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

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D. Martín has written the first draft of the manuscript, done the data analysis and field data collection.

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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 six 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.

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.

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 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 to 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 (Barrigner et al. 2014). 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 *Quercus ilex* at annual and intra-annual scales? Second, can the costs of reproduction in *Quercus 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 use of stratified sampling so that different diametric classes were considered. Keeland and Young (2014) provide details of band dendrometer theory and construction.

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 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 to 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: *(i)* a model for estimating annual growth; *(ii)* a model for estimating winter-spring growth; and *(iii)* a model for estimating late summer-autumn growth (when acorns fatten and disseminate). The initial structure of each model was:

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

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,....,18 and j = 1, 2 under the hypothesis $b_{i(j)} \sim N(0, \mathbf{G})$; α_j is a plot fixed-effect with j = 1, 2; γ_l is a year fixed-effect with l = 2006, 2007,..., 2011; $(\alpha\gamma)_{jl}$ is the plot × year interaction (fixed effect); and e_{ijl} is the residual error under the hypothesis $e_{ijl} \sim N(0, \mathbf{R})$.

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 x 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:

$$\mathrm{cov}\,(b_{i(j)}, b_{i'(j)}) = \sigma^2_b \rho^{d_{ii'}} \qquad (2)$$

where $d_{ii'}$ is the distance between trees i and i' in location j; σ^2_b 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 Scheffe´ 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 **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 **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 **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 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 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 1996; 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 is also greater competition among trees in HR because of the 2-fold greater stand density. According to Reznick et al. (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.

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Conflict of Interest

The authors declare that they have no conflict of interest.

References

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723

Ashman TL (1994) A dynamic perspective on the physiological cost of reproduction in plants. Am Nat 144:300–316

Alejano R, Tapias R, Fernández M, Torres E, Alaejos E, Domingo J (2008) Influence of pruning and the climatic conditions on acorn production in holm oak (*Quercus ilex* L.) dehesas in SW Spain. Ann For Sci 65(2):209-217

Alejano R, Vázquez-Piqué J, Carevic F, Fernández M (2011) Do ecological and silvicultural factors influence acorn mass in Holm Oak (southwestern Spain)? Agrofor Syst 83:25-39

Barringer BC, Koenig WD, Knops JMH (2012) Interrelationships among life-history traits in three California oaks. Oecologia 171:129-139

Camarero JJ, Albuixech J, López-Lozano R, Casterad MA, Montserrat-Martí G (2010) An increase in canopy cover leads to masting in *Quercus ilex*. Trees 24:909–918

Campelo F, Gutiérrez E, Ribas M, Nabais C, Freitas H (2007) Relationships between climate and double rings in *Quercus ilex*from northeast Spain. Can J For Res 37:1915–1923

Carevic FS, Fernández M, Alejano R, Vázquez-Piqué J, Tapias R, Corral E, Domingo J (2010) Plant water relations and edapho-climatic conditions affecting acorn production in a holm oak (*Quercus ilex* L. ssp. *ballota*) open woodland. Agrofor Syst 78:299–308

Cook ER, Kairiukstis LA (1990) Methods of Dendrochronology. Applications in the Environmental Sciences. Kluwer, NL

Cubera E, Moreno G (2007) Effect of land-use on soil water dynamics in dehesas of Central-Western Spain. Catena 71:298–308

Despland E, Houle G (1997) Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in eastern North America. Am J Bot 84:928–37

Escudero A, del Arco JM, Sanz IC, Ayala J (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different wood species. Oecologia 90:80–87

Gea-Izquierdo G, Cherubini P, Cañellas I (2011) Tree-rings reflect the impact of climate change on *Quercus ilex* L. along a temperature gradient in Spain over the last 100 years. Forest Ecol Manage 262:1807-1816

Greenberg CH (2000) Individual variation in acorn production by five species of Southern Appalachian oaks. Forest Ecol Manage 132:199–210

Gutiérrez E, Campelo F, Camarero JJ, Ribas M, Muntán E, Nabais C, Freitas H (2011) Climate controls act at different scales on the seasonal pattern of *Quercus ilex* L. stem radial increments in NE Spain. Trees 25:637–646

