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Growth response to climate and drought change along an aridity gradient in the southernmost *Pinus nigra* relict forests

J. Julio Camarero · Rubén D. Manzanedo ·
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Abstract

• **Context** Tree populations at the rear edge of species distribution are sensitive to climate stress and drought. However, growth responses of these tree populations to those stressors may vary along climatic gradients.
• **Aims** To analyze growth responses to climate and drought using dendrochronology in rear-edge *Pinus nigra* populations located along an aridity gradient.

• **Methods** Tree-ring width chronologies were built for the twentieth century and related to monthly climatic variables, a drought index (Standardized Precipitation–Evapotranspiration Index), and two atmospheric circulation patterns (North Atlantic and Western Mediterranean Oscillations).

• **Results** Growth was enhanced by wet and cold previous autumns and warm late winters before tree-ring formation. The influence of the previous year conditions on growth increased during the past century. Growth was significantly related to North Atlantic and Western Mediterranean Oscillations in two out of five sites. The strongest responses of growth to the drought index were observed in the most xeric sites.

• **Conclusion** Dry conditions before tree-ring formation constrain growth in rear-edge *P. nigra* populations. The comparisons of climate-growth responses along aridity gradients allow characterizing the sensitivity of relict stands to climate warming.

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Contribution of the co-authors JJC contributed new methods or models, analyzed data, and wrote the paper; RDM conceived the study, performed research, analyzed data, and contributed new methods or models, wrote the paper; RSS conceived the study, analyzed data, performed research, and wrote the paper; RMNC conceived the study, analyzed data, performed research, and wrote the paper.

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1 Introduction

According to climatic models, a generalized rise in temperature and a potential decline in water availability are expected in the Circum-Mediterranean area within the current century (Giorgi and Lionello 2008). In this drought-prone region, marginal rear-edge tree populations forming the southernmost distribution limit of the species (usually regarded as the climatic or xeric margin) are considered to be more sensitive to climate warming and related aridification trends (Hampe and Petit 2005; Macias et al. 2006). Moreover, the predicted changes in local climatic conditions and drought are linked

to alteration in regional atmospheric circulation patterns such as a decrease in the frequency of Mediterranean cyclones (Camarero 2011; Pasho et al. 2011).

The related effects of atmospheric circulation patterns, climatic conditions, and drought stress on tree growth at several spatial scales are rarely considered in the same research framework (e.g., Oberhuber et al. 1998; Lebourgeois 2000; Martín-Benito et al. 2010). Marginal Mediterranean mountain forests located at the rear edge of species distribution may serve as valuable model for assessing how sensitive are tree populations in response to climate along regional climatic gradients (Macias et al. 2006; Linares et al. 2009). The high spatio-temporal variability in climatic conditions of Mediterranean areas, particularly regarding precipitation patterns, suggests that the relevance of local factors and drought stress as drivers of growth changes along aridity gradients (e.g., Oberhuber et al. 1998). Furthermore, drought effects on growth may be time-dependent. In *Pinus halepensis*, Sarris et al. (2007) reported that the growth response to drought was more extended under low soil moisture conditions than under less xeric situations.

Atmospheric circulation patterns drive local climatic conditions and may be linked to tree growth along climatic gradients (Camarero 2011). The North Atlantic Oscillation (NAO) is a north–south dipole in geopotential heights that determines the position of the Icelandic low pressure and the Azores high pressure systems, and therefore the direction and strength of westerly winds in southern Europe. Consequently, the NAO has a strong influence on winter climate in the Iberian Peninsula, where increased westerlies (high NAO values) lead to dry and cold conditions mainly in winter (Hurrell et al. 2003). The Western Mediterranean Oscillation (WeMO) reflects the variability in precipitation and cyclogenesis in the western Mediterranean basin. The negative phase of the WeMO is linked to high levels of autumn and winter precipitation over the Spanish Mediterranean coast (Martín-Vide and López-Bustins 2006).

Iberian and Moroccan mountain conifer forests include the rear edge of pine species widely distributed in the Mediterranean Basin, such as *Pinus nigra* Arn. (Black pine). The southernmost populations of the species occur in southeastern Spain (Andalusia), northern Morocco (Rif), and Algeria (Djurdura) (Barbéro et al. 1998). Previous dendrochronological forests showed that *P. nigra* growth is mainly enhanced by wet spring conditions during the year of tree-ring formation (Martín-Benito et al. 2010; Linares and Tiscar 2010). However, none of these studies considered a hierarchical approach by linking different spatial scales and factors affecting tree growth along climatic gradients. Such factors affecting tree growth include large-scale atmospheric circulation patterns, climatic conditions, and drought stress.

Here, we use a dendrochronological network to compare the growth responses to climate and drought stress along an

aridity gradient. We consider five relict stands located at the rear edge of *P. nigra* distribution in southeastern Spain (four sites) and northern Morocco (one site). We analyze climate–growth relationships through time as a function of drought stress taking advantage of the fact that our sites comprise both mesic and xeric *P. nigra* sites. Our objectives were: (1) to describe the local patterns of temperature, precipitation, and radial growth for each population in twentieth century; (2) to quantify the local growth responses to the aforementioned climatic factors and drought intensity; and (3) to characterize the patterns of drought–growth responses along the aridity gradient. We expect that the southernmost *P. nigra* populations subjected to the most xeric local conditions will be the most responsive to precipitation and drought stress regardless of regional influences.

2 Material and methods

2.1 Study sites

P. nigra Arn. is a Circum-Mediterranean conifer which dominates mountains with calcareous substrates at high and intermediate elevations (Barbéro et al. 1998). The study area includes five *P. nigra* relict populations located at Baetic (southern Spain) and Rif (northern Morocco) mountains along the species southernmost xeric distribution limit in the Western Mediterranean Basin (Supplementary material, Fig. S1; Table 1). Those forests are located in several protected areas such as Spanish Natural Parks in Andalusia (from east to west: “Sierra de María-Los Vélez,” hereafter MA, “Sierra de Filabres,” hereafter FI, “Sierra de Mágina,” hereafter MG, “Sierra de Tejada, Almjara y Alhama,” hereafter AL) and the Moroccan Talassemtane National Park (hereafter TL) (Supplementary material, Fig. S1). The scattered distribution of *P. nigra* has produced a high intraspecific morphological and ecological variability among sites. In fact, the southernmost European *P. nigra* forests are considered a threatened habitat in the European Union Habitats Directive.

