Contrasting growth and mortality responses to climate warming of two pine species in a continental Mediterranean ecosystem

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ABSTRACT

The long lifespan of trees makes them sensitive to climate warming, particularly when abrupt changes in climatic conditions occur and when trees are already growing near to their climatic tolerance thresholds. In many Mediterranean pine forests, drought stress induced by warmer temperatures and increased aridification compromise tree survival, causing growth decline and, eventually, triggering tree mortality. We evaluated the effect of climate on radial growth and mortality comparing dead and living trees of two pine species, *Pinus sylvestris* and *Pinus nigra* subsp. *salzmannii*, in a continental Mediterranean area over a 50-year long period. We used linear mixed models and correlations to evaluate the effect of climate on basal area increment (BAI) and on ring-width indices, respectively. In *P. nigra*, growth was enhanced by wet and cold conditions, whilst growth increased with temperatures in *P. sylvestris*. A gradual BAI reduction was detected in *P. nigra* trees since the late 1970s, becoming more pronounced in recently dead trees. Contrarily, *P. sylvestris* growth did not show such decline, whilst death events in this species were linked to severe and punctual droughts. Our findings show that warming and drought stress trigger contrasting responses in functionally and phylogenetically similar tree species, and suggest climate-mediated important changes on competitive dominance in Mediterranean forests.

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1. Introduction

Many cases of forest dieback and tree mortality attributed to drought- or heat-induced stress have been described worldwide over the last decades (Allen et al., 2010, 2015). The long lifespan of trees prevents quick adaptation responses to environmental changes (Lindner et al., 2010), making forests especially vulnerable to climate-warming effects. In the Mediterranean Basin, a decrease of over 25–30% in annual precipitations is expected by the end of the 21st century, together with an increase in the frequency and intensity of dry spells (Beniston et al., 2007). The increase in the variability of precipitations will be likely accompanied by a rise of 4–5 °C in average annual temperatures (Christensen et al., 2007; Giorgi and Lionello, 2008) that could be even higher in mountainous areas (Meehl et al., 2007). Circum-Mediterranean tree populations located at the species' southernmost distribution limits and inhabiting areas prone to drought are particularly susceptible to drought-induced dieback (Sánchez-Salguero et al., 2012). Therefore, drought-induced dieback is expected to affect Mediterranean populations of many tree species, especially conifers showing a high vulnerability to drought-induced embolism such as Scots pine (Camarero et al., 2015b).

Variation in climatic conditions may lead to important changes in tree growth and survival thus altering forest structure and composition (Allen et al., 2010, 2015; Granda et al., 2013). Warm temperatures and reduced precipitation leading to drought stress can trigger tree defoliation and rise mortality rates of dominant trees above basal or background levels (McDowell et al., 2008). Moreover, the differential vulnerability of tree species to climate warming may amplify the changes in composition of forest communities (Valladares, 2008). As a consequence, there is a need to

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increase our understanding on forest dieback processes, and to identify which growth and climatic conditions lead to tree death (Bigler and Bugmann, 2004). This would allow promoting a more sustainable forest management under the ongoing climate change.

A decline in radial growth is a symptom usually associated to forest dieback that can be noticed either immediately during a drought period or several years later (McDowell et al., 2008), and such decline usually precedes tree death (Bigler et al., 2006, 2007). In fact, several studies have reported increases of death risk following a previous period characterized by reduced growth rates (Ogle et al., 2000; Suarez et al., 2004; Bigler et al., 2006). When drought is gradual and maintained over time, it can act in the long term (predisposing factor *sensu* Manion, 1981), progressively weakening the vigor of trees, reducing their growth rates and increasing their vulnerability to recurrent droughts (Tyree and Sperry, 1988; Bigler and Bugmann, 2004). Other factors such as extreme droughts act in the short term (inciting factor *sensu* Manion, 1981) by rapidly reducing the capacity of trees to recover after an acute reduction in water availability. These two types of factors interact with the so-called contribution factors, which are usually opportunistic or secondary pathogens affecting previously weakened trees (Gil Pelegrín et al., 2008; Hereş et al., 2014). Therefore, both long- and short-term reductions in tree growth as a consequence of climate warming and drought stress worsen the capacity of trees to cope with additional stress, increasing the death risk.

There is still a large degree of uncertainty on the patterns behind dieback processes in forests (Allen et al., 2015), including how this phenomenon differently affects tree species along environmental gradients. This is, among other reasons, because climate change induces physiological stress in different ways depending on functional traits like leaf phenology and wood type, and on the phenotypic plasticity of each tree species (Camarero et al., 2015a). For instance, pines are known to close stomata during drought periods to avoid water losses and embolism in the xylem, leading to a decrease in carbon assimilation and, thus, reducing growth and carbon availability (Tyree and Sperry, 1988). However, closely related pine species also respond in different ways to drought, with Scots pine (*Pinus sylvestris* L.) being identified among one of the most susceptible tree species to drought-induced dieback in Western Europe (Martínez-Vilalta and Piñol, 2002). In contrast, Mediterranean pine species as black pine (*Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco) are better able to withstand drought stress (Sánchez-Salguero et al., 2012, 2015a), although cumulative water deficit constrains their growth in the long term (Linares and Tíscar, 2010). In addition, tree growth in continental Mediterranean areas is limited not only by summer drought, but also by winter coldness (Mitrakos, 1980; Camarero et al., 2010), which delays the start of the growing season and shortens the optimal period for tree growth in contrast with milder Mediterranean or wetter areas. Thus, the positive effect of increasing winter temperatures on growth in continental Mediterranean regions (Granda et al., 2013) could be counteracted or canceled out due to rising evapotranspiration rates during the growing season in spring and early summer leading to an exacerbated drought stress (Linares and Tíscar, 2010).

