



Growth projections reveal local vulnerability of Mediterranean oaks with rising temperatures



Guillermo Gea-Izquierdo*, Laura Fernández-de-Uña, Isabel Cañellas

INIA-CIFOR, Ctra. La Coruña km 7.5, 28040 Madrid, Spain

ARTICLE INFO

Article history:

Received 27 February 2013

Received in revised form 20 May 2013

Accepted 25 May 2013

Keywords:

Nonlinear response

Forest decline

Global change

Dendroecology

Quercus pyrenaica

Quercus ilex

ABSTRACT

Growth projections using ecological models fitted to data collected along climatic gradients can help to understand how forests will respond to climate change. Stem growth of two Mediterranean oaks was predicted using nonlinear multiplicative models as a function of precipitation and minimum temperature of the hydrological year fitted to dendrochronological data. The growth of both species increased nonlinearly with accumulated precipitation before reaching an asymptote, but the species with a warmer niche (*Q. ilex*, an evergreen species) required lower levels of precipitation to achieve high relative growth. The species-specific relationship between growth and minimum temperature exhibited an optimum for the two species. Trees were negatively affected by high minimum temperatures whereas they responded negatively (*Q. ilex*) or neutrally (*Q. pyrenaica*, a deciduous species) to low temperatures along the climatic gradient analyzed. Growth would decrease rapidly when minimum temperatures rose above approximately 7 °C for *Q. pyrenaica* and 9 °C for *Q. ilex*. Most growth projections suggest a likely future decrease in productivity along the species range for *Q. pyrenaica* and particularly at species-specific warm, dry locations pointed to a future drastic reduction in productivity as a result of the increase in temperatures without a paired increase in precipitation forecasted by the different climate scenarios considered. In agreement with results from studies modeling future distribution of species this suggests that *Q. pyrenaica* could be threatened by climate change at the species local dry edge where, in addition, stands often present a lack of seed regeneration. More drought tolerant *Q. ilex* might profit from warming temperatures at cold northern locations but would also reduce productivity at warm, dry locations. Stem growth was successfully modeled using biologically meaningful species-specific responses to climate which provided key ecological information to understand the functional response of the two species. The models used have much potential to be applied with dendroecological data to study the response of forests to climate change.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Global change will likely trigger major changes in species distribution and productivity (Boisvenue and Running, 2006; Lenoir et al., 2008; Thuiller et al., 2005). In water limited ecosystems plant acclimation processes such as changes in phenology and increased water-use efficiency (Gordo and Sanz, 2009; Peñuelas et al., 2011; Andreu-Hayles et al., 2011) have not been able to preclude local forest decline induced by the recent enhancement of water stress caused by rising temperatures (Adams et al., 2009; Allen et al., 2010; McDowell et al., 2011). Although warming temperatures may have increased growth of certain species locally at cold, humid sites, in summer drought-limited Mediterranean ecosystems the expected reduction in productivity at species' dry limits in response to rising overall water stress (Vicente-Serrano et al.,

2010; Gea-Izquierdo et al., 2011; Di Filippo et al., 2010, 2012) is believed to portend modifications in species' distributions at the regional scale (Sanchez de Dios et al., 2009; Ruiz-Labourdette et al., 2012, 2013). Consequently, to assess the best strategies that minimize adverse ecological and socio-economic impacts it is crucial to know how forests will respond to changes in climatic conditions and detect plant ecological thresholds at which species start to decline.

Limits in plant responses to climate can be difficult to detect if species did not cross them in the period sampled or if the current distribution of species does not express the complete potential niche. Therefore, to accurately fit the theoretical nonlinear relationship between climate and plant performance it is necessary to sample species along full gradients for specific climatic covariates (Canham and Uriarte, 2006). The nonstationarity and nonlinearity (including the 'Divergence Problem') in the response of growth to climate and the derived implications for growth and climate simulations have received much attention in recent years

* Corresponding author. Tel.: +34 91 3476772; fax: +34 91 3476767.

E-mail addresses: gea.guillermo@inia.es, guigeiz@gmail.com (G. Gea-Izquierdo).

(e.g. D'Arrigo et al., 2008; Evans et al., 2006; Bär et al., 2008; Loehle, 2009). Nonlinear relationships can be approximated to linear if analyzed in short segments of the covariate range and given we do not have a maximum or minimum within that range (Vaganov et al., 2006). However, this will bias projections outside the observed range (Loehle, 2009). Dendrochronological data have been used to build long time series to readily increase the climatic range sampled. Several growth models directly addressing the nonlinear nature of the growth-climate relationships have been used with dendrochronological data, including empirical (D'Arrigo et al., 2004; Bär et al., 2008; Gea-Izquierdo et al., 2011) and ecophysiological approaches (Fritts et al., 1991; Foster and Leblanc, 1993; Misson et al., 2004; Vaganov et al., 2006; Tolwinski-Ward et al., 2011). Nonlinear models with a physiological basis should be more skillful outside the calibration interval than empirical additive linear models (Federer et al., 1989; Foster and Leblanc, 1993; Tolwinski-Ward et al., 2011) like those traditionally used in climate reconstructions or those often used to project growth under different climatic scenarios (Girardin et al., 2008; Lapointe-Garant et al., 2010; Martin-Benito et al., 2011). In empirical models, existing nonlinearities in the climate-growth response have been modeled using Neural Networks (Woodhouse, 1999; Zhang et al., 2000), piecewise relationships (Wilmking et al., 2004) or second-order polynomials (D'Arrigo et al., 2004; Bär et al., 2008), and as shown for repeated forest inventory data, they could be further modeled using flexible non-parametric methods such as B-splines (Nothdurft et al., 2012).

To investigate how trees will respond to climate change we projected growth of one evergreen and one deciduous Mediterranean *Quercus* species using climatic factors as predictors and three different scenarios from IPCC4 (IPCC, 2007) run within three different General Circulation Models (GCMs). We used a parametric multiplicative nonlinear model similar in structure to those utilized at different time scales in forestry and ecology (Ung et al., 2001; Canham et al., 2006), in models of primary productivity (Landsberg and Waring, 1997; Yuan et al., 2007; Mäkelä et al., 2008) or in physiologically oriented models with dendrochronological data (Foster and Leblanc, 1993; Vaganov et al., 2006). By using the proposed parametric approach we can assess the nonlinearity in the response to key climatic covariates and investigate hypothesis on the existence of ecological thresholds as expressed by fitted parameters. To fit the model we used dendrochronological data sampled along climatic gradients and modeled stem growth using functions of precipitation and temperature with a biological basis. We specifically compared functional responses supporting different ecological assumptions regarding species-specific climatic envelopes. In the studied summer drought limited Mediterranean ecosystem we hypothesize that the functional response of growth to precipitation will increase monotonically towards an asymptote whereas the functional response of growth to temperature will exhibit a species-specific optimum and decreasing growth with increasing temperature thereafter. Particularly, we were interested on running predictions to investigate whether instability in growth related to the modeled response thresholds reveals local vulnerability of trees to future climate, accepting that an abrupt decrease

in growth driven by enhanced water stress would indirectly express vulnerability to climate change (e.g. Suárez et al., 2004; Voelker et al., 2008; Sarris et al., 2011; Di Filippo et al., 2012).

2. Material and methods

2.1. Growth data and climatic covariates

To model the relationship between stem growth and climate we used a set of 14 chronologies from two Western Mediterranean oak species (*Quercus ilex* L. and *Quercus pyrenaica* Willd.; hereafter QUIL and QUPY, respectively). *Q. ilex* is an evergreen widespread species in the Mediterranean and presents a higher tolerance to drought than deciduous *Q. pyrenaica* (Corcuera et al., 2006; Montserrat-Marti et al., 2009), which is confined to supramediterranean areas with acidic soils in the West Mediterranean (Costa et al., 2005). These two species can occupy overlapping niches. QUPY was sampled along latitudinal and altitudinal gradients in the Iberian Peninsula whereas QUIL was sampled along a temperature gradient at four locations (Table 1 and Fig. 1). In the studied area mean temperature decreases with increasing altitude and latitude and precipitation increases with altitude. All trees sampled were dominant or co-dominant in stands thriving on sandy soils derived from acidic bedrock (Gutiérrez-Elorza, 1994). These stands were similar in structure, monospecific with only one social class of dominant-codominant trees, often with less than full canopy cover. These conditions are representative of dominant oak woodlands in the area. See Table 1, Appendices A and B for data characteristics.