The study sites are located in topographically complex areas, such as rocky outcrops and steep slopes, and mainly on calcareous substrates (Table 1). Climate in all sites is Mediterranean with wet spring and autumn seasons and warm dry conditions from June to September (Supplementary material, Fig. S1). Maximum seasonal rainfall amounts are usually recorded in winter or autumn in western and eastern sites, respectively (see climate diagrams in Supplementary material, Fig. S1). Annual precipitation varies from 316 mm in site FI to 629 mm in site TL, and these sites can be regarded as the most xeric and mesic sites, respectively (Table 1). MG, AL, MA, and FI experience drier, warmer summers (with mean July temperatures ranging from 22.9 to 24.5 °C and precipitation varying from 4.0 to 7.7 mm) and colder winters (mean January

Table 1 Geographical, topographical, climatic and ecological characteristics of the five *P. nigra* study sites including the meteorological stations used to obtain local climate data (codes are indicated between parentheses)

Variables	Talassemtane (TL)	Tejeda-Almijara-Alhama (AL)	Filabres (FI)	María-Los Vélez (MA)	Mágina (MG)
Latitude (N)	35° 15'	36° 58'	37° 22'	37° 39'	37° 43'
Longitude (W)	5° 15'	3° 52'	2° 50'	2° 05'	3° 28'
Elevation range (m)	1,700–2,000	1,500–1,600	1,800–1,900	1,700–1,900	1,600–1,900
Aspect	NW	N	N–NE	W	S–SE
Slope (%)	25	30	32	25	30
Diameter at 1.3 m (cm)	62.3±8.9	55.40±8.10	76.31±5.13	60.24±4.25	80.75±4.67
Height (m)	9.2±0.5	10.0±0.5	8.5±0.2	9.1±0.6	11.7±1.0
Age at 1.3 m (years)	243±22	268±56	215±10	160±19	231±16
Meteorological station (latitude N, longitude W, elevation in m)	Chefchaouen (35° 10', 5° 18', 630)	Fornes (36° 57', 3° 49', 900)	Bacares (37° 15', 2° 27', 1200)	María (37° 42', 2° 09', 1197)	Jimena (37° 50', 3° 28', 609)
Mean annual temperature (°C)	15.0	14.7	14.9	14.8	14.5
Mean temperature of the coldest–warmest months (°C)	8.8–22.9	6.7–24.2	7.5–24.5	6.8–24.4	6.5–23.7
Total annual precipitation (mm)	629	392	316	366	417
Precipitation of the driest–wettest months (mm)	5–96	4–53	5–38	8–44	6–54
Annual water balance (mm)	–150	–350	–470	–435	–320
Water balance of the driest–wettest months (mm)	–121–71	–130–33	–136–15	–133–23	–128–35

Values are ranges or means±SE

temperatures range from 6.5 to 8.8 °C, respectively) (Table 1). Regarding forest composition, the Iberian stands contain some individuals of *Pinus pinaster* Ait. and *Juniperus* species, whereas in the more humid Moroccan site *P. nigra* forms mixed forests with Atlas cedar (*Cedrus atlantica* (Endl.) Hook. F.) and Moroccan fir (*Abies pinsapo* subsp. *maroccana* (Trab.) Emb. & Maire) (Barbéro et al. 1998).

2.2 Climate data

To analyze climatic trends in the study area at a regional scale and also to quantify climate–growth relationships, we used monthly climatic data (mean temperatures and total precipitation) from the CRU TS 3.1 dataset for the period 1901–2009, produced by the Climate Research Unit. This dataset corresponds to interpolated data of instrumental records recorded by a dense network of local meteorological stations, which have been subjected to homogeneity tests and relative adjustments, and finally gridded onto a 0.5° network (Mitchell and Jones 2005). Previous analyses indicate that gridded and local climatic data showed similar trends and mean values in the study area (Sánchez-Salguero et al. 2012).

To assess spatial and temporal climate variability at local scales, monthly data of mean temperatures and total precipitation were obtained for the period 1960–2009. Data were provided by the Spanish Meteorological Agency from several meteorological stations (Table 1, Supplementary material,

Fig. S1). In the Moroccan site, climatic data were obtained from local sources (Table 1). Stations were always located not further than 30 km from sampled sites, and we checked for the homogeneity of data. Then, annual and monthly water balances were calculated, as the differences between precipitation and potential evapotranspiration for each site. Evapotranspiration was estimated as a function of the mean monthly temperatures and the geographical latitude (see Vicente-Serrano et al. 2010). Temporal trends of monthly mean temperature and monthly total precipitation for each study site were estimated using Pearson and Mann–Kendall coefficients, respectively. Mann–Kendall tests were calculated using the *Kendall* package in the R software (R Development Core Team 2011).

To study the impact of drought severity on growth, we employed a multiscale drought index, the Standardized Precipitation–Evapotranspiration Index (SPEI), which is calculated using precipitation and temperature data from the same homogeneous and spatially dense dataset of local observatories than CRU climate data (Vicente-Serrano et al. 2010). The SPEI is useful to identify time-dependent growth response to drought scales in a better way than other most widely used indices, such as the Palmer Drought Severity Index (see Pasho et al. 2011). Briefly, we used the SPEI to analyze the influence of drought on tree growth at time scales ranging from 1 to 48 months, which according to the aforementioned authors encompass the growth responses to drought of most Iberian tree species.

The NAO and WeMO indices are calculated as a normalized pressure difference (between Gibraltar and Rykjavik in the case of NAO; between San Fernando and Padova in the case of the WeMO). NAO index values were obtained from CRU website (<http://www.cru.uea.ac.uk/cru/data/nao/>), while WeMO index series was downloaded from the Climatology Group website at the University of Barcelona (<http://www.ub.es/gc/English/wemo.htm>). Both NAO and WeMO indices show a high temporal variability, and no significant correlation was observed between them (Martín-Vide and López-Bustins 2006).

