Tree-rings reflect the impact of climate change on *Quercus ilex* L. along a temperature gradient in Spain over the last 100 years

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**A B S T R A C T**

We analyzed tree rings over the past 100 years to understand the response of *Quercus ilex* L. to climate change at four different sites along a temperature gradient in a highly anthropogenically transformed ecosystem. To test the hypothesis of a climate change related decrease in productivity at warmer sites, we discuss the effect of historical management on the growth of forest stands and the spatio-temporal variability of growth in response to climate, analyzing departures from linearity in that relationship. We reconstructed stand history and investigated past growth trends using tree-rings. Then we used a dendroecological approach to study the regional, local and age-dependent response to climate, analyzing the relationship between precipitation and tree growth using non-linear mixed models. Tree rings reflected the origin of the studied landscape, mainly a simplification of an original closed forest and progressive canopy opening for agrosilvopastoral purposes after the mid 1800s. As expected, trees were principally responding to water availability, and regional growth (as expressed by the first principal component from the matrix of chronologies) was highly responsive to hydrological year precipitation ($r=0.7$). In this water limited ecosystem, the response of growth to precipitation was asymptotic and independent of age, but variable in time. Maximum growth was attained at the variable sites and the non-linear function of growth saturated (i.e. reached an asymptote) at temperature dependent site specific precipitation levels within the range considered in the region to lead a shift towards deciduous species dominated woodlands (around 600 mm, variable with mean temperature). Only trees at warmer sites showed symptoms of growth decline, most likely explained by water stress increase in the last decades affecting the highly transformed open (i.e. low competition) tree structure. Stands at colder locations did not show any negative growth trend and may benefit from the current increase in winter temperatures. Coinciding with the decrease in productivity, trees at warmer sites responded more to moisture availability, exhibited a slower response to precipitation and reached maximum growth at higher precipitation levels than at colder sites. This suggests that warmer stands are threatened by climate change. The non-linear response of growth to precipitation described is meaningful for different ecological applications and provides new insights in the way trees respond to climate.

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1. Introduction

Tree growth responds to different external environmental factors, including climate. Climate change is likely to have the highest influence on species at the limit of their distribution area, both through changes in ecophysiological adaptations and spatial shift (Peñuelas and Boada, 2003; Dulamsuren et al., 2010). There is a debate on how growth of individual trees responds to climate change (e.g. D’Arrigo et al., 2008). However, we can expect those trees growing in colder climates where water is not a limiting factor to respond to warming over recent decades by increasing growth (e.g. Salter et al., 2009) whereas at those sites where water is the major limiting factor to growth, the opposite phenomenon has been observed (e.g. Piovesan et al., 2008; Dulamsuren et al., 2010). Growth decline following increasing water stress can anticipate tree dieback (e.g. McDowell et al., 2008; Allen et al., 2010). The growth response to climate has been generally modelled with linear relationships (Cook and Kairiukstis, 1990). Nevertheless, biologically we could expect more complex, non-linear responses to climate exhibiting thresholds with specific factors, as photosynthesis is also a non-linear process (D’Arrigo et al., 2004; Loehle, 2009). It is important to describe these relationships properly in order to accurately predict species growth in response to changes in climate. The relationships between growth and climate are complex and are prone to change interactively with a combination of factors such as species specific traits (e.g. Carrer and Urbinati, 2004; Rozas et al., 2009), space and time-dependent climatic conditions (e.g.
Carrer and Urbinati, 2006; Andreu et al., 2007) and stand competition (e.g. Martín-Benito et al., 2008; Gea-Izquierdo et al., 2009).

In highly anthropogenically transformed ecosystems, human disturbances in addition to climate play a major role in shaping forests. Separating the effect of each factor determining growth at different scales is not always straightforward, particularly if only short time series are available (Cherubini et al., 1998; Bigler et al., 2006). Therefore it is particularly important to study the impact of climate change in conjunction with its interactions with the human influence on forest ecosystems (Peñuelas and Boada, 2003). Human activities in the Mediterranean region have been transforming the landscapes for more than 7000 years and consequently, the composition and structure of natural ecosystems have drastically changed (Jalut et al., 2009; Valbuena-Carabaña et al., 2010). Together with human transformation of forests, these ecosystems limited by water availability in summer have been forced to adapt to an increase in water stress since carbon fertilization reducing the negative effect of stomata closure in drier conditions (Huang et al., 2007; McDowell et al., 2008).