Hoff C, Rambal S, Joffre R (2002) Simulating carbon and water flows and growth in a Mediterranean evergreen *Quercus ilex* coppice using the FOREST-BGC model. Forest Ecol Manage 164:121–136

IUSS Working Group WRB (2007) World Reference Base for Soil Resources 2006, first update 2007. World Soil Resources Reports No. 103. FAO, Rome

Janzen DH (1971) Seed predation by animals. Annu Rev Ecol Evol Syst 2:465–92

Keeland BD, Young PJ (2014) Installation of traditional dendrometer bands. U.S. Geological Survey. National Wetlands Research Center. http://www.nwrc.usgs.gov/topics/Dendrometer/. Accessed 23 January 2014

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9:465–70

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–47

Knops JMH, Koenig WD, Carmen WJ (2007) Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. Proc Natl Acad Sci USA 104:16982–16985

Knops JMH, Koenig WD (2012) Sex allocation in California oaks: trade-offs or resource tracking? PLoS ONE 7(8): e43492

Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. Nature 396:225–226

Korner C (2003) Carbon limitation in trees. J Ecol 91:4–17

Larcher W (2003) Physiological plant ecology. Springer, Berlin

Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) SAS system for mixed models. SAS Institute, Cary

Martín D, Vázquez-Piqué J, Fernández M, Alejano R (2014) Effect of ecological factors on intra- annual stem girth increment of holm oak. Trees 28:1367-1381

Mediavilla S, Escudero A (2003) Stomatal responses to drought at a mediterranean site: a comparative study of co-ocurring woody species differing in leaf longevity. Tree Physiol 23:987–996

Monks A, Kelly D (2006) Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). Austral Ecol 31:366–375

Mund M, Kutsch WL, Wirth C, Kahl T, Knohl A, Skomarkova MV, Schulze ED (2010) The influence of climate and fructification on the inter-annual variability of stem growth and net primary productivity in an old-growth, mixed beech forest. Tree Physiol. 30:689–704

Norton DA, Kelly D (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Funct Ecol 2:399–408

Obeso JR (2002) The costs of reproduction in plants. New Phytol 155:321–348

Obeso JR (2004) A hierarchical perspective in allocation to reproduction from whole plant to fruit and seed level. Perspect Plant Ecol Evol Syst 6:217–225

Patterson H D, Thompson R (1971) Recovery of inter-block information when block sizes are unequal. Biometrika 58:545–554

Pérez-Ramos IM, Ourcival JM, Limousin JM, Rambal S (2010) Mast seeding under increasing drought: results from a long-term dataset and from a rainfall exclusion experiment. Ecology 91:3057–3068

Quézel P, Médail, F (2003) Ecologie et Biogéographie des Forêts du Bassin Méditerranéen. Elsevier, Paris

Reekie EG, Bazzaz FA (1987) Reproductive effort in plants. 1. Carbon allocation to reproduction. Am Nat 129: 876–896

Reznick R (1985) Cost of reproduction: An evaluation of the empirical evidence. Oikos 44:257–267

Rodríguez-Calcerrada J, Pérez-Ramos IM, Ourcival JM, Limousin JM, Joffre R, Rambal S (2011) Is selective thinning an adequate practice for adapting *Quercus ilex* coppices to climate change? Ann Forest Sci 68:575-585

Sala A, Tenhunen JD (1994) Site-specific water relations and stomatal response of *Quercus ilex* L. in a Mediterranean watershed. Tree Physiol 14:601–617

Sánchez-Humanes B, Sork VL, Espelta JM (2011) Trade-offs between vegetative growth and acorn production in *Quercus lobata* during a mast year: the relevance of crop size and hierarchical level within the canopy. Oecologia 166(1):101-110

Searle SR (1971) Linear Models. John Wiley & Sons, New York

Siscart D, Diego V, Lloret F (1999) Acorn ecology. In: Rodà F, Retana J, Gracia CA, Bellot J (eds) Ecology of Mediterranean evergreen oak forests. Springer-Verlag, Berlin, pp 75–86

Sork VL (1993) Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp). Plant Ecol 107–108:133–147

