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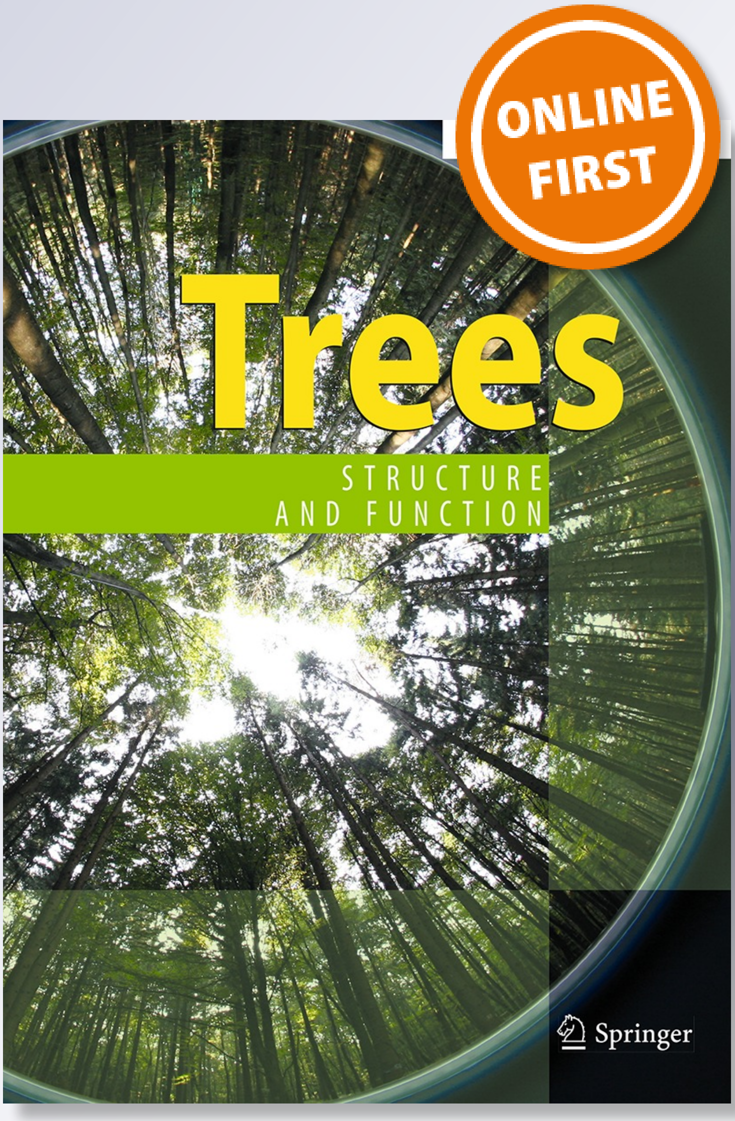

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ORIGINAL PAPER

Trade-off between stem growth and acorn production in holm oak

**Daniel Martín · Javier Vázquez-Piqué ·
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Abstract

Key message **There were trade-offs between acorn production and stem growth in individuals of *Quercus ilex*, and these occurred with annual and intra-annual periods. The costs of reproduction differed significantly between two study sites.**

Abstract Reproduction in trees often requires significant resources, and previous studies have documented trade-offs between reproduction and growth in numerous tree species. In the present study, we assessed the relationships of acorn production with annual and intra-annual stem growth of *Quercus ilex* L. (holm oak) at the level of the individual tree over 6 years (2006–2011) at two study sites in southwestern Spain. There were negative correlations between acorn production and annual and late summer–autumn stem growth during masting years. In other words, the growth rates were lower in trees that had greater acorn production. These results suggest the existence of trade-offs between growth and reproduction in *Q. ilex*. However, there was no relationship between acorn production and winter–spring growth. Moreover, the costs of reproduction varied between the two study sites. There were negative correlations between acorn production and late summer–autumn growth in both study sites, but there were only negative correlations between acorn production and annual growth in one study site. Trade-offs appear to be greater in smaller trees living under more stressful conditions. These results show the importance of making intra-annual measurements of tree growth for appropriate interpretation of potential trade-offs.

Keywords Holm oak · Masting · Reproduction · Resource allocation

Introduction

The growth of forest trees is important for commercial wood production. In addition, growth also shows the response to ecological factors (Cook and Kairiukstis 1990), and it is an indicator of fitness and resources allocation in trees (Stearns 1989). Stem growth generally occupies a low position in the carbon allocation hierarchy (Hoff et al. 2002; Rodríguez-Calcerrada et al. 2011). Trade-offs represent the cost paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another (Stearns 1989).