2.3 Field sampling and dendrochronological methods

The sampling process took place during the autumns of 2009, 2010, and 2011. At each site, we selected dominant, mature, and living trees separated by at least 20 m from each other and located in harsh sites (steep slopes, rocky soils). We sampled a minimum of 15 trees per site (except in site AL, with only five living trees in the whole population) up to a maximum of 24 trees (TL) (Table 3). Two cores per tree at 1.3 m height were collected with a Pressler increment borer along the perpendicular direction to maximum slope. In protected areas (sites MA and TL), only one core per tree was allowed to be collected, and then more trees were sampled. Cores were prepared according to standard dendrochronological procedures (Fritts 2001). Samples were air-dried, sanded, and visually cross-dated, and their ring width series were measured to the nearest 0.001 mm using a LINTABTM measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was verified using COFECHA program (Grissino-Mayer et al. 1992) by checking the consistency of the different ring width series among trees coexisting within the same site.

Each ring-width series was double-detrended and then standardized using the ARSTAN software (Cook 1985), fitting a negative exponential function followed by a 50-year long spline to retain high-frequency variability. Detrending allowed transforming tree-ring widths to dimensionless growth indexes by dividing observed ring width values by fitted values. The resulting series were pre-whitened by autoregressive models to remove temporal autocorrelation. Finally, a biweight robust mean was computed to obtain a residual chronology for each site which was used in all subsequent analyses.

The quality of chronologies was assessed by using several dendrochronological statistics: the mean and standard deviation (SD) of raw tree-ring width data; the first-order autocorrelation of raw data (AC1), which measures the year-to-year persistence in ring width; the mean sensitivity (MS) of the residual ring-width series, which measures the year-to-year variability in the width index; the mean between-trees correlation within each site (r_{bt}), which quantifies the similarity in residual width indices among trees; and the expressed

population signal (EPS) of residual series, which assesses the representativeness of the sample size compared with theoretical infinite population (Fritts 2001). We selected the common period 1901–2009 to calculate these statistics and to perform further analyses since all chronologies showed EPS values above 0.85, considered as minimum threshold for a chronology to be considered well replicated (Wigley et al. 1984). Finally, to characterize the similarity in growth between sites, we calculated a Principal Component Analyses (PCA) based on the covariance matrix of the residual chronologies of the five study sites for the period 1901–2009 (Fritts 2001).

2.4 Statistical analyses

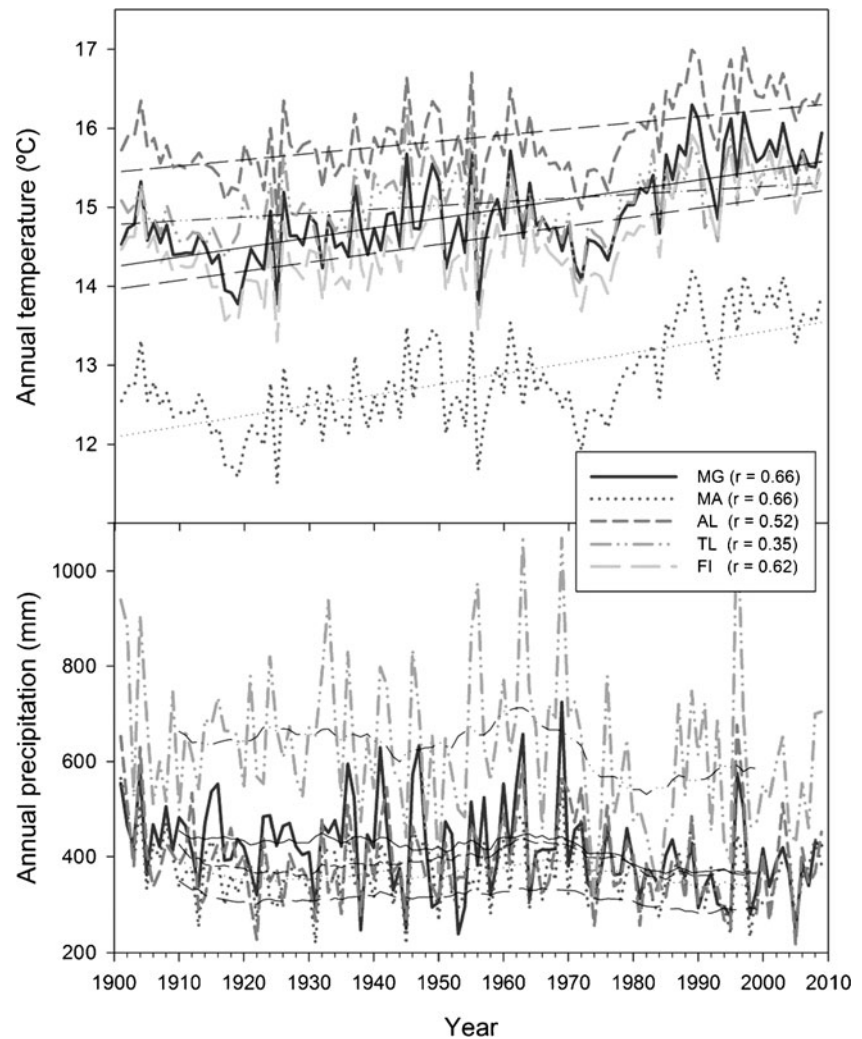
To determine the influence of atmospheric circulation patterns and climatic variables (precipitation, temperature, and drought intensity) on *P. nigra* growth, we related tree-ring width indexed chronologies to monthly climate data, using Pearson correlation coefficients and response functions based on bootstrapped stepwise multiple regressions computed on the principal components of climatic variables (Fritts 2001). Climate–growth relationships were analyzed from May of the previous year, the one before tree-ring growth, up to October of the year of tree-ring formation (Sánchez-Salguero et al. 2012). Moving climate–growth correlations using a 40-year temporal window were also calculated for those climatic variables. We used seasonal values for the NAO and WeMO indices (previous autumn, September–October–November; previous winter, December–January–February; winter–spring transition, February–March–April; current spring, March–April–May) and monthly ones for climatic variables following Camarero (2011) to determine their associations with tree-ring width indices. Correlation, bootstrapped response functions, and moving correlations were calculated using the software Dendroclim2002 (Biondi and Waikul 2004). The significance of correlations was evaluated by using 95 % confidence limits and compared with bootstrapped regression coefficients.

