

SITE AND AGE CONDITION THE GROWTH RESPONSES TO CLIMATE AND DROUGHT OF RELICT *PINUS NIGRA* SUBSP. *SALZMANNII* POPULATIONS IN SOUTHERN SPAIN

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ABSTRACT

To assess if tree age may modulate the main climatic drivers of radial growth, two relict *Pinus nigra* subsp. *salzmannii* populations (María, most xeric site; Mágina, least xeric site) were sampled in southern Spain near the limits of the species range. Tree-ring width residual chronologies for two age groups (mature trees, age ≤ 100 years (minimum 40 years); old trees, age > 100 years) were built to evaluate their responses to climate by relating them to monthly precipitation and temperature and a drought index (DRI) using correlation and response functions. We found that drought is the main driver of growth of relict *P. nigra* populations, but differences between sites and age classes were also observed. First, growth in the most xeric site depends on the drought severity during the previous autumn and the spring of the year of tree-ring formation, whereas in the relatively more mesic site growth is mainly enhanced by warm and wet conditions in spring. Second, growth of mature trees responded more to drought severity than that of old trees. Our findings indicate that drought severity will mainly affect growth of relict *P. nigra* populations dominated by mature trees in xeric sites. This conclusion may also apply to similar mountain Mediterranean conifer relicts.

Keywords: Andalusia, climate change, correlation function, dendroclimatology, drought stress, Mediterranean forests, *Pinus nigra*, relict forests.

INTRODUCTION

Climate effects on intrinsic tree traits such as growth depend not only on regional climate but they are also contingent on the tree sensitivity to local factors such as site conditions or tree age (Linares *et al.* 2013). The long-term growth responses to climate of relict circum-Mediterranean pine populations provide a valuable system to investigate the role played by ongoing climatic warming at the southern distribution limit of these species where they usually face severe drought

stress (Sánchez-Salguero *et al.* 2012a; Camarero *et al.* 2013). Drought stress may selectively affect trees as a function of their ages, often with older trees being more sensitive to drought stress than young ones (Knapp and Soule 2011; Linares *et al.* 2013). Such age-dependent control of growth has been related to hydraulic limitations in old trees affecting photosynthesis, water-use efficiency and carbon allocation within the tree (Ryan *et al.* 2006). Site characteristics for the pine stands at the rear-edge (southernmost limit) of the species distribution make them potentially sensitive to drought stress because they are usually located in sites with soils showing a poor water-holding

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capacity as happens in southern Spain (Sánchez-Salguero *et al.* 2012b). In this area climatic trends during the last half of the 20th Century indicate a notable reduction in annual precipitation at a mean rate of -5 mm yr^{-1} (de Luis *et al.* 2009). An improved retrospective understanding of the growth responses of relict Mediterranean pine populations subjected to contrasting local climatic conditions and dominated by different age classes may improve our predictions of the future dynamics of these drought-prone forests (see also Camarero *et al.* 2013).

The European black pine subspecies *Pinus nigra* Arn. subsp. *salzmannii* (Dunal) (hereafter abbreviated as *P. nigra*) is widely distributed in the Western Mediterranean Basin, forming in eastern Andalusia, southern Spain, the southernmost European populations. *P. nigra* is a species widely used in dendrochronology because of its sensitivity in response to climate stress and its high longevity, with some living individuals up to *ca.* 1000 years old (Creus 1998). In Spain, little research has been performed to quantify growth-climate relationships in relict multi-age *P. nigra* populations where xeric conditions usually prevail and living tree individuals may achieve great age.

In this study, we assessed whether the climatic responsiveness of growth at the individual level in two *P. nigra* relict populations is modulated by local climatic conditions and tree age. We addressed the following specific objectives: (a) to compare the growth responses to climate as related to local climatic variability and tree age by comparing two climatically contrasting sites (more *vs.* less xeric site) and two age groups (old *vs.* mature trees), and (b) to assess individually and retrospectively the role played by climate as a driver of growth in the two marginal sites subjected to different drought severity.