Here we evaluate the response of radial-growth patterns to climatic conditions of living and asymptomatic trees (*i.e.* not showing symptoms indicating they are prone to die such as severe defoliation) together with nearby, recently dead trees in two major pine species of Iberian forests showing dieback, namely Scots and black pine (*P. sylvestris* and *P. nigra* subsp. *salzmannii*, respectively). Since climatic factors determining growth shift along altitudinal gradients (Babst et al., 2013) we also evaluated radial growth patterns at different altitudes in the most widely distributed black pine. We aimed at answering three questions: (1) do growth patterns

differ between asymptomatic living trees from those of recently dead trees? (2) How sensitive are the two pine species studied to drought? And (3) do growth patterns vary with altitude? We expected dead trees to show lower growth rates than asymptomatic trees for several years prior to death, since a diminishing growth in response to drought in a given year can affect growth of the following years due to legacy effects (Anderegg et al., 2013) including reduced conductivity and photosynthetic rates. Further, recurrent droughts could also deteriorate the hydraulic capacity of trees and cumulate stress over time. Given that the Iberian Peninsula represents the southernmost distribution limit of Scots pine, we also expected higher growth sensitivity to drought in Scots pine as compared to the Mediterranean black pine. Finally, since climatic conditions are colder and more humid at higher than at lower elevations in Mediterranean inland sites, we expected higher growth rates at higher elevations due to a reduced drought stress, and therefore a less evident growth decline prior to tree death.

2. Materials and methods

2.1. Study area and species

The study area is located in the "Alto Tajo" Natural Park (Guadalajara province, central Spain) (see Appendix 1). Soils are poorly developed on limestone and dolomite substrates, and the bedrock frequently outcrops (Carcavilla et al., 2008). Climate is continental Mediterranean, with warm and dry summers and cold winters (Table 1). This area is largely covered by pine, oak and juniper forests. Spanish black pine (*P. nigra* Arn. subsp. *salzmannii* (Dunal) Franco) covers a total of 21,826 ha, representing 11.9% of the Natural Park area (data obtained from the Spanish Forest Map on scale 1:50,000, MFE50; Banco de Datos de la Naturaleza, 2006). It is replaced by Scots pine (*P. sylvestris* L.) in colder and more humid places (25,161 ha, 13.7% of the area) and by Spanish juniper (*Juniperus thurifera* L.) in the most continental ones. The most abundant oak species are holm oak (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.) and Portuguese oak (*Quercus faginea* Lam.) (Ferrero et al., 2006). We selected two study sites, Peñalén and Buenafuente del Sistal, dominated respectively by Scots pine and black pine (Table 1). Additionally, we sampled at three different elevations in Buenafuente del Sistal to cover an altitudinal gradient for black pine.

In the Iberian Peninsula, the Scots pine appears in mesic and mountainous areas due to its relatively high water requirements (Richardson, 1998), whereas black pine dominates in Circum-Mediterranean mountainous areas and it is more drought tolerant than the Scots pine (Sánchez-Salguero et al., 2012).

2.2. Climatic data

To characterize the climatic conditions of the two study sites we used the Climatic Atlas of the Iberian Peninsula containing mean data for the 1951–1999 period (Ninyerola et al., 2005). Climatic characteristics at the different elevations at Buenafuente del Sistal site were also described by recording meteorological data *in situ* between 2007 and 2009 using three HOBO weather stations (model H21-001; Onset Computer Corporation, USA) (Table 1).

Monthly mean temperatures and total precipitation for the whole study area from 1951 to 2010 were obtained from the nearby Molina de Aragón meteorological station located at 28 km from the study sites (40°50′40″N, 1°53′07″W, 1063 m a.s.l., Spanish National Meteorological Agency, AEMET). Mean and total annual precipitations were calculated for the whole available period from August of the previous year (year $t-1$) to September of the

Table 1

Description of the two study sites. Mean annual temperature and total annual precipitation for the period 1951–1999 were obtained from the Climatic Digital Atlas of the Iberian Peninsula (Ninyerola et al., 2005) and local records were obtained with three HOBO climatic stations (data are 3-year averages ± SD). Number of sampled asymptomatic or living (A) and dead pines (D) per site (No. trees), number of measured radii (No. radii), mean age per group estimated at breast height (± SD), series intercorrelation (Int.) mean sensitivity (MS) and DBH (mean ± SD) for the common period 1950–2007 are also shown.

Site (Lat. N, Long. W)	Species	Elevation (m a.s.l.)	Mean annual temperature (°C)		Annual precipitation (mm)		Tree status	No. trees	No. radii	Age (years)	Int.	MS	DBH (cm)
			Atlas	HOBO	Atlas	HOBO							
Peñalén (40°39′46″, 02°07′13″)	Scots pine	1250–1381	10.0	–	725	–	A	27	54	105 ± 38	0.535	0.251	39.56 ± 12.14
							D	25	48	100 ± 46	0.455	0.273	39.78 ± 12.13
Buenafuente del Sistal (40°48′56″, 02°12′41″)	Black pine	1100	11.0	10.6 ± 1.2	678	505.8 ± 26.1	A	14	26	139 ± 29	0.832	0.631	26.52 ± 4.98
							D	14	26	144 ± 16	0.705	0.586	25.54 ± 4.70
		1000	12.0	11.4 ± 1.2	588	484.1 ± 26.5	A	14	28	130 ± 28	0.778	0.498	26.19 ± 6.65
							D	15	30	129 ± 48	0.695	0.559	25.02 ± 6.63
		900	12.0	11.2 ± 1.0	671	455.5 ± 20.6	A	15	30	122 ± 43	0.761	0.448	26.01 ± 5.89
							D	11	18	134 ± 40	0.699	0.627	22.78 ± 5.89

current year when the tree-ring is formed (year *t*), since this is the approximated period relevant for pine growth in the study area (Richter et al., 1991; Camarero et al., 2010).