The anatomy and characteristics of QUIL challenges the construction of long chronologies because it is necessary to analyze cross sections. The species is protected, making rather difficult the collection of a sufficient number of old individuals, which makes the dataset available particularly precious (see Gea-Izquierdo et al., 2011 for a complete description of the QUIL dataset). For *Q. pyrenaica* trees two or three cores were taken at 1.30 m and annual ring-width measured and crossdated following standard dendrochronological methods (Fritts, 1976; see Gea-Izquierdo et al., 2012, for more details on data processing). Radial growth was transformed to basal area increment values (BAI, Biondi and Qeadan, 2008). By using BAI (cm²) we intended to keep both the high and the low frequency response of growth and also to preserve the direct relationship between covariates (i.e. their dimension) within the range sampled, so that the model could reflect differences in mean productivity between sites. However we aimed to specifically model the nonlinear shape of the relationship between growth and climatic covariates using a likelihood approach that requires independence between observations (Bolker, 2008). Depending on the goal, within data correlation should be treated in different ways because eventually it includes part of the ecological information to be analyzed. We decided to smooth data by filtering out serial correlation within each individual tree-ring series as regularly implemented in dendrochronological methods (Cook and Kairiukstis, 1990) using an autoregressive moving average model ARMA(1,1) (Monserud, 1986) scaled to the tree

Table 1

Mean observed climatic and growth variables per species for the period 1951–2004. # Obs = number of observations. BAI = annual basal area increment; Ppt = precipitation of hydrological year; T_{min} = minimum monthly average temperature of hydrological year. Max = maximum; Min = minimum. In Latitude and Altitude we show maximum and minimum values for the different species sampled. More details on specific sites are presented in Appendix A and Appendix B.

Species	# Sites	# Trees	Latitude (°)	Altitude (m)	Density (trees/ha)	BAI (cm ² /year)				Ppt (mm)				T_{min} (°C)			
						# Obs	Mean	Max	Min	Mean	Max	Min	Range	Mean	Max	Min	Range
QUIL	4	91	41.8–39.4	740–390	30–191	110	16.7	47.2	4.5	497.0	1066.0	210.1	855.9	8.3	12.0	5.4	6.6
QUPY	10	197	42.1–37.0	1650–760	65–325	550	18.2	32.9	1.1	647.1	1497.0	225.8	1271.2	6.2	10.8	2.9	7.9

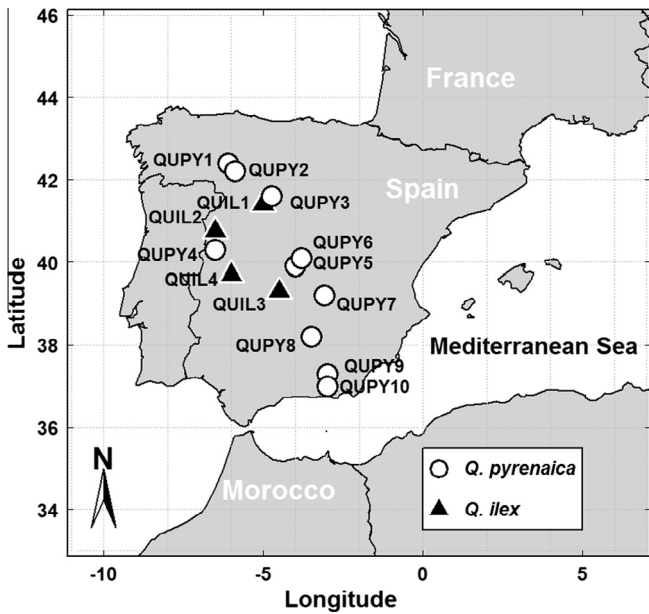


Fig. 1. Map showing the distribution of chronologies in Appendix B. Overlapping points mean different chronologies coming from a single site either because of sampling along altitudinal gradients or because the two species occurred within the same site.

average BAI to preserve the low-frequency information. Finally, we built mean site BAI chronologies to fit the growth models.

Climatic gridded CRU TS 3.10 data (Mitchell and Jones, 2005) including monthly precipitation and mean, minimum and maximum temperature were obtained from the KNMI explorer (http://climexp.knmi.nl/get_index.cgi) for the period 1901–2004. Gridded data were linearly corrected using local data from AEMET (<http://www.aemet.es/es/portada>) when available and along altitudinal gradients temperatures were corrected considering a mean lapse rate of 0.6 °C for every 100 m in elevation range (Nobel, 2009). To select those covariates showing the highest relationship with growth, in a preliminary analysis we tested climatic covariates for target periods of maximum growth response in the studied Mediterranean species (Tessier et al., 1994; Gea-Izquierdo et al., 2011): hydrological year (from November $t - 1$ to October t), winter (from January to March), spring (from April to June) and June–July. After exploring these different climatic covariates we decided to fit models as a function of precipitation and minimum temperature for the hydrological year (hereafter Ppt and T_{min} respectively), which in Mediterranean ecosystems includes the two periods of maximum environmental stress: the cold winter and the summer shortage of water availability (Mitrakos, 1980). Models based on empirical climatic covariates can relate well to plant performance because ecophysiological processes including productivity depend on different biochemical and ecological conditions ultimately governed by moisture and temperature (Schenk, 1996). Additionally, different climatic scenarios including monthly precipitation and temperature data are readily available, which facilitates projecting growth at different locations using Ppt and T_{min} as predictors.

2.2. Growth model

Excluding other biotic and abiotic disturbances, growth can be modeled as a function of tree age, size, stand competition and site fertility, which includes soil and climatic factors (Fritts, 1976; Zahner et al., 1989; Canham et al., 2006). Soil conditions were assumed to be comparable along the studied gradients, thus overall differences among sites should not bias the relationship between

growth and climate fit by the model. Then a simplified generic empirical model of growth with a multiplicative structure could be as follows:

$$\text{Growth}_j = MG \cdot f_1(\text{age}) \cdot f_2(\text{competition}) \cdot f_3(\text{climate}) + \varepsilon_j \quad (1)$$

all $f(\cdot)$ are unitless functions of value [0,1] which can take into account different functional relationships with specific covariates, MG is a parameter representing maximum growth in growth units (in our case BAI in cm^2/year) and ε_j is a random error for observation j . To eliminate the effect of juvenile growth (f_1) on BAI and minimize the effect of competition (most sites showed little evidence of management during that period) we used data from the period 1951–2004 to fit the model and 1925–1950 to validate the final selected model. Additionally, by using non-juvenile mean chronologies we reduced any possible effect of individual tree size on BAI. With dendrochronological data we have readily available long time spans of growth under a wide climatic range but we lack information on changes in competition in time that will likely influence radial growth. To assess the influence in time of changes in competition on growth (f_2) we would require information from permanent plots. However, permanent plots usually have limited geographical range compared to dendroecological data and rarely span more than few decades (Biondi, 1999). The effect of competition in our study should be comparable between stands and reduced compared to more complex, denser forests. With the exception of crowding increase with stand development (which should be similar at all sites) the influence of competition was minimal in the period studied: sampled dominant trees experienced no crown competition, there were very few release events (i.e. major disturbances) after 1950 in the studied sites (data not shown) and stand densities were not high and within the normal range of stocking levels of mature oak woodlands in the area (Gea-Izquierdo and Cañellas, 2009). Additionally, no stand presented a dense shrub understory. In fact, on a preliminary analysis we observed that the inclusion of present stand density did not improve the model (not shown). Therefore, f_1 and f_2 were considered negligible for our study compared to f_3 and the growth response fitted to climatic factors should be robust when analyzed in the spatio-temporal climatic gradients sampled. The general form of the model to be fitted was:

$$\text{BAI}_j = MG \cdot g_1(Ppt) \cdot g_2(T_{min}) + \varepsilon_j \quad (2)$$

As mentioned above, climate was represented in the final model by functions of precipitation (Ppt) and mean minimum temperature (T_{min}) of the hydrological year. The model is based on the principle of the limiting factor and the growth projections assume the principle of uniformitarianism (Fritts, 1976). Although relationships with empirical covariates can depend on the time scale (Schenk, 1996) ideally physiological responses will follow either sigmoid or bell-shaped curves (Vaganov et al., 2006). In model (2) we compared the following functional relationships (see Fig. 2).

2.2.1. Precipitation effect: g_1

Under the studied Mediterranean climate where summer water stress is a main ecological driver, we considered that the functional form of the underlying physiological relationship between growth and precipitation will increase monotonically to an horizontal asymptote as in a sigmoidal function or the cumulative exponential distribution (Vaganov et al., 2006; Gea-Izquierdo et al., 2011). Thus the relationship between hydrological year precipitation and growth would fit a logistic function, of the form:

$$g_1(Ppt) = 1 / (1 + (Ppt/p_1)^{p_2}) \quad (3)$$

where $g_1 \sim [0,1]$, p_1 is the precipitation at which growth is half of the maximum potential value (half saturation) and p_2 is a scale parameter, negative to make the function monotonically increasing.

