Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: Past trends and future perspectives

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ABSTRACT

Positive and negative effects of climate change on forest growth have been observed in different parts of the world. However, much is still unknown about how forest structure and productivity might affect climate–growth relationships in the future. We examined the effects of climate, site quality, and competition on tree basal area growth of black pine (*Pinus nigra* Arn.) between 1964 and 2005 in 21 sites in the Iberian Peninsula. We used a new approach to simultaneously account for climate–growth relationships, inter-annual growth variability, and stand structural changes, by fitting a linear mixed effects model (LMEM) for basal area increments (BAI) using climate data, tree-ring chronologies, and repeated forest inventory data. This approach showed the potential to improve our understanding of climate effects on tree growth and to include climate in empirical forest growth models. We used the LMEM to make projections of BAI growth under two CO_2 emission scenarios and two global circulation models (GCM). The main climate drivers for growth were precipitation from previous autumn to summer and winter temperature with a positive effect, and temperature in spring–summer which had a negative effect. Tree response to climate was modulated by stand conditions, tree competition, and productivity. The more productive stands showed greater ability to either maintain or increase growth at warmer spring–summer temperatures under different levels of autumn–summer precipitation. Growth projections showed important regional differences. In general, growth under future climate is predicted to decrease although moderate growth increases might be expected in the northern region for highly and moderately productive stands.

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1. Introduction

In the Mediterranean basin drought is the most limiting factor for tree growth (Specht, 1981). In this region, climate warming and increasing summer drought have caused a general decline in forest growth during the past decades (e.g. Jump et al., 2006; Macias et al., 2006; Sarris et al., 2007; Piovesan et al., 2008), although positive growth trends have also been reported (Martínez-Vilalta et al., 2008; Vila et al., 2008). In some cases, both positive and negative trends have been shown for different trees within the same forest stands (Wilmking et al., 2004; Martínez-Vilalta et al., 2008; Piovesan et al., 2008; Martín-Benito et al., 2010a). Further growth reductions could be expected in the future should the predicted drop of precipitation (Gibelin and Déqué, 2003) and warming temperatures (IPCC, 2007) occur in these already drought stressed forests. However, tree response to climatic variability is affected by competition, stand dynamics, and characteristics such as tree social status (Orwig and Abrams, 1997; Martín-Benito et al., 2008a) or stand density (Piutti and Cescatti, 1997; Misson et al., 2003; Martín-Benito et al., 2010b). These endogenous factors and their interactions affect growth at the forest-stand scale by modulating the amount of water, nutrients, and energy available for tree growth and their utilization by trees (Aussenac, 2000).

The impact of future climate change on forest tree growth has been extensively analyzed through tree rings (e.g. Girardin et al., 2008; Chen et al., 2010; Lapointe-Garant et al., 2010) a technique also used to infer past growth trends (e.g. Cook and Kairiukstis, 1990; Macias et al., 2006; Piovesan et al., 2008). Tree rings offer an annually resolved proxy to explore tree growth at times when no forest inventories or meteorological instrumental records were available (Cook and Kairiukstis, 1990). Unfortunately, most tree ring studies lack the contextual data on forest stand dynamics that modulate climate change impacts on tree growth (Canham et al., 2004) which are in general only available through repeated forest inventories (RFI). However, RFI are fairly recent (~100 years) and their time

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resolution is usually lower than 5 years. Several studies have successfully included stand variables in tree-ring based growth models although, they either had a subannual resolution (Laubhann et al., 2009) or used categorical variables (e.g. managed vs. not-managed) (Martínez-Vilalta et al., 2008). Therefore the combination of RFI and dendrochronology offers a great potential to explore the effect of the stand structure on tree-ring growth (Biondi, 1999), while enabling the introduction of annually resolved environmental variables (such as climate or atmospheric CO_2 concentration) into empirical forest models (Laubhann et al., 2009).

Long term responses of tree growth to climate change will most likely differ at the regional or sub-regional scale (O'Neill et al., 2008; Griesbauer et al., 2011) calling for a detailed analysis of the variables that affect forest growth in order to make future projections. In addition, inter- and intra-population variability might cause regional differences on both the effects of future climate on other forest processes such as tree mortality (Breshears et al., 2005) or regeneration, and on their potential for adaptation to climate change (Griesbauer et al., 2011). Climate predictions from the general circulation models (GCM) also have very strong regional components (Ruosteenoja et al., 2007) particularly in the Mediterranean basin because of its complex topography (Gibelin and Déqué, 2003).

In the Mediterranean basin, pine forests have been greatly affected by climate change during the recent decades (Andreu et al., 2007; Sarris et al., 2007; Leal et al., 2008; Martín-Benito et al., 2010a). Black pine (*Pinus nigra* Arn.) is one of the most extended pines in the Mediterranean and among the most affected pines species in the area. Growth trends of different magnitude and sign, either positive or negative, have been reported for this drought sensitive species (Leal et al., 2008; Martín-Benito et al., 2010a). In the western part of its distribution area, black pine forests commonly occupy the supramediterranean altitudinal belt between the more thermophilic pines (*Pinus halepensis* Mill., *P. pinea* L., *Pinus pinaster* Ait.), and the more mesic-temperate Scots pine (*Pinus sylvestris* L.) (Barbéro et al., 1998). In the Iberian Peninsula, black pine covers a wide latitudinal gradient from the Baetic mountain range in the south to the Pyrenees in the north. In this study, we analyze radial growth of black pine from 1964 to 2005 in 21 stands distributed along a 500 km latitudinal transect in eastern Iberia. We hypothesize that climate change will force decreasing radial growth because of increasing temperatures and decreasing precipitation (Macias et al., 2006; Piovesan et al., 2008). In addition, we consider that responses to climate change could be modified by stand structure, namely intraspecific competition and site productivity (Piutti and Cescatti, 1997; Spiecker, 1999), and specific regional population differences (Chen et al., 2010; Martín-Benito et al., 2010a; Griesbauer et al., 2011). Our main goal was to determine the most important stand and climatic drivers of tree growth in order to interpret past growth as well as predict future growth changes under several greenhouse gas (GHG) emission scenarios and several GCMs. We develop a basal area increment (BAI) model combining tree-ring measurements, forest inventory records, site productivity, and climate by a linear mixed effects model. This approach enabled us to account for both exogenous and endogenous factors, as well as growth variability across regions, sites, and trees. Our specific objectives were to (i) quantify the effects of climate and competition on radial growth and (ii) project basal area growth and future black pine forest development under expected climate change.