2.3. Tree sampling and growth measurements

We used dendrochronology to quantify radial growth (Fritts, 2001). Standing dead trees without external signs of perturbation (burned bark, stems presenting fire scars, broken branches, etc.) were chosen along transects located perpendicular to the slope, recording their diameter at breast height (DBH) measured at 1.3 m. Tree density was estimated to characterize each transect, counting the number of trees in plots of 100 m² per site. Wood samples were collected between spring and autumn of 2010 at Peñalén for Scots pine (1250–1381 m a.s.l., Table 1) and at Buenafuente del Sistal for black pine stands located at high, mid and low elevations (1100, 1000 and 900 m a.s.l., respectively). Trees were bored at breast height (1.3 m) with a Pressler increment borer, obtaining two radial cores per individual. We also cored living or asymptomatic trees located near each sampled dead tree and showing a similar DBH. Samples were visually cross-dated and tree ring-width was measured with a LINTAB semiautomatic device with a 0.01 mm resolution and registered through the use of the software TSAPWIN (Rinn, 2003). Visual cross-dating was statistically checked using the software COFECHA (Holmes, 1983). Measurements of the two cores per tree were averaged to obtain individual tree growth series. The year of death of each tree was considered as the year when the last ring was formed in both cores. Because sometimes trees can keep alive without forming new rings for several years (Bigler et al., 2007), these estimations must be held with caution when only two cores per tree are measured. To estimate tree age at 1.3 m when samples did not include the pith we used a geometric method based on the curvature of the innermost tree ring to estimate the number of missing rings up to the theoretical pith (Duncan, 1989). For each site or tree species, we calculated the series average mean sensitivity, which quantifies the relative variability in ring-width of consecutive years, and the series intercorrelation.

Two different methods were used to analyze growth data: (1) we obtained ring-width indices to characterize the relationships between tree growth and monthly climatic variables; and (2) we calculated basal area increment (BAI) to analyze the associations between growth, annual climatic trends and tree features (DBH, status –asymptomatic vs. dead tree). On the one hand, we used the ARSTAN software (Cook and Holmes, 1996) to standardize and detrend tree-ring width data by using a double detrending procedure (first adjustment to a negative exponential curve, then adjustment to a 60-year frequency polynomial spline) so as to retain high-frequency growth variability. We also removed part

of the first-order autocorrelation to obtain residual chronologies of tree-ring width indices. On the other hand, BAI was calculated from raw tree-ring widths as the difference between consecutive cross-sectional basal areas to obtain a biologically meaningful variable showing growth trends irrespective of tree age and size (Biondi and Qeadan, 2008). Mean group chronologies (that is, for asymptomatic and dead individuals of each species, also considering the three elevations for black pine) were obtained by averaging individual tree values.

2.4. Statistical analyses

Linear regressions were used to quantify climatic trends in mean annual temperature and accumulated precipitation from 1970 to 2010.

We used linear mixed-effects models (Pinheiro et al., 2015) to analyze the relationships between tree growth (normalized logarithm of BAI values from each tree for the 1952–2010 period) and the fixed factors DBH, tree status –asymptomatic or dead–, annual mean temperature and total precipitation calculated from previous August to current September. We also included as fixed factors the interactions between climatic variables and tree status and, in the case of black pine, elevation and the first-order interactions between elevation, tree status and climatic variables. Besides, we performed a model studying the two species together. In this model, we considered as fixed factor the species and its interactions with the tree status, elevation, annual mean temperature and total precipitation, additionally to all the variables and interactions cited before. Tree identity, the year of each tree ring formation and the combination of year nested in tree identity were considered random components of the models.

Candidate models were adjusted by the Maximum Likelihood method (ML). We selected the best model by choosing the best random component structure first, and then selecting the best fixed-factor structure by minimizing the Akaike Information Criterion (AIC), following the criteria proposed by Zuur et al. (2009). Finally, we adjusted the best model by the restricted maximum likelihood method (REML). For the black pine model, residuals failed the homoscedasticity assumption. To solve this problem we applied a correction by including different functions to specify the variance structure of the residuals according to the DBH and elevation (Zuur et al., 2009). Percentage of variance explained by fixed and random effects of the best model was obtained according to Nakagawa and Schielzeth (2013). These analyses were performed using the *nlme* (Pinheiro et al., 2015) and *MuMIn* (Barton, 2015) packages in the R statistical environment ver. 3.0.0 (R Core Team, 2015).

To analyze the relationships between tree growth and monthly climatic variables, we calculated Pearson correlations between the

residual chronology index of each group (species and tree status, i. e. asymptomatic and dead trees) and mean monthly temperatures and total monthly precipitations from previous August (year $t − 1$) to September of the year of ring formation (t). We split the data in two sub-periods (1952–1978 and 1979–2005) to analyze separately changes in the relationships between growth indices and climate over time. We chose these two sub-periods due to the observed climate evolution, following the methodology and results of a previous study performed in the area (García-Cervigón et al., 2012), and to have similar-length periods. Years after 2005 were discarded due to the small number of dead trees reaching this date. Stepwise linear regressions were also calculated to detect significant correlations but avoiding the temporal autocorrelation between months. Changes in significant growth responses to monthly climatic variables between the two studied periods were checked by means of paired t-Student tests. These analyses were run with the software SPSS 18.0 (PASW Statistics for Windows, Inc., USA).