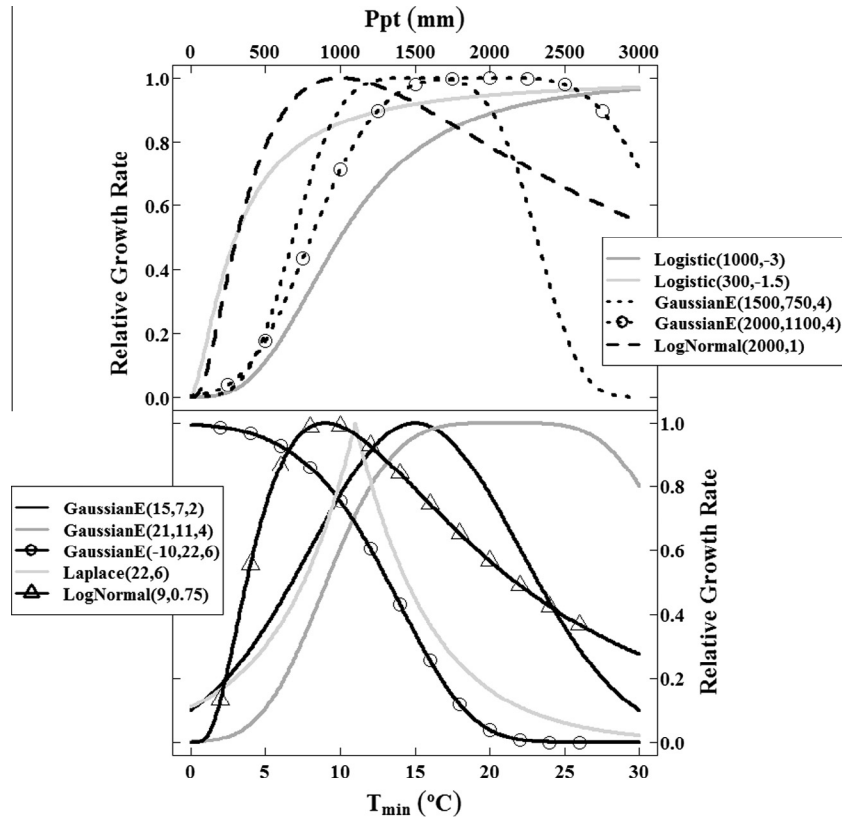


Fig. 2. Examples of hypothetical functional relationships for the growth response to precipitation (above) and temperature (below) as tested in the empirical multiplicative model. In the legends we show the parameters of the different distributions used in the figure, see functions (3)–(7) in main text for meaning of parameters. GaussianE = expanded Gaussian function. Dashed lines correspond to a shape that we do not consider realistic for the studied species in a Mediterranean climate with climatic scenarios of non-increasing precipitation. We test them for comparison and since it might be expressed in more humid ecosystems. Parameters in functions were randomly selected to depict different shapes and do not correspond to any model fit.

We did not expect a quadratic response of growth to precipitation (Fig. 2) in the ecosystem studied both because it was suggested empirically (Fig. 3) but also because it has been shown that, under the studied climate, precipitation does not reach such high levels that make growth decline (Gea-Izquierdo et al., 2011). However, to demonstrate this assumption we compared the logistic function to a symmetric response as in the Gaussian function:

$$g_1(Ppt) = \exp(-0.5 \cdot ((Ppt - p)/b_p)^2) \quad (4)$$

$g_1 \sim [0,1]$, p is the optimum precipitation at which maximum growth occurs and b_p is the standard deviation or breadth of the function (Canham et al., 2006). To discard also that the relationship between growth and precipitation was asymmetric with a maximum we tested a lognormal distribution:

$$g_1(Ppt) = \exp(-0.5 \cdot ((\log(Ppt/a_1)/a_2)^2) \quad (5)$$

where a_1 is the optimum value of Ppt at which potential growth occurs and a_2 is the standard deviation or breadth of the function (Fig. 2).

2.2.2. Temperature effect: g_2

We expect species to exhibit optimal temperatures for growth (Schenk, 1996; D'Arrigo et al., 2004; Vaganov et al., 2006; Loehle, 2009). Therefore, theoretically, we should use non-monotonic, unimodal (the mode being either a single value or an interval), either symmetric (e.g. Gaussian or Laplace) and asymmetric (e.g. Lognormal and Weibull, Beta), concave up, parabolic functions to fit the relationship between growth and temperature (Fig. 2). Several functional relationships between growth and temperature were

compared. A generic smooth symmetric response to temperature was tested using a modified Gaussian function, of the form:

$$g_2(T_{min}) = \exp(-0.5 \cdot ((T_{min} - t)/b)^a) \quad (6)$$

with $g_2 \sim [0,1]$, where t is the optimum temperature at which maximum growth occurs, b is the standard deviation or breadth of the function (Canham et al., 2006) and a is a third parameter to make the function flexible to fit platykurtic relationships. The possibility of having an asymmetric functional response was tested using a log-normal distribution equivalent to function (5) but with minimum temperature as the driving covariate. Since the relationship between growth and temperature for *Q. ilex* (QUIL) was very leptokurtic we also tested the Laplace function, a symmetric pointy distribution with a single maximum:

$$g_2(T_{min}) = (1/2t'_2) \cdot \exp(-abs(T_{min} - t'_1)/t'_2) \quad (7)$$

with $g_2 \sim [0,1]$, t'_1 is the optimum temperature at which optimum growth occurs and t'_2 a scale or breadth parameter.

2.3. Model calibration and verification

To select the best model (period 1951–2004) we compared formulations including different functional relationships (Eqs. (3)–(7)) between growth and climate in models with different parameters by species compared with models with unique parameters independent of the species. We tested the hypothesis of nonlinearity in the growth response by comparing the nonlinear multiplicative models to a linear model with the same climatic covariates (Model #1 in Table 2). Several models with different

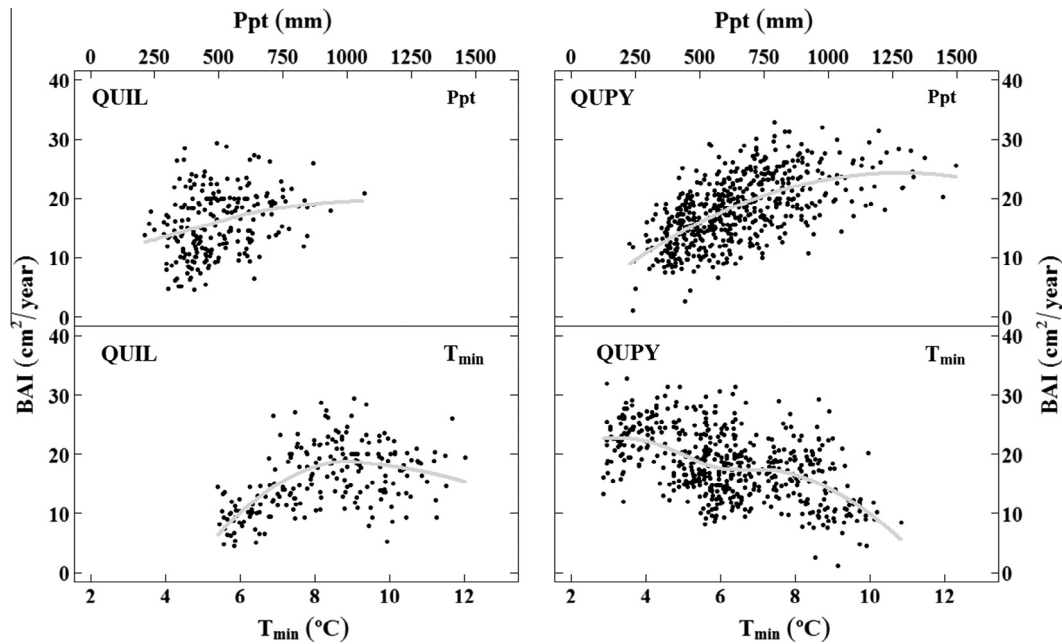


Fig. 3. Relationships between BAI from the 14 chronologies used to fit the growth model and minimum temperature (T_{min} , lower panels) and precipitation (Ppt , upper panels) of the hydrological year. In grey we show a smoother applied to highlight the nonlinear nature of the relationship between BAI and climatic covariates.

parameterization were compared and the best was selected based on the coefficient of determination (R^2), root mean square error (RMSE) and Akaike Information Criterion (AIC) using the Δ_i notation as $\Delta_i = AIC - AIC_{i_{min}}$ (i.e. the best model is that with $\Delta_i = 0.0$). By minimizing AIC we maximize likelihood but penalize for the number of parameters to assure parsimony and avoid overfitting (Burnham and Anderson, 2004; Johnson and Omland, 2004). Models were fitted using maximum likelihood with a Gamma distribution which directly addresses heterokedasticity inherent to growth data and performed better than other probability distributions like the Gaussian, the Lognormal or the Power Variance (not shown). The maximum likelihood parameters and asymptotic two-unit support intervals for each parameter were estimated using simulated annealing in the *likelihood* package vers. 1.5 (http://www.sortie-nd.org/lme/lme_R_code_tutorials.html) and R vers. 2.14.1. Two-unit support intervals for specific parameters are analogous to 95% confidence intervals but calculated as those reducing two units the maximum likelihood function maximized for the other parameters (Bolker, 2008). Models were validated using independent data (1925–1950) and compared based on the correlation coefficient (r) calculated between estimated BAI and independent data and the reduction of error statistic (RE), which is equivalent to R^2 but calculated using independent data (Cook and Kairiukstis, 1990).