Investment in reproduction may be considered a hierarchical process (Obeso 2004). Hence, it is expected that the extraordinary resource allocation to reproduction during "mast years" (when there is high production of seeds) could lead to reduced stem growth. Masting seems to be triggered by climate, in that more seeds are produced when the climate is better (resource matching hypothesis; Norton and Kelly 1988). However, masting may also be a strategy to reduce the percentage of seeds lost by predation (predator satiation hypothesis; Janzen 1971) or to synchronize seed production in good climatic years, and thereby

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improve seedling establishment (environmental prediction hypothesis; Kelly 1994). Masting as reproductive strategy requires a resource allocation mechanism that increases the variation of seed production among years (resource switching or trade-off hypothesis; Kelly and Sork, 2002; Monks and Kelly 2006; Sánchez-Humanes et al. 2011). Thus, a large investment in reproduction could reduce the energy available for growth in long-lived plants (Koenig and Knops 1998), such as *Quercus* species (Camarero et al. 2010; Sánchez-Humanes et al. 2011; Barringer et al. 2012). However, the phenomenon of resource switching is not a universal explanation for masting (Knops et al. 2007), and there can even be positive correlations between plant growth and reproduction (Despland and Houle 1997).

Quercus ilex L. (holm oak) is a widespread species in the Mediterranean Basin that covers more than 6.5 million ha (Quézel and Médail 2003). It is one of the dominant species in “dehesas”, traditional agroforestry systems consisting of an open woodland forest (10–60 trees ha^{-1}) and an herbaceous layer (Cubera and Moreno 2007). *Q. ilex* has highly variable annual acorn production (Alejano et al. 2011), as other oak species (Sork 1993; Sánchez-Humanes et al. 2011). Previous studies of trade-offs between growth and reproduction in trees have generally examined annual growth data, such as tree-ring width or annual dendrometer measurements (e.g., Monks and Kelly 2006; Knops et al. 2007; Barringer et al. 2012). However, *Q. ilex* typically has two intra-annual periods of stem growth (Gutiérrez et al. 2011; Martín et al. 2014); in late winter to early summer and after the summer drought throughout the autumn. This second period of growth overlaps with acorn fattening (Siscart et al. 1999), the period of maximal investment in acorns (Knops et al. 2007). Hence, the relations between stem growth and acorn production in holm oak may change at the intra-annual level.

Even when there is a negative correlation between life history traits, this may not be due to trade-offs due to resource limitation (Barringer et al. 2012). For example, Knops et al. (2007) reported the presence of a negative correlation between annual growth and acorn production in several *Quercus* species and they suggested that spring rainfall caused increased growth and decreased pollination (apparent or putative trade-offs). The analysis of trade-offs at the intra-annual level in holm oak, particularly during the second intra-annual growth period in late summer and autumn, could be a method to test the hypothesis of a true trade-offs between growth and reproduction. This is because late summer and autumn growth are not driven by spring rainfall, and autumn is the period of acorn fattening, when a large amount of tree resources could be derived to reproduction.

This study addressed two main questions. First, are there trade-offs at the level of the individual tree between acorn production and stem growth in *Q. ilex* at annual and intra-annual scales? Second, can the costs of reproduction in *Q. ilex* vary between study sites due to differences in ecological traits? Answering these questions will improve our understanding of the growth process and the influence of endogenous biological factors on individual growth variability of *Q. ilex* that is not driven by climate, competition, or microecological factors (Martín et al. 2014). Ultimately, understanding these issues will be useful for the development of accurate and full-parameterized growth models for Mediterranean ecosystems and will provide guidance for their sustainable management.

Materials and Methods

Field plots

This study was performed in two experimental plots in the Huelva province of southwestern Spain (Table 1). The Huerto Ramirez (HR) plot is in an open woodland of *Q. ilex* where sheep and Iberian pigs are raised. Its soils have different degrees of development from acrisols, alisols, and lixisols to regosols and cambisols (IUSS Working Group WRB 2007). There is a sparse understory of mainly *Cistus ladanifer* and *C. crispus* and an abundant herbaceous layer of mainly grasses. The San Bartolomé (SB) plot is in an open woodland of *Q. ilex* where bulls are raised. Its soils are endoleptic regosols (episkeletic) or endoleptic luvisols (dystric), with deeper soils in depositional or concave areas (IUSS Working Group WRB 2007). SB has a very sparse understory due to frequent tillage, and an abundant herbaceous layer of mainly grasses. Both plots were fenced-in to avoid predation on acorns and damage of field equipment. The climate of both plots is Mediterranean, with highly variable temperature and rainfall within and among years. The nearby ocean modulates air temperature and increases precipitation relative to the more continental areas in the Iberian Peninsula. There were no large variations in temperature during the study period (2006–2011), but there was large monthly and annual variability in precipitation (Figs. 1, 2; Table 2).

Measurement of stem growth and location of trees

31 aluminum band dendrometers that were developed by the University of Huelva were installed at breast height (1.30 m) on 18 trees in HR and 13 trees in SB, with care taken to avoid stem deformities. Trees were selected within plots by the use of stratified sampling so that different diametric classes were considered. Keeland and Young (2014) provide details of band dendrometer theory and construction.