Evergreen oak woodlands dominate many lowland landscapes in the Mediterranean region (Costa et al., 2005). In Western Iberia, historical records suggest that large areas covered today by evergreen open oak woodlands originate from more complex closed forests, transformed by humans for agrosilvopastoral uses (Costa et al., 2005; Martín-Vicente and Fernández-Alés, 2006). The future of these woodlands, dominated by Quercus ilex L. (holm oak), is severely threatened by a lack of regeneration (e.g. Pulido and Díaz, 2005; Plieninger et al., 2010) along with tree dieback triggered by sudden oak death, which is induced by the pathogen Phytophthora cinamomii Ram. Together with several contributing stress factors, including drought (Brasier, 1996). Mediterranean evergreen broadleaf species have great dendroecological potential. However, due to the complexity of their wood anatomy and difficulty associated with obtaining cross-sections from older trees (the species are protected) these species have only recently been used by several authors for tree-ring studies (e.g. Zhang and Raman, 1991; Cherubini et al., 2003; Córceuera et al., 2004; Leal et al., 2008; Campelo et al., 2009; Gea-Izquierdo et al., 2009).

For these studies analyze chronologies longer than 50–70 years (Campelo et al., 2009; Gea-Izquierdo et al., 2009) and furthermore they only analyze single sites. To our knowledge, none of these studies compares long chronologies along climatic gradients in this system. We used holm oak stands sampled in Western Iberia following a temperature gradient to analyze long-term growth trends and investigate their relationships with climate. We expect a climate change related decrease in productivity at warmer sites that will be expressed by a growth reduction in time together with a higher response to moisture availability at those sites. To separate the impact of human disturbance from that of climate change on the forest response, we first studied whether tree-rings reflect the drastic change suffered in stand structure in the late 1800s from formerly closed forests to the current open stands (Costa et al., 2005; Martín-Vicente and Fernández-Alés, 2006). Having analyzed how stand structure and competition have changed over time, we studied whether growth trends can be explained by an increase in water stress over recent decades and whether the open forests we observe today were originated under conditions of less water stress. To do so, we studied the climate–growth spatio-temporal variability, discussing whether the relationship between growth and precipitation is linear and whether this relationship can be used to understand the described growth trends.

2. Material and methods

2.1. Sample sites and data characteristics

Holm oak samples were collected at four sites in Western Spain (namely Cáceres–CÁC, Madrid–MAD, Salamanca–SAL, Zamora–ZAM) following a temperature gradient (Table 1), where water stress increases with mean temperature. All sites have similar sandy, acidic soils with low water retention capacities. Cross-sections rather than cores are strictly necessary for holm oak dendrochronological studies. Rather than following an orthodox planned sampling strategy, as the species is protected, the samples had to be collected as they became available through road and railway works. As a consequence, the samples from the different sites were obtained over a period of five years (2005–2009). A total of 233 holm oak basal sections were collected: 26 from ZAM, 115 from SAL, 40 from MAD and 52 from CÁC (Table 2). In SAL and CÁC, samples were collected from plots of 10 trees of variable radius located systematically along the strip being logged and the five central trees were harvested (see Gea-Izquierdo and Cañellas, 2009 for further details). In the cases of MAD and ZAM, it was not possible to measure plot characteristics but all individuals from available stands were taken along the clearcut strip, including all diameter classes. With the exception of shrubby coppice stands and some of the highest density stands in SAL, regeneration was generally not observed. Stand densities are shown in Table 1. Most series included in the SAL chronology belonged to low density plots (Gea-Izquierdo et al., 2009). Most of the MAD samples also came from the lowest densities (Table 1). The procedure followed to select samples for the final chronologies is further discussed in Gea-Izquierdo et al. (2009). The age and diameter distributions are shown in Fig. and in Appendix A1 respectively.