Staudhammer CL, Wadt LHO, Kainer AK (2013) Tradeoffs in basal area growth and reproduction shift over the lifetime of a long-lived tropical species. Oecologia 173:45–57

Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3:259–268

Zhang SH, Romane F (1991) Variations de la croissance radiale de *Quercus ilex* L. en fonction du climat. Ann Forest Sci 48:225–234

Tables

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

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

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

Year	**Precipitation (mm)**								**Temperature (ºC)**					
	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	1019	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

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

	Annual growth			**Winter-spring growth**			**Late summer-autumn growth**		
Effect	**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

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

Figure captions

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

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 indicate significant differences for each growth model ($p < 0.05$). Bottom: Mean annual acorn production per tree at both plots (g m^{-2} ± standard error). * indicates that acorn production reduced the variance of annual stem growth at the individual tree level. ** indicates that acorn production reduced the variance of late summer-autumn growth at the individual tree level

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 indicate significant differences for each growth model ($p < 0.05$). Bottom: Mean annual acorn production per tree at each plot (g m^{-2} ± standard error)

Fig. 1

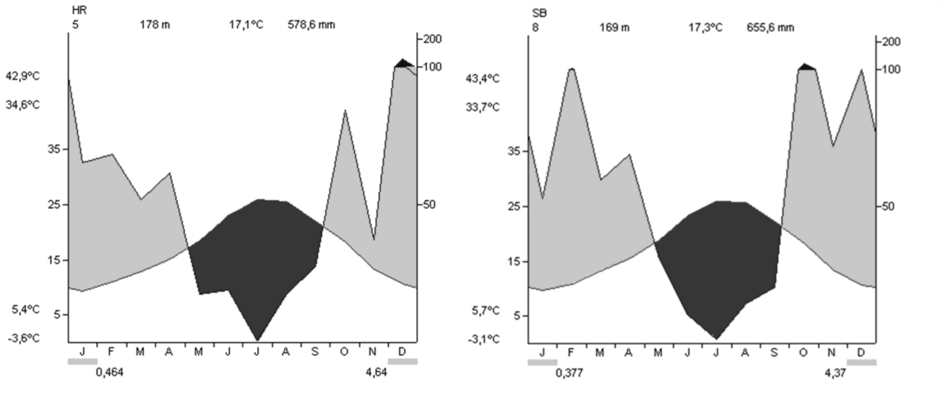
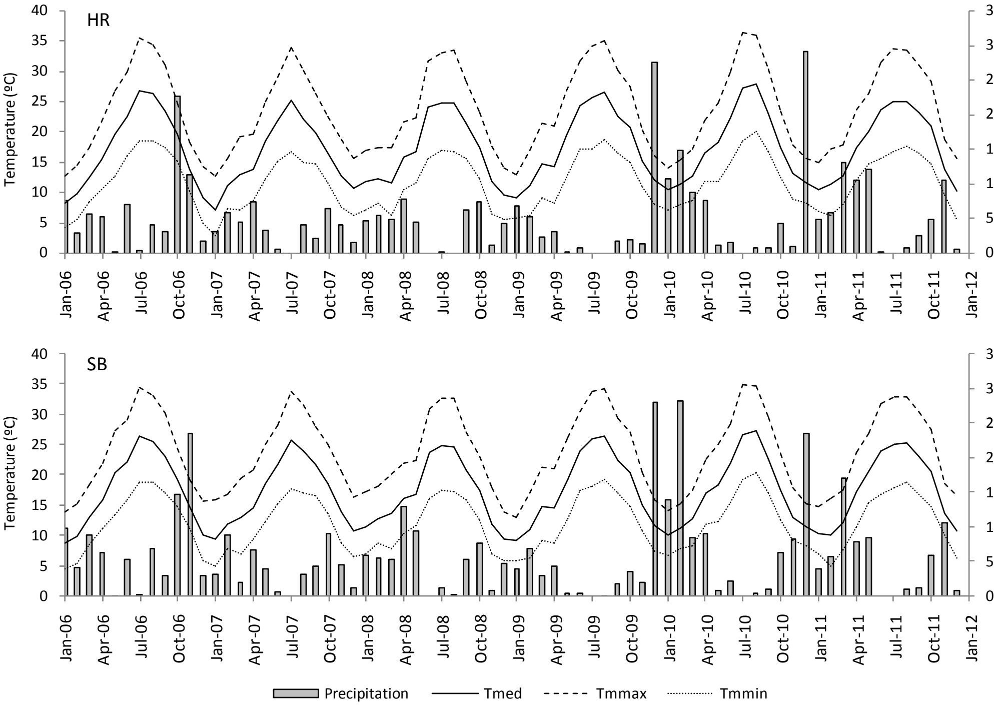

