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Assessing climate–growth relationships under contrasting stands of co-occurring Iberian pines along an altitudinal gradient

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ABSTRACT

Current decreasing precipitation and increasing temperatures, together with the growing likelihood of extreme drought events, may heighten the vulnerability of several tree populations in Mediterranean areas. In this study, we analysed tree-ring-width chronologies of three coexisting pine species (*Pinus nigra* Arn., *Pinus pinaster* L., and *Pinus sylvestris* L.) across an altitudinal gradient in the Cuenca Mountain Range (central-eastern Spain), along with soil conditions and stand structure. We quantified climate–growth relationships between basal area increment indexes and regional mean temperature and precipitation minus potential evapotranspiration (P-PET); drought sensitivity was defined as the percentage of growth reduction during an extreme drought event. Local climatic data spanning the 20th century yielded a warming trend and increasing extreme drought events since the onset of the 1980s. The *P. nigra* populations located at the lower altitudinal border showed the most significant correlation (negative) between mean temperature and declining growth trends. Contrasting to *P. nigra*, the studied *P. pinaster* population, also located at lower elevations, showed the higher correlations (positive) between P-PET and the higher mean growth. Aside from growth–climate relationships our results suggest a major effect of soil conditions and stand structure on tree growth and climate–growth responses. Old *P. nigra* stands showed the lower mean growth, while thinned stands, about 130 years old, located at the core of the elevation range showed positive growth trends resembling a positive relationship with winter-to-spring temperatures and the higher soil organic matter content. *P. nigra* and *P. sylvestris* trees growing on soils with low total nitrogen seem to be more negatively affected by drought than would be expected under a linear elevation-related response.

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1. Introduction

Climate observations at a global scale indicate a general warming trend (IPCC, 2007), though uncertainties remain concerning the responses of coexisting tree species to ongoing climate change (Allen et al., 2010). Although some studies have investigated the potential impacts of such change on drought-prone forests dynamics (Peñuelas et al., 2010), much less attention has been devoted to the long-term growth trends of coexisting tree species under such conditions, which are expected to reveal contrasting drought sensitivity (Orwig and Abrams, 1997; He et al., 2005; Eilmann et al., 2006; Pichler and Oberhuber, 2007; Das et al., 2007). Climate effects on tree growth will likely depend on the specific changes in climatic conditions at the regional scale, tree species' inherent sensitivity,

and their ability to cope with the new conditions (Lindner et al., 2009).

Conifer climate–growth relationships have been investigated mainly in temperate, boreal, and high-altitude species (Antonova et al., 1995; Rossi et al., 2006; Ko Heinrichs et al., 2007; Camarero et al., 2011; Carrer, 2011). In contrast, less is known about secondary growth in conifers from Mediterranean mountain ranges, which are, on one edge, subjected to both water–stress and high elevation-related low temperatures, but also, at lower elevations, to overcome relatively high temperature during the dry summer period (but see De Luis et al. (2007), Martín-Benito et al. (2010, 2011), Sánchez-Salguero et al. (2011), and Linares and Tíscar (2010, 2011)).

Regional climate models predict lower annual mean precipitation for the Mediterranean Basin (Sumner et al., 2003; IPCC, 2007). However, precipitation variability could be of much more importance since extreme events, such as extended droughts, could have far more drastic consequences on tree growth and survival than would gradual changes in the mean climate conditions

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(Loustau et al., 2005; Granier et al., 2007). If extreme droughts in Mediterranean areas become more frequent in the future, forest productivity could diminish, altering species composition (Martínez-Vilalta et al., 2008; Allen et al., 2010).

Different researchers have found either greater or lesser tree growth with rising temperatures (Briffa et al., 1998; Boisvenue and Running, 2006; Adams et al., 2009; Linares and Tíscar, 2011), which alone would benefit some populations or tree species. However, higher temperatures are not expected to exert positive effects in Mediterranean forests due to the soil-water deficits brought about by increasing evapotranspiration rates (Pereira and Chaves, 1995; Sabaté et al., 2002). Indeed, mountain ranges in the Mediterranean Basin may undergo somewhat higher temperature increases compared to the surrounding regions (IPCC, 2007), thereby increasing the vulnerability of the Mediterranean mountain forests to climate change.

Moreover, growth–climate relationships will be mediated by several abiotic and biotic factors, as elevation-related water availability, stand density and age structure, and soil properties. A quantification of radial growth responses to climatic constraints, soil conditions and stand–age structure could improve our understanding of mechanisms allowing the growth and persistence of Mediterranean mountain conifers under a changing climate scenario (Martínez-Vilalta et al., 2008; Linares and Tíscar, 2010). Several studies have shown that tree species had higher water-use efficiency at the lowest and presumably driest sites; however, it also appears that changes in stand density could compensate for changes in water availability (Linares et al., 2010; Martín-Benito et al., 2010). On the other hand, key soil properties such as water holding capacity, organic matter and nutrient content are strongly influenced by stand structure and forest management (Williams et al., 1995; Bastida et al., 2007).

In this work we have examined radial-growth variability, climate–growth relationships and drought sensitivity in three coexisting pine species under contrasting climatic conditions in order to assess the degree to which trees were affected by long-term climate change, either adversely or beneficially, and the extent to which climate–growth relationships and drought sensitivity are modulated by forest age and density and soil properties along an altitudinal gradient. Growth patterns and climate responses have been analysed on *Pinus pinaster* L., *Pinus nigra* Arn. subsp. *salzmannii* Dunal (Franco), and *Pinus sylvestris* L. (*P. pinaster*, *P. nigra*, and *P. sylvestris*, respectively, hereafter), coexisting along an altitudinal gradient. Our specific aims were: (i) to quantify the climate–growth relationship of a widely distributed (*P. nigra*) and two coexisting pine species (*P. pinaster* at lower elevations and *P. sylvestris* at higher elevations) in the Cuenca Mountain Range (central-eastern Spain); and (ii) to quantify the age and size structure, BAI trends, and drought sensitivity of these three species. We hypothesise that, at the higher elevation, both *P. nigra* and *P. sylvestris* trees should exhibit a positive growth trend in response to temperature increase, modulated by their respective densities, while, at the lower elevation, *P. nigra* should show a higher drought sensitivity and drought-induced growth reduction than the better drought-adapted *P. pinaster*.

2. Materials and methods

2.1. Climatic data

Altitudinal trends for mean temperature and total precipitation were obtained from local data of 12 meteorological stations available in the study area (see Appendix, Table S1). These trends are the fit lines from the simple linear regression. The data sets were afterwards combined into a robust and long-term regional climate series, for further climate–growth relationships analysis, using the MET routine from the Dendrochronology Program Library (Holmes, 1992). Mean regional climate series were used for climate–growth analysis instead of local data available from individual weather stations due to the lack of long-term data set for some sites. The annual water budget was calculated from the sum of the monthly differences between precipitation (P) data and potential evapotranspiration (PET) estimated by a modified version of the Thornthwaite method (Willmott et al., 1985). Annual means were based on data from September of one year to August of the next one. Finally, from the regional climate series long-term trends were estimated for the last century (1908–2010). For the temperature estimates, the trends were calculated by means of a simple linear regression between mean temperature and time; for the estimation of trends in drought events, we performed a Spearman rank order correlations on the P-ETP data of the drier locality (AR).

2.2. Study sites and soil physicochemical properties

The study was conducted in the Cuenca Mountain Range (central-eastern Spain) during October and November of 2010. This mountainous area belongs to the Iberian System Mountains, which is composed of numerous haphazard and motley series of mountain ranges, massifs, plateaus and depressions without a definite common lithological composition and overall structure. Cuenca Mountain elevations range from 610 to 1866 m above sea level. *P. nigra* is naturally distributed in this area between 1000 and 1700 m a.s.l. and dominates the forest composition, as nearly pure stands, along this altitudinal range. However, *P. nigra* and *P. pinaster* mixed stands appear at lower elevations (c. 1000–1100 m) while at the upper elevation limit of the study area, *P. nigra* and *P. sylvestris* arrange as mixed stands (c.a. 1400–1700 m). At the edges (both lower and upper) of the altitudinal gradient, *P. nigra* appears as isolated or relict populations that are further fragmented into smaller stands (Lucas-Borja et al., 2010a, 2010b). The main soil types in the region overlie calcium-rich and mainly shallow calcareous bedrock (Soil Survey Staff, 1999), being Lithic haploxeroll to Typical xerorthent the dominant soils of the study area (Lucas-Borja et al., 2011).