Table 1 Characteristics of the two study plots (SD: standard deviation)

Plot	Coordinates (UTM. Zone 29) (m)	Area (ha)	Density (trees ha^{-1})	Mean diameter ± SD (cm)	Mean height ± SD (m)
Huerto Ramírez (HR)	X:644288 Y:4161376	2.94	73.0	30.0 ± 7.7	6.6 ± 1.6
San Bartolomé (SB)	X:669638 Y:4145966	2.70	36.0	35.4 ± 7.2	6.5 ± 1.1

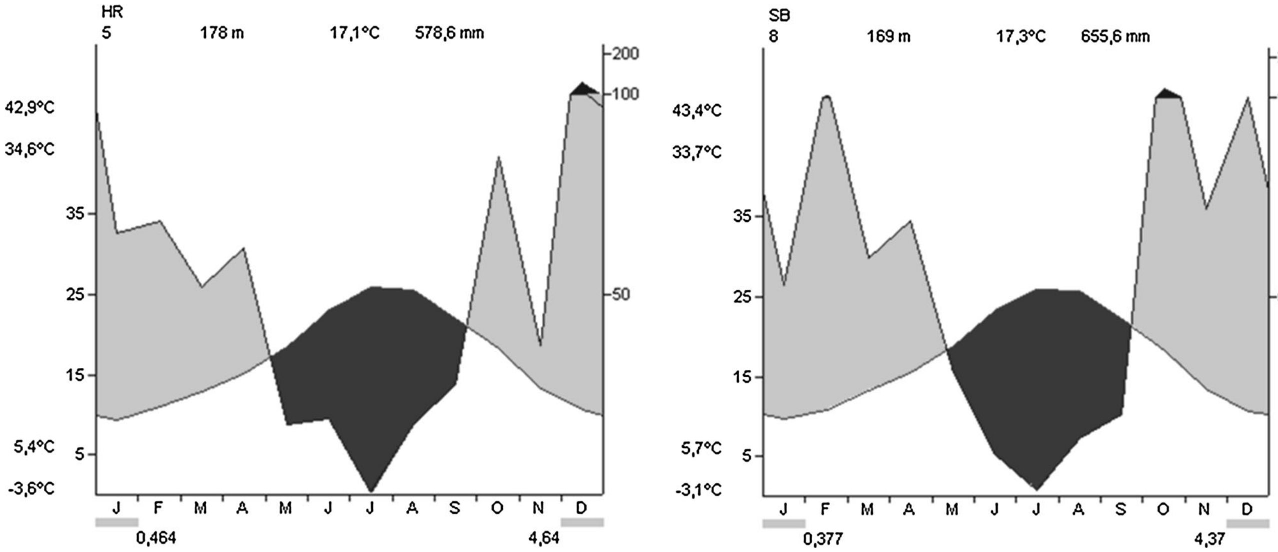

Fig. 1 Walter-Lieth climate diagrams of the plots in Huerto Ramírez (*left*) and San Bartolomé (*right*)

Fig. 2 Monthly precipitation and temperature of plots in Huerto Ramírez (*top*) and San Bartolomé (*bottom*) during the study period. *Tmed* mean temperature, *Tmmax* mean maximum daily temperature, *Tmmin* mean minimum daily temperature