3 Results

3.1 Climate trends

Annual mean temperature in the study area increased during the twentieth century (Fig. 1). All the studied sites showed significant ($P < 0.05$) warming trends during that period with the highest temperature rises in sites FI and MA ($0.013 \text{ } ^\circ\text{C year}^{-1}$) and the lowest ones in sites AL ($0.008 \text{ } ^\circ\text{C year}^{-1}$) and TL ($0.005 \text{ } ^\circ\text{C year}^{-1}$). Annual precipitation showed a strong variability between decades and years with wet periods (1960s, 1970s) alternating with dry ones (1980s, 1990s). We observed that, after the 1960s, total annual

Fig. 1 Climatic trends in annual mean temperature and total precipitation for the five study sites. Linear regressions and correlation coefficients for temperature series are displayed ($P < 0.05$), while 20-year moving mean averages are presented in the case of precipitation series (see Table 2 for an analysis of precipitation trends). Sites' codes are as in Table 1



precipitation decreased in all sites with significant monthly declines being detected in March and November (Table 2, Fig. 1). The reduction of rainfall in these wet months was particularly severe in sites MG, TL, FI, and MA. Moreover, precipitation decreased in June in mesic sites (TL, MG, AL).

3.2 Growth characteristics

The mean tree-ring width for the common period 1901–2009 was higher in the wet site TL (0.95 mm) than in the xeric ones (MG, 0.60 mm; FI, 0.77 mm) (Table 3). The first-order autocorrelation was the highest in the xeric site FI, suggesting an elevated year-to-year persistence in growth of drought-prone sites, whereas the mean sensitivity was the lowest in the mesic site TL, indicating a lower year-to-year variability in width indices there as compared with the other sites. The correlation of growth series among trees (r_{bt}) within each stand varied from 0.49 (site TL) to 0.60 (site MG) (Table 3), and the EPS was also maximum (minimum) in site MG (TL) confirming a higher (lower) growth coherency among trees

Table 2 Mann–Kendall statistic and related probability levels assessing precipitation trends for selected months during the period 1901–2009 and considering the five *P. nigra* study sites

Month	TL	AL	FI	MA	MG
January	-0.18	0.02	-0.22	-0.06	-0.05
February	-0.25	-0.02	-0.04	0.15	-0.20
March	-1.34***	-0.71*	-0.94**	-0.99***	-1.39***
April	-0.54	-0.34	-0.44	-0.42	-0.71*
May	-0.13	-0.41	-0.22	0.12	-0.17
June	-0.69*	-0.81**	-0.56	-0.33	-0.68*
July	-0.05	0.42	-0.12	-0.24	-0.03
August	0.70**	0.79**	0.70*	0.52	0.77**
September	0.11	-0.14	-0.35	-0.38	-0.13
October	-0.26	-0.21	-0.26	-0.12	0.02
November	-0.81**	-0.69*	-0.97**	-0.92**	-0.93**
December	-0.05	0.04	0.13	0.16	-0.15

*0.05 < $P \leq 0.10$; **0.01 < $P \leq 0.05$; *** $P \leq 0.01$, levels of significance

there than elsewhere. Lastly, the first two components of the PCA captured 60.5 % and 13.3 % of the total growth variability. The second component separated the wet Moroccan site from the other more xeric sites.

3.3 Climate–growth relationships

Tree growth in the five regions was mainly enhanced by wet and cold conditions during the previous autumn (September, October), whereas warm conditions during late winter and early spring (February, March) also promoted the production of wider rings (Fig. 2). In the most xeric sites (FI, MA), the positive association between previous autumn rainfall and growth was the highest while, in mesic sites (e.g., TL), current spring temperature was the main driver of growth. In the site TL, March temperatures influenced positively growth more than February thermal conditions. Overall, radial growth correlated more strongly with the climatic conditions of the year prior to tree-ring formation than with those of the year of growth.

The moving correlations revealed a stronger influence of previous September precipitation on growth in the driest sites (e.g., FI) during the late twentieth century, whereas high rainfall in the previous September was more relevant for growth in the wet site TL during the early past century (Fig. 3). Previous October precipitation showed significant and stronger effects in the second half of twentieth century, only in the wettest site TL. The relationships between growth and current March precipitation increased in the MG site, whereas such association gradually lost significance in site AL (Fig. 3). Current February temperatures showed a rising positive correlations with growth for MG and TL sites, while

March temperatures lost relevance for growth with growth for MG and MA sites. Contrastingly, in the wettest site, TL March temperatures influenced growth as strongly at the beginning as at the end of the twentieth century. In fact, the site TL illustrates a trend of increasing importance of the negative effects of warmer previous September conditions on growth.

3.4 Growth responses to drought

Most of the studied trees presented a neat decline in growth during the last 50 years, excepting those in site TL where most trees were positive or neutral tenders (data not shown). We observed similar high-frequency growth patterns as compared with those of the drought SPEI index with noticeable growth reductions in 1939, 1940, 1994, 1999, and 2005 and growth increases in 1914, 1941, 1964, and 1997. Some of these sharp growth reductions and increases, which were evident in the most xeric sites (FI, MA), corresponded to severe droughts (e.g., 2005) and very wet years (e.g., 1997), respectively.

The correlation analyses between tree-ring width indices and the drought index (SPEI) revealed a significant association between growth and drought intensity and severity for all sites but with different magnitudes. We found a positive and significant relationship between SPEI recorded at short time scales (1–8 months) corresponding to short dry (or wet) periods occurring at a high frequency (Figs. 4 and 5). In all study sites, significant SPEI-growth correlations were found for time scales from 1 to 8 months, being higher in the most xeric sites (FI, MA) than in the less xeric sites (TL, MG) (Fig. 5). In the most xeric, these significant correlations were observed at scales up to 16 months long and from the previous September up to the current March, while in the less xeric sites the