2.2. Analyses of stand disturbance and competition history

To study stand development over time we built a disturbance chronology using cross-dated raw ring width. Percentage growth change (GC) was calculated annually using a 10-year window:

\[
G_C = \frac{\sum^{i=10}_{i=1} RW_i - \sum_{i=1}^{i=10} RW_i}{\sum_{i=1}^{i=10} RW_i} \times 100, \text{ with } RW \text{ being ring-width from year } i \text{ of an individual tree-ring series. Disturbance chronologies were constructed per site by averaging GC in all trees and a threshold of 25% was considered for canopy disturbances (Nowacki and Abrams, 1997).}
\]

2.3. Analyses of changes in mean site growth in the 1900s

We estimated ages by counting rings to the pith in all cross-sections. To evaluate whether tree growth was declining as a consequence of increased water stress, individual tree-ring series were grouped in three cambial age clusters: ‘Young’ (Age < 65 years), ‘Medium’ (65 < Age < 100) and ‘Old’ (Age > 100 years old). If there is a growth reduction over time in the ecosystem, this can be explained primarily by two factors: (1) climate forcing through increased water stress; (2) non-comparable competition levels, higher today than when ‘Old’ trees were established. It could also be that growth differences would arise from differences in the sprout-seeding origin of different classes. From our observations in the field and since stands at different sites were similar, we assume that they all have a similar origin. Thus we consider this explanation to be secondary compared to the two others. Smoothing splines were fitted to mean cambial age-aligned growth of different age clusters and compared for the four sites. The comparison between growth trends of different age groups within a site is based on the following rationale: if the hypothesis that the low
density of the current stand was created by thinning over time is applicable, then ‘Old’ trees at an early cambial age were growing under conditions of greater competition than ‘Young’ trees in the open stands found today. Hence, if trees in the ‘Young’ age class at the same cambial age are growing less than those included in the ‘Old’ age class, this reflects long-term reduction in stand growth and productivity forced by changes in climate.

2.4. Dendrochronological methods and studied covariates

Cross-sections were processed and chronologies built following standard dendrochronological methods (Cook and Kairiukstis, 1990). Annual ring width (RW) was measured using a moving table coupled to a stereomicroscope, visually cross dated and then verified statistically using COFECHA (Grissino-Mayer, 2001). To study growth–climate relationships we calculated mean site chronologies of growth indices (GI). Annual GIs were obtained by standardizing individual RW series using 30 year splines and removing the autocorrelation from the residuals before using biweight means (Cook and Kairiukstis, 1990). A flexible function was used because this species is subject to management practices and we were mainly interested in analyzing the high-frequency response of growth to climate. Studied covariates included site-wise monthly climatic data (CRU, 1901–2004), the Palmer Drought Severity

Table 1

<table>
<thead>
<tr>
<th>Name</th>
<th>Longitude (North)</th>
<th>Latitude (West)</th>
<th>Altitude (m a.s.l)</th>
<th>Climate</th>
<th>Stand density</th>
<th>Dbh</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZAM</td>
<td>41° 49'</td>
<td>5° 55'</td>
<td>740</td>
<td>P</td>
<td>Tmean Tmax Tmin Tmamax85</td>
<td>Range (Min-Max)</td>
<td>Mean (sd) Max (Min)</td>
</tr>
<tr>
<td>SAL</td>
<td>40° 37'</td>
<td>6° 40'</td>
<td>700</td>
<td>P</td>
<td>Tmean Tmax Tmin Tmamax85</td>
<td>Range (Min-Max)</td>
<td>Mean (sd) Max (Min)</td>
</tr>
<tr>
<td>MAD</td>
<td>40° 25'</td>
<td>4° 10'</td>
<td>600</td>
<td>P</td>
<td>Tmean Tmax Tmin Tmamax85</td>
<td>Range (Min-Max)</td>
<td>Mean (sd) Max (Min)</td>
</tr>
<tr>
<td>CAC</td>
<td>39° 25'</td>
<td>6° 25'</td>
<td>390</td>
<td>P</td>
<td>Tmean Tmax Tmin Tmamax85</td>
<td>Range (Min-Max)</td>
<td>Mean (sd) Max (Min)</td>
</tr>
</tbody>
</table>

Table 2

Chronology characteristics. VFPC = Variance in the first principal component. Common interval analyses: 1950–2004. Standard deviation, Mean sensitivity and AR(1) are series averages. EPS and the three types of correlation are calculated for the mean chronology and growth indices. SNR = signal to noise ratio (Cook and Kairiukstis, 1990). Length is the period with two or more cross-dated series. The final site chronologies include only years replicated with at least five series (Appendix A5).