3. Results

3.1. Climate, growth trends and death events

The Scots pine study site was more humid and had lower mean temperature than any of the black pine sites. Precipitation increased with elevation in black pine sites (Table 1), and temperature was lower at the high-elevation site as compared with the other two sites. Annual average temperature increased progressively from 1970 to 2010, rising 0.4 °C per decade ($r = 0.70$, $P < 0.001$), but precipitations did not show a clear linear trend ($r = 0.30$, $P = 0.053$) (Fig. 1a). Tree density at the Scots pine site was 700 tree/ha, while for black pines density was 2000, 2500 and 1800 tree/ha at the high, mid and low elevation sites respectively.

Mean sensitivity and intercorrelation values were higher in black pine than in Scots pine chronologies (Table 1) and for dead than for asymptomatic living trees, except in the case of black pines at the high elevation site, where mean sensitivity was higher in asymptomatic trees. Basal area increment (BAI) of black pines was lower (2.53 cm^2) and more variable (CV, coefficient of variation = 43.7%) than BAI of Scots pine (9.23 cm^2, CV = 24.3%) considering the common period 1950–2005 (Fig. 1b–e). Black pine showed a progressive growth decline since the 1970s, which was more evident and sharper in recently dead trees and at the highest elevation. Moreover, black pines showed a high frequency of missing rings (1.8% and 3.5% for asymptomatic and dead trees, respectively) compared with Scots pine, which did not present missing rings. The dead black pines located at the low elevation site had higher growth rates in wet years with favorable climatic conditions than asymptomatic trees until the mid 1930s (data not shown). In
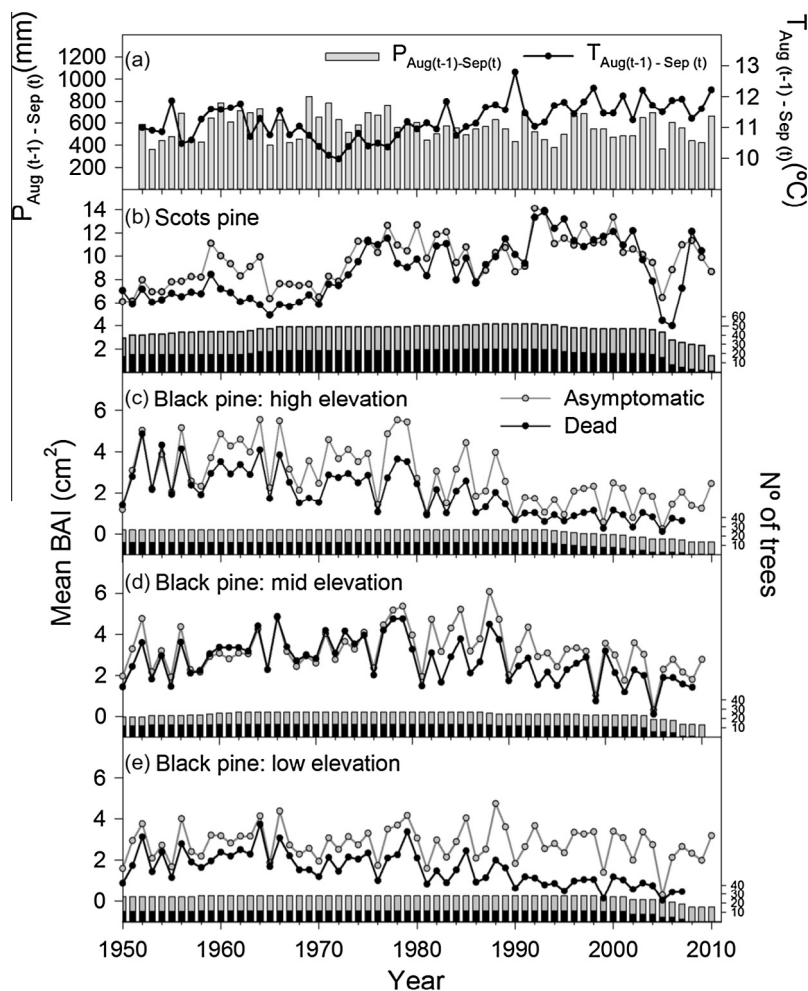

Fig. 1. Temporal evolution of mean basal area increment (BAI, lines) as related to mean temperatures ($T_{Aug(t−1)–Sep(t)}$) and total precipitation ($P_{Aug(t−1)–Sep(t)}$) from August of the previous year to September of the current year (a) in Scots pine (P. sylvestris) (b), and black pine (P. nigra) trees growing in the high (c), mid (d) and low (e) elevation sites. The right y-axes show the number of measured trees (black bars, dead trees; gray bars, living trees) for the period 1950–2010.

Table 2
Statistics obtained for the linear mixed-effects models of basal area increment (BAI) for Scots pine and black pine considering the 1952–2010 period. Only the fixed factors included in the most parsimonious model selected by minimizing the Akaike Information Criterion are shown. Abbreviations: SE: standard error; DF: degrees of freedom; DBH: diameter at breast height; TS: tree status (dead vs. asymptomatic or living trees); E_m: mid elevation; E_l: lower elevation; $T_{Aug(t-1)-Sep(t)}$: mean temperature from August of the previous year to September of the current year; $P_{Aug(t-1)-Sep(t)}$: total precipitation from August of the previous year to September of the current year. The reference level for the categorical factor *elevation* is the high elevation site. For *Tree status*, reference level is dead.