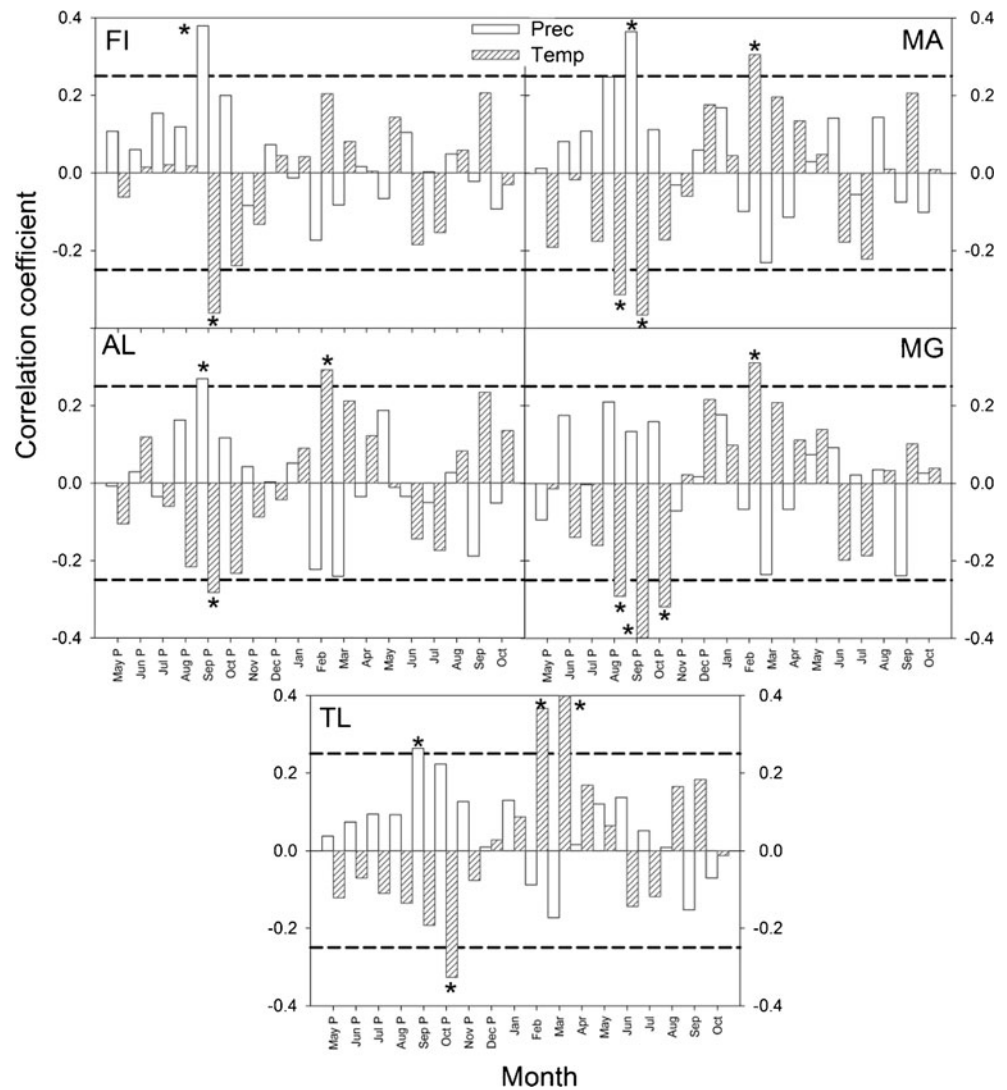
Table 3 Characteristics of the tree-ring width chronologies for the common period 1901–2009

Variables	Sites				
	TL	AL	FI	MA	MG
No. trees (radii)	24 (35)	5 (10)	18 (22)	22 (32)	15 (29)
Tree-ring width (mm)	0.95±0.02	0.81±0.03	0.77±0.03	0.87±0.04	0.60±0.02
SD (mm)	0.05±0.02	0.03±0.01	0.04±0.01	0.04±0.01	0.03±0.01
AC1	0.57	0.61	0.73	0.65	0.61
MS	0.23±0.01	0.37±0.02	0.32±0.01	0.34±0.01	0.29±0.01
r_{bt}	0.49	0.54	0.53	0.52	0.60
EPS	0.86	0.89	0.95	0.94	0.96
PC1 score	0.47	0.40	0.42	0.49	0.45
PC2 score	0.82	−0.16	−0.42	−0.30	−0.26

The last two lines show the scores of the first (PC1) and second (PC2) principal components of a principal component analysis considering the five indexed tree-ring width chronologies. Sites' codes are as in Table 1

Statistics: mean and standard deviation (SD) of raw tree-ring width data; *AC1*, first-order autocorrelation of raw data, which measures the year-to-year persistence in ring width; *MS*, mean sensitivity of the residual ring-width series, which measures the year-to-year variability in the width index; r_{bt} , the mean between-trees correlation within each site which quantifies the similarity in residual width indices among trees; *EPS*, expressed population signal of residual series, which assesses the representativeness of the sample size compared with theoretical infinite population

Fig. 2 Correlations (Pearson coefficients) calculated between tree-ring width indices and monthly climatic variables (mean temperature, *filled bars* and total precipitation, *empty bars*). The correlations were calculated from May of the previous year (months abbreviated and followed with “P”) to October of the current year of tree-ring formation. *Dashed horizontal lines* and *asterisks* indicate significant ($P < 0.05$) correlations and response coefficients, respectively. Sites’ codes are as in Table 1



strongest correlations were observed at shorter time scales (1–8 months) from the previous September up to the current January. The wettest and coldest sites did not show strong associations between growth and SPEI during late winter and early spring.

3.5 Growth response to regional atmospheric circulation patterns

The first principal component of all ring-width series and the TL site chronology were significantly correlated in a negative way with the previous autumn NAO index, and positively with the winter–spring NAO index (Table 4). Only the previous autumn WeMO index was significantly and negatively related to growth in the FI site. Previous autumn and winter NAO and autumn WeMO indices showed significant correlation with precipitation in TL and FI sites, respectively (data not shown).

4 Discussion

We have evaluated the impact of regional and local climate variability and drought stress on growth of relict rear edge *P. nigra* populations during the twentieth century along an aridity gradient. The arrangement of the sampled stands along this gradient going from xeric sites in southeastern Spain up to a mesic site in northern Morocco allowed us detecting how growth responses varied as a function of drought stress.

Independently of the magnitude of the association and the SPEI time scale analyzed, the highest correlation coefficients between growth and that drought index were obtained in previous autumn and winter months, the period when thermal limitations and positive water balance occurs. First, this suggests the importance of the ability of soils to store water as a major driver of tree growth. This was confirmed by climate–growth correlations which were similar among sites (positive roles of previous wet and cold autumn and warm late winter) but changed slightly as a function of local xericity. Indeed, the