MATERIAL AND METHODS

Study Area

We selected two study sites located in two natural parks in southeastern Spain: Sierra de María-Los Vélez (hereafter abbreviated as María) (37°41'N, 2°14'W) and Sierra de Mágina (hereafter abbreviated as Mágina) (37°44'N, 3°28'W)

(Figure 1). These sites were selected because they share similar physiographic and lithological characteristics, and their structures allowed sampling dominant trees belonging to a wide range of age classes (Table 1). Climate in both sites is Mediterranean with wet spring and fall seasons and a marked summer drought lasting from June to September. However, climate in María (the most xeric site) is semiarid, whereas in Mágina (the least xeric site) wetter and more temperate conditions occur (Camarero *et al.* 2013). The estimated annual precipitation in María and Mágina sites for the period 1990–2008 were 354 mm and 494 mm, whereas mean annual temperatures were 12.8°C and 16.3°C, respectively. Soils have a greater water-holding capacity in Mágina than in María, with the most abundant soil types: leptosols, regosols and cambisols on limestone and dolomites in Mágina, and entisols and inceptisols on limestones in María. In both study sites, slopes are steep. The current structure of both studied forests is characterized by dominant and isolated trees.

Field Sampling and Dendrochronological Methods

Because of the protection status of study areas, it was not feasible to sample a large number of trees and cores per site, as is recommended in standard dendrochronological studies (Fritts 2001; but see Woodall 2008). Therefore, single increment cores from 32 (María) and 44 (Mágina) trees per site were collected at 1.3 m using an increment borer. At each site, care was taken to select trees greater than 50 years old growing under similar microsite and competition conditions and located at least 20 m apart from each other across a rectangular area of 5 ha. Two age groups were finally established based on previous analyses and considering mature (age \leq 100 years, minimum 40 years) and old individuals (age $>$ 100 years).

In the laboratory, all wood samples were air dried and carefully polished with successively finer sandpapers until tree rings were clearly visible. The tree-ring series were dated, and missing or false rings were identified by crossdating with all the cores of all the trees per site. Visual crossdating