2.4. Growth projections

The best model selected was then used to project growth under nine different climatic scenarios. We used downscaled climatic data from three different GCMs (MPEH5, CNM3 and BCM2) run for three different emissions scenarios from IPCC4 (IPCC, 2007): A2, A1B and B1. Climatic scenarios were obtained from a grid with 0.2° geographic resolution from the University of Cantabria (www.meteo.unican.es/thredds/catalog/PNACC2012/Rejilla/dato_diario/catalog.html). For the period 2090–2099 relative to 1980–1999, B1 predicts that warming will range between 1.1 and 2.9 °C, A1B between 1.4 and 3.4 °C and A2 between 2.0 and 5.4 but none of these climatic scenarios predicted significant

increases in precipitation in the next 100 years. Growth projections were implemented at different sites of contrasting climate (including marginal locations) among those sampled for the two species using the nine different sets of climatic scenarios for the period 2001–2100 (Fig. 1, Table 1, and Appendices A and B). The annual growth projections were smoothed using cubic splines with a 50% frequency cutoff at 30 years to highlight the long-term response and for clarity to compare results from the different climate scenarios.

3. Results

Multiplicative nonlinear models performed better than an additive linear model with species-specific parameters both in calibration and verification statistics (Table 2) and a model with species-specific parameters was the best (Model #6 in Table 2). Several models behaved similarly in the verification step but the difference in Δ_i between Model #6 and the closest (Model #9, $\Delta_i = 9.4$) was big enough to support considering Model #6 as the unique best candidate (Burnham and Anderson, 2004). To eliminate any trade-off between parameters (Canham and Uriarte, 2006) once we had selected the best model (Table 2) we fixed *a priori* parameter b in the final model for QUPY (Table 3). The final model fit was good for both species (Table 3 and Fig. 4).

The functional response of growth to Ppt was a logistic function in both cases (Table 2). This shows that in the studied stands accumulated precipitation was never too high to reduce annual growth which in turn stopped responding to increasing moisture availability above given species-specific precipitation thresholds (the response was asymptotic). QUIL reached high growth rates at lower precipitation levels than QUPY (Fig. 5). The best functional relationship selected by the model between T_{min} and growth was species-specific. It was fitted by a modified Gaussian function for QUPY and by the Laplace function for QUIL (Table 2) as shown in Fig. 5. The relationship between growth and T_{min} was symmetric only for QUIL. This symmetric relationship reached a unique global maximum around 9 °C, with growth rapidly decreasing with increasing temperatures after that maximum.

Table 2

Comparison among different models. Models fitted to data from 14 chronologies of *Q. ilex* and *Q. pyrenaica* for the period 1951–2004 and validated for the period 1925–1950. Model #1 is the linear model $BAI = b_i + a_{1i} \cdot Ppt + a_{2i} \cdot T_{min} + a_{3i} \cdot Ppt \cdot T_{min}$ (note that b_i is a species-specific intercept and not maximum growth). The rest are multiplicative models of expression $BAI = MG_i \cdot g_1(Ppt) \cdot g_2(T_{min})$ (model (2) in the main text) where $g_1(\cdot)$ and $g_2(\cdot)$ are different functions, as selected from those in (3)–(7) in the main text. MG_i is the maximum growth parameter. The subindex i means that a specific parameter is fitted for each species. Small letters correspond to parameters to be fitted in the model. Par_k is either the intercept b in the linear model of the maximum growth parameter (MG) in the nonlinear models; Ppt = precipitation of hydrological year; T_{min} = mean monthly minimum temperature of hydrological year; ML = maximum likelihood estimation; AIC_i = corrected Akaike information criterion of model i , $\Delta_i = AIC_i - AIC_{i_{min}}$; # pars = number of parameters; r = linear correlation; RE = reduction of error.

Model #	Covariate functional form			Calibration				Validation	
	Par_k	$g_1(\cdot)$	$g_2(\cdot)$	# Pars	ML	Δ_i	R^2	r	RE
1	b_i	$a_{1i} \cdot Ppt + a_{2i} \cdot T_{min} + a_{3i} \cdot Ppt \cdot T_{min}$	–	9	–2251.4	140.2	0.381	0.544	0.254
2		$1/(1 + (Ppt/p_{1i})^{p_2})$	–	6	–2292.2	217.7	0.313	0.401	0.119
3	MG_i	–		8	–2292.7	222.8	0.287	0.622	0.362
4		$1/(1 + (Ppt/p_1)^{p_2})$	$\begin{cases} \exp(-0.5 \cdot ((T_{min} - t)/b)^a) & \text{if QUPY} \\ \exp(-abs(T_{min} - t'_1)/t'_2) & \text{if QUIL} \end{cases}$	10	–2185.0	11.2	0.449	0.616	0.365
5	MG			10	–2200.1	41.4	0.432	0.628	0.380
6				12	–2177.4	0.0	0.460	0.625	0.365
7		$1/(1 + (Ppt/p_{1i})^{p_{2i}})$	$\exp(-0.5 \cdot ((\log(T_{min}/t_i)/t_{si})^2)$	11	–2184.2	11.6	0.453	0.529	0.321
8			$\exp(-0.5 \cdot ((T_{min} - t_i)/b_i)^a)$	13	–2289.0	225.3	0.317	0.420	0.127
9	MG_i	$1/(1 + (Ppt/p_{1i})^{p_2})$		11	–2183.0	9.4	0.451	0.625	0.379
10		$\exp(-0.5 \cdot ((Ppt - p_i)/b_i)^2)$	$\begin{cases} \exp(-0.5 \cdot ((T_{min} - t)/b)^a) & \text{if QUPY} \\ (1/2t'_2) \cdot \exp(-abs(T_{min} - t'_1)/t'_2) & \text{if QUIL} \end{cases}$	12	–2226.2	97.6	0.407	0.565	0.302
11		$\exp(-0.5 \cdot ((\log(Ppt/p_i)/p_{si})^2)$		12	–2192.1	29.5	0.442	0.635	0.379

Table 3

Parameter estimates and goodness of fit statistics of the final model selected (Model #6, Table 2) for the two species. ML = maximum likelihood estimation; # Pars = number of parameters; RMSE = mean root square error (cm²/year). MLE = maximum likelihood estimate; S.I.=support interval. Model: $BAI = MG \cdot g_1(Ppt) \cdot g_2(T_{min}) \sim \mu$, with error following a Gamma distribution $\Gamma \sim (\text{mean} = \mu, \text{variance} = \mu \cdot \alpha)$. The model for QUIL:

$$BAI_{qi} = MG_{qi} \cdot [1/(1 + (Ppt/p_{1qi})^{p_{2qi}})] \cdot [(1/2t'_2) \cdot \exp(-abs(T_{min} - t'_1)/t'_2)].$$

The model for QUPY:

$$BAI_{qp} = MG_{qp} \cdot [1/(1 + (Ppt/p_{1qp})^{p_{2qp}})] \cdot [\exp(-0.5 \cdot ((T_{min} - t)/b)^a)].$$

Model part	Parameter	Species	MLE (± 2 S.I.)	
MG (cm ² /year)	MG_i	QUIL	338.9988 (329.0288, 349.1688)	
		QUPY	27.3749 (27.02744, 27.9840)	
Ppt (mm)	p_1	QUIL	333.0670 (300.4216, 364.3928)	
		QUPY	351.0876 (338.555, 361.6203)	
		QUIL	–0.8373 (–1.1012, –0.6684)	
		QUPY	–1.71490 (–1.9169, –1.5958)	
T_{min} (°C)	t	QUPY	–173.1005 (–175.0588, –171.1591)	
		QUIL	8.9677 (8.7904, 9.0574)	
		QUPY	182.9	
		QUIL	4.6216 (4.4371, 4.8064)	
		QUPY	132.9170 (114.4487, 164.3211)	
Gamma	α	QUIL	1.1370 (0.9596, 1.3852)	
		QUPY	0.9457 (0.8622, 1.0906)	
<i>Goodness of fit</i>				
Species	ML	# Pars	RMSE	R^2
QUIL	–622.6	6	4.207	0.385
QUPY	–1551.4	6	4.050	0.466

QUPY was sampled across a wider climatic range and its functional relationship with T_{min} was also realistic, with neutral response to low temperatures and decreasing growth rates with minimum temperatures over 7 °C (Table 3; Figs. 5 and 6). T_{min} over 12 °C would be too limiting for the species to grow according to our model (Figs. 5 and 6).

In Fig. 7 we projected growth at different sites of contrasting climate where we had collected data. There was high variability in the projections, as can be expected from using nine different climatic scenarios and a model which also has uncertainty associated. However, the growth projections suggested some clear future trends, particularly under scenarios forecasting a maximum increase in temperature (i.e. A2). Growth projections of QUIL on a

cold site at the north of its distribution (QUIL_{high} in Fig. 7) suggested that this species would not decrease productivity and even might be positively influenced by the increase in temperature without a major change in precipitation forecasted by the different scenarios. Conversely, this species would reduce productivity at the warmest location from those we had sampled (QUIL_{low} in Fig. 7). Predictions suggest that QUPY productivity would decline in the next decades all along its distributional range in the Iberian Peninsula for all the climate scenarios studied. This decline would be more dramatic at low altitudes at warmer Southern locations, with most projections converging to zero at the warmest site sampled (QUPY_{low1} in Fig. 7), which can be considered a marginal population.