2. Materials and methods

2.1. Study areas and sample sites

Black pine is the dominant species in the supramediterranean altitudinal belt in the mountains of eastern Spain, often forming mixed stands with *P. pinaster* or *P. sylvestris*. In 1964, the Spanish Forest Research Centre (CIFOR-INIA) established 50 permanent sample plots (PSP) covering the complete range of stand ages, density, and productivity found across black pine distribution in Spain. These PSPs were divided latitudinally in three regions: the "south" region is located in the Sierra de Cazorla mountain range, the "center" region is located in 'Serranía de Cuenca' mountains, and the "north" region located in the Sierra de Gúdar-Javalambre and Puertos de Beceite in the mountains that surround the southern margin of the Ebro valley (Fig. 1). The study areas cover a wide ecological gradient from the south where black pine forms the timber line to the north where it thrives near European beech (*Fagus sylvatica* L.) The main soil types are based on dolomite or calcareous bedrocks which create leptosols (rendzinas) on higher slopes, and luvisols on flat terrain (Sánchez-Palomares et al., 1990). Our study focused on the 21 PSPs that existed in 2006, between 37.86° N and 40.73° N, and between 3.01° W and 0.22° E. Elevation of these sites varies from 1100 to 1470 m a.s.l (Table 1). Inventories of PSPs, covering different ages and site qualities, were carried out at 5–9 year intervals between 1964 and 2006 (see electronic supplementary material, Table S1 and Martín-Benito et al. (2008b) for details on the PSPs). In each inventory, diameter (dbh) of all trees with dbh > 7.5 cm and height of all dominant trees (100 trees per hectare with the largest diameter) were measured. Inventory information available at these 5–9 year intervals was linearly interpolated to annual values between two consecutive inventories.

2.2. Climate data

Mean monthly temperatures and precipitation data were provided by the Spanish National Meteorological Agency (AEMET) from several meteorological stations (Fig. 1). We used a homogenized precipitation dataset for the period 1899–1999 (González-Rouco et al., 2001), to which we added AEMET data for the period 2000–2005. Temporal trends of monthly temperature and precipitation were estimated for the three regions considered. Average climate description of each region is shown in the electronic supplementary material, Fig. S1. For projections of future growth under expected climate change, we used climate predictions from two GCMs (ECHAM4 and CGCM2) under two GHG emission scenarios (Nakicenovic et al., 2000) covering 50% of the range of the nine IPCC scenarios in terms of GHG concentration (A2 and B2) downscaled using the FIC analog method and provided by AEMET. These are the only two GHG emission scenarios and two GCMs downscaled currently available for the Iberian Peninsula.

2.3. Dendroecological approach

Trees were sampled in fully-stocked forest stands by taking two cores at breast-height from 14–16 dominant trees from each PSP. A total of 293 trees were used (Table 1; Fig. 2). Cores were mounted and sanded to produce clearly visible ring boundaries (Stokes and Smiley, 1968) and total ring width (TRW) was measured to the nearest 0.01 mm with a measuring table and the software TSAP (Rinn, 2003). TRW series were visually and statistically crossdated with TSAP by the *Gleichläufigkeit* (measures the year-to-year agreement between the interval trends of two chronologies, based upon the sign of agreement and expressed as percentage), *t*-values (determines the correlation between series) and the cross-date index (CDI), which is a combination of both. Accuracy of crossdating and measurement were checked using the COFECHA program (Grissino-Mayer, 2001).

Tree-ring series standardization as commonly done in dendrochronological studies removes an uncontrolled amount of potentially important variability and the standardization method might have an effect on observed long-term trends of tree-ring series
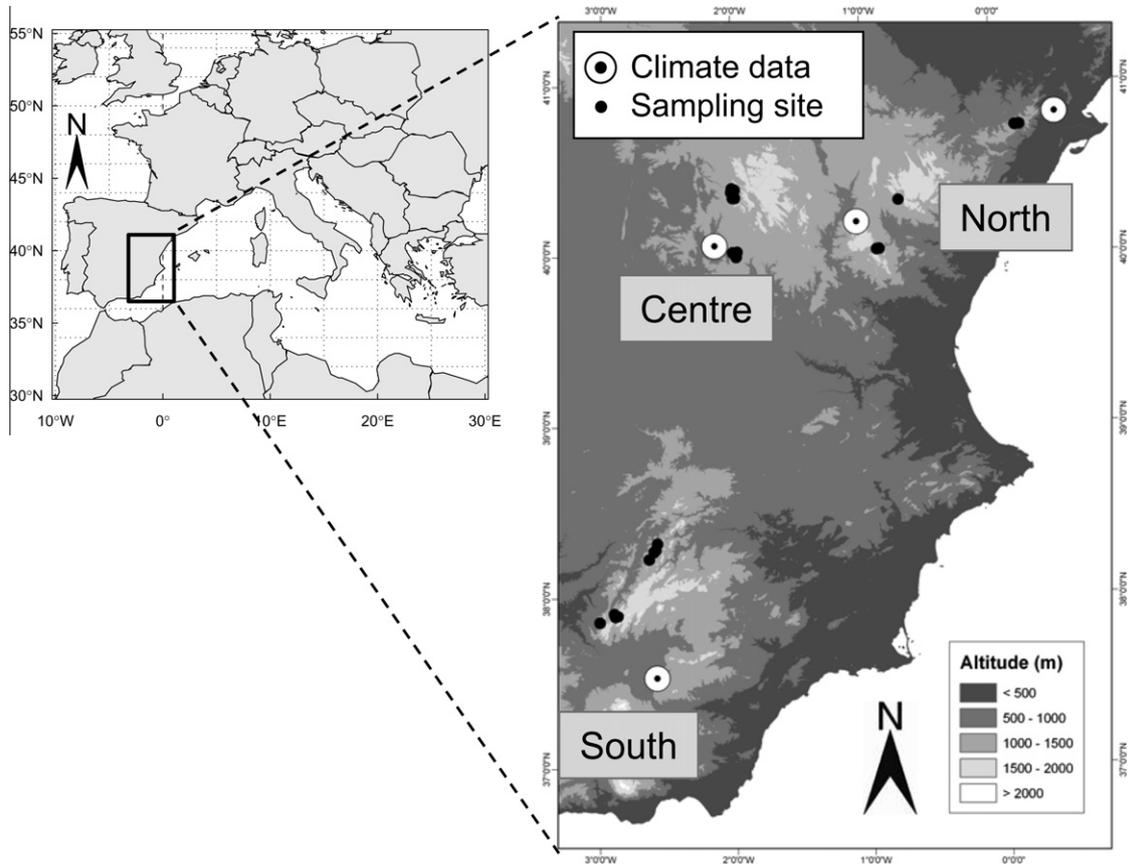
Fig. 1. Distribution of sampling sites and climate stations in the Eastern Iberian Peninsula.