Species	Factor	Estimate	SE	DF	t	P
Scots pine	(Intercept)	0.1083	0.11053	2753	0.0917	0.331
	DBH	0.0137	0.00206	54	6.551	<0.001
	$T_{Aug(t-1)-Sep(t)}$	0.0256	0.00626	2753	4.083	<0.001
Black pine	(Intercept)	3.2226	0.25024	4272	12.878	<0.001
	DBH	0.0222	0.00227	74	9.810	<0.001
	$T_{Aug(t-1)-Sep(t)}$	−0.3272	0.02157	4272	−15.167	<0.001
	$P_{Aug(t-1)-Sep(t)}$	−0.0036	0.00038	4272	−9.486	<0.001
	TS	−0.3438	0.09210	74	−3.733	<0.001
	E_m	−0.2218	0.12933	74	−1.715	0.091
	E_l	−0.6128	0.11808	74	−5.189	<0.001
	$T_{(t-1)-Sep(t)} \times P_{Aug-Sep}$	0.0004	0.00003	4272	10.871	<0.001
	$T_{(t-1)-Sep(t)} \times TS$	0.0366	0.00788	4272	4.646	<0.001
	$T_{(t-1)-Sep(t)} \times E_m$	0.0330	0.01044	4272	3.162	0.002
	$T_{A(t-1)-Sep(t)} \times E_l$	0.0668	0.00945	4272	7.068	<0.001
	$P_{(t-1)-Sep(t)} \times E_m$	−0.0001	0.00005	4272	−2.747	0.006
	$P_{(t-1)-Sep(t)} \times E_l$	−0.0002	0.00005	4272	−4.173	<0.001

Note: The random effect that explained the highest variability in both models was the identity of each tree. The standard deviation of the random effect was 0.182 (residual: 0.191) for Scots pine and 0.110 (residual: 0.111) for black pine.

the same period, asymptomatic living Scots pines also presented lower but rapidly increasing BAI values (from 2 to 6 cm²) as compared with dead trees, while dead trees maintained more constant rates. During the 1960s, asymptomatic Scots pine individuals had slightly higher growth rates than conspecific dead trees, but BAI values of both groups were similar for the rest of the study period.

The lowest BAI values were recorded in 2005 for both pine species (Fig. 1b–e). Most of the mortality events in black pine were found in 2005 and 2008, when 61.54% of the sampled trees died, whereas Scots pine mortality was more uniformly distributed through time, with the strongest mortality event occurring in 2006 (20% of sampled trees).

3.2. Factors affecting growth

The best-fitted (most parsimonious) growth model in Scots pine (Table 2) showed a significant positive effect of DBH and the annual mean temperature on BAI (Fig. 2). The percentage of variance explained by fixed and random effects was 28.96% and 33.78%, respectively (62.74% in total). In this species, we did not find significant differences in the predictors of BAI between dead and asymptomatic living trees.

In black pine, the best-fitted model included all fixed factors (DBH, mean temperature, precipitation, tree status and elevation), as well as the first-order interactions between them, except the interaction between tree status and precipitation (Table 2). The percentage of variance explained by fixed and random effects was 63.43% and 23.64%, respectively (97.07% in total). In this species, BAI was predicted to decrease with rising temperatures (Fig. 2), especially in the case of recently dead trees. The interaction between temperature and precipitation on BAI indicated minimum growth with air temperatures above 12 °C when precipitation was lower than 500 mm, but maximum BAI values occurred when annual precipitation was higher than 700 mm (Fig. 3). Growth peaked at the mid-elevation site, and was enhanced by climatic
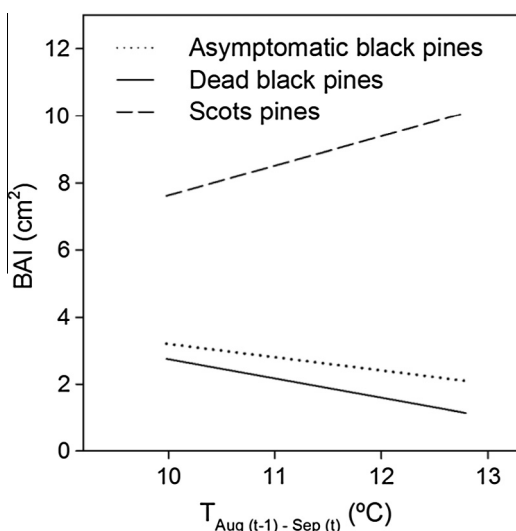
Fig. 2. Regression lines showing the relationships between basal area increment (BAI) and the mean temperature from August of the previous year to September of the current year ($T_{Aug(t-1)-Sep(t)}$) for the dead and asymptomatic or living black pine (*P. nigra*) trees, and for all Scots pine (*P. sylvestris*) trees.
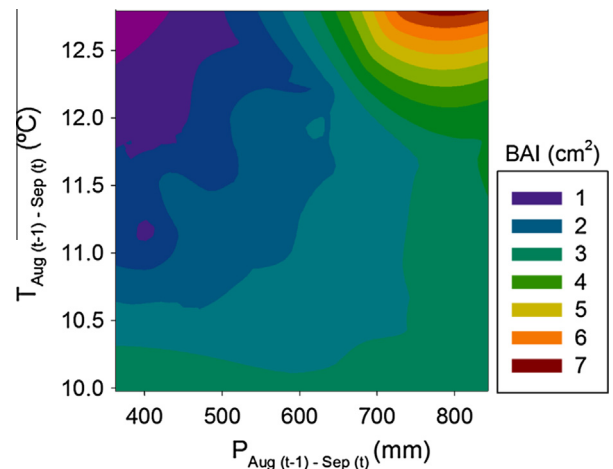
Fig. 3. Predicted effects of the interaction between mean temperature ($T_{Aug(t-1)-Sep(t)}$) and the total amount of precipitation ($P_{Aug(t-1)-Sep(t)}$) from August of the previous year to September of the current year on the basal area increment (BAI) of black pine (*P. nigra*) trees. For simplicity, the figure legend shows color variation every 1 cm² of BAI change, but note that colors vary every 0.5 cm² in the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
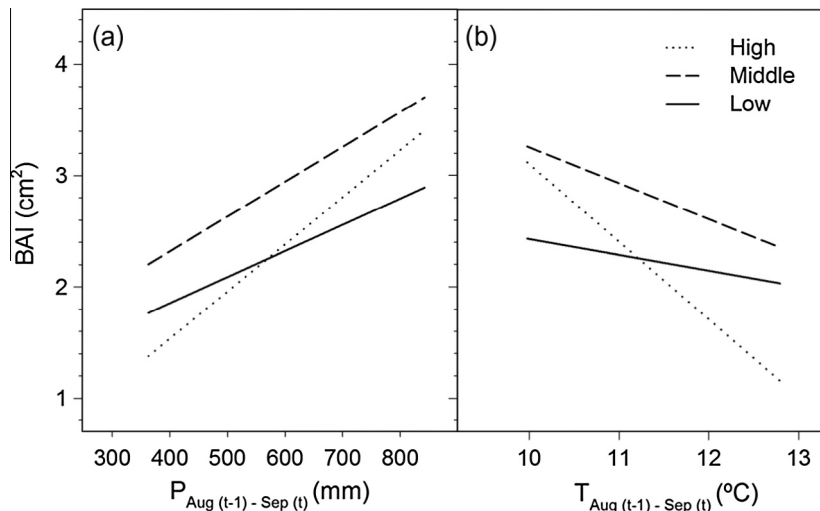
Fig. 4. Variation of the basal area increment (BAI) of black pine (*P. nigra*) individuals growing at three different elevations, according to (a) the total amount of precipitation ($P_{Aug(t-1)-Sep(t)}$); and (b) the mean temperature ($T_{Aug(t-1)-Sep(t)}$) from August of the previous year to September of the current year.