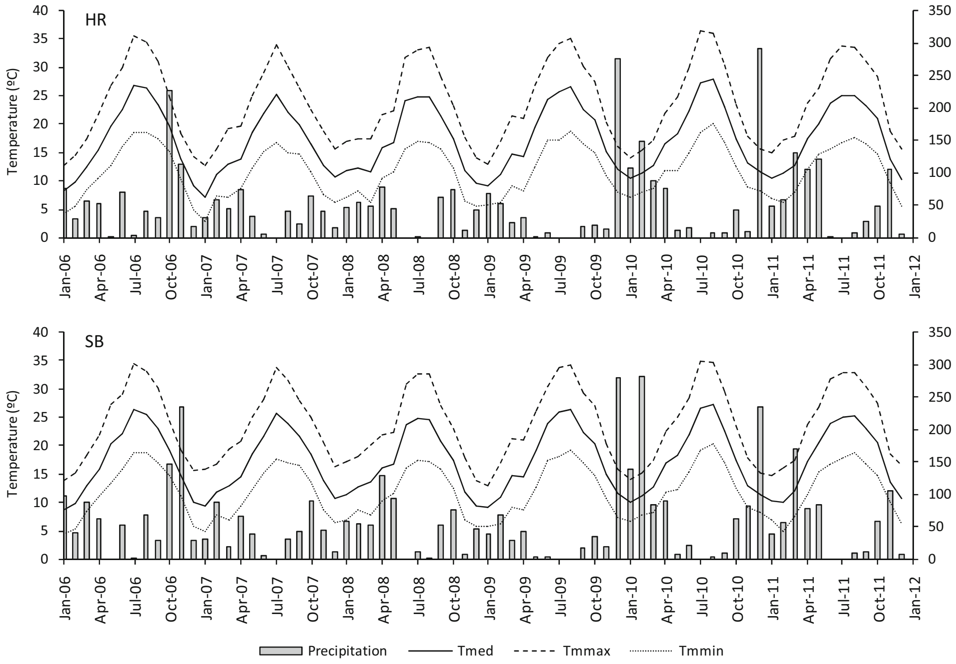

Table 2 Precipitation and temperature of the two plots during the study period

Year	Precipitation (mm)								Temperature (°C)					
	SB				HR				SB			HR		
	Psp	Psm	Pat	P	Psp	Psm	Pat	P	TM	Tm	T	TM	Tm	T
2006	115	99	411	850	123	74	356	713	34.4	4.5	17.4	35.6	4.2	17.4
2007	111	75	148	473	110	60	118	421	33.8	4.9	17.0	33.9	2.8	16.1
2008	222	66	130	584	121	64	126	458	32.7	5.7	17.0	33.4	5.5	16.8
2009	50	18	334	538	38	16	305	502	34.1	5.7	17.9	35.0	5.7	18.0
2010	120	12	379	1,019	99	14	342	799	34.9	6.7	17.5	36.3	7.1	17.6
2011	162	21	107	618	226	31	158	651	32.8	5.0	17.7	33.2	6.0	17.4

Psp spring precipitation, *Psm* summer precipitation, *Pat* autumn precipitation, *P* annual precipitation, *TM* mean maximum temperature of the hottest month, *Tm* mean minimum temperature of the coldest month, *T* mean annual temperature

Measurements were recorded each month with a digital caliper (0.01 mm precision) from 2006 to 2011 and these data were used to calculate annual stem girth increment (hereafter, annual growth), January to June stem girth increment (hereafter, winter–spring growth) and August to December stem girth increment (hereafter, late summer–autumn growth). The calculation of these values as the accumulation of monthly measurements is more accurate than single-season or annual measurements because it allowed detection and correction of measurement errors. Changes in girth were not transformed into diameter because *Q. ilex* has high within-tree variability in stem growth, and because the stems were not sufficiently cylindrical for this transformation. At the beginning of the study, the topographic location of each of the 31 trees was measured using a Sokkia 3B total station.

Estimation of acorn production

Acorns were harvested from the same trees whose growth was measured by the use of a trapping method (Greenberg 2000). Four containers (0.45 m diameter at the top) were placed on the ground under selected trees at the north, south, east, and west positions, at three-quarters of the distance from the stem to the edge of the crown. This trapping method allowed sampling of a fraction of the projection of the crown surface where acorns were assumed to fall. Acorns were collected from each container every 2 weeks during the six dissemination periods (2006/2007–2011/2012) from September to January. The acorns were transferred to the laboratory in polyethylene bags for counting and determination of fresh weight. Alejano et al. (2011) reported that acorn water content of *Q. ilex* did not vary significantly among trees in months and years. Thus, we used fresh acorn mass in this study, which we consider a more accurate measurement. Acorn production (AP) was calculated as fresh weight of acorns per m^2 of the orthogonal projection of the crown on the ground (g FM m^{-2}). Acorn production estimated by this container method is consistent with total acorn yield of the whole tree (Alejano et al. 2008).

Data analysis

We used three linear mixed models for data analysis: (a) a model for estimating annual growth; (b) a model for estimating winter–spring growth; and (c) a model for estimating late summer–autumn growth (when acorns fatten and disseminate). The initial structure of each model was:

$$y_{ijl} = \mu + b_{i(j)} + \alpha_j + \gamma_l + (\alpha\gamma)_{jl} + e_{ijl} \quad (1)$$

where y_{ijl} is the girth increase (mm) of tree i at plot j of year l for the entire year in the annual model, from January to June of year l in the winter–spring model, or from August to December of year l in the late summer–autumn model; μ is the general mean; $b_{i(j)}$ is a tree random effect within each plot with $i = 1, 2,\ldots, 18$ and $j = 1, 2$ under the hypothesis $b_{i(j)} \sim \mathrm{N}(0, \mathbf{G})$; α_j is a plot fixed effect with $j = 1, 2$; γ_l is a year fixed effect with $l = 2006, 2007,\ldots, 2011$; $(\alpha\gamma)_{jl}$ is the plot × year interaction (fixed effect); and e_{ijl} is the residual error under the hypothesis $e_{ijl} \sim \mathrm{N}(0, \mathbf{R})$.

The following procedure was used to select the best model structure

First, the models were adjusted by consideration of tree random effect, temporal correlations between observations of different years for each tree, and different variances for different years. Hence, **G** was initially considered a diagonal matrix and **R** a block diagonal matrix, with each block corresponding to a 6 × 6 submatrix of observations for each tree. We considered the following alternatives for the structure of blocks in the **R** matrix: autoregressive order 1, autoregressive heterogeneous, Toeplitz up to 6 bands, heterogeneous Toeplitz up to 6 bands, unstructured up to 6 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).

Second, 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, which follows a χ^2 distribution with 1 degree of freedom. An α value of 0.05 was considered to indicate an improved covariance structure.