Table 1
Summary information of the tree-ring width chronologies from the studied regions. Information refers to raw tree ring width (TRW).

Region	Altitude (m a.s.l.)	No. of trees	No. of cores	Period	Mean length (min–max)		Mean (cm year^{-1})	SD	MS	AC(1)
North	1100–1400	73	139	1833–2006	128	(53–196)	1.061	0.664	0.332	0.718
Center	1130–1470	126	227	1891–2006	85	(57–119)	1.420	0.932	0.295	0.758
South	1270–1430	99	173	1833–2005	105	(60–201)	1.662	1.009	0.276	0.761

SD, is the standard deviation; MS, is the mean sensitivity; AC(1), is the first order autocorrelation coefficient.

(Fritts, 1976; Biondi, 1999). In order to preserve high and low frequency (multi-decadal) variability and allow for their simultaneous analysis and possible interactions between phenomena such as competition and drought, we used raw BAI of individual dominant trees (Visser and Molenaar, 1990; LeBlanc, 1992; Van Deusen, 1992; Piovesan et al., 2008) as our predicted variable and introduced cambial age as an explanatory variable in our model.

Annual basal area increments (BAI) were derived from the mean ring width of two cores per tree, assuming concentric rings according to:

$$BAI_t = \pi(R_t^2 - R_{t-1}^2)$$

where R_t and R_{t-1} are the tree radius at breast height on the year of ring formation (t) and previous year, respectively. Radius was derived by adding up all ring widths from the pith. For trees in which pith was not reached, we applied the average growth of all trees in the same plot until the first available ring of the subject tree. Because BAI distribution was right-skewed, data were log-transformed in order to achieve normality so the modeled variable was ln (BAI + 1) where one was added to avoid negative values of the transformed variable.

2.4. Linear mixed effects model approach (LMEM)

The presence of a hierarchical structure in our data (i.e. rings in trees, trees in plots, and plots in regions) results in the lack of independence between observations and causes spatial and temporal correlation within the data. Hence, we used a linear mixed model approach (with fixed and random effects) which allows for the parameterization of the variance–covariance matrix of the error terms. These models also enable to further analyze the variance not explained by their fixed effects by allocating it to the different hierarchical levels and/or random effects.

First, we started by finding the "*beyond optimal*" model only including fixed effects (Diggle et al., 2002) based on previous dendrochronological studies for the climatic variables (Martín-Benito et al., 2010a) and all biologically realistic interactions, to find the explanatory variables more likely to be significant (Zuur et al., 2009). The model was expressed as:

$$\ln(BAI + 1) = a + b \cdot SIZE + c \cdot COMP + d \cdot SITE + e \cdot CLIM$$

where a is the intercept, SIZE is a vector of variables describing the age-dependent radial growth pattern, COMP a vector describing tree competition, SITE a descriptor of site quality and CLIM a vector
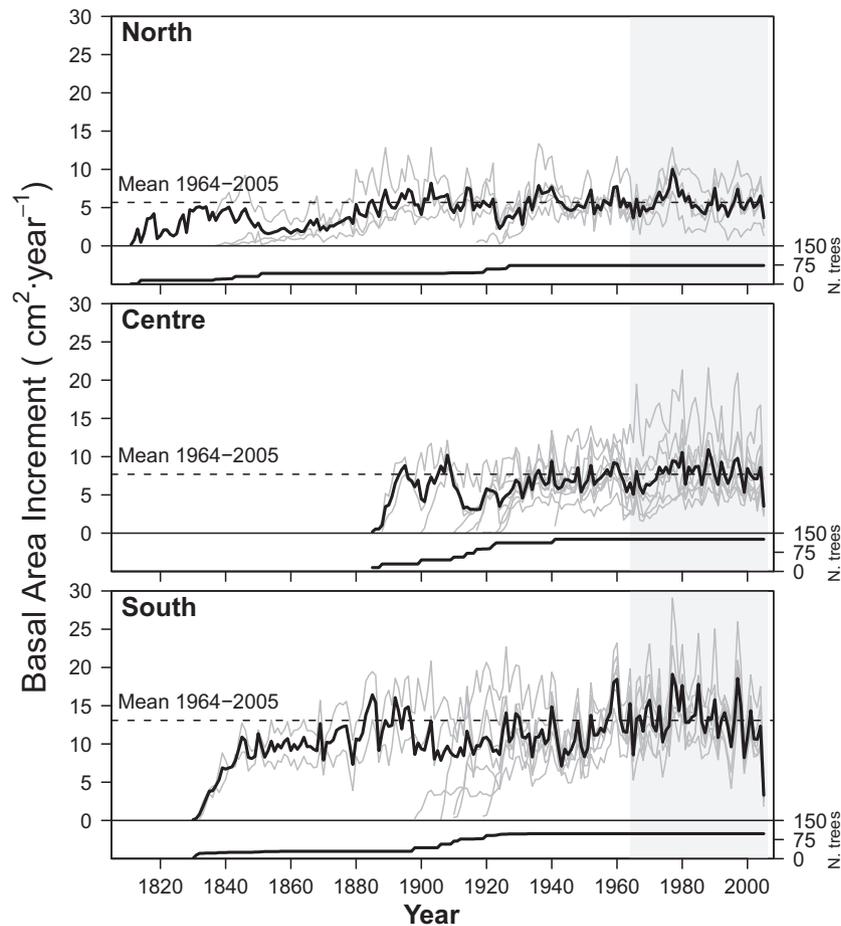
Fig. 2. Mean tree basal area increments (BAI) for each plot (gray lines) and regional mean (black line) in the three regions considered. Gray shaded area represents the period 1964–2005.