conditions characterized by high precipitation and mild temperatures (Fig. 4). Black pine individuals growing at the high-elevation site were predicted to present higher BAI values than those growing at the low-elevation site when precipitation was abundant or average temperature was mild. However, BAI in the high-elevation site was predicted to decrease more rapidly when temperatures were high or precipitation scarce, suggesting a more sensitive behavior of trees to both climatic variables there than at lower elevations.

The model that considered the two species together (see Appendix 2) showed that there are significant differences between the growth responses of both species. These results are similar to the obtained in the models performed for each species: while BAI of scots pine responded positively to increasing temperatures and slightly negatively to precipitation, black pine responded in the opposite direction in both cases. The secondary growth of both species responded positively to DHB, but this response was stronger in the case of the Scots pine.

3.3. Climate–growth relationships

Climatic response of secondary growth was similar in dead and asymptomatic trees of both species. Significant negative correlations were found between ring-width indices of dead and asymptomatic Scots pine trees and June temperatures for the 1979–2005 sub-period (Fig. 5; see also Appendix 3). Asymptomatic trees also showed a significant positive correlation with the previous September precipitation. Dead and asymptomatic black pine trees responded similarly to precipitation, showing significant positive correlations between ring-width indices and January and May rainfall.

Dead Scots pines presented significant positive correlations between ring-width indices and August precipitation during the 1952–1978 sub-period (see Appendix 3), whilst black pine grew more under mild winters (positive correlation with December temperatures) and high precipitation in the previous October and the current spring (May and June). The asymptomatic black pine trees presented also significant positive growth correlations with precipitation of the previous November.

We found significant changes between the two sub-periods (1952–1978 and 1976–2005) in the calculated climate–growth correlations (see Appendix 4). The negative correlations of Scots pine ring-width indices and June temperatures intensified, going

from −0.11 to −0.49 for the asymptomatic trees and from −0.10 to −0.47 for the dead trees. Besides, the positive correlation found between ring-width indices of asymptomatic black pines and May precipitation also increased from 0.37 to 0.54, whilst dead trees of this species had only a marginally significant increase from 0.40 to 0.57. The correlation between ring-width indices of asymptomatic black pines and January precipitations also increased from 0.20 to 0.35. There was a decrease in the association between June precipitation and the ring-width indices of black pines regardless their status, being significantly positive in the first sub-period (1952–1978) but becoming non-significant in the second sub-period (1979–2005). Similarly, the correlation observed in black pine between ring-width indices and previous October precipitation decreased from 0.32 to 0.07 and from 0.36 to 0.05 in asymptomatic and dead trees, respectively.

4. Discussion

Regional climate warming intensified since the 1970s in the study area and differentially affected death processes and growth patterns of Scots pine and black pine. Mortality events peaked between 2005 and 2008, when severely dry and very warm conditions prevailed and growth rates (BAI) reached minimum values. Rising temperatures enhanced growth of Scots pine growing in a mesic site with enough water availability. However, warmer conditions amplified drought stress and negatively drove growth in black pine, particularly in the case of dead trees and in the driest mid- and low-elevation sites. Therefore, warmer and drier conditions differentially affect the dynamics of pine species in Mediterranean forests, with their responses being also dependent on local site conditions such as topography (slope, aspect and steepness) and soil depth.