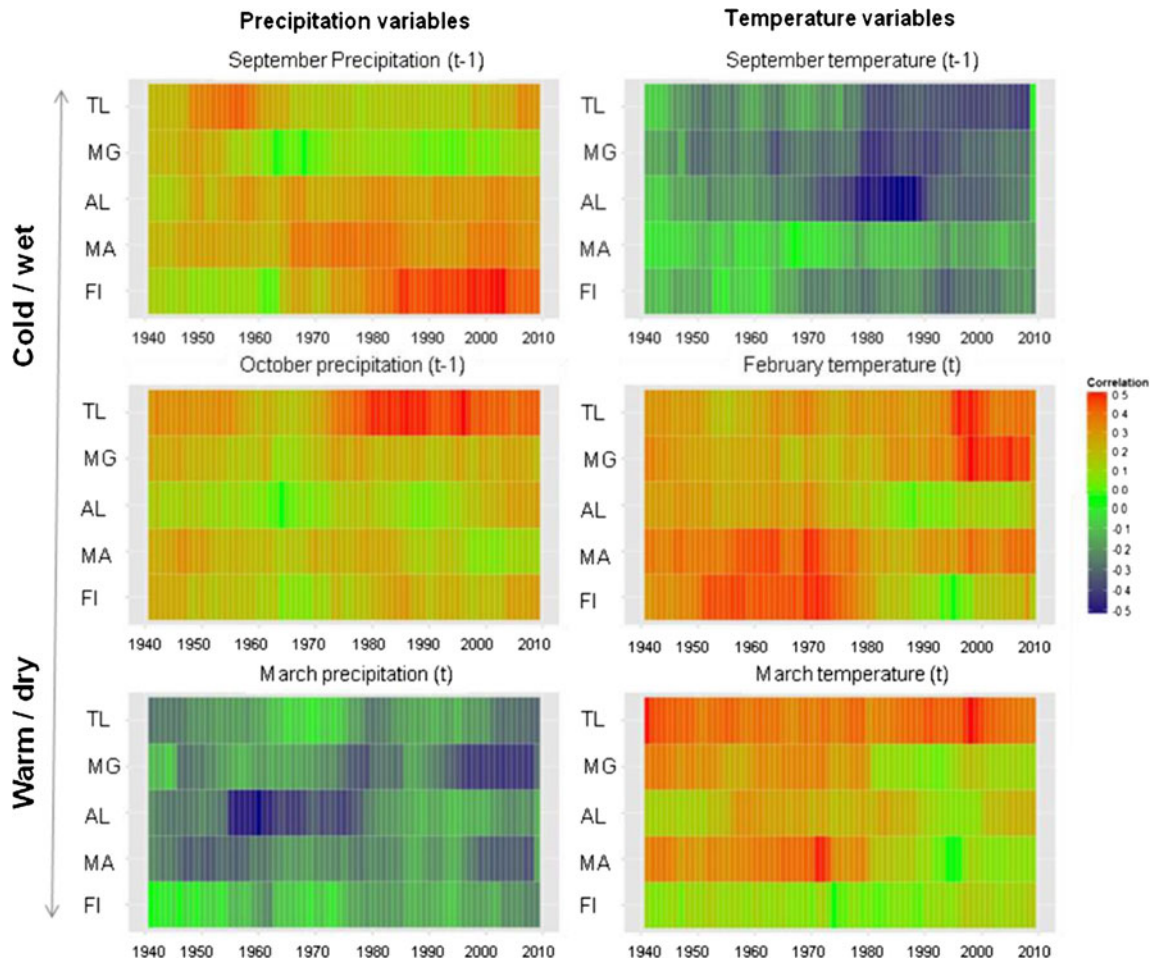


Fig. 3 Moving correlation analyses between selected climatic variables (total precipitation, *left*; mean temperature, *right*) and radial-growth for the five study sites: precipitation and temperature of the previous (year $t-1$) September; precipitation of the previous October; temperature of current (year t) February; precipitation of current March; and temperature of current March. The stands were arranged following a climatic gradient

from warm and dry to cold and wet conditions (see *arrows*). Correlations (Pearson coefficients) were calculated for 40-year intervals considering the period 1901–2009 (each major tick along the x -axis shows the last value of the corresponding 40-year interval, e.g., 1940 stands for the period 1901–1940, etc.). Sites' codes are as in Table 1

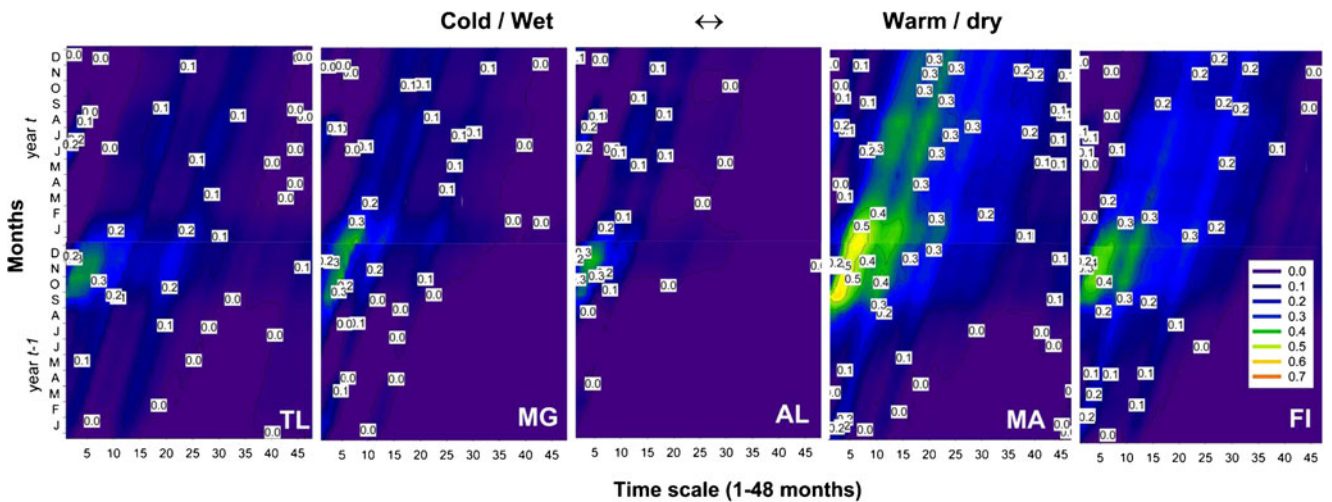
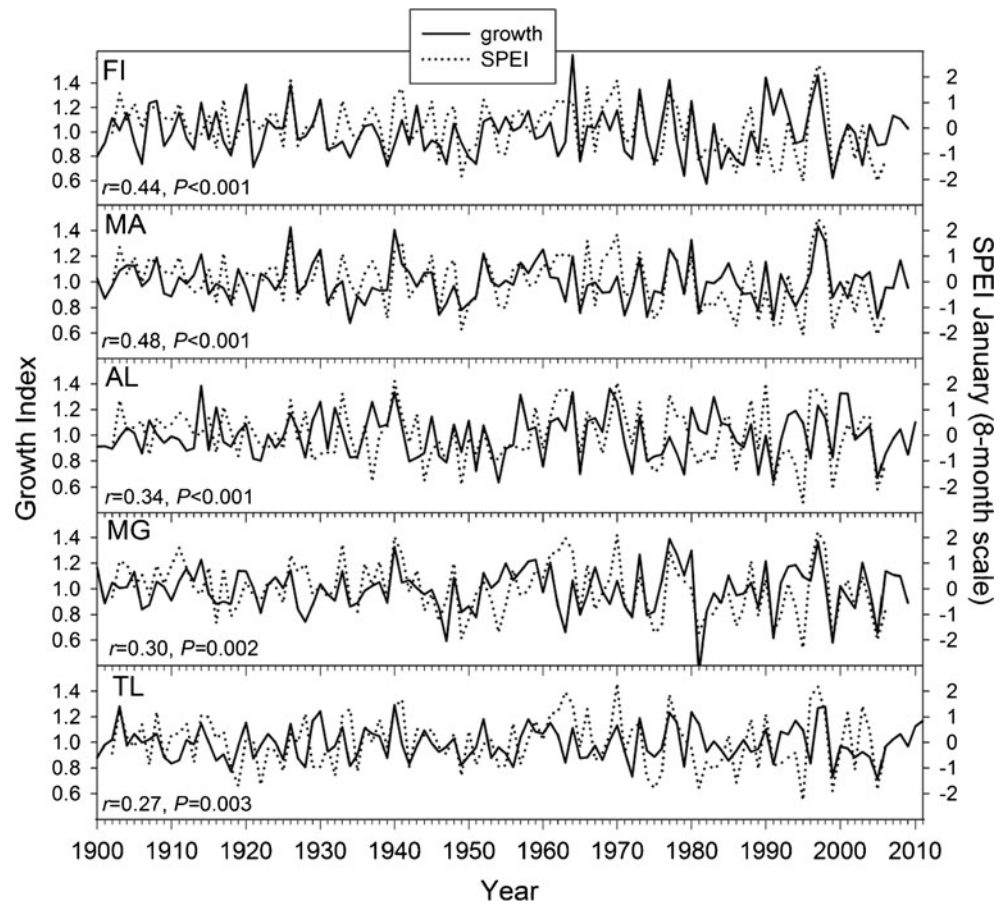