Fig. 1. Estimated age of establishment distribution. Where ages were non-crossdated basal and 1.30 m sections ages estimated were compared to find an agreement: the estimation is robust for 10 year age classes. Saplings and younger ages, although scarce, are lacking since trees of dbh > 10 cm were prioritized.
Index (PDSI) and time series (1981–2001) of NDVI (normalized difference vegetation index), which were obtained from http://cli-

cmexp.knmi.nl. NDVI is an indirect estimate of leaf area index, pho-

tosynthetic capacity and, hence, net primary productivity (e.g.

Kaufmann et al., 2008; Liang et al., 2009). NDVI series used are

monthly means of maximum NDVI values from 15-day datasets

averaged within 1° × 1°.

2.5. Analysis of variability in the growth response to climate

To see whether differences in growth trends between sites were

expressing differences in the climate–growth response we ana-

lyzed separately the regional climatic signal shared by the four

sites from that of individual sites. To extract the common regional

signal of the four sites we performed a principal component anal-

ysis (PCA, Legendre and Legendre, 1998) for the common period

1902–2002. PCA has been frequently used in tree-ring studies since

chronologies of growth indices are independent and normally dis-

tributed (Cook and Kairiukstis, 1990). The principal component

associated with the first of the four eigenvectors of the 4 × 101 ma-

trix will maximize the shared variability explained by the four sites

(Legendre and Legendre, 1998). We carried out an exploratory cor-

relation analyses between the four ring-width chronologies and

monthly climatic data, PDSI and NDVI, and between seasonal cli-

mate and PC1.

To check whether differences in growth between age classes in

time can be related to a differential response to climate of different

classes, we compared the relationship between growth and hydro-

logical year precipitation (from August (t−1) to September (t), for

the shared period 1950–2003) of the three different age classes

and all data together. We examined whether the response to pre-

cipitation is non-linear and discussed how the non-linear relation-

ship can explain spatio-temporal variability in the growth

response to climate. We used growth indices from the four site

chronologies as the dependent variable and hydrological year pre-

scription as the independent variable. A linear response was com-

pared to the exponential distribution (GI = \( G_{\text{max}}/(1 + \exp(b \cdot (P-Ip))) \)).

P is precipitation in mm, \( G_{\text{max}} \) is maximum growth, Ip the inflec-

tion point, b the shape curvature parameter and GI the growth in-

dex. We used non-linear regression mixed models (Diggle et al.,

2002). In non-linear regression models at least one of its param-

ters is on a nonlinear form (Ratkowsky, 1990). Mixed models can

include correlated error structures and non-linear random effects,

meaning that the regression parameters \( \beta \) can vary randomly

between subjects (Diggle et al., 2002). The expression is:

\[ Y_i = \mu(x_i; \beta) + Z_i, \]

where \( \mu(\cdot) \) is a non-linear function of explanatory

terms, \( x_i \) measured on the ith subject, \( j \)th observation with-

in subject. Deviations \( Z_i \) can be correlated within the ith subject,

and \( \beta \) is a random multivariate Gaussian vector with mean \( \beta \) and

variance matrix \( V_\beta \) (Diggle et al., 2002). All analyses were carried

out in R software (ver. 2.11.1), using library dplR to standardize

data, library nlme to fit the mixed models and vegan to run the

PCA. All tests were at α = 0.05, except when indicated.

3. Results

Mean annual temperature increased almost 3 °C in the region in

the 1900s while mean annual precipitation did not show any trend

(Appendix A2). This combination resulted in higher winter NDVI

indices in the study area in the last years (Appendix A3).

3.1. Stand history

There was one big release event situated at the beginning of all

the four chronologies (Fig. 2 and Appendix A4). There were release

events in ZAM around 1910 and 1980 and in MAD around 1880 and

1975. Similarly, in SAL there was a big release event around 1890

and another smaller release episode around 1920. In the warmest

stand (CAC) there was a big release event at the beginning of the

chronology (after 1880) and peaks of growth suppression around

1900 and 1940 (Fig. 2 and Appendix A4). Generally, release events

coincided with peaks in the age distribution function (Fig. 1), and

CAC was the oldest stand (Fig. 1; Table 1; Appendix A1).