HR
5
178 m
17,1°C
578,6 mm
200
100
50
42,9°C
34,6°C
35
25
15
5
5,4°C
-3,6°C
J
F
M
A
M
J
J
A
S
O
N
D
0,464
4,64
SB
8
169 m
17,3°C
655,6 mm
200
100
50
43,4°C
33,7°C
35
25
15
5
5,7°C
-3,1°C
J
F
M
A
M
J
J
A
S
O
N
D
0,377
4,37

Fig. 2



HR
SB
Temperature (ºC)
Precipitation (mm)
0
5
10
15
20
25
30
35
40
0
50
100
150
200
250
300
350
Jan-06
Apr-06
Jul-06
Oct-06
Jan-07
Apr-07
Jul-07
Oct-07
Jan-08
Apr-08
Jul-08
Oct-08
Jan-09
Apr-09
Jul-09
Oct-09
Jan-10
Apr-10
Jul-10
Oct-10
Jan-11
Apr-11
Jul-11
Oct-11
Jan-12
Precipitation
Tmed
Tmmax
Tmmin

Fig. 3

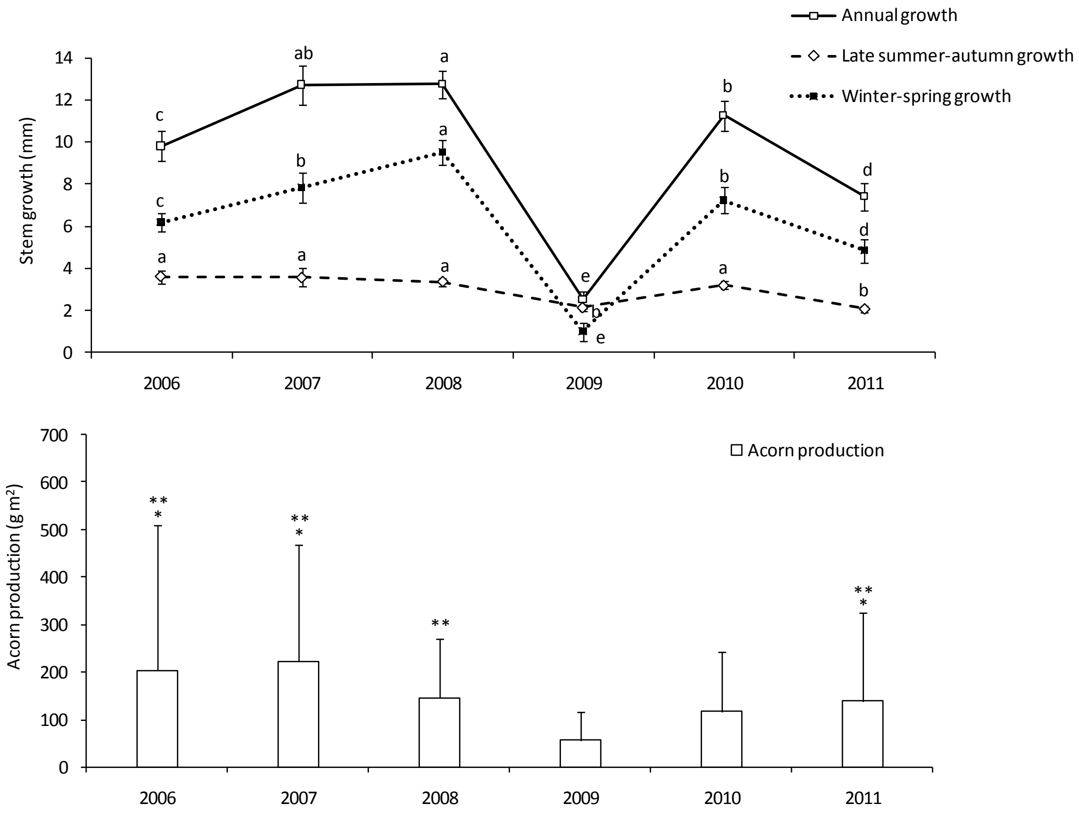
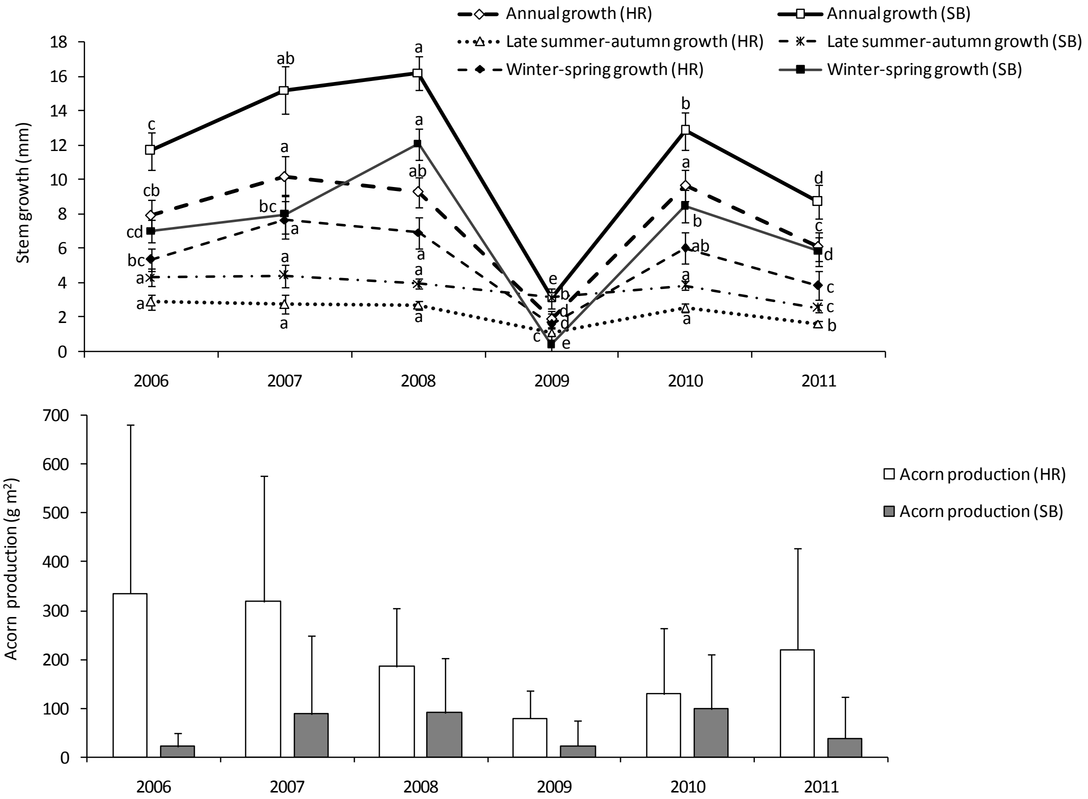

Annual growth
Late summer-autumn growth
Winter-spring growth
Stem growth (mm)
0
2
4
6
8
10
12
14
c
ab
a
e
b
d
c
b
a
e
b
d
a
a
a
b
a
b
2006
2007
2008
2009
2010
2011
Acorn production
Acorn production (g m^2)
0
100
200
300
400
500
600
700
***
***
**
***
2006
2007
2008
2009
2010
2011

Fig. 4


Annual growth (HR)
Annual growth (SB)
Late summer-autumn growth (HR)
Late summer-autumn growth (SB)
Winter-spring growth (HR)
Winter-spring growth (SB)
Stem growth (mm)
0
2
4
6
8
10
12
14
16
18
2006
2007
2008
2009
2010
2011
Acorn production (HR)
Acorn production (SB)
Acorn production (g m²)
0
100
200
300
400
500
600
700
2006
2007
2008
2009
2010
2011