Third, if the tree random effect was significant, the presence of spatial correlation was determined by use of the following isotropic power covariance model:

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

where $d_{ii'}$ is the distance between trees i and i' in location j; σ_{2b} is the variance component at the tree level; and ρ is a parameter to be estimated with $|\rho| < 1$. The spatial covariance between observations at different locations was considered zero.

Fourth, after selection of the best variance–covariance structure, the fixed effects were estimated by a generalized least squares (GLS) equation (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. Different levels of significance were compared by the Scheffé test.

Fifth, acorn production of the current year was introduced into the models as an additive linear effects covariate, and its significance was assessed with an F test. To analyze the significance of covariates, the variance components were estimated by maximum likelihood (ML). Significant covariates were tested in each plot by covariance analysis (Littell et al. 2006). All statistical analysis was performed with SAS/ETS (ver. 9.2).

Results

Annual growth

The best structure of the variance–covariance matrix for the 6×6 blocks of the $\mathbf{R}$ matrix was heterogeneous Toeplitz with 5 bands. The tree random effect was significant ($p = 0.039$), but spatial covariance was not ($p = 0.499$ in HR; $p = 0.145$ in SB). This indicates the presence of significant growth differences between trees that is not explained by tree location within a plot. The selected model indicates that plot effect, year effect, and the plot × year interaction were highly significant (Table 3). In other words, the annual stem growth varied between plots and among years. For both plots, annual growth was greatest during 2007 and 2008 (12.71 ± 0.91 mm in 2007 and 12.75 ± 0.65 mm in 2008) and lowest during 2009 (2.51 ± 0.39 mm, Fig. 3). At the plot level, growth in the SB plot was significantly greater than in the HR plot (11.30 ± 0.82 vs. 7.51 ± 0.60 mm, $p = 0.001$). Growth was greatest during 2008 in the SB plot (16.23 ± 0.99 mm) and during 2007 in the HR plot (10.21 ± 1.19 mm). Growth was lowest during 2009 for both plots (3.12 ± 0.60 mm in SB and 1.90 ± 0.51 mm in HR). Trees in the SB plot grew more than trees in the HR plot during all 6 years (Fig. 4).

Winter–spring growth

The best structure of the variance–covariance matrix for the 6×6 blocks of the $\mathbf{R}$ matrix was heterogeneous Toeplitz with 5 bands. The tree random effect was significant ($p = 0.027$), indicating significant growth differences among trees. We could not calculate spatial covariance because the model did not converge. The selected model indicates that the year effect and the plot × year interaction were highly significant, but the plot effect was not significant (Table 3). Thus, there were generally no significant differences in winter–spring growth between study sites, but these differences were significant in some years. For both plots, winter–spring growth was greatest during 2006 (9.51 ± 0.59 mm) and lowest during 2009 (0.99 ± 0.42 mm). At the plot × year level, winter–spring growth was maximal during 2008 at SB (12.08 ± 0.91 mm) and during 2007 at HR (7.67 ± 0.94 mm). Both plots had the lowest growth during 2009 (0.42 ± 0.64 mm in SB and 1.57 ± 0.55 mm in HR). Trees in the SB plot grew more than trees in the HR plot in all years except 2009 (Fig. 3).

Late summer–autumn growth

The best structure of the variance–covariance matrix for the 6×6 blocks of the $\mathbf{R}$ matrix was heterogeneous autoregressive of order 1.The tree random effect was significant ($p = 0.036$), indicating significant growth differences among trees. We could not calculate spatial covariance because the model did not converge. The selected model indicates that plot effect, year effect, and plot × year interaction were highly significant (Table 3). For both plots, late summer–autumn growth was greatest during 2006 (3.60 ± 0.32 mm) and lowest during 2011 (2.08 ± 0.15 mm, Fig. 3). At the plot level, the growth at SB was significantly greater than growth at HR (3.71 ± 0.22 vs. 2.28 ± 0.19 mm, $p < 0.001$). At the

Table 3 Significance of fixed effects in the annual, winter–spring, and late summer–autumn growth models

Effect	Annual growth			Winter–spring growth			Late summer–autumn growth		
	Year	Plot	Plot × year	Year	Plot	Plot × year	Year	Plot	Plot × year
F value	107.11	12.42	6.85	88.18	3.82	9.25	20.57	24.78	2.56
Pr > F	<0.0001	0.0014	<0.0001	<0.0001	0.0604	<0.0001	<0.0001	<0.0001	0.0301