Five study areas were selected, based on records from the literature (Lucas-Borja et al., 2010b, 2011) and several extensive field surveys that covered the distribution area of *P. nigra* in the Cuenca Mountain Range: from lower to higher sites, "Arcas del Villar" (AR), "Los Palancares" (PA), "Buenache de la Sierra" (BU), "Las Majadas" (MA) and "Tragacete" (TA). The elevation of the study area ranges from 1100 to 1641 m a.s.l. (see Table 1 for more details of each experimental area). All these forests are naturally regenerated stands which were traditionally managed using the shelterwood method, with a shelter-phase of 20–25 years and a rotation period of 100–125 years.

Due to the different characteristics of the study sites along the Cuenca Mountain Range, we investigated physical and chemical parameters of the soil in each of them. Three soil samples (0–25 cm depth), composed by six sub-samples (total of c. 500 g), were collected in each site. Soil samples were sieved (<2 mm), all debris and plant remains were removed to avoid any influence on the attributes analysed in the laboratory, and the samples were stored at 4 °C until analysed. Analyses were performed according to the following methodologies: pH was measured in a 1/5 (w/v) aqueous solution by means of a Crison mod 2001 pH meter (Crison Instruments S.A., Derio); total organic carbon (TOC) was determined by oxidation with K_2CrO_7 in an acid medium followed by the evaluation of the excess of dichromate with $(NH_4)_2Fe(SO_4)_2$ (Yeomans and Bremmer, 1989); organic-matter content was determined by multiplying the TOC content by 1.728 (Lucas-Borja et al., 2010a) bioavailable phosphorus was determined following the

Table 1
Geographical, topographical, edaphic, and structural characteristics of the study sites along the Cuenca Mountain Range, Spain. Values are means.

Experimental forest[*]	AR	PA	BU	MA	TA
Latitude (N)	39°54′24	40°00′36	40°06′45	40°15′21	40°20′32
Longitude (W)	2°03′57	1°57′36	1°56′11	1°56′53	1°47′22
Elevation (m a.s.l.)	1100	1186	1283	1465	1641
Slope (%)	3	0.5	14.7	6.5	8.4
Aspect	SO	Flat	NE	S	SE
Mean temperature (°C)	10.9	10.4	9.8	9.1	7.5
Total annual precipitation (mm)	735	818	912	1004	1258
pH	7.0	6.8	6.5	6.2	6.8
Organic matter (%)	37.4	69.5	97.7	47.9	65.9
Total organic carbon (%)	4.7	6.2	6.5	7.0	6.9
P (mg kg^{-1})	9.6	27.6	16.8	31.2	43.5
Total N (%)	0.2	0.7	0.4	0.5	0.3
C/N	23.2	12.1	17.0	13.4	27.3
Sand (%)	87.0	70.0	75.5	80.5	67.0
Silt (%)	7.0	8.0	8.0	4.5	12.0
Clay (%)	6.0	22.0	16.5	15.0	21.0
Mean stand dbh (cm)	29	22	24	14	22
Mean stand Height (m)	11	16	14	13	14.5
Stand density (tree ha^{-1})	421	955	622	756	863
Stand basal area (m^2 ha^{-1})	48	75	82	35	37
Number of living regenerated trees (individuals ha^{-1})	0 *P. nigra* 0 *P. pinaster*	253 *P. nigra*	19 *P. nigra*	139 *P. nigra*	27 *P. nigra* 82 *P. silvestrys*

[*] Arcas del Villar (AR), Los Palancares (PA), Buenache de la Sierra (BU), Las Majadas (MA) and Tragacete (TA).

method described by Olsen and Sommers (1982); finally, total N was determined by the Kjeldahl method modified by Bremmer and Mulvaney (1978).

2.3. Stand structure and dendrochronological methods

For the description and quantification of the stand-structure variability along the altitudinal gradient, seven stands with contrasting elevation and species composition were selected (Table 2). Two stands were selected at the lower elevation site, a pure *P. nigra* lower-elevation population and a mixed *P. nigra–P. pinaster* lower-elevation population (ARPn hereafter and ARPp hereafter, respectively). Three pure *P. nigra* stands were sampled in the core of the altitudinal range (PAPn, BUPn, and MAPn, respectively). Finally two stands were considered at the higher-elevation site, a pure *P. nigra* higher-elevation population (TAPn thereafter) and a mixed *P. nigra–P. sylvestris* higher-elevation population (TAPs thereafter).

Within each of the seven stands, two plots (c. 0.13 ha, located around 1 km apart) were sampled in order to characterise stand structure. According to Lucas-Borja (2008) and several extensive field surveys, we can argue that these forests displayed lower

spatial heterogeneity of tree composition and densities, being the plots large enough to capture the range of variability. All the trees with a diameter greater than 3 cm at 1.3 m from the base (diameter at breast height; dbh) were identified, tagged, and mapped, and their diameters were measured (see Fig. S1 at Supplementary material).

Experimental sites and trees were selected in order to find the maximum tree growth response to climate changes and the best signal to noise ratio, respectively (Carrer, 2011). None of the stands selected showed evidence of intense perturbations such as fires or windstorm. Stumps were found in some stands since management by the Public Forest Administration under the shelterwood system is applied over the study area. For the quantification of secondary growth across the altitudinal gradient, wood cores were obtained from 70 trees (10 dominant trees per stand) to build seven tree-ring chronologies. Two-three cores per tree at dbh were extracted with a borer, perpendicular to the terrain slope (Fritts, 1976). Trees with asymmetrical growth and a non-circular bole were avoided.

Cores were sanded and visually cross-dated using the marker year's method and their ring-width series were measured to the nearest 0.001 mm by menas of a stereomicroscope coupled with

Table 2
Growth features for the study sites along the Cuenca Mountain Range, Spain, during the 1921–2010 period.

Site	AR			PA		BU		MA		TA			
Species	*P. pinaster*		*P. nigra*	*P. nigra*		*P. nigra*		*P. nigra*		*P. nigra*		*P. sylvestris*	
dbh (cm)	56.80	b	48.65 a	55.50	b	47.50	a	58.45	b	47.20	a	43.55	a
Age dbh (years)	81.70	a	124.50 b	157.20	c	129.35	b	295.30	d	157.05	c	160.05	c
Mean BAI 1921–1950 (cm^2)	18.17	d	12.32 c	10.00	bc	7.10	ab	5.25	a	8.62	ab	7.14	ab
Mean BAI 1951–1980 (cm^2)	20.70	c	8.48 ab	9.53	b	7.88	ab	4.97	a	9.39	b	5.69	a
Mean BAI 1981–2010 (cm^2)	14.38	d	6.10 ab	8.69	bc	9.78	c	4.65	a	7.65	abc	5.02	a
BAI Trend 1921–1950 (cm^2 year^{-1})	0.48	b	0.03 a	0.01	a	0.00	a	−0.01	a	0.04	a	0.02	a
BAI Trend 1951–1980 (cm^2 year^{-1})	−0.03	a	−0.05 a	−0.02	a	0.04	a	−0.04	a	−0.05	a	0.07	a
BAI Trend 1981–2010 (cm^2 year^{-1})	0.00	a	−0.10 a	−0.08	a	0.17	b	0.00	a	−0.02	a	0.00	a
Mean among trees BAI correlation 1921–1950	0.54	bc	0.40 ab	0.41	ab	0.60	bc	0.27	a	0.68	c	0.66	c
Mean among trees BAI correlation 1951–1980	0.75	b	0.40 a	0.62	b	0.65	b	0.46	a	0.68	b	0.58	ab
Mean among trees BAI correlation 1981–2010	0.63	bc	0.55 abc	0.68	c	0.63	bc	0.37	a	0.60	bc	0.46	ab
Mean within trees BAI variance 1921–2050	54.00	c	28.84 b	11.37	a	7.96	a	3.96	a	9.22	a	5.10	a
Mean within trees BAI variance 1951–1980	49.46	b	13.60 a	10.99	a	13.88	a	5.51	a	9.27	a	3.89	a
Mean within trees BAI variance 1981–2010	37.23	c	9.38 ab	8.55	ab	17.04	b	2.98	a	6.65	ab	2.45	a