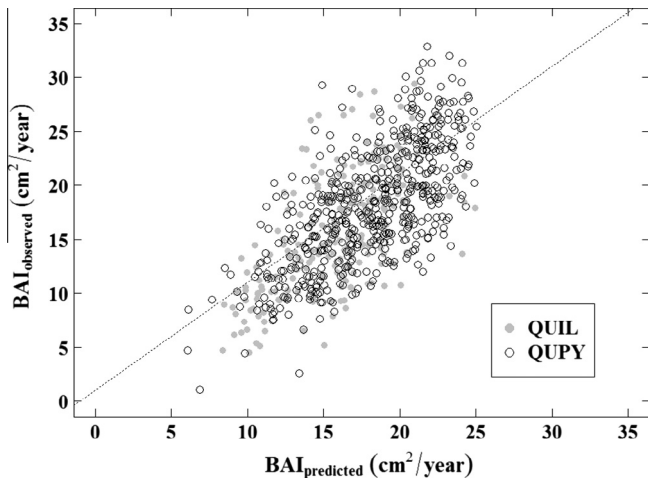


Fig. 4. Plot of predicted vs. observed BAI for the two species studied. Residuals are calculated applying Model #6 in Table 2 with parameters from Table 3 to the data used to fit the models.

4. Discussion

4.1. Ecological implications of the relationship between oak growth and climate

Oaks exhibited species-specific, nonlinear and ecologically-sound functional responses to climate. The relationship between growth and precipitation was nonlinear and asymptotic for all species (Vaganov et al., 2006; Gea-Izquierdo et al., 2011). This means that the highest precipitation levels reached in the studied ecosystem are not detrimental for tree performance in opposition to what has been suggested for oak species growing in rainy oceanic temperate forests (Rozas and Garcia-Gonzalez, 2012) and could be a rule in more humid climates. *Q. ilex* has a warmer realized niche

(Costa et al., 2005) and exhibited faster growth for a given level of precipitation than *Q. pyrenaica*, maybe expressing that evergreen trees at warmer sites with less limiting winter low temperatures are able to profit more from rainy periods in winter (Baldocchi et al., 2010). Maximum growth for *Q. ilex* occurred at higher mean minimum temperatures (9 °C) than for the less drought-tolerant *Q. pyrenaica* (7 °C), with temperatures over 9 °C increasingly reducing *Q. ilex* growth. Given the climate in our data, *Q. pyrenaica* productivity would decline over mean minimum annual temperatures of 7 °C and our model suggested that mean minimum temperatures above 12 °C would be too warm with current precipitation levels for the species to grow. Contrary to *Q. ilex*, growth of *Q. pyrenaica* was not enhanced by increasing low temperatures up to an optimum. However, this species could have expressed a limitation by low temperatures had we fitted the model with data from a colder period like that before the 1900s. The model performance looks realistic given the climatic scenarios considered (increasing temperature without a paired increase in precipitation) and the negative response to warming temperature expressed by the relationships fitted in the model.

4.2. Growth projections for *Q. pyrenaica* and *Q. ilex* suggest local vulnerability to climate change

The distribution of species in the studied area depends mostly on moisture availability and temperature conditions (Costa et al., 2005; Sanchez de Dios et al., 2009). Therefore, as expressed by our model it seems reasonable to assume that an increase in water stress triggered by increasing temperatures without increased precipitation should be detrimental for most species after species-specific climatic thresholds have been surpassed. Similarly to other studies reporting growth constraints with global change drought increase (e.g. Zahner et al., 1989; Sarris et al., 2011; Di Filippo et al., 2012), the expected temperature increase without a paired increase in rainfall under all the climate scenarios assessed (IPCC, 2007) seem to be negative for *Q. pyrenaica* productivity. Particularly, the model forecasts a drastic reduction in mean growth at the warmest locations (like QUPY_{low1}, a marginal stand from Sierra

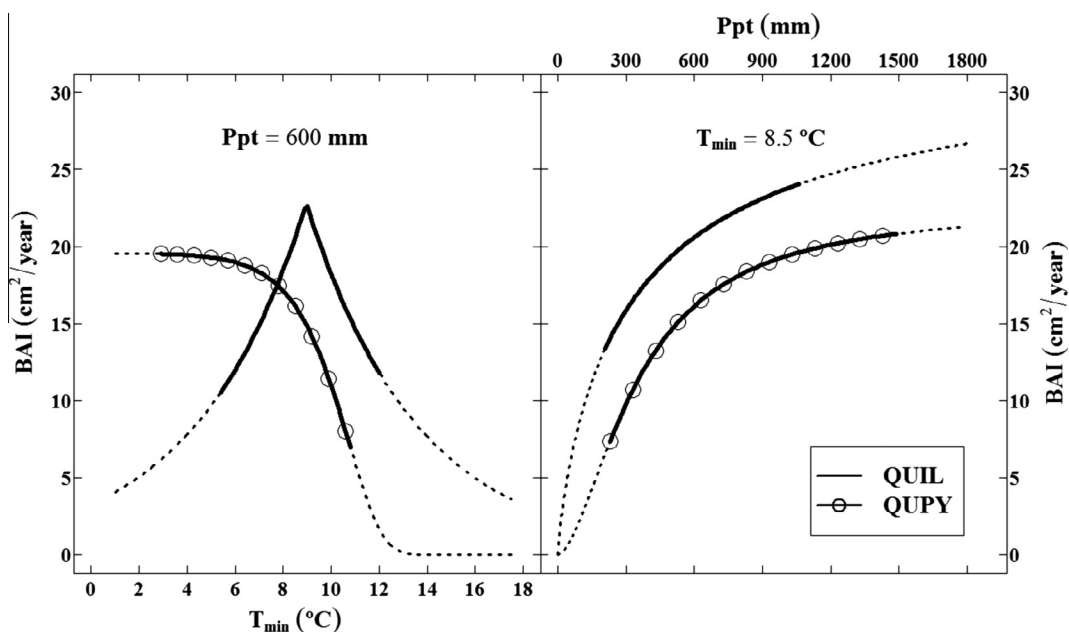


Fig. 5. Model simulation for $Ppt = 600$ mm (left panel) and $T_{min} = 8.5$ °C (right panel). These values were selected because they represent common climatic values within the range where the two species can coexist. Solid lines correspond to the range of covariates sampled and included in the model fit whereas dashed lines correspond to extrapolation of the model outside the range observed for specific covariates and species.

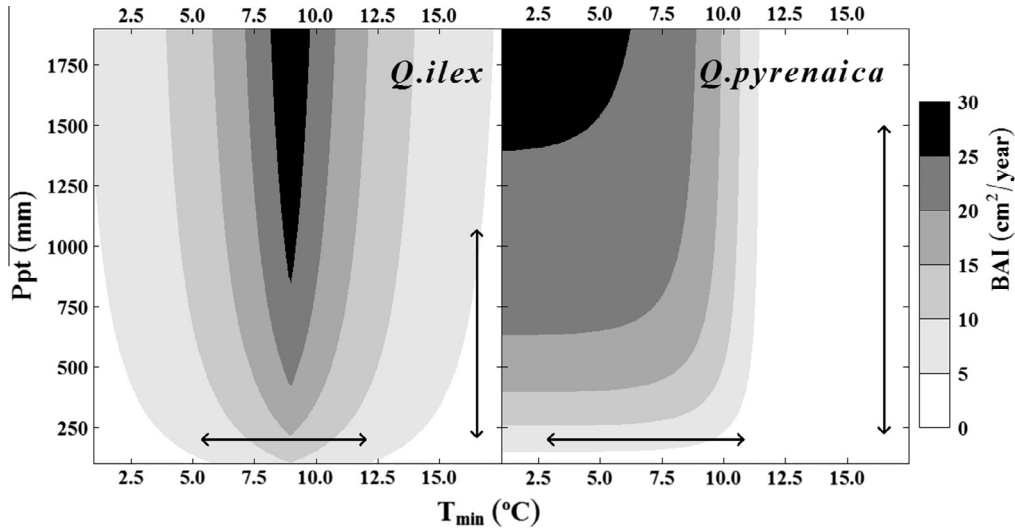


Fig. 6. Response surfaces of basal area increment as a function of hydrological year precipitation and minimum temperature. Arrows show the observed range in the covariates (as in Table 1) used in the model calibration for the two species.