of climatic variables. We included a quadratic function of R_{t-1} and cambial age to capture the age-dependent tree growth pattern, and basal area of larger trees (BAL, $m^2 ha^{-1}$) as a measure of the competitive ranking of a tree within the plot that behaves well under all types of thinning (Monserud and Sterba, 1996). For competition, we also tested the ratio between diameter of the subject tree and the mean quadratic diameter (size ratio, Sr). In addition, stand basal area (BA) and density (N) were tested to incorporate the effect of crowding. As a proxy for site productivity at plot level, site index [SI, dominant height at the age of 80 years of age (Martín-Benito et al., 2008b)] was included. Regarding climate, we introduced variables from previous June to current October, either monthly or seasonal values. Annual mean atmospheric CO_2 concentration (www.esrl.noaa.gov/gmd/ccgg/trends/) was also considered as a possible covariate for BAI based on previous studies that showed its important effect on growth of other pine species (Knapp et al., 2001; Martínez-Vilalta et al., 2008).

Second, we explored the most parsimonious random effect structure considering both intercepts and slopes of all explanatory variables as possible random effects at three hierarchical levels (tree, plot, and region). At each step, Akaike's Information Criterion (AIC) decrease was compared to the previous more parsimonious model and a likelihood ratio test was performed to check for a significant model improvement. A level of $p = 0.01$ was used for significant testing of variables in the model.

While parameter estimates are not biased by autocorrelated data (Gregoire et al., 1995) their variance is, which results in biased estimates for the confidence interval of the parameters, and

invalidates hypothesis tests performed on them (Searle et al., 1992). We tested autoregressive moving average (ARMA) with different orders of autocorrelation as the covariance structure for the error terms. We finally used an ARMA(2,0), which imposes a decreasing correlation between error terms as the distance between measurements increases. Linear mixed effects models (LMEM) were fitted in R version 2.10.1 (R Development Core Team, 2009), using the package *nlme* (Pinheiro et al., 2009) and the REML method, except when simplifying the fixed structure of models when ML was used (Zuur et al., 2009).

2.5. Projections of future growth

Basal area growth was estimated individually for each tree using climate variables derived from each of the two GCMs and two GHG emission scenarios (a total of four GCM–GHG combinations) treated with equal probability (IPCC, 2007) and the developed model considering only the first hierarchical level (region) in order to account for regional differences in the response to future climate (O'Neill et al., 2008). For each tree and GCM–GHG combination, mean growth projections for three 30-year periods (2011–2040, 2041–2070, 2071–2100) were expressed as percentage of the mean estimated growth for the control period (1961–1990). Growth projections were further analyzed for different categories of stand variables. In each 30-year period, all non-climatic variables were considered equal to those of the control period (i.e. stand and tree variables were the same for 1971, 2021, 2051, and 2081).

3. Results

3.1. Climate trends

For the period 1964–2005, spring–summer temperatures (March–August) increased significantly ($p < 0.001$) in the three regions at 0.45 °C decade^{-1} on average, accelerating to 0.76 °C decade^{-1} after 1970 (Fig. S2). However, winter temperatures (December–February) did not increase as much, being only significant in the central and northern regions (0.48 °C decade^{-1}, $p < 0.001$; 0.23 °C decade^{-1}, $p = 0.042$, respectively). After 1970, this increase remained only in the central region (0.63 °C decade^{-1}; $p < 0.001$). From 1964 to 2005, previous September to current July precipitation (PP$_{9-7}$) decreased in the south and center (−75.8 mm decade^{-1}; $p = 0.006$, and −37.6 mm decade^{-1}; $p = 0.016$, respectively), but only in the south after 1970 (−108.4 mm decade^{-1}; $p < 0.001$). Similar climate trends were shown by GCM predictions, although individual predicted values for spring–summer and winter temperatures were in some cases higher than any observed value in the south and center regions for the period 1964–2005 whereas predicted precipitation values were within the observed range for all regions and periods (Fig. S3).

3.2. Tree growth and limiting factors

Mean annual BAI between 1964 and 2005 decreased from south to north, being 13.08, 7.66, and 5.64 cm^2 year^{-1} in the south, center, and north, respectively (Fig. 2). Mean tree-ring sensitivity followed the opposite trend increasing from south to north (Table 1). These growth trends were explained by our LMEM that included nine variables and five interactions (Table 2). Previous radius (R_{t-1}) entered the model with a positive single-order coefficient and a negative second-order coefficient indicating a decrease of radial growth rate as tree size increased. Growth decline was predicted for older trees by the negative coefficient associated with cambial age. Tree size and age had a significant positive interaction on growth (Table 2).

Several stand variables from RFI entered into the model to take into account changes in tree and stand characteristics. As expected, higher competition was associated with lower growth by the negative coefficients of both BAL and N, while productivity (expressed as SI) had a positive coefficient (Table 2). The positive interaction between productivity and stand density indicated that trees at the

Table 2
Summary of the fitted linear mixed effects model of BAI.

Fixed effect	Value	SE	DF	t-value	p-value
Intercept	5.1587	0.4046	12,502	12.749	<0.001
R_{t-1}	0.1647	0.0189	12,505	8.694	<0.001
R_{t-1}^2	−0.0061	0.0008	12,505	−7.282	<0.001
Age	−0.0110	0.0023	12,505	−4.848	<0.001
BAL	−0.0776	0.0055	12,505	−14.105	<0.001
N	−0.0002	0.0003	12,505	−7.977	<0.001
SI	0.0496	0.0138	17	3.598	0.002
T_{win}	0.0543	0.0024	12,505	22.234	<0.001
T_{ss}	−0.1706	0.0049	12,505	−34.827	<0.001
PP$_{9-7}$	−0.0031	0.0001	12,505	−33.099	<0.001
Age × R	0.0006	0.0001	12,505	4.174	<0.001
SI × N	3.3×10^{-5}	6.9×10^{-6}	12,502	4.821	<0.001
T_{ss} × PP$_{9-7}$	0.0002	0.0001	12,505	38.210	<0.001
SI × T_{ss}	0.0049	0.0007	12,502	6.703	<0.001
SI × PP$_{9-7}$	1.1×10^{-5}	3.4×10^{-6}	12,502	3.087	0.002