Fig. 2. Disturbance chronology (mean growth change, calculated for 10 year intervals, see text for details) and mean annual ring growth per site. Bars correspond to GCs (growth changes) whereas lines to annual mean growth. Dashed grey horizontal lines correspond to a threshold of ±25% (Nowacki and Abrams, 1997).
3.2. Analyses of growth trends in the 1900s along the temperature gradient

Mean growth at earlier cambial ages showed that at all sites, ‘Medium’ trees originating after the described release events in the early 1900s were growing more than ‘Old’ trees at the same early cambial ages (Fig. 3). ‘Young’ trees, established in ZAM, MAD and SAL (around 1960) when competition was likely to have been higher again (according to Fig. 2), reacted to competition releases, like in ZAM around 1980. In ZAM and SAL (colder sites), the growth attained by ‘Young’ trees (Fig. 3) was similar to that of older age classes at cambial age 30 (i.e. around 25 years ago for ‘young’ trees). In CAC and MAD the growth of ‘Young’ trees was lower than that of older trees at the same age (Fig. 3). In CAC, which is the warmest site, both ‘Young’ and ‘Medium’ trees were growing less than ‘Old’ trees at the same cambial age for at least the last 50 years (CAC, Fig. 3).

3.3. Spatio-temporal variability in the climate-growth response: correlation analyses

The characteristics of the final chronologies (Appendix A5) are shown in Table 2. Inter-correlation among chronologies (from 0.27 to 0.52) showed the existence of a shared regional signal, which was also reflected in the high variance explained by PC1 (54.7%). The shared regional signal, as explained by the PC1, was mainly reflecting the common response to overall moisture availability. The correlation of PC1 with hydrological year precipitation was $r = 0.71$, with precipitation in winter $r = 0.58$ and with PDSI$_{Feb.-Aug.}$ $r = 0.54$. Additionally, there was a correlation between PC1 and winter temperatures (Tmean$_{Dec.-Feb.}$, $r = 0.45$). These correlations increased in the last years (Appendix A6). The high response to precipitation and drought indices varied between sites (Figs. 4A and 5A). Correlations with hydrological year precipitation were $r_{ZAM} = 0.45$, $r_{SAL} = 0.35$, $r_{MAD} = 0.45$ and $r_{CAC} = 0.63$. Temperatures, particularly in winter and late fall, were also influencing growth, yet correlations were lower than those with precipitation. The response of the two Southern most, warmest sites was separated from that of the two colder sites situated more to the North. Warmer sites were responding to precipitation in winter and early spring, whereas cooler sites were also responsive to later precipitation events (Fig. 5A). Mild winter minimum temperatures had a beneficial effect on growth in the coldest site. Mild late fall minimum temperatures from the previous year were positive for all sites, whereas high maximum summer temperatures were negative for growth at SAL (Fig. 4). These relationships were further reflected by positive correlations with summer canopy conditions as expressed by NDVI (Fig. 5B). There was a negative correlation with NDVI from January of the previous year at all sites (Fig. 5B).

3.4. Spatio-temporal variability in the climate-growth response: non-linearities and age-dependence in the response to precipitation

There were no big differences in the relationships between growth at different ages and precipitation (Table 3) and the influence of age on the growth response to precipitation was smaller than that of site (non-significant random effect for ‘age class’ in the final non-linear mixed model; $p = 0.998$). The biologically meaningful sigmoid relationship between growth and precipitation (expressed by the logistic function) improved the fit in comparison to the linear and exponential models (Table 3 and Fig. 6). The final non-linear mixed model random effects for parameters k and Gmax (Table 4) reflected differences in the sigmoid shape between the different sites along the temperature gradient and the common inflection point was 285 mm (although there was only data from MAD below that threshold; Table 4). The mean maximum growth response was around 600 mm (Fig. 6), and larger maximum growth responses were attained at higher precipitation levels with increasing mean site temperatures (Table 4). This analysis showed that there was a slower response to precipitation at warmer sites.

4. Discussion

4.1. Disentangling the influence of management and climate on growth trends: are trees from warmer locations relicts from former, more humid conditions?