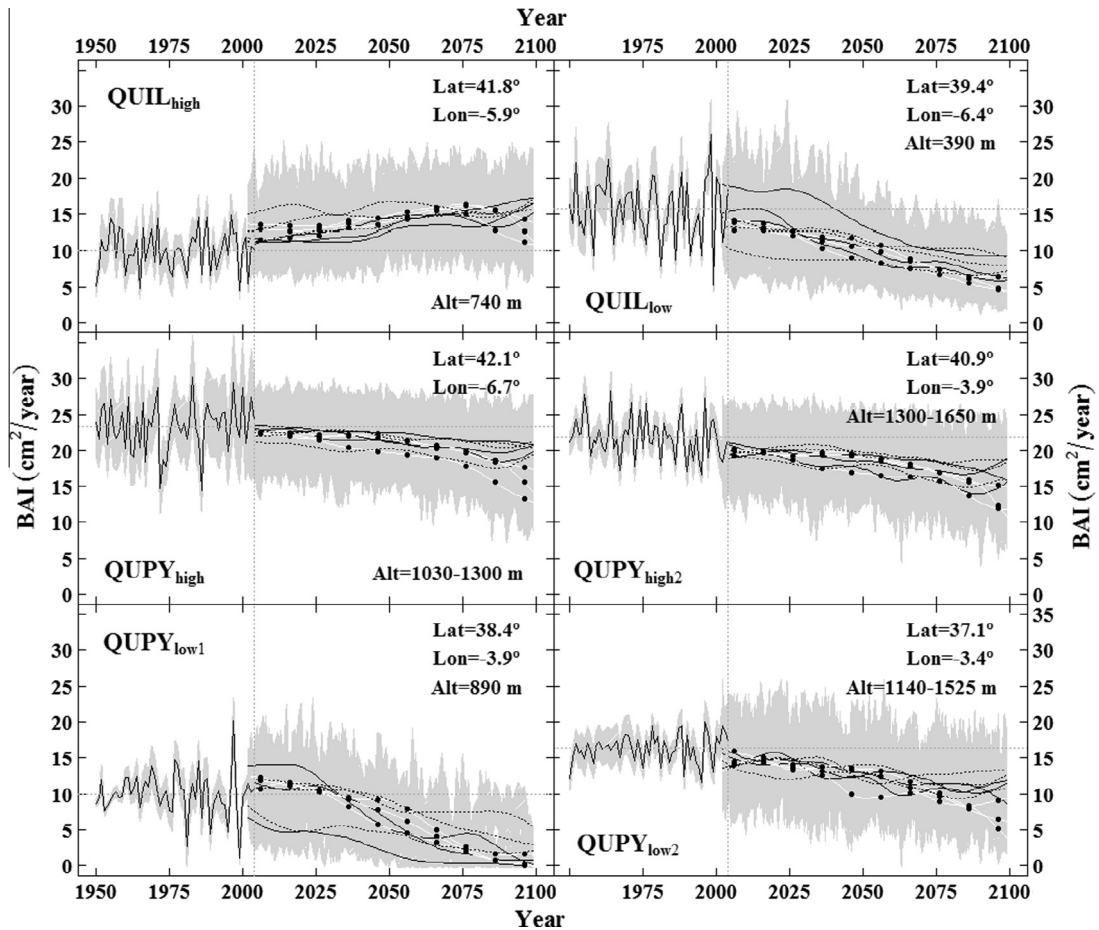


Fig. 7. Growth projections using IPCC4 scenarios (period 2001–2100) A2 (solid white lines with black circles), A1B (solid black lines), and B1 (dotted black lines) with three different GCMs (see main text). The composed confidence intervals of the nine simulations are shown as grey polygons. Growth projections (period 2000–2100) were smoothed with cubic splines with a 50% frequency cutoff at 30 years. For the period 1950–2004 the observed mean annual BAI data sampled at the projected sites is shown with a black line overlaid to grey polygons representing the confidence intervals of the standard error. Dashed thin grey horizontal lines correspond to the mean observed BAI for the period 1951–2004. Subscript 'high' means the high latitude site sampled for the species whereas 'low' means low latitude site. Correspondence of data below to those in Fig. 1 is as follows: QUIL_{high} = QUIL1; QUIL_{low} = QUIL4; QUPY_{high} = mean of QUPY1–QUPY2; QUPY_{high2} = mean of QUPY5–QUPY6; QUPY_{low1} = QUPY8; QUPY_{low2} = mean of QUPY9–QUPY10. Coordinates (Latitude and Longitude) and altitude are specified on each graph.

Morena, Spain) with most climatic scenarios. Although we did not observe yet any major episode of mortality in the sampled stands, natural seed regeneration seemed absent or very reduced in most sites excepting those in the north of the sampled area. Other studies analyzing the climatic envelope of Western Mediterranean tree species concluded that *Q. pyrenaica* is threatened by climate change and forecast a regression of the species and the submediterranean range in the Iberian Peninsula (Sanchez de Dios et al., 2009; Ruiz-Labourdette et al., 2012). Increasing drought could enhance the susceptibility of trees to pathogens and portend forest decline, which is generally expressed by low and decreasing growth rates (Foster and Leblanc, 1993; Suárez et al., 2004; Voelker et al., 2008). There is always uncertainty associated to any growth projections and to climatic scenarios. Additionally, with the climatic and growth data available we modeled average growth as representative of overall stand conditions neglecting variability between individuals and variability related to small-scale site conditions which could partially mitigate the negative response to climate change described. However, it seems reasonable to speculate that the drastic growth reduction trend suggested by the model at the warmest and driest sites coincident with the local low-elevation and/or low-latitude dry-edge of the species distribution could express local enhanced vulnerability of trees to increasing overall water stress forced by a warmer climate. Excessively high temperatures can be negative for trees in different manners (Breshears et al., 2009; McDowell et al., 2011). High temperatures increase potential evapotranspiration and plant stress in the dry season (Niinemets, 2010) but also high winter temperatures could be negative for deciduous plants if they increased respiration when they bear no leaves, hence, reducing annual net productivity and also potential conductivity (Fonti and García-González, 2004; Baldocchi et al., 2010; Gea-Izquierdo et al., 2012).

A positive or neutral response to climate change of *Q. ilex* at the northern limit of its distribution is in accordance with the increase in productivity at the species upper latitudinal distribution in Southern France modeled by Gaucherel et al. (2008) and agrees with those studies considering that *Q. ilex* would benefit if there is a regression of submediterranean oaks like *Q. pyrenaica* (Ruiz-Labourdette et al., 2012). However our results also suggest a negative effect of warming on *Q. ilex* growth at warm, dry sites from low elevations and low latitudes ($QUIL_{low}$). Thus, our results agree with studies forecasting species-specific positive effects of climate change only in the northern limit of climatic gradients in boreal forests (Lapointe-Garant et al., 2010; Lloyd et al., 2011), greater changes in Mediterranean forests driven by increased water-stress at low-elevations than at high-elevations (Ruiz-Labourdette et al., 2013) and contrasting future productivity trends at opposite limits of different Mediterranean species distributions (species' warm-dry vs. cold-wet limits) including *Q. ilex* (Vicente-Serrano et al., 2010; Martin-Benito et al., 2011). Following these growth projections, the great extension of woodlands dominated by *Q. ilex* from more southern Iberian locations which withstand warmer climates than those sampled here could be severely threatened by climate change (Carnicer et al., 2011; Gea-Izquierdo et al., 2011). In fact, widespread *Q. ilex* mortality has already been observed in South-Western Spain (Brasier, 1992; personal observation).

The simple stand structure of the studied oak woodlands made our model feasible when fitted to dendroecological data. However, more complex model formulations might be required to properly fit the relationship between growth and climate in multilayer or multispecies forests. A number of different factors affect growth and specific plant species can exhibit contrasting responses to global change depending on local climatic conditions (Spiecker, 1999; Salzer et al., 2009; McMahon et al., 2010; Di Filippo et al., 2012). For instance, in addition to variability in temperature and precipitation, along climatic gradients there will be differences in incident

radiation and the photoperiod which will influence tree performance and its ability to acclimate to other environmental factors. Additionally, non-climatic atmospheric factors such as CO₂ and nitrogen fertilization can interact with climate to modify future growth. Some authors suggest that growth will be enhanced by the CO₂ fertilization effect in Mediterranean ecosystems (Rathgeber et al., 1999, 2003; Gaucherel et al., 2008). Nevertheless, most studies in the Mediterranean report that increased water use efficiency does not counteract the stronger negative effect of higher water stress, resulting on a negligible net positive effect of the CO₂ increase to growth (Andreu-Hayles et al., 2011; Peñuelas et al., 2011; Girardin et al., 2012). These contradictory conclusions between studies could be explained if the effect of CO₂ was nonlinear or only expressed under certain climatic conditions (e.g. if there is an increase in precipitation) or by certain taxa (Rathgeber et al., 2003; Huang et al., 2007). To our knowledge no study has reported in the studied region the existence of a generalized dominant effect of nitrogen fertilization on tree growth over that of water stress. The minor influence on growth of the previous non-climatic factors compared to that of climate would thus contribute to support the robustness of the relationships we modeled between growth and climate. Nonetheless, our growth projections should be complemented with process-based approaches to gain a better understanding on how these different factors will determine tree performance in the future.

5. Conclusions

Projections of future growth using a model specifically addressing the functional nonlinear relationship between climate and growth suggested that *Q. pyrenaica* and *Q. ilex* growing under species-specific dry conditions would drastically reduce productivity in response to local increase in temperatures without a parallel increase in precipitation. The relationship between growth and minimum temperature exhibited a meaningful growth threshold for these two species suggesting that the growth predictions performed under the expected warming climate scenario were realistic. The relationship between growth and precipitation was monotonically increasing with an asymptote. *Q. pyrenaica* would be negatively affected by warming temperatures and modeled growth would show a general decrease in the future at the sampled stands. *Q. ilex* would be also negatively affected by warming at southern warm, dry sites but conversely its growth would experience no change or even be enhanced at the local northern cold limit of its distribution. The novel nonlinear model approach used with dendroecological data successfully fitted the growth trends observed along the sampled gradients and mimicked biologically meaningful relationships between growth and climate, directly avoiding the bias specific to additive linear models. Similar formulations would help to increase the accuracy of future growth predictions through the detection of ecological thresholds in the response to specific climatic factors, which could be used in forest management to minimize the impact of climate change.