Fig. 4 Mean correlation coefficients calculated between tree-ring width residual chronologies and series of the SPEI drought index obtained for different monthly scales (from 1 to 48 months) in the five study sites. Correlation analyses were performed for monthly drought data of the

previous year ($t-1$) and the year of tree-ring formation (t). Sites are arranged from cold and wet (*left*) to warm and dry climatic conditions (*right*). Correlation values above +0.20 and below -0.20 are significant at the $P=0.05$ level. Sites' codes are as in Table 1

Fig. 5 Tree-ring width chronologies obtained for the five *P. nigra* study sites and related January SPEI drought index (calculated at 8-month scale) for the twentieth century. The plotted drought index was the most strongly related to annual tree-ring width indices in four out of five study sites (see tree-ring width–SPEI Pearson correlation coefficients and related probability levels in each plot in Fig. 4). Sites' codes are as in Table 1



maximum growth–SPEI correlation (see Fig. 5) was positively related to the local water balance of each site ($r = -0.88$, $P = 0.05$). Second, previous autumn conditions were more important for growth in the eastern and most xeric sites (e.g., FI) whereas late-winter conditions were more relevant in the western less xeric sites (e.g., TL). This indicates that the

season when the maximum rainfall occurs before the growing season starts (autumn vs. winter) significantly influences growth responses the following year. This is probably caused by restoring soil water reserves after the dry summer conditions or by using the available autumn–winter water to enhance carbohydrate synthesis and storage in plant tissues,

Table 4 Correlations (Pearson coefficients) between seasonal circulation atmospheric patterns (NAO, North Atlantic Oscillation; WeMO, Western Mediterranean Oscillation) and tree-ring width indices of the first two

principal components of all tree-ring width chronologies (PC1, PC2) and *P. nigra* local chronologies for the period 1901–2009

Patterns	Season (year) (months)	Principal components		Sites				
		PC1	PC2	TL	AL	FI	MA	MG
NAO	Autumn ($t-1$) (SON)	-0.23	-0.01	-0.22	-0.08	-0.08	-0.12	-0.15
	Winter ($t-1$) (DJF)	0.04	0.13	0.11	0.09	0.06	-0.03	-0.04
	Spring (t) (MAM)	0.13	-0.10	0.11	0.02	0.15	0.09	0.13
	Winter-spring (t) (FMA)	0.21	-0.02	0.20	0.11	0.14	0.15	0.18
WeMO	Autumn ($t-1$) (SON)	0.01	0.01	0.04	-0.04	-0.21	0.07	-0.10
	Winter ($t-1$) (DJF)	0.08	0.12	0.14	0.13	0.03	0.13	0.07
	Spring (t) (MAM)	0.11	0.02	0.09	0.09	0.05	0.14	0.07
	Winter-spring (t) (FMA)	0.12	0.01	0.12	0.08	0.08	0.10	0.08

The growth is related with circulation atmospheric patterns for the year of tree-ring formation (t) and the previous one ($t-1$). Bold values are significant ($P < 0.05$). Sites' codes are as in Table 1

Seasons: *SON* September–October–November, *DJF* December–January–February, *MAM* March–April–May, *FMA* February–March–April

which can readily be used for spring growth (Pasho et al. 2011). Reloading soil water before spring growth resumption is critical for Mediterranean conifer species inhabiting drought-prone areas with short springs and apparently shallow soils such as the study sites (Table 1). Therefore, even such soils are able to store enough water before the growing season starts given the relevance of rainfall received in the previous autumn or winter for growth. Such findings agree with other research in Mediterranean forests (Linares and Tiscar 2010; Martín-Benito et al. 2010) and also in drought-prone subalpine (Oberhuber et al. 1998) and temperate (Michelot et al. 2012) areas. These results highlight how important is the amount of autumn or winter precipitation stored by soils for tree growth in dry Mediterranean areas which should lead to lagged climate–growth relationships.