Tree-rings suggested that current stands are the result of the transformation of a closed forest thinned over time on several occasions to enable silvopastoral use, revealing that they are not natural
savannas (Costa et al., 2005; Martín-Vicente and Fernández-Alés, 2006). Martín-Vicente and Fernández-Alés (2006) reported that before the 1800s, most holm oak woodlands in Western Spain were closed shrubland whereas today the dominant landscape is open oak woodland. Therefore, trees face less competition today than prior to the first recorded thinning episodes in the late 1800s or early 1900s, which is when they were likely to have been converted to the current open stands (Costa et al., 2005; Martín-Vicente and Fernández-Alés, 2006). Traditionally in this agrosilvopastoral ecosystem, when canopy cover is too high for grassland development, stand density is reduced by thinning, and as reflected by release events, thinning was likely undertaken more than once. Episodes of growth suppression were less dramatic than growth releases (i.e. thinning), and could be related to periods of intense pressure for firewood from these ecosystems (as occurred in CAC directly after the Spanish Civil War, around 1940) and/or increased stand competition before thinning.

Disentangling the effects of climate and management changes over time on tree growth can be difficult since they can co-occur

![Figure 4: Monthly correlation between growth index and climate for the four different sites studied: (A) monthly precipitation; (B) mean monthly minimum temperatures; (C) mean monthly maximum temperatures. Dashed lines correspond to significant levels at 0.05.](image)

![Figure 5: Monthly correlations between ring width, NDVI and PDSI for the different sites studied: (A) correlation with PDSI (1901–2002); (B) correlation with NDVI (1982–2000). Dashed horizontal lines correspond to significant levels at 0.05.](image)
and present synergistic effects. At the warmer sites, trees are growing less today than in the early 1900s, when competition was likely higher. The fact that this occurs in other water limited areas, not only in the Mediterranean (e.g. Peñuelas et al., 2008; Piovesan et al., 2008; Dulamsuren et al., 2010), suggests that declining growth in warmer, southern locations is a result of water stress. And growth decline can lead to tree mortality (Bigler et al., 2006). Growth trends from the two coldest sites (ZAM and SAL) did not suggest any significant change in growing conditions. Moreover, growth at these sites may even be positively affected by an increase in winter temperatures and earlier phenology (Gordo and Sanz, 2009; Vicente-Serrano et al., 2010). Growth decline may also be related to local, non-climatic factors, although we consider this unlikely. Like other Fagaceae species, Q. ilex is able to

### Table 3

Age cohort analyses (1) Correlation analyses between mean age cohort chronologies and selected covariates (1950–2004); (2) comparison of linear, exponential and sigmoidal (logistic function, see text for details) models of growth indices with hydrological year precipitation. AIC = Akaike Information Criterion (minimum is best). Pwinter = precipitation in winter (January–March); Pspring = precipitation in spring (April–June); Phydrol = hydrological year precipitation.

<table>
<thead>
<tr>
<th>Correlation mean annual growth</th>
<th>Model AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Phydrol</td>
</tr>
<tr>
<td>Young</td>
<td>0.450</td>
</tr>
<tr>
<td>Medium</td>
<td>0.521</td>
</tr>
<tr>
<td>Old</td>
<td>0.535</td>
</tr>
<tr>
<td>All</td>
<td>0.501</td>
</tr>
</tbody>
</table>

### Table 4

Sigmoidal (logistic function) mixed effect model results of hydrological year precipitation (August–Sept.) on growth indices. AIC = Akaike Information Criterion. Gmax = maximum growth; Ip = inflection point; k = curvature parameter; μ = mean response; αi = site specific random estimated random effect.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate (SE)</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed effects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gmax</td>
<td>1.2904 (0.072)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>k</td>
<td>-0.0072 (0.0010)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Ip</td>
<td>294.63 (6.09)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Random effects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Covariance estimates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gmax</td>
<td>0.1391</td>
<td>0.0007</td>
</tr>
<tr>
<td>k</td>
<td>0.0018</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Estimated precipitation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>90% Gmax</td>
<td>590</td>
<td>690</td>
</tr>
<tr>
<td>95% Gmax</td>
<td>690</td>
<td>830</td>
</tr>
</tbody>
</table>

Fig. 6. Mixed model results between the four chronologies and hydrological year precipitation. Different coloured dots correspond to observations from the four different sites sampled. The thick black line corresponds to the mean response (fixed effects from sigmoidal mixed model) whereas thinner colored lines correspond to local site functions (fixed + random effects in the sigmoidal model), with the same colours as those of the dots. The vertical grey dashed lines show: (1) the inflection point of the mean response (Ip); (2) the precipitation at which 90% (Gmax90) and 95% (Gmax95) of mean population growth is achieved respectively.
resprout, and the origin of the current stems (either from seedlings or sprouts) would influence long-term stand dynamics (Clarke et al., 2010). Sprouts tend to lose vigour more rapidly than seedlings when intensively coppiced; therefore if the existing tree structure is the result of past coppicing practices, decline could also be partly explained by the stagnation of stools in older woodlands (Clarke et al., 2010; Di Filippo et al., 2010).