R_{t-1}, is tree radius at breast height reconstructed from tree rings; BAL, is basal area of larger trees (m^2 ha^{-1}), N, is stand density (trees·ha^{-1}), SI, is stand site index (m), T_{win} is the mean winter temperature (January–March; °C), T_{ss} is the mean spring and summer temperature (April–September; °C), PP$_{9-7}$ is the total precipitation from September of the year previous to growth to July of the current year (mm). The modeled variable was ln (BAI + 1).

more productive stands may maintain higher growth rates at higher densities although density had a general negative effect on growth across the explored productivity ranges (Table 2). Among the climate variables analyzed, three were found to add significantly to BAI. Winter temperature (T_{win}, December–February) showed a positive effect on growth whereas spring–summer temperature (T_{ss}, March–August) had a negative effect. September–July precipitation (PP$_{9-7}$) had a negative coefficient in the model which would reflect a negative effect of precipitation (Table 2). However, PP$_{9-7}$ should be interpreted in conjunction with its interaction with T_{ss}, indicating a more positive effect of precipitation as T_{ss} increases (Fig. 3). Below a certain level of PP$_{9-7}$ (ca. 800 mm), higher T_{ss} leads to decreasing growth whereas above that precipitation threshold growth might increase (Fig. 3). The effect of atmospheric CO$_2$ concentration was not significant for the analyzed period. Region, tree, and plot random effects on growth were important as intercepts and non-significant for the covariables tested. The final model was:

$$\ln(\text{BAL} + 1) = a + b_1 \cdot R_{t-1} + b_2 \cdot R_{t-1}^2 + b_3 \cdot \text{age} + b_4 \cdot (R_{t-1} \times \text{age})$$
$$+ c_1 \cdot \text{BAL} + c_2 \cdot N + d_1 \cdot \text{SI} + d_2 \cdot N \times \text{SI} + e_1 \cdot T_{ss}$$
$$+ e_2 \cdot T_{win} + e_3 \cdot \text{PP}_{9-7} + e_4 \cdot (T_{ss} \times \text{PP}_{9-7}) + t + p + r$$

where a, b_i, c_i, d, and e_i are estimated parameter of the fixed effects (Table 2) and t, p, and r are tree, plot and region random effects (random-effect variances were 0.047, 0.058, and 0.004 for tree, plot, and region, respectively).

The final LMEM showed a good behavior with high R^2 values (correlation between observed and predicted values) for the model with fixed and random effects ($R^2 = 0.703$) and with the fixed effects part alone ($R^2 = 0.354$) (Table 3), further justifying the use of our LMEM approach. Root mean square error and bias were low in both cases (Table 3). Residuals showed no departure from the assumption of normally distributed error with homogenous variance for the log transformed variable (results not shown). In general, predicted BAI closely followed observed BAI during 1964–2005 in the three regions (Fig. 4), although for the period 1975–1980 the model did not account for much of the BAI variability in the northern region and underestimated growth.

The effects of precipitation and temperature were explored across the full range of stand productivity observed in our dataset (Fig. 5). At low precipitation, tree growth decreased in all productivity classes as temperature warmed and this reduction was more pronounced for the least productive stands. However, at high precipitation tree growth increased with warming temperature except for the least productive stands where it either remained constant or decreased. The positive effect of warm temperatures under high precipitation increased with increasing stand productivity (Fig. 5).

3.3. Growth projections under expected climate change

In absolute terms of BAI, growth projections based on future climate predictions showed maintained declines in the southern and central regions. For the northern region, however, diverging trends and greater tree growth variability could be expected (results not shown). In relative terms (i.e. referred to mean BAI in the control period 1961–1990) the south and center regions showed similar negative trends attaining maximum growth decreases of 10%, 20%, and 40% for the three projected periods (Fig. 6). The northern region presented significant differences because its variability was high enough to allow for both increasing and decreasing growth rates.

Breaking down the projected growth for each region based on several classes of SI and BAL showed important inter and
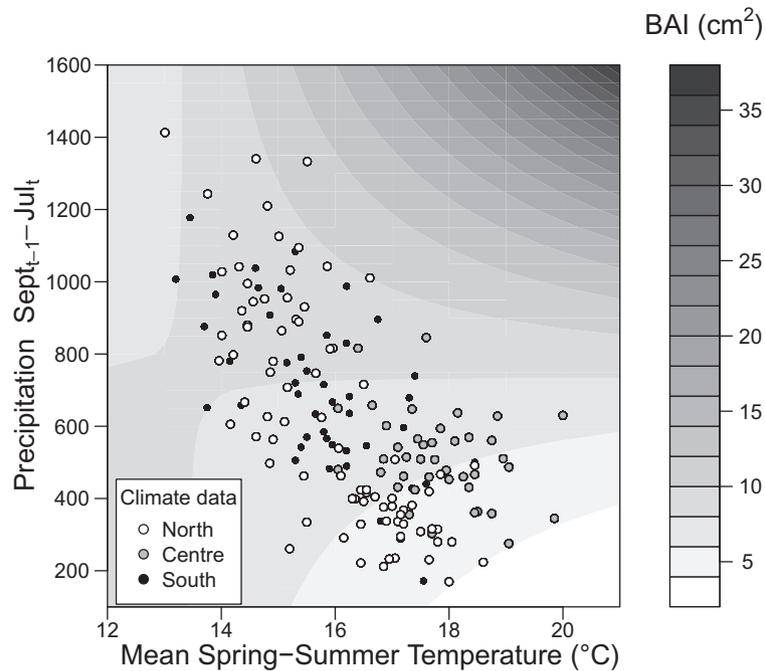
Fig. 3. Surface plot of the predicted effects of the interaction between spring–summer temperature and September–July precipitation on BAI (only fixed effects were used).

Table 3
Goodness of fit statistics for the BAI model.