Different letters indicate significant differences among stands within 30-year periods, determined by one-way ANOVA ($p < 0.05$); differences among BAI trends were tested by two slopes comparison test ($p < 0.05$). Values are means; $n = 10$.

a LINTAB[TM] 5 RINNTECH® device linked to a computer. Cross-dating quality was checked using COFECHA (Holmes, 1983). Basal area increment (BAI) was calculated from tree-ring width as a more accurate evidence of annual radial growth around the circumference of the tree. Age-related long-term BAI trend and BAI autocorrelation were removed by fitting raw BAI data *versus* cambial tree age (tree age at coring height; see Fig. S3, Supplementary material). Long-term BAI trend was then estimated for the whole dataset by polynomial regression (loess) and weights computed from the Gaussian density function (see Zuur et al., 2007). BAI indexes were obtained as the residual chronology, standardised by individuals mean BAI:

$$\text{BAI index}_{ij} = \frac{\text{observed BAI}_j - \text{predicted BAI}_j}{\text{mean BAI}_i}, \qquad (1)$$

where BAI index$_{ij}$ stands for the value calculated for the year j in the tree i; observed BAI$_j$ is the raw BAI value of the year j in the tree i; predicted BAI$_j$ is the BAI value predicted by polynomial regression (loess) for the year j; and mean BAI$_i$ is the mean BAI of the tree i computed for the entire tree chronology; BAI indexes were tested for age-independence and autocorrelation (see Appendix 1 at Supplementary material).

2.4. Growth statistical analysis and drought sensitivity estimation

Growth trends were calculated on each individual as the linear slope computed between raw (not indexed) BAI and time. Mean within tree BAI variance was calculated as the variance of the annual BAI values (i.e. variance of the BAI for a given tree) for three 30-year periods: 1921–1950, 1951–1980, and 1981–2010; individual variance values were then averaged for each stand. Mean within stand BAI correlation was calculated as the among trees BAI correlation (i.e. covariance of the BAI series among the trees sampled for a given stand) for the same three time periods; peer correlation values were then averaged for each stand. Drought sensitivity was defined as the degree to which tree growth was affected by an extreme drought event (Linares and Tíscar, 2010). Based on climatic results, we selected the three worst extreme drought events (the three lower P-PET values; see Fig. 1) in the second half of the 20th century, separated by at least 10 years. Then, drought sensitivity (DS) was estimated, on each individual, using raw BAI values ($n = 10$ trees per site):

$$\text{DS} = \frac{\text{mean}(\text{BAI}_D + \text{BAI}_{D+1})}{\text{mean}(\text{BAI}_{D-10})}, \qquad (2)$$

where BAI$_D$ is the BAI in the year the drought occurred, BAI$_{D+1}$ is the BAI in the year after the drought occurred, and BAI$_{D-10}$ is the BAI calculated for the 10 years prior to the drought. Thereafter, the degree to which trees were susceptible to adverse effects of climate change (i.e. vulnerability) was discussed as a function of key climate trends and drought sensitivity.

Climate–growth relationships analyses were performed using climate data derived from the regional mean for the period of 1950–2010 (see Appendix, Table S1) and the individual BAI indexes ($n = 10$ trees per site). Pearson's correlation coefficients were estimated on each individual tree BAI indexes by using monthly and seasonal calculations of mean temperature and P-PET for the prior and the current growing year.

Mean values of diameter at breast height (dbh), age at dbh, mean BAI, BAI trend, mean among trees BAI correlation and mean within trees BAI variance, for the three time periods (1921–1950, 1951–1980, 1981–2010), were compared by means of a one-way ANOVA ($n = 10$ trees per site). Since DS was estimated for three drought events within each tree, a repeated-measures ANOVA was used to compare BAI (von Ende, 2001). Because our main interest was to test the site effect and its interaction with stand structure, the between-subject factor was the plot, whereas tree age (at dbh) and tree size (dbh) were considered as covariates. The different drought years were regarded as the within-subject factor. DS values were tested for homogeneity of variance and for the assumption of compound symmetry of the variance-covariance matrix using the Bartlett-Box F-test and the Mauchly criterion, respectively. DS data were log-transformed when necessary to meet homoscedasticity. We used the Greenhouse–Geisser statistic to adjust the F-tests. Paired comparisons were corrected using the Bonferroni adjustment. The one-way and the repeated-measures ANOVA were calculated using R software (R Development Core Team, 2011).

3. Results

3.1. Climatic values and soil characteristics

The altitudinal gradient for mean annual temperature decreased linearly by 0.64 °C for every 100 m of elevation ($y = -0.0064x + 17.99$; $R^2 = 0.74$, $p < 0.001$; $n = 9$, ranging from 945 to 1360 m a.s.l.; see Appendix Table S1). Based in the above relationship, the mean annual temperatures ranged from 7.5 to 10.9 °C at the study sites (Table 1). The annual precipitation in the study area increased with elevation by ~ 97 mm for every 100 m of elevation ($y = 0.9663x - 328.05$; $R^2 = 0.73$, $p < 0.001$; $n = 12$, range to that used for temperature). Annual precipitation ranged from 735 to 1258 mm at the study sites (Table 1) when calculated from the above relationship. The regional mean temperature and drought index (precipitation minus evapotranspiration) for the 1950–2010 period are shown in Fig. 1. Mean annual temperature increased in the study area 2.6 °C from 1901 to 2010 (linear regression; $p < 0.001$), while drought events showed a significant worsening trend toward the end of the 20th century, as estimated by Spearman rank correlation (Spearman $R = -0.26$; $p < 0.05$); seven of the eleven worst drought event found between 1901 and 2010, took place after 1980 (1981, 1983, 1994, 1995, 1999, 2000 and 2005). Drought events registered in 1953, 1995, and 2005 were also selected to test tree drought sensitivity.

Regarding soil characteristics, the highest pH values were found at AR while lowest pH values were registered in the older stands of MA; on the contrary, the highest percentage of organic carbon was found in MA while the lowest percentage was found in AR (Table 1). The organic-matter content was significantly higher in the stand located at the core of the altitudinal range (BU) as compared to the lower and upper populations of the *P. nigra* distribution range. The lowest values of organic matter, total organic C, total N, and bioavailable P content were found at the lower altitudinal edge of the gradient (AR). According to soil texture, the PA site showed the highest clay content while the AR site showed the highest percentage of sandy elements.