Acknowledgements

G.G.I. gratefully thanks the Dendro group at WSL for hosting and the Spanish Ministry of Science (MICINN) for funding through a post-doctoral contract. We gratefully thank all foresters who made possible sampling at the different sites. Jaime Ribalaygua kindly helped to obtain the climate scenarios. The first author is particularly grateful to Charles Canham for enriching discussion on the use of likelihood models. This research was supported by projects AGL2010-21153-C02-01, funded by MICINN, and S2009/AMB-1668.

Appendix A.

Characteristics of sampled plots. Lat = latitude, Long = longitude. P=precipitation; Tmean=mean temperature; D = estimated mean stand density. Dbh, age and height are site means. Standard deviations are shown in brackets; PET = potential evapotranspiration for hydrological year using Thornthwaite. Climatic data refer to the period 1960–2004.

Species	Name	Site	Lat (°)	Long (°)	Altitude (m)	Climate			D (trees/ ha)	Dbh (cm)	Age		Height (m)	
						P (mm)	Tmean (°C)	PET (mm)			Mean	Max		
<i>Quercus ilex</i> L.	QUIL1	Tábara	41.8	−5.9	740	478.0	12.2	704.6	30– 125	28.1 (14.4)	98.0 (55.8)	280	5.6 (1.6)	
	QUIL2	Ciudad Rodrigo	40.6	−6.7	700	585.3	13.6	746.3	35– 191	28.9 (11.2)	89.0 (29.6)	175	8.3 (2.3)	
	QUIL3	Chapinería	40.4	−4.2	600	418.3	14.6	792.0	10– 100	34.2 (21.1)	67.0 (41.0)	183	–	
	QUIL4	Cáceres	39.4	−6.4	390	538.6	16.0	841.9	15–85	38.7 (10.4)	115.0 (36.6)	212	6.2 (1.6)	
<i>Quercus pyrenaica</i> Willd.	QUPY1	Sanabria	42.1	−6.5	1030	857.8	9.3	614.3	100	46.8 (19.4)	65.5 (19.3)	111	18.0 (3.0)	
	QUPY2	Sanabria	42.1	−6.7	1310	965.4	7.6	568.8	175	72.7 (22.1)	270.2 (148.3)	502	17.3 (3.4)	
	QUPY3	Tábara	41.9	−6.1	760	478.0	12.2	704.6	70– 125	40.1 (14.5)	75.3 (48.3)	235	14.6 (3.9)	
	QUPY4	Navasfrías	40.3	−6.8	900	783.2	12.7	708.7	20– 275	53.9 (7.2)	149.2 (48.9)	201	19.7 (3.5)	
	QUPY5	Rascafría	40.9	−3.9	1300	692.8	11.8	684.5	325	58.8 (19.9)	142.7 (82.9)	339	14.4 (2.0)	
	QUPY6	Rascafría	40.9	−3.9	1650	791.7	9.7	623.3	200	55.2 (8.7)	165.3 (50.6)	281	11.6 (1.9)	
	QUPY7	Quintos de Mora	39.4	−4.1	900	464.3	14.3	784.0	150	39.2 (6.8)	81.2 (20.3)	118	15.9 (3.7)	
	QUPY8	Andújar	38.4	−3.9	890	507.6	15.6	835.6	275	30.9 (5.2)	90.6 (32.2)	156	12.5 (1.8)	
	QUPY9	Sierra Nevada	37.1	−3.4	1140– 1370	446.1	14.1	738.4	65	33.9 (6.7)	68.0 (18.1)	101	11.5 (2.1)	
	QUPY10	Sierra Nevada	37.0	−3.4	1525	578.8	13.0	731.0	70– 110	43.6 (12.0)	120.5 (52.8)	197	11.6 (1.6)	

Appendix B.

Characteristics of studied mean tree ring chronologies. Ring width (mm, RW), standard deviation (std), Mean sensitivity (MS) and AR(1) are series averages (Fritts, 1976). EPS and Rbt (correlation between series) are calculated for the mean residual chronology of growth indices. Length is the period with five or more series, which are those years included in the final chronologies.

Name	First year	Last year	Length (years)	# Trees	# Radii	RW (mm)		MS	AR(1)	EPS	Rbt
						Mean	Std				
QUIL1	1894	2008	115	21	42	1.58	1.056	0.488	0.546	0.978	0.396
QUIL2	1864	2004	141	25	42	2.29	1.178	0.383	0.512	0.974	0.410
QUIL3	1831	2005	176	25	46	2.57	1.501	0.476	0.393	0.987	0.408
QUIL4	1872	2005	134	20	33	1.87	1.108	0.491	0.464	0.949	0.301
QUPY1	1941	2008	68	19	35	3.08	1.364	0.280	0.598	0.956	0.348
QUPY2	1698	2008	311	19	35	1.16	0.484	0.237	0.617	0.957	0.310
QUPY3	1893	2008	116	22	44	2.41	1.209	0.304	0.671	0.991	0.497
QUPY4	1845	2008	164	22	41	1.54	0.749	0.250	0.744	0.970	0.390
QUPY5	1836	2008	173	22	42	1.92	0.922	0.237	0.730	0.968	0.233
QUPY6	1792	2008	217	20	41	1.39	0.719	0.215	0.797	0.963	0.311
QUPY7	1919	2008	90	17	34	2.19	1.115	0.241	0.739	0.975	0.244
QUPY8	1905	2008	104	20	41	1.62	1.130	0.344	0.747	0.980	0.471
QUPY9	1933	2008	77	16	33	2.20	1.168	0.280	0.728	0.978	0.431
QUPY10	1859	2008	150	20	37	1.50	0.879	0.235	0.798	0.973	0.262