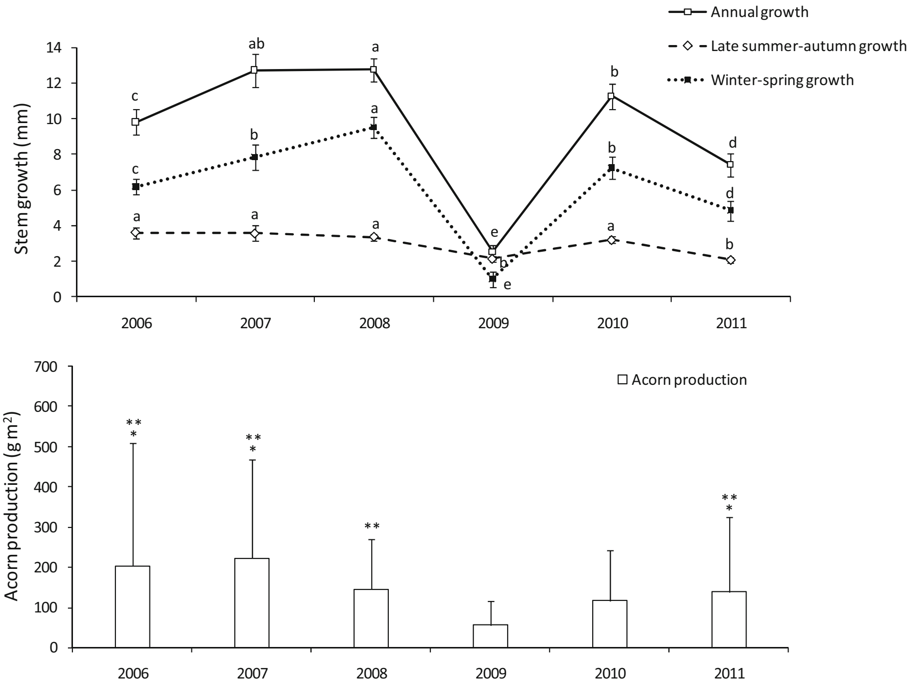

Fig. 3 *Top* least squares estimates of the mean annual, winter–spring, and late summer–autumn stem growth per tree (mm ± standard error) at both plots. *Different letters* significant differences for each growth model ($p < 0.05$). *Bottom* mean annual acorn production per tree at both plots ($g\ m^{-2}$ ± standard error). *Asterisk* that acorn production reduced the variance of annual stem growth at the individual tree level. *Double asterisk* that acorn production reduced the variance of late summer–autumn growth at the individual tree level

plot × year level, late summer–autumn growth was greatest during 2007 at SB (4.43 ± 0.64 mm) and during 2006 at HR (2.89 ± 0.41 mm). The lowest growth was during 2011 at SB (2.55 ± 0.22 mm) and during 2009 at HR (1.13 ± 0.19 mm). Trees in the SB plot grew more than trees in the HR plot in all years (Fig. 4).

Trade-off between acorn production and growth

There were negative correlations between acorn production and annual growth ($p = 0.038$; coefficient = −0.003), and between acorn production and late summer–autumn growth ($p = 0.037$; coefficient = −0.014). The introduction of the acorn production as a covariate reduced the variance of the annual model in years 2006, 2007 and 2011, and reduced the variance of the late summer–autumn model in years 2006, 2007, 2008 and 2011 (Table 4). These results indicate that acorn production explained part of the variability of growth between individual trees in these years. The reduction of variance was remarkable during 2006 (the year of maximal acorn production) in the model of annual growth and in the model of late summer–autumn growth. In contrast, the variance did not decrease after the introduction of this effect in both models during the years of less acorn production, e.g., 2009, indicating that acorn production did not influence stem growth in these years (Table 4; Fig. 3). Covariance analysis showed no significant differences between the plots in the late summer–autumn model ($p = 0.079$), but the presence of significant differences in annual model ($p = 0.019$). Specifically, acorn production was significantly and negatively correlated with growth at HR ($p = 0.001$; coefficient = −0.004), but not at SB ($p = 0.161$). On the contrary, acorn production had no significant effect on winter–spring growth ($p = 0.238$).

Discussion

Patterns of stem growth

The stem growth of *Q. ilex* varied significantly during the 6-year study period, with the highest growth rates in 2007