Region	All effects		Fixed effects	
	Bias (cm^2)	RMSE (cm^2)	Bias (cm^2)	RMSE (cm^2)
North	−0.64	2.23	−0.51	3.02
Center	−0.37	3.01	−0.07	4.54
South	−1.11	4.75	−3.12	7.02
All regions	−0.74	3.58	−1.32	5.27
R^2	0.703		0.354	
AIC = 2928.93	BIC = 3085.52		log Lik = −1449.46	

R^2, refers to the correlation between observed and predicted values.

intraregional differences (Fig. 6). Growth was projected to decrease for all SI and BAL classes in the southern and central regions although this decrease would be smaller as SI increases (Fig. 6a) and BAL decreases (Fig. 6b). The northern region, however, showed future growth acceleration for high SI sites (Fig. 6a) whereas growth in trees under low BAL might show higher variability (e.g. from 40% reduction to 20% increase, Fig. 6b). Excluding the random regional effect from growth projections reduced these differences, further highlighting the importance of unobserved regional factors, included in the random structure of the model.

4. Discussion

### 4.1. Climatic drivers of black pine growth and growth patterns

Our results show that black pine growth is limited by summer drought, i.e. the combination of high spring–summer temperature and low autumn–summer precipitation, and by low winter temperatures, as previously observed in Spain (Richter et al., 1991; Martín-Benito et al., 2010a) and central Europe (Lebourgeois, 2000; Leal et al., 2008). Higher winter temperatures promoted growth most likely reflecting the importance of multiple factors such as winter photosynthesis (Pederson et al., 2004), carbohydrate accumulation

in conifers (Hoch et al., 2003), and the development of roots during the cold season (Hansen and Beck, 1994).

The effect of warm spring–summer temperature was generally negative although it could enhance growth during wetter years (Fig. 3) in accordance with results on other conifers (D'Arrigo et al., 2004; Wilmking et al., 2004; Martínez-Vilalta et al., 2008) indicating that an increase in precipitation could compensate or exceed the increase in evaporative demand associated with higher temperatures. This interaction between spring–summer temperatures and precipitation in the central and southern regions was positive for growth at the beginning of the studied period but later became negative most likely after reaching certain thresholds when the precipitation could not compensate for the higher temperatures (D'Arrigo et al., 2004; Wilmking et al., 2004), causing a convex shape in BAI (Figs. 2 and 4) similar to the growth trends of other drought stressed species in the recent decades (Piovesan et al., 2008). Similar interactions were found for Scots pine in Northeastern Spain where the negative effect of warming was larger for drier sites although the threshold value for growth decline was not exceeded (Martínez-Vilalta et al., 2008). The lack of significant growth decline in the northern region (Figs. 2 and 4), where precipitation has not significantly decreased despite the observed warming, supports the importance of the increasing water deficit as the cause of growth decline. The growth decline observed after 1985 mainly in our southern region (Figs. 2 and 4) corresponds with similar drought-driven declines in other Mediterranean regions (Macias et al., 2006; Sarris et al., 2007; Piovesan et al., 2008) and increased climate sensitivity in pines (Andreu et al., 2007). This negative pattern remains even after taking into account the effects of tree age and size, density changes, and competition (Table 2).

4.2. Effects of stand characteristics on tree growth and interactions with climate

Stand structure and competition are two of the most important factors for tree growth acting either directly or indirectly interacting with other factors such as climate (Piutti and Cescatti, 1997). As expected, trees in lower density plots grew faster than those in
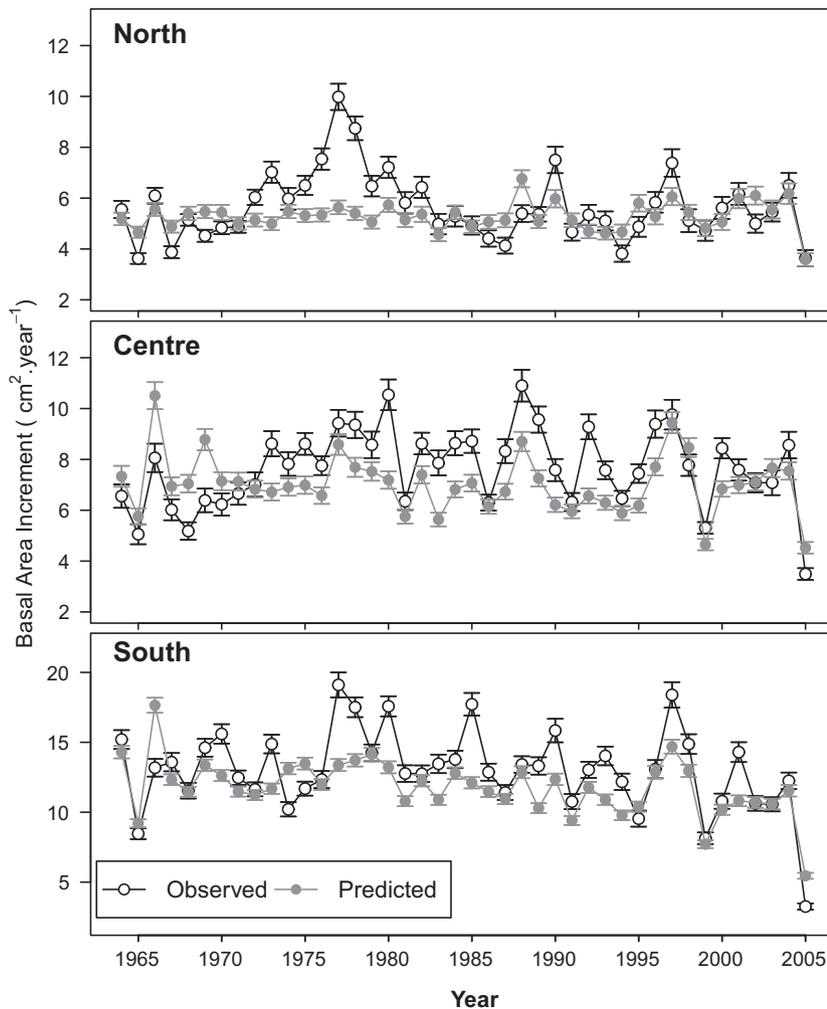
Fig. 4. Mean BAI (observed and predicted) for the three regions as a function of climate, and stand and competition variables in the linear mixed effects model. Error bars represent standard errors for all trees in each region.

denser plots and at the same time the effects of warmer temperatures and lower precipitation on growth increased with stand density and BAL. Management may exert great impacts on future forest response to climate change (Hulme, 2005). In this regard, thinning is a useful forest management measure to adapt forest to global change because of its positive effects on the response of trees to climate (Piutti and Cescatti, 1997; Misson et al., 2003; Martín-Benito et al., 2010b) by reducing rain interception and tree-to-tree competition and therefore making more resources available for each individual tree (e.g. water, light, and nutrients). Therefore, wider initial spacing and higher stand thinning might effectively counterbalance negative effects of future changes in climate, at least in part, if trees have higher relative growth rates which could allow them to better withstand future growth reductions caused by higher water stress. These findings might not be directly extensible to suppressed trees for which opposite results (i.e. lower effect of climate on suppressed tress than on dominant trees) have been found in our southern region (Martín-Benito et al., 2008a) and suggest a non-linear relationship between competition and climate-growth relationships across the complete range of competition classes (Piutti and Cescatti, 1997).