References

- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., et al., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *PNAS* 106 (17), 7063–7066.
- Allen, C.D., Macalady, A.K., Chenchouni, H., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol. Manage.* 259 (4), 660–684.
- Andreu-Hayles, L., Planells, O., Gutiérrez, E., et al., 2011. Long tree-ring chronologies reveal 20th century increases in water-use efficiency but no enhancement of tree growth at five Iberian pine forests. *Glob. Change Biol.* 17 (6), 2095–2112.
- Baldocchi, D.D., Ma, S.Y., Rambal, S., et al., 2010. On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. *Ecol. Appl.* 20 (6), 1583–1597.
- Bär, A., Pape, R., Bräuning, A., Laffler, J., 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *J. Biogeogr.* 35 (4), 625–636.
- Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecol. Appl.* 9, 216–227.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res.* 64, 81–96.
- Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Change Biol.* 12, 862–882.
- Bolker, B.M., 2008. *Ecological Models and Data* in R. Princeton University Press, NJ.
- Brasier, C.M., 1992. Oak tree mortality in Iberia. *Nature* 360, 539.
- Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., Pockman, W.T., 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front. Ecol. Environ.* 7 (4), 185–189.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference – understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33, 261–304.
- Canham, C.D., Uriarte, M., 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecol. Appl.* 16, 62–73.
- Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in new England forests. *Ecol. Appl.* 16 (2), 540–554.
- Camicer, J., Coll, M., Ninyerola, M., et al., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *PNAS* 108 (4), 1474–1478.
- Cook, E.R., Kairiukstis, L.A., 1990. *Methods of Dendrochronology. Applications in the Environmental Sciences*, Kluwer, The Netherlands.
- Corcuera, L., Camarero, J.J., Siso, S., Gil-Pelegrin, E., 2006. Radial-growth and wood-anatomical changes in overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape. *Trees-Struct. Funct.* 20 (1), 91–98.
- Costa, M., Morla, C., Sáinz, H. (Eds.), 2005. *Los bosques ibéricos. Una interpretación geobotánica*. Editorial Planeta, Barcelona, Spain.
- D'Arrigo, R.D., Kaufmann, R.K., Davi, N., Jacoby, G.C., Laskowski, C., Myneni, R.B., Cherubini, P., 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Glob. Biogeochem. Cy.* 18 (3).
- D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'divergence problem' in northern forests: a review of the tree-ring evidence and possible causes. *Glob. Planet. Change* 60 (3–4), 289–305.
- Di Filippo, A., Alessandrini, A., Biondi, F., Blasi, S., Portoghesi, L., Piovesan, G., 2010. Climate change and oak growth decline: dendroecology and stand productivity of a Turkey oak (*Quercus cerris* L.) old stored coppice in Central Italy. *Ann. Forest Sci.* 67 (7), 706.
- Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B., Piovesan, G., 2012. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. *Glob. Change Biol.* 18 (3), 960–972.
- Evans, M.N., Reichert, B.K., Kaplan, A., Anchukaitis, K.J., Vaganov, E.A., Hughes, M.K., Cane, M.A., 2006. A forward modeling approach to paleoclimatic interpretation of tree-ring data. *J. Geophys. Res.* – Biogeosci. 111.
- Federer, C.A., Tritton, L.M., Hornbeck, J.W., Smith, R.B., 1989. Physiologically based dendroclimate models for effects of weather on red spruce basal-area growth. *Agr. Forest Meteorol.* 46 (1–2), 159–172.
- Fonti, P., García-González, I., 2004. Suitability of chestnut earlywood vessel chronologies for ecological studies. *New Phytol.* 163, 77–86.
- Foster, J.R., Leblanc, D.C., 1993. A physiological approach to dendroclimatic modeling of oak radial growth in the Midwestern United States. *Can. J. Forest Res.* 23, 783–798.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Blackburn Press, 567p.
- Fritts, H.C., Vaganov, E.A., Sviderskaya, I.V., Shashkin, A.V., 1991. Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width, number of cells, cell size, cell-wall thickness and wood density. *Clim. Res.* 1, 97–116.
- Gauchere, C., Guiot, J., Misson, L., 2008. Evolution of the potential distribution area of French Mediterranean forests under global warming. *Biogeosci. Discuss.* 5, 573–603.
- Gea-Izquierdo, G., Cañellas, I., 2009. Analysis of holm oak intraspecific competition using Gamma regression. *Forest Sci.* 55, 310–322.
- Gea-Izquierdo, G., Cherubini, P., Cañellas, I., 2011. Tree-rings reflect the impact of climate change along a temperature gradient in Spain over the last 100 years. *Forest Ecol. Manage.* 262, 1807–1816.
- Gea-Izquierdo, G., Fonti, P., Cherubini, P., et al., 2012. Xylem hydraulic adjustment and growth response of *Quercus canariensis* Willd. to climatic variability. *Tree Physiol.* 32, 401–413.
- Girardin, M.P., Raulier, F., Bernier, P.Y., Tardif, J.C., 2008. Response of tree growth to a changing climate in boreal central Canada: a comparison of empirical, process-based, and hybrid modelling approaches. *Ecol. Model.* 213 (2), 209–228.
- Girardin, M.P., Bernier, P.Y., Raulier, F., Tardif, J.C., Conciatori, F., Guo, X.J., 2012. Testing for a CO₂ fertilization effect on growth of Canadian boreal forests. *J. Geophys. Res.* – Biogeosci. 116.
- Gordo, O., Sanz, J.J., 2009. Long-term temporal changes of plant phenology in the Western Mediterranean. *Glob. Change Biol.* 15, 1930–1948.
- Gutiérrez-Elorza, M. (Coord.), 1994. *Geomorfología de España*. Rueda, 526p.
- Huang, J.G., Bergeron, Y., Denneler, B., Berninger, F., Tardif, J., 2007. Response of forest trees to increased atmospheric CO₂. *Crit. Rev. Plant Sci.* 26, 265–283.
- IPCC, 2007. In: Pachauri, R.K., Reisinger, A. (Eds.), *Climate Change 2007: Synthesis Report*. IPCC, Geneva, Switzerland, p. 104p.
- Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecol. Manage.* 95, 209–228.
- Lapointe-Garant, M.P., Huang, J.G., Gea-Izquierdo, G., et al., 2010. Use of tree rings to study the effect of climate change on trembling aspen in Quebec. *Glob. Change Biol.* 16, 2039–2051.
- Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320 (5884), 1768–1771.
- Lloyd, A.H., Bunn, A.G., Berner, L., 2011. A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Glob. Change Biol.* 17, 1935–1945.
- Loehle, C., 2009. A mathematical analysis of the divergence problem in dendroclimatology. *Clim. Change* 94, 233–245.
- Mäkela, A., Pulkkinen, M., Kolari, P., et al., 2008. Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Glob. Change Biol.* 14, 92–108.
- Martin-Benito, D., Del Rio, M., Heinrich, I., Helle, G., Canellas, I., 2011. Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: past trends and future perspectives. *Forest Ecol. Manage.* 262 (6), 1030–1040.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* 26, 523–532.
- McMahon, S.M., Parker, G.G., Miller, D.R., 2010. Evidence for a recent increase in forest growth. *PNAS* 107, 3611–3615.
- Misson, L., Rathgeber, C., Guiot, J., 2004. Dendroecological analysis of climatic effects on *Quercus petraea* and *Pinus halepensis* radial growth using the process-based MAIDEN model. *Can. J. Forest Res.* 34, 888–898.
- Mitchell, T.D., Jones, P.D., 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.* 25, 693–712.
- Mitrakos, K., 1980. A theory for Mediterranean plant-life. *Oecolog. Plantar.* 15, 245–252.
- Monserud, R.A., 1986. Time-series analyses of tree-ring chronologies. *Forest Sci.* 32, 349–372.
- Montserrat-Marti, G., Camarero, J.J., Palacio, S., et al., 2009. Summer-drought constrains the phenology and growth of two coexisting Mediterranean oaks with contrasting leaf habit: implications for their persistence and reproduction. *Trees-Struct. Funct.* 23 (4), 787–799.
- Niinemet, U., 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecol. Manage.* 260, 1623–1639.
- Nobel, P.S., 2009. *Physicochemical and Environmental Plant Physiology*, 4th ed. Academic Press, Elsevier.
- Nothdurft, A., Wolf, T., Ringeler, A., Boehner, J., Saborowski, J., 2012. Spatio-temporal prediction of site index based on forest inventories and climate change scenarios. *Forest Ecol. Manage.* 279, 97–111.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* 20, 597–608.
- Rathgeber, C., Guiot, J., Roche, P., Tessier, L., 1999. *Quercus humilis* increase of productivity in the Mediterranean area. *Ann. Forest Sci.* 56, 211–219.
- Rathgeber, C., Nicault, A., Kaplan, J.O., Guiot, J., 2003. Using a biogeochemistry model in simulating forests productivity responses to climatic change and [CO₂] increase: example of *Pinus halepensis* in Provence (south-east France). *Ecol. Model.* 166, 239–255.
- Rozas, V., Garcia-Gonzalez, I., 2012. Too wet for oaks? Inter-tree competition and recent persistent wetness predispose oaks to rainfall-induced dieback in Atlantic rainy forest. *Glob. Planet. Change* 94–95, 62–71.
- Ruiz-Labourdette, D., Nogues-Bravo, D., Sainz Ollero, H., et al., 2012. Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *J. Biogeogr.* 39, 162–176.

- Ruiz-Labourdette, D., Schmitz, M.F., Pineda, F.D., 2013. Changes in tree species composition in Mediterranean mountains under climate change: indicators for conservation planning. *Ecol. Indic.* 24, 310–323.
- Salzer, M.G., Hughes, M.K., Bunn, A.G., Kipfmüller, K.F., 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *PNAS* 106 (48), 20348–20353.
- Sanchez de Dios, R., Benito-Garzon, M., Sainz-Ollero, H., 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecol.* 204, 189–205.
- Sarris, D., Christodoulakis, D., Korner, C., 2011. Impact of recent climatic change on growth of low elevation eastern Mediterranean forest trees. *Clim. Change* 106, 203–223.
- Schenk, H.J., 1996. Modeling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. *Ecol. Model.* 92, 1–32.
- Spiecker, H., 1999. Overview of recent growth trends in European forests. *Water Air Soil Pollut.* 116, 33–46.
- Suárez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *J. Ecol.* 92, 954–966.
- Tessier, L., Nola, P., Serrebatchet, F., 1994. Deciduous *Quercus* in the Mediterranean region – tree-ring/climate relationships. *New Phytol.* 126, 355–367.
- Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. *PNAS* 102 (23), 8245–8250.
- Tolwinski-Ward, S.E., Evans, M.N., Hughes, M.K., Anchukaitis, K.J., 2011. An efficient forward model of the climate controls on interannual variation in tree-ring width. *Clim. Dynam.* 36 (11–12), 2419–2439.
- Ung, C.H., Bernier, P.Y., Raulier, F., Fournier, R.A., Lambert, M.C., Regniere, J., 2001. Biophysical site indices for shade tolerant and intolerant boreal species. *Forest Sci.* 47 (1), 83–95.
- Vaganov, E.A., Hughes, M.K., Shashkin, A.V., 2006. *Growth Dynamics of Conifer Tree Rings: Images of Past and Future Environments*. Springer, New York.
- Vicente-Serrano, S.M., Lasanta, T., Gracia, C., 2010. Aridification determines changes in forest growth in *Pinus halepensis* forests under semiarid Mediterranean climate conditions. *Agr. Forest Meteorol.* 150, 614–628.
- Voelker, S.L., Muzika, R.M., Guyette, R.P., 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. *Forest Sci.* 54, 8–20.
- Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.S.J., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Glob. Change Biol.* 10 (10), 1724–1736.
- Woodhouse, C.A., 1999. Artificial neural networks and dendroclimatic reconstructions: an example from the Front Range, Colorado, USA. *Holocene* 9, 521–529.
- Yuan, W., Liu, S., Zhou, G., et al., 2007. Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. *Agr. Forest Meteorol.* 143 (3–4), 189–207.
- Zahner, R., Saucier, J.R., Myers, R.K., 1989. Tree-ring model interprets growth decline in natural stands of loblolly-pine in the Southern United States. *Can. J. Forest Res.* 19, 612–621.
- Zhang, Q.B., Hebda, R.J., Zhang, Q.J., Alfaro, R.I., 2000. Modeling tree-ring growth responses to climatic variables using artificial neural networks. *Forest Sci.* 46, 229–239.