable for growth. This could be due to the flat or smooth undulated topography of our plots. Holm oak has a well-developed root system, with a main penetrating root and several secondary and extending roots (Ruiz de la Torre 2006), getting deeper soil layers when growing with competition (Rolo and Moreno 2012). This could allow trees to take water from the surface and at different depths, hence minimizing the effect of topography. No previous studies of *Q. ilex* evaluated this hypothesis. However, Miller et al. (2001) reported that topography modulated the effect of precipitation on growth in *Prosopis glandulosa* in a subtropical savanna-type forest in Texas, with a higher growth at lower elevations.

Trees with larger potentially available area (i.e., more access to resources such as water, nutrients, and light) had higher stem increment rates. In addition, the selected index in the category of distance-weighted ratio indexes indicated that there was a large radius of competition for each tree. This suggests that the severe water limitation in these ecosystems leads to competition among trees mainly at the root level. On the other hand, our results indicated a significant and positive influence of initial stem diameter on stem increment. This may be because larger trees have more developed root systems, so are better able to extract water from deeper soil layers. If so, this would give larger trees an extended growth period during the end of spring and beginning of summer. The positive influence of stem size on growth of *Q. ilex* has also been reported by Cartan-Son et al. (1992). As reported by Rivest et al. (2011), trees in forests with limiting climatic and soil conditions, such as the open woodlands of the Mediterranean, frequently compete for water and nutrients at the intra- and interspecific levels. Trees in the HI plot had lower stem increment rates than those in the other two plots, and this may be due to higher competition for resources in HI. According to Pulido and Díaz (2005), in water-limited ecosystems, the suppression of a proportion of the trees due to limited water availability means that the standing trees have a larger soil volume available per tree, leading to improved productivity and health and increased growth. This has also been reported for *Q. ilex* (Rodríguez-Calcerrada et al. 2011). Nevertheless, most of the indexes that we tested were not significant, so the validity of these results should be evaluated in further studies.

We explained 12 % of the stem increment variability among trees by the stem diameter and 12–25 % by competition. However, *Q. ilex* forests have high genetic variability, so there could also be physiological adaptations at the tree level that modify the response of cambial activity to climate (Baas 1976).

Conclusions

Q. ilex showed two periods of intra-annual stem increment, typically with a higher peak in spring and a lesser peak in autumn. However in years with a dry spring, this pattern changed, with autumn stem increment being higher than spring increment. In some years, stem increment did not completely stop in winter. Stem contractions always occurred in summer because of water stress, but we cannot determine whether cambial activity stopped entirely. Stem increment varied significantly among plots and among trees within each plot.

Climate strongly drives the stem increment pattern within and among years, with water availability acting as the main climatic factor. This species appears to respond to the summer drought by simply decreasing its vegetative activity. The effect of temperature was mostly related to the reduced water availability due to evapotranspiration rather than reduced vegetative activity during the winter. Therefore, the forecasted climatic change, in which decreased rainfall in spring and increased summer drought are expected in the Mediterranean region, may be a significant threat to the forests and open woodlands of *Quercus ilex.* The intra-annual stem increment model developed in this study might be used to build large-scale ecological models or geographical mapping of vulnerable areas under different climate change scenarios.

Tree size and competition can modulate the growth response to climate. These findings might help to design silvicultural management practices to mitigate some of those climate effects by reducing competition (i.e, selective harvesting), especially in dense forests.

Author contribution statement D. Martín has written the first draft of the manuscript, done the data analysis and field data collection. J. Vázquez-Piqué has participated in the data analysis, co-written the manuscript, collaborated in data collection and in plot establishment.M. Fernández has reviewed the manuscript, collaborated in data collection and in plot establishment. R. Alejano has co-written the manuscript, participated in data collection and in plot establishment.

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Conflict of interest The authors declare that they have no conflict of interest.

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