3.2. Forest structure and BAI values

Forest structure (based on tree dbh and age and stand density) differed for each study site (Fig. S1 and Table 1). The highest mean stand dbh and, also, the lowest stand density were found in the lower-elevation *P. nigra* stand (AR). The population in the PA stand showed the highest values of mean stand height and density, while the *P. nigra* population located at the core of the elevation range (BU stand) showed the highest basal stand area, which was reduced by logging, as reflected by the relatively high presence of stumps. The lowest stand mean dbh and basal area values were found at the MA site, probably as a result of the presence of young regenerated trees (Table 1). All sampled trees were of similar size
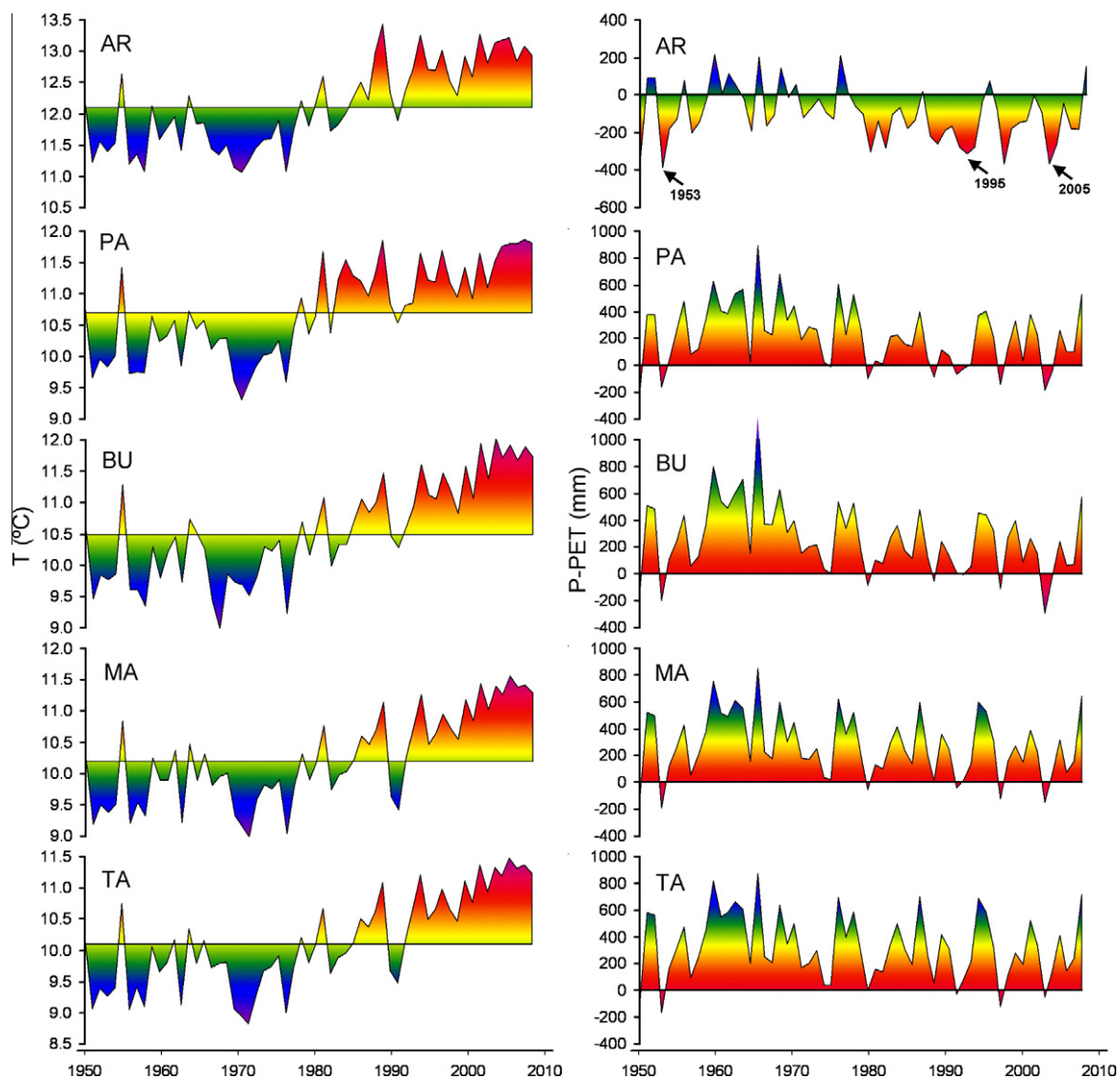
Fig. 1. Regional mean temperature and drought index (precipitation minus evapotranspiration, P-ETP) for the 1950–2010 period in the study sites along the Cuenca Mountain Range, Spain. The arrows indicate the extreme drought events (1953, 1995 and 2005) selected to quantify drought sensitivity.

($\sim$50–60 cm dbh); however, tree age and radial growth showed significant differences ($p < 0.05$) (Table 2). The mean age of the trees sampled in the AR and BU stands was lower than 130 years, whereas trees located at PA, TA, and MA were older than 150 years. In terms of the different species, *P. pinaster* trees (ARPp) were younger than *P. nigra* (PAPn, BUPn, MAPn and TAPn) and *P. sylvestris* trees (TAPs) but greater in diameter and mean BAI. The time span for the chronologies varied from 82 to 295 years; the mean stand age was not significantly correlated with elevation, the youngest trees located at the ARPp and BUPn stands and the oldest ones at the MAPn and TA stands (Fig. 2 and Table 2).

Mean BAI values were significantly higher (ANOVA, $n = 10$, $p < 0.05$) in *P. pinaster* trees than in the other two species during the whole time span (1921–2010). On average, lower mean BAI values were found in the populations located at higher elevations; however, the lower-elevation *P. nigra* population (ARPn) yielded a distinct growth decline, from c. 12 cm^2 year^{-1} to c. 6 cm^2 year^{-1} between the 1921–1950 and 1981–2010 spans (Table 2).

Mean growth rate (estimated from BAI trends) for the 1921–1950 period was positive or steady, (i.e. increasing or steady BAI) for all of the seven stands studied (Table 2). The *P. pinaster* popula-

tion showed a significantly ($p < 0.05$) higher growth rate (Table 2). For the 1951–1980 period, all the stands showed a similar steady BAI trend, while for the 1981–2010 period, the population at the BU stand (located at the core of the *P. nigra* distribution range), showed a significantly ($p < 0.05$) higher growth rate (Table 2).

According to the ANOVA analyses (Table 2) the mean among-trees BAI correlation decreased at higher elevations (mainly for *P. sylvestris*) but increased at the lower elevations. The mean within-tree BAI variance was significantly ($p < 0.05$) higher for *P. pinaster* over the entire time span (1921–2010). *P. nigra* and *P. sylvestris*, on average, showed significant ($p < 0.05$) differences (Table 2, Fig. 2).