Despite the general negative growth trends observed, our results show that site productivity is an important factor modulating tree response to climate. Taking into account the effects of all other variables, warmer and drier climate leads to lower growth in the least productive forests (Fig. 5). Low productivity is caused by a combination of environmental factors (mainly topography, soil, and climate) that limit the full development of a species' potential growth (Seynave et al., 2008). The same edaphic factors associated with higher forest productivity, such as higher water retention capacity, better aeration, or nutrient availability (Bravo and Montero, 2001), could to some extent counteract the effects of higher spring–summer temperatures at low precipitation by maintaining a higher soil moisture balance. A lower response to climate of the more productive stands was also reflected in their lower mean sensitivity (Table 1). At low productivity sites, on the other hand, any additional abiotic stress (e.g. more drought or warmer temperatures) might not be buffered by site conditions and could lead to slower growth. However, we also report important regional differences in the interactions between climate and site productivity.

4.3. Projected future growth

Our results supported the hypothesis that drought causes the general negative trends of tree growth found around the Mediterranean (e.g. Macias et al., 2006; Sarris et al., 2007; Piovesan et al., 2008). However, our growth projections suggested that in black pine forests located in mountainous regions of the Mediterranean the general balance between summer drought and winter cold will result in maintained growth decreases in southern and central
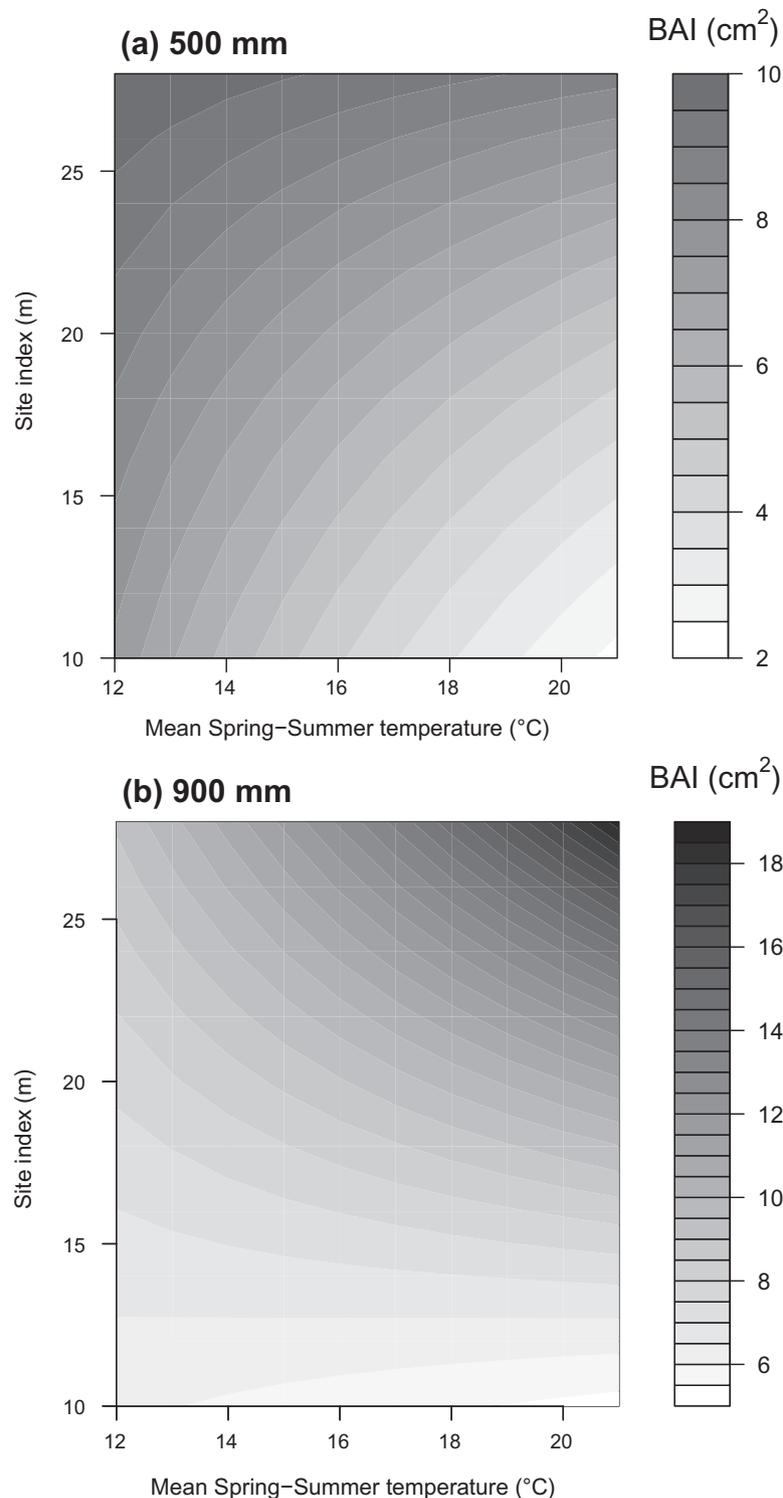
Fig. 5. Surface plot of the predicted effects of the interaction between spring–summer temperatures and site productivity (as estimated by site index, dominant height at age 80 years) on BAI two different precipitation regimes (a) low (500 mm year^{-1}) and, (b) high (900 mm year^{-1}) (only fixed effects used).