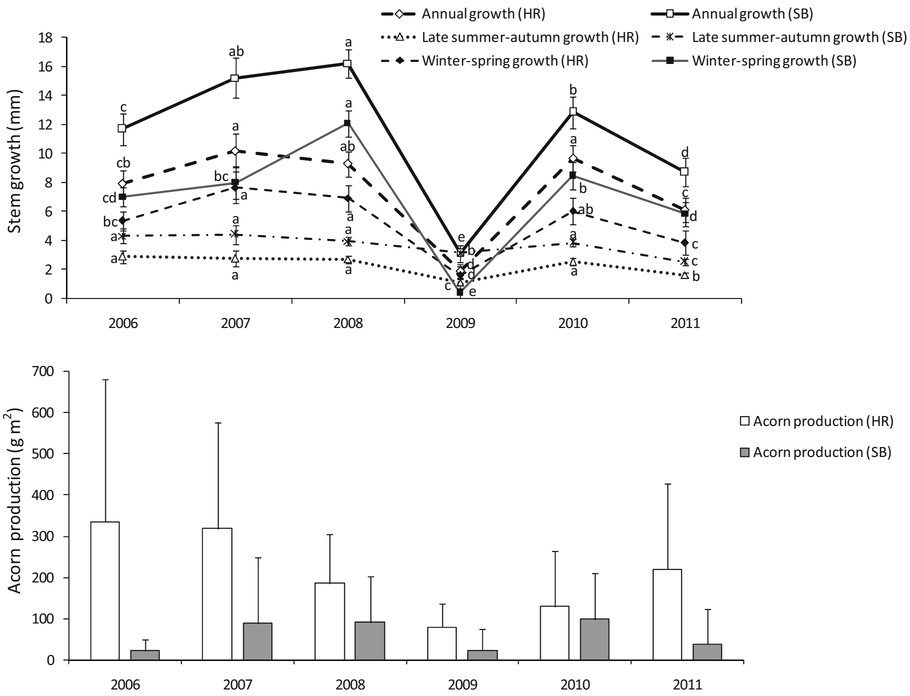

Fig. 4 *Top* least squares mean estimates of annual, winter–spring, and late summer–autumn stem growth per tree (mm ± standard error) at each plot. *Different letters* significant differences for each growth model ($p < 0.05$). *Bottom* mean annual acorn production per tree at each plot (g m^{-2} ± standard error)

Table 4 Effect of acorn production on the variance in annual and late summer–autumn growth models during each year (% reduction of variance)

Year	Annual growth	Late summer–autumn growth
2006	6.68	8.26
2007	5.56	2.23
2008	−1.32	3.22
2009	−9.17	−4.57
2010	−3.96	−4.18
2011	0.33	1.59

and 2008, and the lowest rates in 2009. Most of the annual growth occurred during spring, as reported in previous studies of this species (e.g., Gutiérrez et al. 2011; Martín et al. 2014), but there was also a second (generally shorter) growth period after the summer drought that correlated with late summer or early autumn precipitation. However, in years with dry springs and rainy autumns, such as 2009, most annual stem growth can occur during the second growth period, indicating that intra-annual growth patterns can be switched by climate.

Martín et al. (2014) reported high between-year variability in the timing of the second period of stem growth in holm oak. However, our results indicated that between-year variability in the late summer–autumn growth was less marked than annual growth and winter–spring growth, even though precipitation and temperature variability were greater during summer and autumn than spring. Hence, other biological processes during this period, such as acorn production, apparently compete for the limited available resources, and this modulates the between-year variability in late summer–autumn growth.

Our results showed that differences of growth among trees were not due to spatial differences. In other words, different locations within a plot were about equally favorable for growth. Thus, processes such as acorn production may explain the observed growth differences. The growth differences between plots, both annual growth and late summer growth, are probably related to the greater soil depth and development, reduced competition (because of lower stand density), and better climate (higher precipitation, milder temperatures) at SB than HR. On the contrary, during winter–spring, growth differences between the plots were not significant. Spring is generally the most favorable season for growth in Mediterranean climates because of the mild temperatures and greater water availability (Gea-Izquierdo et al. 2011). Hence, a greater water supply due to precipitation may have modulated the differences in soil type and stand density.

Trade-offs between acorn production and growth

Our results showed negative correlations between acorn production and annual growth and late summer–autumn growth in good masting years (2006, 2007, 2008, and 2011). Camarero et al. (2010) reported similar results for *Q. ilex* and Barringer et al. (2012) reported similar results for *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*. However, we found no correlations between acorn production and winter–spring growth. Several studies (e.g., Kelly and Sork 2002; Monks and Kelly 2006; Mund et al. 2010) suggested that a negative correlation between fruit production and stem growth generally indicates a switching of resources from vegetative growth to reproduction. Hence, when a tree of *Q. ilex* produces a large acorn crop during a mast year, this leads to reduced allocation for stem growth.

It may be questionable whether our observed negative correlations between acorn production and stem growth were due to a true trade-off of resources, or occurred simply because different environmental factors regulate growth and reproduction. Knops et al. (2007) suggested that the negative correlation between acorn production and annual stem growth in California oaks may be explained by this later mechanism. Thus, spring precipitation could enhance stem growth, but have a detrimental effect on pollination, leading to low acorn production and greater growth in years with more rainfall (Knops et al. 2007). Alejano et al. (2011) found that April precipitation was associated with decreased acorn production of *Q. ilex* in dehesas of southwestern Spain. However, we found negative correlations between stem growth and acorn production in late summer–autumn growth, which probably does not depend on spring rainfall, but there were no such correlations between winter–spring stem growth and acorn production. These results are not consistent with the hypothesis of Knops et al. (2007), and suggest that the negative correlations between growth and reproduction were not driven by spring rainfall. Mund et al. (2010) found negative correlations between stem growth and fruit production in *Fagus sylvatica*, and demonstrated that this was a causal relationship, rejecting the existence of apparent or putative trade-offs.