3.3. Climate–growth relationships. BAI indexes and climate correlations and drought sensitivity

BAI indexes (BAIx) used to estimate climate–growth relationships are shown in Fig. 3. On average, the lower-elevation stands of both *P. pinaster* and *P. nigra* showed the highest positive correlation coefficients between BAIx and P-PET (Fig. 4). P-PET calculated in September and October, prior to the growing season, and May to
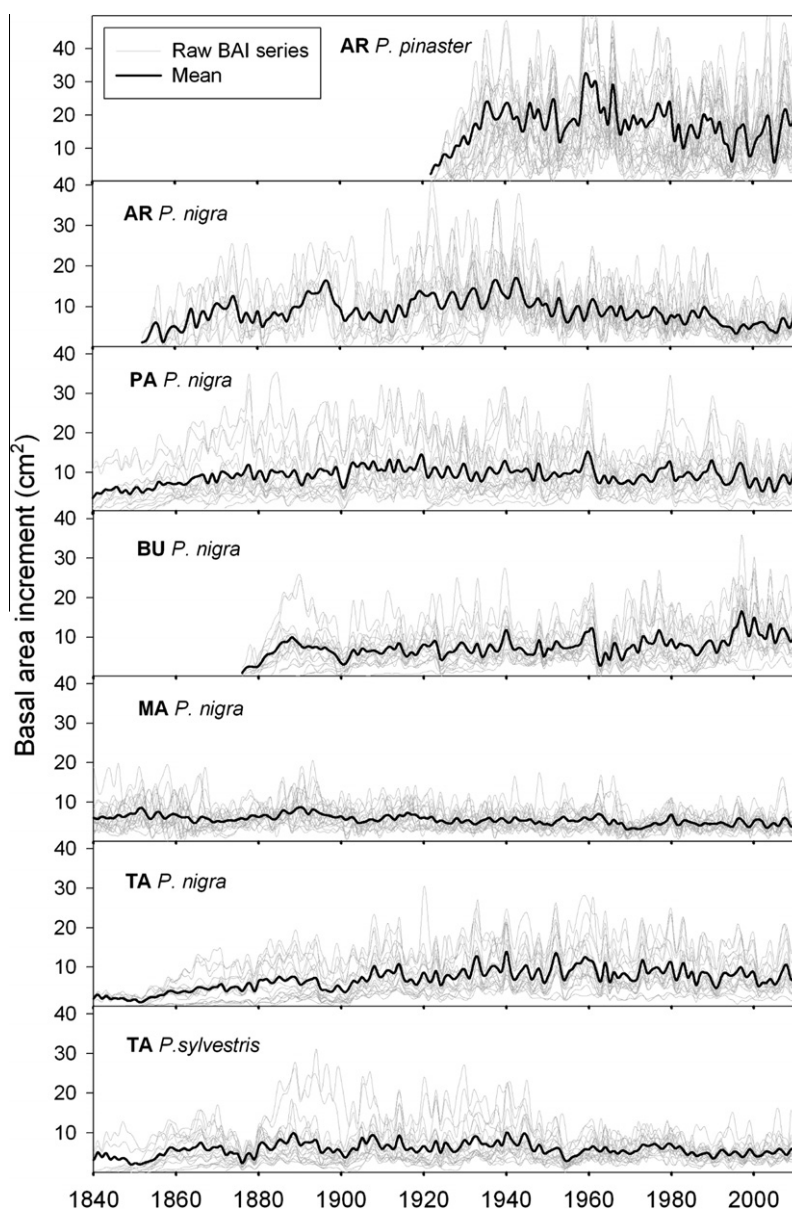
Fig. 2. Individuals raw data of tree basal-area increment (BAI) (narrow lines) and mean values (black line; n = 10 trees) in the study sites along the Cuenca Mountain Range, Spain.

July of the current year were positively correlated to BAIx in all the studied sites; in the case of *P. sylvestris* July P-PET was the only variable showing significant differences (summer P-PET at a seasonal scale). The relationships between BAIx and the monthly (and seasonal) mean temperature were strongly negative for the lower-elevation *P. nigra* stand (ARPn). The following low-elevation stand (PAPn) showed a significant negative correlation with prior and current autumn and summer temperature. On the other hand, the stand located at the core of the altitudinal gradient (BUPn) showed a positive correlation with winter and spring temperature (Fig. 4).

On average, BAI dropped during extreme drought events by around 40% (ranging between 0% and 70%), indicating broad variations in drought sensitivity (DS) among *P. nigra* populations. For the extreme drought event registered in 1953 and 1995, the highest DS was found at the lower and higher elevation limits of the altitudinal gradient studied, respectively. However, during the 2005 drought event, DS decreased with elevation (Fig. 5).

4. Discussion

4.1. Climate and forest growth trends

Our results support a 20th-century warming trend in the study area (2.2 °C during the 20th century; although a milder increase, 1.94 °C, from 1970 to 2010), as well as a higher likelihood of extreme drought events toward the end of the 20th century (as we obtained by Spearman correlation test). This is in agreement with recent climate change models that forecast similar trends towards 2100 (IPCC, 2007). An increase of 3–4 °C (4–5 °C in summer and 2–3 °C in winter) is expected for the mean temperature of Europe towards 2100, while annual rainfall is likely to drop by as much as 20% (reaching 50% for summer precipitation in some Mediterranean regions), whereas winter precipitation is expected to increase (IPCC, 2007).

Moreover, we illustrate that the productivity of Mediterranean-mountains tree species might not be limited by temperature, since
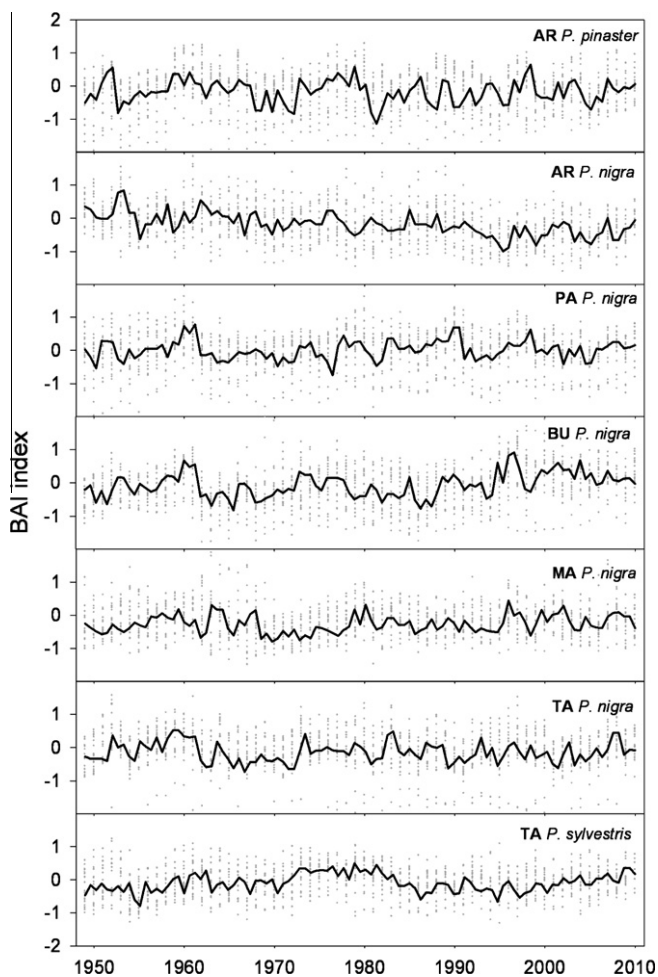
Fig. 3. Individuals BAI indexes (points) and mean BAI index chronology (black line; n = 10 trees) in the study sites along the Cuenca Mountain Range, Spain. BAI indexes were calculated as the residual chronology of BAI data *versus* cambial tree age, standardised by mean tree BAI.

no positive relationships have been found between winter-spring temperatures and BAI indexes at the higher-elevation stand of *P. nigra* or *P. sylvestris* (see also Linares and Tíscar, 2010, 2011; Martínez-Vilalta et al., 2008; Lebourgeois, 2000; Fernández et al., 1996). Increasing temperatures could extend the available growing period (Wullschleger et al., 2002; Boisvenue and Running, 2006); however, a simultaneous decrease in water availability may reduce the length of the trees growing period, due to a drought-induced declining in C uptake (McDowell et al., 2010).

Growth increases could generally be expected in sites hypothetically limited by low temperatures (i.e. forests at higher elevations) as a result of warming (Tardif et al., 2003; Büntgen et al., 2007). However, our results do not support this hypothesis, since, contrasting to our initial hypothesis about a positive effect of temperature increase on tree growth at higher elevations, we have found negative correlation trends between temperature and BAI indexes at the higher-elevation stands, although only significant for prior autumn temperature at higher elevation *P. nigra* stand. However it should also be noted that this higher-elevation stands presented southern aspect (S and SE), which are comparatively hotter and drier than that slopes with a northern aspect, and they showed the higher soil C/N ratio (about 27), which may indicate a lower nitrogen availability than in soils with a lower C/N ratio. The same characteristics of aspect and soil C/N ratio were obtained at the lower elevation *P. nigra* stand (SO aspect and a soil C/N value

around 23), which has been previously associated to a higher drought sensitivity (Bastida et al., 2007).

Temperature was negatively correlated with BAI indexes in *P. nigra* stands at lower elevations. Moreover, a lagging negative correlation with autumn temperatures of the previous year was found in the lower- and higher-elevation *P. nigra* stands. Lower BAI indexes after a warm previous autumn suggest a temperature-induced decrease on carbohydrate accumulation (or increasing respiratory costs) and declining size of the dormant cambium zone, developed during the previous autumn (Richter et al., 1991; Fernández et al., 1996).