Our results agree with previous dendroecological research performed in *P. nigra* forests from France (e.g., Lebourgeois 2000) and also concur with other findings obtained for Scots pine forests from the dry inner Swiss Alps (Eilmann et al. 2009) and for Greek Aleppo pine forests (Sarris et al. 2007). The growth in the studied rear-edge *P. nigra* populations was enhanced by wet and cold conditions during the previous autumn and by warm late winters as has been found in other Iberian forests (Andreu et al. 2007; Martín-Benito et al. 2010). The effects of the climatic conditions during the previous autumn and winter are probably related to increased autumn and winter carbohydrate synthesis and possible reduced respiration costs (Gimeno et al. 2012). On the other hand, the positive effect on growth caused by warmer February conditions may trigger an earlier cambial resumption and enhance secondary growth as has been postulated for other Mediterranean conifers (Camarero et al. 2010).

Relict pine forests in the Mediterranean Basin are likely to experience strong negative effects on growth associated to warming-enhanced drought stress (Sarris et al. 2007). Higher year-to-year climatic variability and increased long-term aridity may reduce tree growth of pine species as has been shown in the Iberian Peninsula (Andreu et al. 2007). But we must also assess how much of this growth variability driven by local factors is mediated by regional factors. For instance, growth in the most (FI) and less xeric (TL) sites responded to different atmospheric circulation patterns during the previous autumn (WeMO and NAO, respectively), and this is probably modulating local precipitation regimes (Camarero 2011).

During the wet season, the NAO and WeMO arise as the main modes of Iberian precipitation variability, mainly in western and eastern areas of that Peninsula respectively, and play a significant role in tree growth through changes in precipitation and soil water availability (Bogino and Bravo 2008; Camarero 2011). The recharging of soil moisture depends on the amount of the autumn (east) and winter (west) precipitation, and the latter is inversely correlated with the

NAO and WeMO. Therefore, regional atmospheric circulation indices (NAO, WeMO) influence *P. nigra* growth variability at local scales through changes in local precipitation pattern and drought stress. In agreement with the results obtained by Camarero (2011) in NE Spain, a similar spatial gradient in the effect of the NAO and WeMO on tree growth was found here. The spatially constrained negative relationship between the autumn NAO index and growth at the site TL in northern Morocco is linked to the positive effect of winter temperature on growth (Camarero 2011). However, growth at the FI site is also negatively related to the autumn WeMO index, which can be explained by more water storage previously to the start of radial growth in spring during negative phases of the WeMO index (Camarero 2011). The impact of NAO on growth in the western less xeric sites and that of the WeMO in the eastern most xeric sites resembled the observed pattern of tree growth variability obtained by means of the PCA. This confirms a distinct spatial influence of the atmospheric circulation patterns observed at regional scales on precipitation recorded at local scales.

As expected, the southernmost *P. nigra* populations subjected to the most xeric local conditions where trees face the species' aridity tolerance limit were those presenting the highest responsiveness to precipitation and drought stress. These xeric rear-edge stands are the most vulnerable against drought-induced forest dieback (Sánchez-Salguero et al. 2012). In the studied areas, temperature rose and precipitation declined, particularly in spring and autumn, during the second half of twentieth century, showing a long-term trend toward aridification as has been observed elsewhere in southeastern Spain (Linares et al. 2009; Sánchez-Salguero et al. 2012). The recurrence of severe drought events has caused a progressive reduction in available soil water in that area (Esteban et al. 2012). These results suggest that climatic change might cause divergent growth trends in different *P. nigra* rear-edge populations as a function of drought stress. Warming late-winter could favor growth in wet sites such as TL while warmer and drier autumn conditions could cause growth decline in xeric sites such as FI.

The radial growth in the most xeric forests (FI, MA) showed a high sensitivity to water availability in the previous autumn, whereas growth in the less xeric one (site TL) responded more to late-winter temperature before tree-ring formation started. Increasing drought stress during the second half of the twentieth century might be the cause of the higher synchrony in tree growth for the most xeric sites where the highest mean sensitivity values were observed. A longer drought-stress period might explain why *P. nigra* climate–growth relationships shifted in the mid 1970s with a clear divergence between dry and mesic sites. For instance, in the most xeric FI site, previous September precipitation became more important for growth, whereas current February–March temperature became more relevant in the less xeric site TL.

This divergence in unstable climate–growth associations was also observed in eastern Spain by Martín-Benito et al. (2010).

Our analyses revealed two distinct patterns in terms of the growth responses to drought, depending on the aridity of the studied site. The driest semi-arid sites (FI, MA) showed stronger growth responses to long-term (1–16 months) droughts compared with those growing in less xeric mountainous areas which responded much less and only to short-term (1–8 months) droughts (AL, MG, TL). It has been found previously that in xeric Mediterranean areas tree growth is mainly limited by low precipitation, while in mesic areas the main factors constraining growth are low temperatures in winter time (Pasho et al. 2011). Overall, our results confirmed different growth response of rear edge *P. nigra* forests to drought as a function of local climate conditions. Trees growing in the driest sites responded to the SPEI drought index at long time scales, which indicates that cumulative precipitation conditions during 1 year impact tree growth as illustrated by Sarris et al. (2007) and Pasho et al. (2011) for *P. halepensis*. We argue that trees at these xeric sites are locally adapted to those conditions through morphological (e.g., deep roots, small crown and tree size) and physiological (e.g., tight control of water potential through stomatal closure) adaptations. In the less xeric sites, short-term water shortages slightly constrain growth probably through warming in autumn and winter leading to reduced soil water reserves during the following spring (Camarero 2011). We speculate that these mesic sites would be the most sensitive to warmer and drier conditions during the previous autumn and winter, and these changes may be related to NAO shifts.

To conclude, our study emphasizes how growth responses to drought change along an aridity gradient in relict *P. nigra* tree populations. Dry conditions before tree-ring formation constitute the major constrain of growth in these rear-edge populations. Preserving marginal populations adapted to very xeric conditions is critical for storing genotypes which can withstand the drier and warmer conditions predicted for the Mediterranean Basin (Giorgi and Lionello 2008). However, an increased variability in extreme drought events may also threaten these populations if functional thresholds are crossed leading to forest dieback. For these reasons, knowing how regional and local climatic conditions modulate drought stress and drive tree growth is essential to understand how Mediterranean forests will respond to the future climate.

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