Today, age-related differences in rooting depth partly explain lack of regeneration establishment in the ecosystem, along with low stand densities, overgrazing and the absence of a shrub layer enabling seedling facilitation (e.g. Pulido and Díaz, 2005; Plieninger et al., 2010). The absence of differences between age classes in terms of the response to annual precipitation has also been reported by other authors (e.g. Esper et al., 2008; Di Filippo et al., 2010). However, as regards the response to climate, we expected to identify age related differences (e.g. Carrer and Urbinati, 2004; Rozas et al., 2009) because young trees were expected to be more responsive to precipitation as a result of age-related differences in carbon allocation and shallower root systems. The fact that the two warmest sites exhibited higher correlations with winter precipitation (greater percolation to deeper horizons when the annual grass layer is less active) and less correlation with late spring precipitation (greater percolation to deeper horizons (Sarris et al., 2007). Along with the observed growth reduction observed in warmer, southern stands, this might be an indication that the adult tree structure encountered today became established when more humid or cooler conditions existed during the 1800s (Rodrigo et al., 2000; Touchan et al., 2010).

4.2. Spatio-temporal variability in the response to climate explain growth trends

Species response is plastic and varies spatially (e.g. Cherubini et al., 2003) according to differences in microsite conditions which determine the ecophysiological response and changes in phenology of the trees (La Mantia et al., 2003), Q. ilex, like other species in winter-warmer double-stress ecosystems, shows a mixed temperature-precipitation signal (e.g. Zhang and Romane, 1991; Tressier et al., 1994; Cherubini et al., 2003). However, higher response to precipitation is to be expected when analyzing the monthly or seasonal response (Gutiérrez et al., 2011) in water limited ecosystems and warm climates (e.g. Andreu et al., 2007; Brien et al., 2010; Clark et al., 2010). Trees were found to be highly dependent on moisture availability, as expected. Overall, response to precipitation was highest in early winter and spring. Spring is the period of maximum growth for the species, although after a facultative cambial stop in summer, it is able to resume growth in fall (Gutiérrez et al., 2011). The shared regional response of growth to hydrological year precipitation was very high (r = 0.71) and above that of individual site responses (r < 0.55). There was a later response to precipitation in colder stands and higher response to drought at the warmest site (CAC), coinciding with the observed reduction in growth over time. Variability in individual correlations with climate at the different sites was similar to those previously reported for the species in the Iberian Peninsula (e.g. Corcuerà et al., 2004; Campelo et al., 2005; Gutiérrez et al., 2011) as well as for other Mediterranean species (e.g., Leal et al., 2008; Martín-Benito et al., 2008; Di Filippo et al., 2010).

The relationship between growth and climate varies over time (e.g. Carrer and Urbinati, 2006; Andreu et al., 2007; D’Arrigo et al., 2008), and the responsiveness of many Western Mediterranean forests to precipitation has increased over the last three decades (e.g. Andreu et al., 2007; Gea-Izquierdo et al., 2009). This is further reflected by NDVI increase in February, the increase in annual temperatures and earlier phenology (Gordo and Sanz, 2009). There is a complex reverse effect on growth caused by an increase in both winter and summer temperatures. Although the negative effect of summer stress on trees might be expressed on a different time scale through carbon storage and reallocation, the fact that trees do not show a negative response to summer temperatures might mean that they are generally able to control drought through stomatal control and uptake of water from deep horizons (Nardini et al., 2000; Infante et al., 2003; Baldocchi et al., 2010). The positive response to winter temperatures suggests that these evergreens may be photosynthesizing and storing carbohydrates in milder winters (Baldocchi et al., 2010). Furthermore, this increase in winter temperatures means that trees are less threatened by the indirect effect of frost on the photosynthetic apparatus and tree carbon pools (Nardini et al., 2000; Corcuerà et al., 2005). The overall effect on growth and carbon pools of these two contrary effects of rising temperatures merits further research. Relationships between photosynthesis and growth can help us to understand pathways in carbon allocation and their role in climate change mitigation. Tree rings have proved to be useful to reconstruct NDVI in other ecosystems, and both variables responded to similar climatic forcing in Liang et al. (2009). The positive correlation between growth and NDVI after spring was well related to physiological reactions expressed by correlations between growth and climate. Contrary to what Kaufmann et al. (2008) report for deciduous trees but similar to findings for evergreen conifers. The growth of our evergreen broadleaves was mainly correlated with summer canopy status, reflecting better canopy conditions and carbon pools after humid springs and winters. The negative correlation with the NDVI from January of the previous year is difficult to explain, but we could speculate that it might reflect trade-offs in growth-carbon allocation to crowns as a consequence of evergreen leaves remaining in the canopy for a longer time.