At lower elevations, rising temperatures and diminishing rainfall should magnify *P. nigra* drought stress and growth decline. This hypothesis is supported by our results and also by previous short- and long-term studies on temperate mountain conifers (Lebourgeois, 2000; Fernández et al., 1996; Martín-Benito et al., 2011). Significant radial-growth reductions in response to severe droughts have been reported by Eilmann et al. (2006) in *Pinus sylvestris*. Moreover, although secondary growth of *P. sylvestris* has increased during the 20th century in Catalonia (NE Spain), increasing temperatures have already negatively affected drier sites (Martínez-Vilalta et al., 2008). Climate warming and harsher water stress appear to be the main causes of growth decline in *Abies alba* forests near the southern limit of the species distribution (Camarero et al., 2011; Macias et al., 2006) and should also lead to a severe BAI reduction in drought-sensitive Mediterranean conifer as *Abies pinsapo*, *P. nigra* and *Cedrus atlantica* according to dendrochronological studies (Linares et al., 2010; Allen et al., 2010; Martín-Benito et al., 2011; Linares and Tíscar, 2011).

Contrasting to lower-elevation *P. nigra* stands, our results support a positive effect of February–April temperature in the *P. nigra* stand located at the core of the altitudinal gradient (BUPn), which also yielded a higher mean BAI than in the other *P. nigra* stands, as well as the highest soil organic matter content. This BUPn stand was the only sample unit presenting northern aspect (NE) and was also the only stand that showed a significant positive BAI trend, and low drought sensitivity for the three extreme drought events computed.

4.2. Interacting effects of forest soil, stand age and structure on climate–growth relationships

Recent researches performed in the same study area found that soil with low organic matter content yielded the lower soil moisture and reduced biochemical and microbiological activity (Candel et al., 2011). It is well known that soils with higher organic matter content may exhibit higher water availability and nutrients content, affecting tree growth and the activity of soil microorganisms (Bartelt-Ryser et al., 2005). Thus, favourable soil conditions might partially compensate the negative effect of drought on tree growth at the core of the *P. nigra* distribution range in our study area. However, a more detailed sample design should be applied in order to quantify and confirm soil effects.

On the other hand, since the forests from our study area have historically undergone different management intensities, by means of forestry methods such as shelterwood, a strong interaction between stand structure and climate–growth relationships (Martín-Benito et al., 2010) could be expected. Indeed, logged stands at the core of the altitudinal gradient showed positive BAI trends and sudden BAI releases, which are most probably related to 1990s logging (Lucas-Borja, 2008). Notably, this stand showed a substantial number of stumps, suggesting that these populations present a favourable thinning-induced stand structure for *P. nigra* growth (trees about 130 year old and reduced tree-to-tree competition). Thinning generally allows a less constrained growth of the remaining trees by reducing competition (Oliver and Larson, 1996).
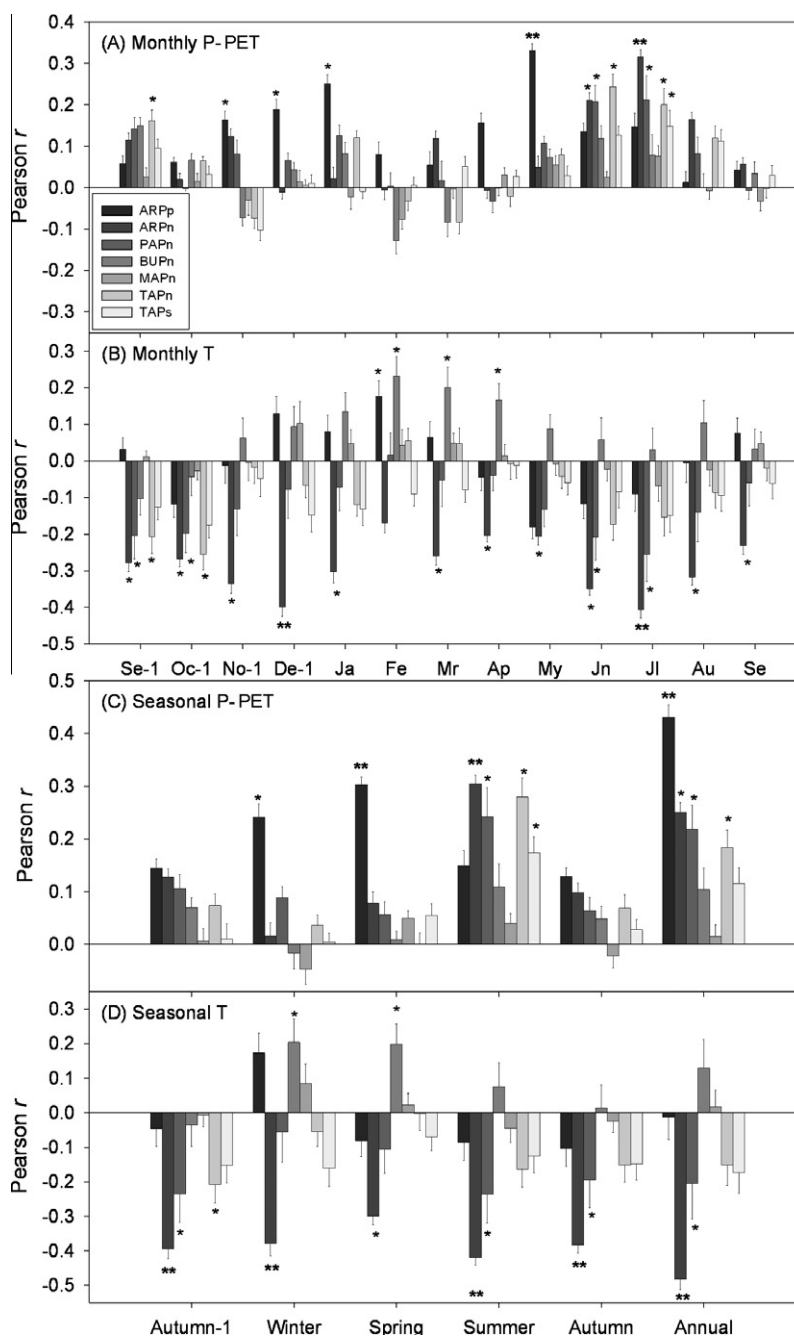
Fig. 4. Pearson correlation coefficients for the relationships between basal area increment (BAI) indexes of *Pinus pinaster* (*Pp*), *Pinus nigra* (*Pn*), and *Pinus sylvestris* (*Ps*), and the monthly difference between precipitation and evapotranspiration (P-PET; 5A), mean monthly temperature (T; 5B), seasonal difference between precipitation and evapotranspiration (5C) and mean seasonal temperature (5D); time span 1950–2010, *n* = 10 trees per site. Climatic variables corresponding to the previous year to tree-ring formation are indicated by (−1). $^*p < 0.05$; $^{**}p < 0.01$.

Thus, the reduction by thinning of intra-specific competition, as evidenced by the presence of stumps, might also be an effective way to reduce the negative effect of drought on Mediterranean mountain dense conifer forests (Linares et al., 2010; Martín-Benito et al., 2010 and references therein).

Substantial differences have been observed between higher and lower elevations. In this way, high-elevation stands of *P. nigra* and *P. sylvestris* (MAPn, TAPn and TAPs), presented uneven aged structures, with a high number of small trees from both species, matching with the older individuals sampled in our study. Contrarily, although *P. pinaster* at low-elevation stands showed the highest growth rates in our study, regeneration was absent. Mean BAI was reduced for *P. nigra* at both higher (where the older trees were found) and lower elevations; however, higher-elevations stands yielded suitable stand regeneration and favourable soil conditions (total organic C, P, and N), while the lower-elevation *P. nigra* stand showed low tree density at the smaller dbh classes (i.e. below 25 cm), declining growth trends and the lowest values of soil organic matter, organic C, P, and N.