Our results showed that the negative correlation between growth and reproduction was greater during intra-annual growth periods, when there was greater resource allocation to reproduction. Late summer–autumn growth partially overlaps with the fattening of acorns, which is typically a period of lower resource availability (Carevic et al. 2010). In spring, only male flowering overlaps with stem growth. In general, female plants invest up to 10-fold more resources to reproduction than males (Obeso 2004), and in oaks, female allocation closely matches total reproductive allocation (Knops and Koenig 2012). Although summer and autumn had a higher intra-annual variability than spring in terms of climate (especially precipitation), the growth differences between years were smaller for late summer–autumn growth than for winter–spring and annual growth. On the contrary, variation in acorn production between years closely followed variations in precipitation. For example, greater acorn production occurred in years with greater summer and autumn precipitation (e.g., 2006), and lower production occurred in years with scarce summer and autumn precipitation (e.g., 2009). Stem growth has a low position in the resource allocation hierarchy (Hoff et al. 2002; Rodríguez-Calcerrada et al. 2011), and has lower sink strength than fruit production (Mund et al. 2010). Therefore, a resource allocation hierarchy may explain the greater inter-year variability in acorn production than in late summer–autumn stem growth in holm oak. In years of high resource availability, trees seem to devote the surplus to reproduction, while sustaining stem growth at moderate rates (as in normal years); however, in years with low resource availability (e.g., 2009) stem growth and acorn production were both low and a negative correlation between growth and reproduction could not explain the between-tree differences in stem growth. According to Kelly and Sork (2002), when resources are very scarce, there can even be positive correlations between growth and reproduction.

Our results clearly indicated negative correlations between acorn production and stem growth at the level of the individual tree. However, our results also showed that years with greater acorn production at the population level had greater stem growth, and that years with lower acorn production at the population level had lower stem growth. Pérez-Ramos et al. (2010) found a positive correlation between acorn production and stem growth at the population level in a stand of *Q. ilex* in Southern France, consistent with the resource matching hypothesis (Norton and Kelly 1988). Our study indicates that acorn production and stem growth in *Q. ilex* may be mainly driven by climate at the population level, consistent with the resource matching hypothesis. However, trade-offs between growth and reproduction occur at the level of the individual tree, with less stem growth in trees that allocate more resources to acorn production, consistent with the resource switching hypothesis (Kelly and Sork 2002; Monks and Kelly 2006; Sánchez-Humanes et al. 2011). Hence, resource switching and resource matching can co-occur in different periods and at different ecological levels, depending on resource availability. These findings highlight the importance of analyzing data at the individual level in examination of potential trade-offs, as suggested by Barringer et al. (2012).

Regarding the association of limited resources with trade-offs, growth in oaks is not limited by carbon availability even in mast years (Korner 2003). However, the costs of reproduction may be measured by considering photosynthesis, respiration, and resorption (Reekie and Bazzaz 1987; Ashman 1994; Sánchez-Humanes et al. 2011), which can be limited by water availability (Escudero et al. 1992; Sala and Tenhunen 1994; Mediavilla and Escudero 2003). Water shortage can cause premature abortion of fruits at the beginning of seed development (Larcher 2003; Carevic et al. 2010), thereby decreasing acorn production (Alejano et al. 2011). Stem growth is also highly dependent on water availability, especially during summer and autumn (Zhang and Romane 1991; Gutiérrez et al. 2011; Martín et al. 2014). Therefore, it is likely that the trade-offs we identified were related to intra-plant competition between stem growth and acorn production for water.

At the plot × year level, there were significant differences in stem growth and acorn production between the two plots, and covariance analyses showed that acorn production only correlated with annual stem growth in HR. HR had greater acorn production and lower stem growth than SB in all years, suggesting a preference in resource allocation to acorn production, especially in mast years. The HR plot has shallower and less developed soils and a slightly drier climate, with hotter summers and colder winters. There was also greater competition among trees in HR because of the twofold greater stand density. According to Reznick (1985), the costs of reproduction are greater in ecosystems with limited resource availability or other causes of stress. Thus, stress in the HR plot could increase resource allocation to acorn production, thereby ensuring successful reproduction and a greater density of seedlings (Kelly 1994). On the other hand, trees in HR were smaller than those in SB. Staudhammer et al. (2013) studied a tropical tree species and found that trade-offs between growth and reproduction decreased as trees increased in size and maturity; thus a phase in which there is a trade-off between growth and reproduction may slowly shift to a phase in which growth and reproduction are more independent. Acorn production was negatively correlated with late summer–autumn growth in both of our plots, and this suggests that in this more critical growth period (when acorns fatten), there were trade-offs in both plots.

Conclusions

1. During masting years, there were trade-offs between stem growth and acorn production at the level of the individual tree in *Q. ilex*.
2. The trade-offs between stem growth and acorn production occurred during late summer–autumn growth (the period of acorn fattening), but not during winter–spring growth. This result shows the importance of making intra-annual measurements of tree growth for appropriate interpretation of potential trade-offs.
3. The costs of reproduction differed between the two study sites. Trade-offs between stem growth and acorn production were greater in smaller trees that grew in conditions with greater pedological and climatic stress.

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. F. S. Carevic has participated in the data collection and reviewed the manuscript. M Fernandez 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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