regions whereas the northern region could experience equal or enhanced growth (Fig. 6). This increase in growth rates in the northern populations is in accordance with results found for black pine in France (Lebourgeois et al., 2000) and other boreal and Mediterranean species (Jump et al., 2006; Martínez-Vilalta et al., 2008; Vila et al., 2008; Lapointe-Garant et al., 2010) and would seem to contrast with those in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) where southern populations would be less impacted by

climate change (Chen et al., 2010). However, breaking down the analysis for different levels of SI showed that in the north, where mean SI is lower, the interactions between precipitation and temperatures might still be positive even for the last projection period (2071–2100) in high and medium SI stands (Fig. 6a). These results suggest important regional differences and would support results of lower productivity reductions for outlying tree populations better adapted to drought conditions (Chen et al., 2010), not
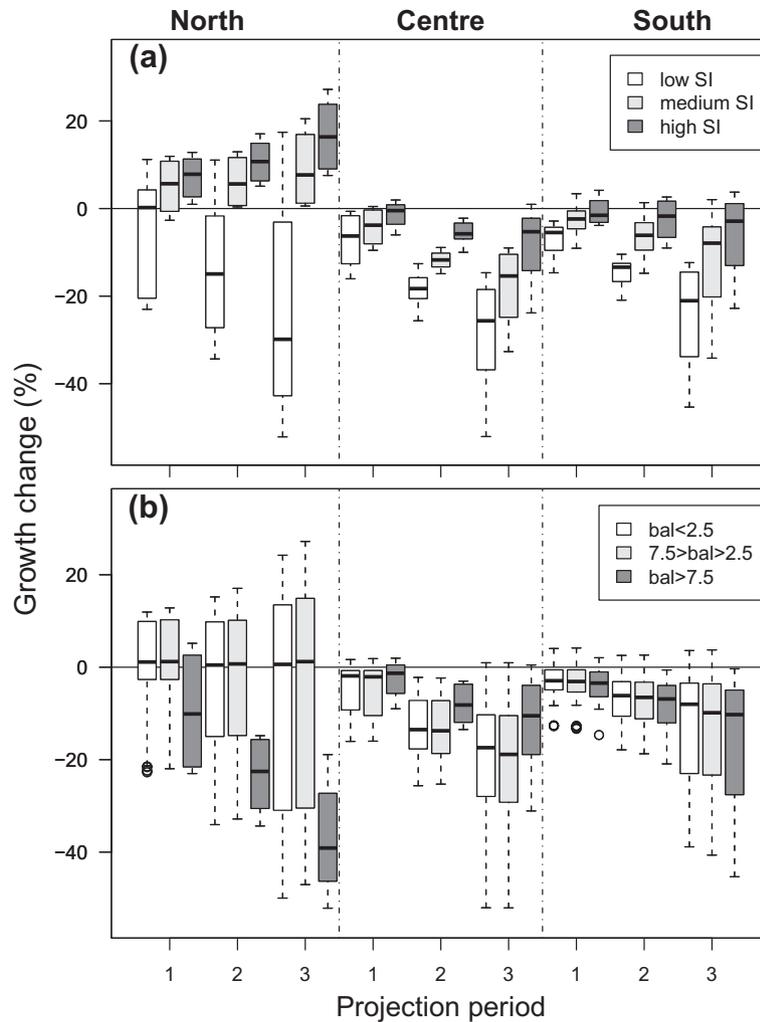
Fig. 6. Growth projections based on two GCMs under two GHG emission scenarios. Relative growth changes are expressed as percent change from average growth in the reference period 1961–1990. Regional projections are broken-down by (a) low, medium, and high productivity (as estimated by site index, dominant height at age 80 years), and (b) basal area of larger trees (BAL, m^2 ha^{-1}). Prediction periods are: (1) 2011–2040, (2) 2041–2070, and (3) 2071–2100.

necessarily those in the southern distribution limits. Higher intra-population genetic variability in our northern region (Martín-Albertos and Gonzalez-Martínez, 2000) and adaptations to local dryer environments might have an impact in the observed regional growth patterns (Davis and Shaw, 2001).

Higher growth rates of trees in productive sites might allow them to reduce their growth and still survive whereas trees at low SI sites might be approaching their minimum survival growth threshold which might lead to higher mortality (Bigler and Bugmann, 2004). Surviving trees will most likely adapt to drier and warmer conditions in the future, a process in which the reduction of competition among surviving trees could play an important role (Martínez-Vilalta and Piñol, 2002). In the central and northern regions of its distribution area in Spain, black pine occupies a drier and lower altitudinal belt than Scots pine (Barbéro et al., 1998). The fact that Scots pine has shown important mortality in the northern region (Martínez-Vilalta and Piñol, 2002) where black pine growth was predicted to increase (Fig. 6) might result in an extension of black pine at the expense of Scots pine (Debain et al., 2007) in accordance with expected altitudinal and latitudinal shifts for tree species (Lenoir et al., 2008). It is important to note, however, that tree regeneration and tree growth are not necessarily affected by the same environmental factors.

The present results need to be interpreted with caution, especially as we approach the end of the projection period, because of

the empirical nature of our model and the uncertainty of SRES scenarios (Nakicenovic et al., 2000). In addition, stand characteristics commonly considered constant, such as productivity, might also be affected by climate change (Boisvenue and Running, 2006), adding further uncertainty to our results. Furthermore it is important to consider that observed and predicted BAI decreases, and thus also that of aboveground wood production, does not necessarily imply reductions of net primary production (NPP) as tree carbon allocation might have shifted towards root growth which might in turn lead to a higher tree drought resistance (Mokany et al., 2006).

5. Conclusion

The observed radial growth decline in the West-Mediterranean populations of black pine in Spain is consistent with increasing drought in the area, and in accordance with previous tree growth studies in dry-temperate regions. However, our LMEM approach combining forest inventory data and tree rings allowed us to quantitatively analyze the role of stand characteristics on modulating this negative trend. In fully stocked forests, different processes of competition or facilitation greatly influence the combined effect of precipitation and temperature on tree growth. A weaker effect of climate was found for trees in stands that enhanced growth (high productivity). Growth projections under four climate

scenarios and similar stand conditions allowed us to evaluate different regional vulnerabilities, found to be lower at the northern region.

Our results have implications for forest management and measures aiming to adapt forest stands to global change. In order to avoid or limit further growth declines in dominant trees, foresters could promote less dense stands and increase their productivity. However, it is important to note that other important processes for forest development not analyzed in this study, such as natural regeneration, might need different stand conditions.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.05.038.

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