Stand age could also play a central role in explaining among-site variance in BAI and climate responses (Linares and Tíscar, 2010; Tíscar, 2002, 2007). Mean BAI was found to be lower in older trees (MAPn), and drought sensitivity seems to be higher than expected for trees growing at higher elevation (Rossi et al., 2006), where the water deficit is significantly lower. These findings could imply age-related changes in endogenous parameters possibly linked to the
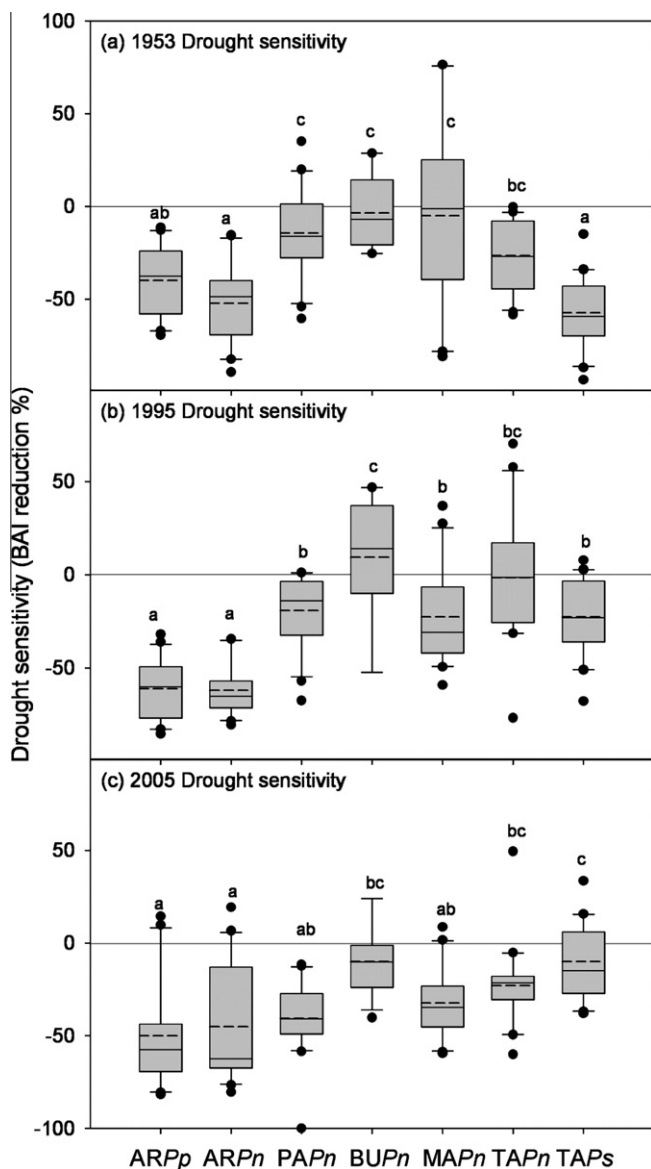
Fig. 5. Drought sensitivity estimated as BAI reduction percentage, related to the mean BAI of the decade prior to the droughts registered in 1953, 1995 and 2005. In the box-plot figure, error bars represent the 5th/95th percentiles; boxes stand for the standard error ($n = 10$ trees per site); solid lines represent the median; dashed lines are the mean values, and points are outliers. Drought sensitivity values below the horizontal line indicate growth reductions (lower BAI) during the drought event, as compared to mean BAI prior to the drought event; values of drought sensitivity above the horizontal line indicate growth increases (higher BAI values), as compared to mean BAI prior to the drought event. Different letters indicate significant differences ($n = 10$ trees), repeated-measures ANOVA, $p < 0.05$.

water status and the tree C balance (Hunt et al., 1999). Such onto-genetic changes affect xylogenesis (Rossi et al., 2008) and alter growth–climate relationships (Carrer and Urbinati, 2004). The increased size and structural complexity of older trees raise maintenance respiration costs and lower the efficiency of the hydraulic pathway, which may explain the lower growth rate, low climate–growth correlations and relatively high drought sensitivity found in old trees (MAPn site; see also Ryan and Yoder, 1997).

5. Conclusions

The growth of *P. nigra* progressively declined as aridity increased at the lower elevation limit of our study area; however, soil condition also appeared as a limiting factor on these stands. The stands having favourable climatic and soil conditions showed lower drought sensitivity and significantly higher growth trends, as these populations showed a positive response to forest management. Temperature-induced stress and sensitivity to extreme drought events appeared to become increasingly limiting as *P. nigra* and *P. sylvestris* became older, whereas diminishing precipitation exerted a greater impact on radial growth in lower-elevation stands. This contrasting climatic sensitivity may be wielding a significant impact on future forest dynamics in Iberian pine forests at a regional scale, since both a warming trend and a precipitation decline have been forecasted for coming decades.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2012.02.010.

References

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality: implications for regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. USA 106, 7063–7066.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684.

Antonova, G.F., Cherkashin, V.P., Stasova, V.V., Varaksina, T.N., 1995. Daily dynamics in xylem cell radial growth of Scots pine (*Pinus sylvestris* L.). Trees-Struct. Funct. 10, 24–30.

Bartelt-Ryser, J., Joshi, J., Schmid, B., Brandl, H., Balser, T., 2005. Soil feedbacks of plant diversity on soil microbial communities and subsequent plant growth. Perspect. Plant Ecol. 7, 27–49.

Bastida, F., Moreno, J.L., Hernández, T., García, C., 2007. The long-term effects of the management of a forest soil on its carbon content, microbial biomass and activity under a semi-arid climate. Appl. Soil. Ecol. 37, 53–62.

Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity-evidence since the middle of the 20th century. Global Change Biol. 12, 1–12.

Bremmer, J.M., Mulvaney, R.L., 1978. Urease activity in soils. In: Burns, R.G. (Ed.), Soil Enzymes. Academic Press, New York, pp. 149–196.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G., Vaganov, E.A., 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391, 678–682.

Büntgen, U., Frank, D.C., Kaczka, R.J., Verstege, A., Zwijackz-Kozica, T., Esper, J., 2007. Growth responses to climate in a multi-species tree-ring network in the Western Carpathian Tatra Mountains, Poland and Slovakia. Tree Physiol. 27, 689–702.

Camarero, J.J., Bigler, C.J., Linares, J.C., Gil-Pelegrín, E., 2011. Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. For. Ecol. Manage. 262, 759–769.

Candel, D., Andrés, M., Bastida, F., López, F.R., Lucas-Borja, M.E., 2011. Soil characteristics in relation to tree stand composition across an altitudinal gradient in Mediterranean mountain areas: establishing forest management strategies. In: Conference Proceedings of the International Symposium of Interactions of Soil Minerals with Organic Components and Microorganisms, 26thJune–1stJuly, Montpellier, France.

Carrer, M., Urbinati, C., 2004. Age-dependent tree ring growth responses to climate of *Larix decidua* and *Pinus cembra* in the Italian Alps. Ecology 85, 730–740.

Carrer, M., 2011. Individualistic and time-varying tree-ring growth to climate sensitivity. PLoS ONE 6 (7), e22813. doi:10.1371/journal.pone.0022813.

Das, A.J., Battles, J.J., Stephenson, N.L., van Mantgem, P.J., 2007. The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. Can. J. For. Res. 37, 580–597.

De Luis, M., Gričar, J., Čufar, K., Raventós, J., 2007. Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. IAWA J. 28, 389–404.

Eilmann, B., Weber, P., Rigling, D., Eckstein, D., 2006. Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. Dendrochronologia 23, 121–132.

Fernández, A., Génova, M., Creus, J., Gutiérrez, E., 1996. Dendroclimatological investigation covering the last 300 years in central Spain. In: Dean, J.S., Meko, D.M., Swetman, T.W. (Eds.), Tree Rings, Environment and Humanity. University of Arizona, Tucson, Radiocarbon, pp. 181–190.

Fritts, H.C., 1976. Tree Rings and Climate. Blackburn Press, Caldwell, New Jersey.

Granier, A., Reichstein, M., Bréda, N., Janssens, I.A., Falge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Köstner, B., Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., Wang, Q., 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agr. Forest Meteorol. 143, 123–145.