4.1. Species-specific sensitivity to climatic stress

The study pine populations showed growth trends over the last decades that were idiosyncratic for each species, pointing to a more vigorous status of the Scots pine high-elevation population. In fact, black pines frequently exhibited missing rings during the driest years such as 1994–1995, 1999, 2005 and 2008. The higher intercorrelation and mean sensitivity of black pine series also supports these findings, as trees with increased year-to-year variability in growth are considered to be more sensitive to drought and
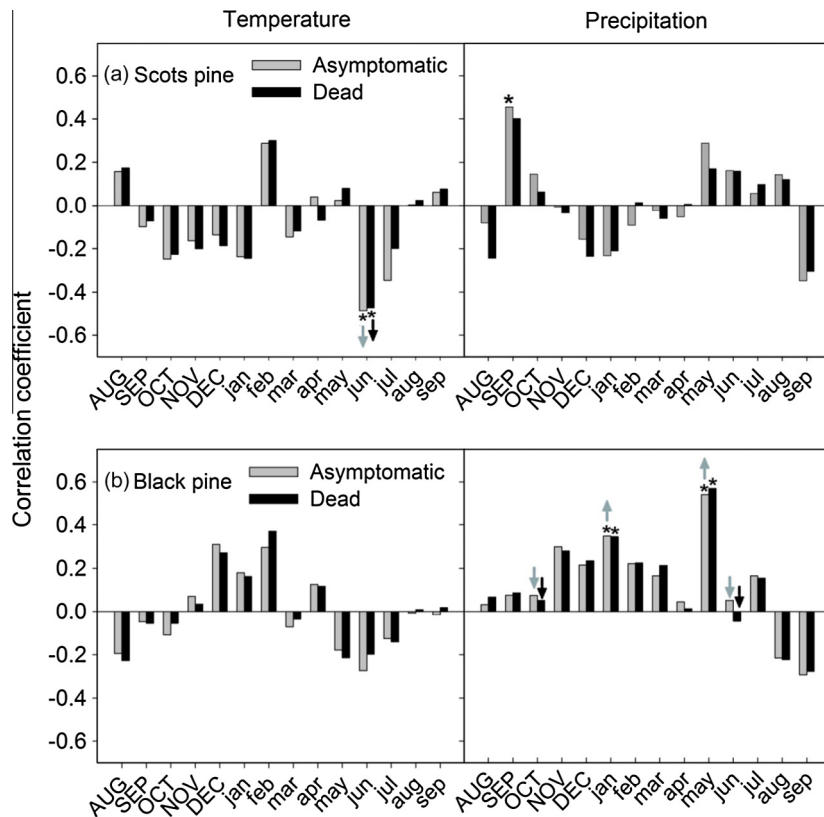
Fig. 5. Correlations obtained by relating ring-width indices of (a) Scots pine (*P. sylvestris*) and (b) black pine (*P. nigra*) trees and the monthly mean temperature and total precipitation considering the 1979–2005 period. Months in uppercase letters correspond to the previous year ($t - 1$), while those in lowercase letters correspond to the current year of tree-ring formation (t). Significant coefficients ($P < 0.05$) of multiple regression analyses are indicated with asterisks. Upward and downward arrows indicate significant increases and decreases, respectively ($P < 0.05$, Student *t*-test), of the correlation between the two compared sub-periods (1952–1978 *vs.* 1979–2005).

prone to die (Ogle et al., 2000; Macalady and Bugmann, 2014). Scots pine presented higher BAI values, and its growth responded positively to warmer temperatures in late winter. This positive effect of temperature could be related to an earlier onset of xylogenesis that promoted the existence of a longer growth period and the formation of wider rings (Rossi et al., 2008). These results indicate a reduced sensitivity of this Scots pine population to precipitation despite this species being considered as very sensitive to water shortage in warmer conditions (Sánchez-Salguero et al., 2012, 2015a), particularly near its southernmost distribution limit.

Differences found in growth patterns between both species were largely driven by environmental local conditions due to the contrasting elevations of their corresponding populations. This could also explain the different growth patterns found here with respect to those previously described by Granda et al. (2013) for black pine in nearby locations. Our research confirms that local climatic conditions are very important regarding the effects of drought and changing average temperatures on secondary growth (Linares and Tíscar, 2010; Sánchez-Salguero et al., 2015a). The study Scots pine stand dominated a site with slightly cooler and more mesic conditions than the black pine sites, especially considering rainfall during the most favorable seasons to grow, spring and autumn. Moreover, Scots pine tends to dominate in sites with gentle slopes and more developed soils with higher water holding capacity (Carcavilla et al., 2008), which would probably increase soil water availability more than in the case of black pine steeper sites. Tree density was also lower in this site than in the black pine site. Overall, the habitat characteristics of the Scots pine population seemed to be more favorable for tree growth, which could explain why precipitation was not a limiting factor for growth in contrast with black pine

populations. This contrasts with other drought-induced dieback events described for Scots pine in sites subjected to similar climatic conditions which indicate that warming triggered drought stress affecting mainly trees growing in soils with a low water retention capacity (Camarero et al., 2015b).

The effects of elevation on secondary growth of black pine trees could not be clearly detected, probably because the selected gradient was not ample enough or due to the lower sample sizes compared to Scots pine. Nonetheless, and contrary to our expectations, we observed a higher sensitivity to climate in trees from the high-elevation site, where growth was the lowest and showed a more pronounced decline during the last three decades. This is likely a consequence of the presence of less developed soils and steeper slopes at the high elevation site (personal observation), which in some cases may drive growth more strongly than climatic conditions (Oberhuber et al., 1998). That could explain the differences with the results found by Sánchez-Salguero et al. (2012) in southern Spain, where they described increased growth for black pine and Scots pine with increasing elevation, as climatic conditions were wetter and colder upwards. Although competition modulates long-term growth responses to drought (Sánchez-Salguero et al., 2015b), tree density was similar in all elevations of the black pine site. Thus, we consider improbable that competition is playing an important role on the clime sensitivity differences found between the elevation sites. Besides, Granda et al. (2013) studied growth trends in different species, including black pine, in nearby locations, and found no significant influence of competition on growth.

Our results for the black pine showed that when precipitation was not limiting, higher temperatures favored growth, similarly to what other studies observed with this species in other Iberian

locations (Linares and Tíscar, 2010; Navarro-Cerrillo et al., 2014). However, when precipitation was scarce, temperatures affected growth negatively due to the increased drought stress during the growing season. These results support the idea that in Mediterranean areas tree growth is mainly limited by precipitation during or before the growing season in xeric areas, while in continental areas long winter and cold spring temperatures can also constrain growth by delaying the start of the growing season (Pasho et al., 2011).