Theoretically, species should display thresholds where they start or stop responding to external forcing factors (D’Arrigo et al., 2004, 2008), therefore we might expect a sigmoidal growth response to individual factors. Non-linearities are more likely to be evident when applied to a wide gradient including ecological limits of a specific dominant climatic factor, as in the present study. The limits drawn by the sigmoid response to precipitation are meaningful for species ecology in response to climate change in the sense that they would determine the limit at which the species is more competitive and expressed interactions with mean site temperature. Variability in the logistic function curvature and maximum growth (as indicated by the site random coefficients) expressed the influence of overall site moisture balances. Warmer sites showing a decrease in productivity responded more slowly to precipitation and required greater precipitation amounts to achieve maximum growth. Together with Pinus halepensis, Q. ilex is one of the most drought tolerant tree species of those found in the Mediterranean region. It is often the dominant tree species forming woodlands in the ecotone with sub-desertic or drier shrubland ecosystem types. The ecotone occurs with precipitation levels of around 250–300 mm (Costa et al., 2005), the precipitation limit indicated by the inflection point of the sigmoidal response. Furthermore, it is interesting to note the absence of a growth response to precipitation levels above 600–700 mm (Table 4), as indicated by the sigmoid. This is roughly the limit considered in the Western Mediterranean area which implies a shift from evergreen broadleaf dominated woodlands to less water stress tolerant or broadleaf deciduous forests (Costa et al., 2005). The high regional response to precipitation identified might attract climate reconstruction modellers. However, for this species, the extension of chronologies into the past and the reconstruction of precipitation would seem cumbersome for three reasons: (1) the response is non-linear and sensitivity is non-stationary, hence linear extrapolations into the past may not be correct (Loehle, 2009); (2) the limited availability of a representative sample of old trees
Baldocchi, D.D., Ma, S.Y., Rambal, S., Misson, L., Ourcival, J.M., Limousin, J.M., Pereira, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., the growth trends and response to climate of Quercus ilex L. (>200 years old) without rotten centers; (3) the problem of disentangling the low frequency climatic signal from the effects of human impact.

5. Conclusions

The opportunity arose to analyze a unique dataset with a time span longer than 100 years, providing valuable information on the growth trends and response to climate of Q. ilex. All stands studied had a very similar disturbance history, likely reflecting the transformation by humans of the original closed, mixed forest following socio-economic changes and redistribution of land in Spain in the mid 1800s. Disentangling the impact on growth of warming over recent decades from that of management is challenging, not only due to the lack of reliable information on the local history of forests but also because of the total transformation of landscapes in the Mediterranean area. Warming is increasing water stress and it seems that growth constraints have increased along the last decades in warmer stands. In warmer stands (those located more to the South) the response of trees to moisture availability was highest and we observed a decline in growth, meaning that trees are very likely threatened by climate warming. Regionally, we observed a very high level of common response to precipitation. The relationship between growth and precipitation was sigmoidal, and both the growth-saturating precipitation level and the shape of the sigmoid function provided valuable insights into the ecology of the species in relation to climate. In terms of growth, Q. ilex stopped responding to increasing precipitation at levels above 600–700 mm. These values coincide with the general range of precipitation considered to trigger a change from evergreen dry woodlands to deciduous dominated woodlands in the studied area. Our results provide some new evidences on the response to warming of an endangered ecosystem.

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Appendix A. Supplementary data


References