He, J.S., Zhang, Q.B., Bazzaz, F.A., 2005. Differential drought responses between saplings and adult trees in four co-occurring species of New England. Trees-Struct. Funct. 19, 442–450.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 68–78.

Holmes, R.L., 1992. Dendrochronology Program Library. Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Hunt, E.R., Lavigne, M.B., Franklin, S.E., 1999. Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model. Ecol. Model. 122, 151–164.

IPCC, 2007. Climate Change, Fourth Assessment Report. Cambridge University Press, London.

Ko Heinrichs, D., Tardif, J.C., Bergeron, Y., 2007. Xylem production in six tree species growing on an island in the boreal forest region of western Quebec, Canada. Can. J. Bot. 85, 518–525.

Lebourgeois, F., 2000. Climatic signals in earlywood, latewood and total ring width of Corsican pine from western France. Ann. For. Sci. 57, 155–164.

Linares, J.C., Camarero, J.J., Carreira, J.A., 2010. Competition modulates the adaptation capacity of forests to climatic stress: Insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. J. Ecol. 98, 592–603.

Linares, J.C., Tíscar, P.A., 2010. Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. Tree Physiol. 30, 795–806.

Linares, J.C., Tíscar, P.A., 2011. Buffered climate change effects in a Mediterranean pine species: range limit implications from a tree-ring study. Oecologia 167, 847–859.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2009. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 162, 73–86.

Loustau, D., Bosc, A., Colin, A., Ogée, J., Davi, H., François, C., Dufrêne, E., Déqué, M., Cloppet, E., Arrouays, D., Le Bas, C., Saby, N., Pignard, G., Hamza, N., Granier, A., Bréda, N., Ciais, P., Viovy, N., Delage, F., 2005. Modelling climate change effects on the potential production of French plains forests at the sub-regional level. Tree Physiol. 25, 813–823.

Lucas-Borja, M.E., 2008. La regeneración de los montes de *Pinus nigra* Arn. en la Serranía de Cuenca. Base de la gestión forestal del Monte de Utilidad Publica n 106, Los Palancares y Agregados (CU). Ph. D. thesis, Universidad de Castilla-La Mancha.

Lucas-Borja, M.E., Bastida, F., Nicolás, C., Moreno, J.L., Del Cerro, A., Andrés, M., 2010a. Influence of forest cover and herbaceous vegetation on the microbiological and biochemical properties of soil under Mediterranean humid climate. Eur. J. Soil Biol. 46, 273–279.

Lucas-Borja, M.E., Silva-Santos, P., Fonseca, T.F., Tíscar Oliver, P.A., López-Serrano, F.R., Andrés Abellán, M., Martínez García, E., Del Cerro Barja, A., 2010b. Modelling Spanish black pine postdispersal seed predation in Central-Eastern Spain. Forest Syst. 19 (3), 393–403.

Lucas-Borja, M.E., Fonseca, T., Parresol, B.R., Silva-Santos, P., García-Morote, F.A., Tíscar-Oliver, P.A., 2011. Modelling Spanish black pine seedling emergence. Establishing management strategies for endangered forest areas. For. Ecol. Manage. 262, 195–202.

Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir *Abies alba* (Mill.) water stress in its south-western distribution limit. Clim. Change 79, 289–313.

Martín-Benito, D., Heinrich, I., Helle, G., del Río, M., Cañellas, I., 2010. Response of climate–growth relationships and water use efficieny to thinning in a *Pinus nigra* afforestation. For. Ecol. Manage. 259, 967–975.

Martín-Benito, D., Kint, V., del Río, M., Muys, B., Cañellas, I., 2011. Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: past trends and future perspetives. For. Ecol. Manage. 262, 1030–1040.

Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L., Ninyerola, M., 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. Global Change Biol. 14, 2868–2881.

McDowell, N., Allen, C.D., Marshall, L., 2010. Growth, carbon isotope discrimination, and climate-induced mortality across a *Pinus ponderosa* elevation transect. Global Change Biol. 16, 399–415.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics, update ed. John Wiley, New York.

Olsen, S.R., Sommers, L.E., 1982. Phosphorus. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. American Society of Agronomy, Madison, Wisconsin, pp. 403–427.

Orwig, D.A., Abrams, M.D., 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees-Struct. Funct. 11, 474–484.

Peñuelas, J., Gracia, C., Filella, I., Jump, A., Carnicer, J., Coll, M., Lloret, F., Yuste, J.C., Estiarte, M., Rutishauser, T., Ogaya, R., Llusià, J., Sardans, J., 2010. Introducing the climate change effects on Mediterranean forest ecosystems: observation, experimentation, simulation, and management. Forêt méditerranéenne XXXI, 357–362.

Pereira, J.S., Chaves, M.M., 1995. Plant responses to drought under climate change in mediterranean-type ecosystems. In: Moreno, J.M., Oechel, W.C. (Eds.), Global Change and Mediterranean-Type Ecosystems. Springer, New York, pp. 140–161.

Pichler, P., Oberhuber, W., 2007. Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. For. Ecol. Manage. 242, 688–699.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Richter, K., Eckstein, D., Holmes, R.L., 1991. The dendrochronological signal of pine trees (*Pinus* spp.) in Spain. Tree Ring Bull 51, 1–13.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol. 170, 301–310.

Rossi, S., Deslauriers, A., Anfodillo, T., Carrer, M., 2008. Age-dependent xylogenesis in timberline conifers. New Phytol. 177, 199–208.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. Bioscience 47, 235–242.

Sabaté, S., Gracia, C., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean Region. For. Ecol. Manage. 162, 23–37.

Sánchez-Salguero, R., Navarro-Cerrillo, R.M., Camarero, J.J., Fernández-Cancio, A., 2011. Selective drought-induced decline of pine species in southeastern Spain. Climatic Change. doi:10.1007/s10584-011-0372-6.

Soil Survey Staff, 1999. Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys, second ed. United States Department of Agriculture, Washington.

Sumner, G., Romero, R., Homar, V., Ramis, C., Alonso, S., Zorita, E., 2003. An estimate of the effects of climate change on the rainfall of Mediterranean Spain by the late twenty first century. Clim. Dyn. 20, 789–805.

Tardif, J., Camarero, J.J., Ribas, M., Gutiérrez, E., 2003. Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. Ecol. Monogr. 73, 241–257.

Tíscar, P., 2002. Capacidad reproductiva de *Pinus nigra* subsp. *salzmannii* en relación con la edad de la planta madre. Invest. Agr. Sist. Recur. For. 11 (2), 357–371.

Tíscar, P., 2007. Dinámica de regeneración de *Pinus nigra* subsp *salzmannii* al sur de su área de distribución: etapas, procesos y factores implicados. Inv. Agr. Sis. Rec. For. 16 (2), 124–135.

von Ende, C.N., 2001. Repeated-measures analysis: growth and other time-dependent measures. In: Scheiner, S.M., Gurevitch, J. (Eds.), Design and Analysis of Ecological Experiments. Oxford University Press, Oxford, pp. 134–157.

Williams, A., Ternan, J.L., Elmes, A., González del Tánago, M., Blanco, R., 1995. A field study of the influence of land management and soil properties on runoff and soil loss in Central Spain. Environ. Monit. Assess. 37, 333–345.

Willmott, C.J., Rowe, C.M., Mintz, Y., 1985. Climatology of the terrestrial seasonal water cycle. Int. J. Climatol. 5, 589–606.

Wullschleger, S.D., Tschaplinski, T.J., Norby, R.J., 2002. Plant water relations at elevated CO_2 – implications for water-limited environments. Plant Cell Environ. 25, 319–331.

Yeomans, J., Bremmer, J.M., 1989. A rapid and precise method for routine determination of organic carbon in soil. Commun. Soil Sci. Plant Anal. 19, 1467–1476.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analysing Ecological Data. Springer, Berlin-Heidelberg.