4.2. Temporal changes in climate–growth relationships

The relationships observed between growth and monthly climatic variables differed between the two sub-periods considered. The growth dependency on climatic variables during the growing season increased for both species (June temperature for Scots pine and May precipitation for black pine), and this was probably linked to the temperature rise occurred since the late 1970s. Previous studies have shown an increasing correlation between growth and spring precipitations from the 1970s onwards for several Iberian conifers (Bogino and Bravo, 2008; García-Cervigón et al., 2012), as well as an increase of the drought stress, which limits tree growth (Macias et al., 2006; Andreu et al., 2007). These patterns are especially worrisome for our study populations, since the average temperature rise in the study area has not been uniform throughout the year, but higher relative increments have occurred in spring and summer (Granda et al., 2013). Warmer conditions starting in the 1980s were more intense in those months when Mediterranean pines have their maximum cambial activity, *i.e.* between April and June (Camarero et al., 2010). This warming trend might be thus exacerbating the negative effects of climate on tree growth and vigor through increasing evapotranspiration rates (Azorin-Molina et al., 2015) and trigger tipping-points in forest vitality (Camarero et al., 2015b).

Although we did not find significant differences between the radial growth of dead and asymptomatic Scots pine trees since the 1950s, the group of dead trees apparently had more vigorous growth prior to the 1940s than the group of asymptomatic living trees (data not shown). Camarero et al. (2012) found similar results when comparing European silver fir (*Abies alba* Mill.) trees with different degrees of drought-induced crown defoliation in the Pyrenees. Their results suggest that trees showing higher radial growth under better climatic conditions tend to show lower response capacity to face drought events and may be more prone to die. This may be a consequence of lower investment in root growth and/or greater crown development during the mild period, which would be unfavorable under severe water deficits (Delucia et al., 2000).

The increasing growth dependency on climatic variables was translated into a progressive decline of BAI in black pine, as described for other species sensitive to drought for the same period (Linares et al., 2009; Gea-Izquierdo et al., 2014). Less favorable climatic conditions produce a loss of vigor on individuals, and thus an increased vulnerability to drought events and other stress factors such as pests (Bigler et al., 2007). Nevertheless, the effect of climatic variables on growth trends is not similar for all Mediterranean conifer species. The Spanish juniper, a more drought tolerant species, has experienced an increase in secondary growth (Camarero et al., 2010; Granda et al., 2013) probably due not only to the rise in temperature, but also to a possible fertilization effect due to the increment in atmospheric CO_2 concentrations (Martínez-Vilalta et al., 2008).

4.3. Tree mortality patterns: abrupt or gradual?

Mortality patterns differed between the study species, being more gradual in black pine and more abrupt in Scots pine. The average age of dead and asymptomatic living trees was similar in both cases, suggesting that differences in growth or mortality patterns were not a consequence of the natural age-related decline process. Black pine dead trees suffered a more drastic previous decline in BAI than asymptomatic trees, which is consistent with a death process induced by negative environmental factors acting at long-term scales (*e.g.* aridification) and/or by the effect of repeated drought events over time (Bigler et al., 2006; Linares and Tíscar, 2010; Hereş et al., 2012). Lower radial growth in a given year implies lower water transport capacity, and thus less potential to growth and to synthesize carbohydrates the next growing season (Tyree and Sperry, 1988). In turn, this may affect the vigor and capacity of trees to respond to drought and heat stress, weakening them and eventually causing their death. Since most black pines died during or after extremely dry and warm years (*e.g.* 2005, 2008), this could indicate that these drought events might have triggered the mortality of already predisposed individuals (Bigler et al., 2006; Macalady and Bugmann, 2014).

In the case of Scots pine, we did not find significant differences in growth patterns or in the growth responses to temperature of asymptomatic and dead trees. Although no previous weakening was detected, growth of some trees begun to show the negative effects of increasing summer temperatures in the late 1970s, being drastically reduced after a particular dry year like 2005. This extreme drought event triggered tree death in many of the sampled dead trees, which showed therefore a fast response to water shortage and elevated temperatures (see also Guarín and Taylor, 2005; Bigler et al., 2007). Abrupt deaths in pines after intense drought events have been also described by Ogle et al. (2000) and Macalady and Bugmann (2014). This indicates that an isolated but severe drought event may have important and long-lasting consequences on the dynamics of pine forests in drought-prone areas as the study Scots pine population.

5. Conclusions

We detected a clear effect of climate warming from 1950 onwards on growth performance of the study pine populations. Our findings indicate that the survival of individuals of both pine species will be compromised in contrasting ways. In the case of black pine, a progressive and extended reduction of growth since the late 1970s weakened trees and predisposed them to die after dry spells. On the contrary, growth of Scots pine trees was severely reduced after severe droughts, leading to sudden peaks in mortality. Dieback and related mortality events in Mediterranean pine forests would become more frequent if temperatures and drought severity keep increasing as observed in the late 20th century and as predicted for the 21st century. These results warn about possible changes in forest community composition in continental Mediterranean areas under future climatic and land-use scenarios, with the more drought sensitive species (*e.g.* Scots pine) being replaced by those that are more competitive under warmer and arid conditions (*e.g.* Spanish juniper) (Camarero et al., 2010; Granda et al., 2013; Gea-Izquierdo et al., 2014). However, site conditions play a very important role in driving growth patterns and could buffer mortality episodes. Therefore, further research should include mixed pine forests (*e.g.* ecotones) or pine stands growing under different abiotic (*e.g.* climatic gradients) or biotic (*e.g.* competition intensity or forest composition) conditions to characterize other factors than climate that may become more relevant for growth and survival of Mediterranean pine forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.12.038.

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