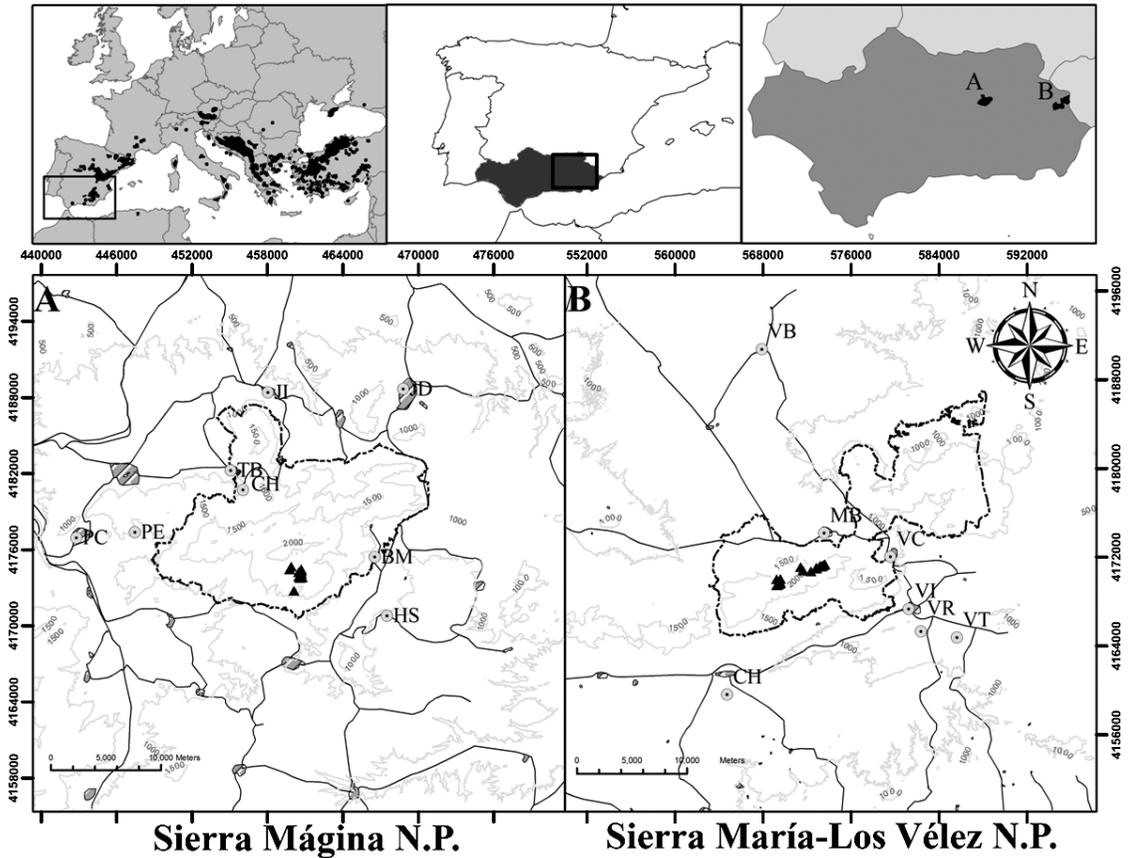


Figure 1. Location of the two study sites (A, B) in eastern Andalusia, southeastern Spain. Sampling points (solid triangles), meteorological stations used (grey circles), limits of the Natural Parks surrounding each study site, and elevation isolines are displayed in each detailed map. The two-letter codes for each station are the same as those displayed in the Supplementary Material. The upper maps show the distribution of *Pinus nigra* and the location of the study area in Europe, Spain and Andalusia.

of samples was conducted before measuring the samples to a resolution of 0.001 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany) (Stokes and Smiley 1996). Crossdating

was verified using COFECHA (Holmes 1983; Grissino-Mayer 2001). Four annual tree-ring width chronologies were built for the two site and age groups. The mean tree-ring width

Table 1. Characteristics of the two studied relict *Pinus nigra* populations. The last two lines show mean values \pm standard errors.

Variables	Sites	
	María	Mágina
Forest surface (ha)	700	1860
Elevation range (m a.s.l.)	1700–1900	1600–1900
Aspect	W	S-SE
Slope (%)	25	30
Maximum age at 1.3 m (years)	469	400
Mean age at 1.3 m of mature trees (years)	83	85
Mean age at 1.3 m of old trees (years)	260	235
Diameter measured at 1.3 m (cm)	60.25 \pm 4.25	63.69 \pm 5.84
Height (m)	9.10 \pm 0.62	9.91 \pm 0.76

Table 2. Descriptive statistics (mean \pm SE) of the four chronologies built with two age groups (mature vs. old trees) in the two *Pinus nigra* study sites (María, Mágina) for the common interval A.D. 1917–2009.

	María		Mágina	
	Mature Trees	Old Trees	Mature Trees	Old Trees
No. trees	18	14	15	29
Timespan	1917–2009	1541–2009	1890–2009	1613–2009
Tree-ring width (mm) ^a	1.87 \pm 0.05 ^{bc}	1.03 \pm 0.62 ^{ad}	2.36 \pm 0.12 ^{bd}	1.35 \pm 0.10 ^{ac}
SD ^b	0.57 \pm 0.03 ^{bd}	0.17 \pm 0.06 ^{ac}	0.85 \pm 0.07 ^{bd}	0.14 \pm 0.01 ^{bd}
AR1	0.55 \pm 0.03 ^{ad}	0.72 \pm 0.05 ^{bd}	0.79 \pm 0.03 ^{ac}	0.85 \pm 0.02 ^{bc}
MS	0.26 \pm 0.01	0.27 \pm 0.01	0.31 \pm 0.02	0.32 \pm 0.01
r _{bt}	0.47 \pm 0.02 ^a	0.54 \pm 0.01 ^b	0.44 \pm 0.03 ^a	0.55 \pm 0.01 ^b
EPS	0.94	0.96	0.93	0.97
Period EPS > 0.85 ^c	1900–2009	1732–2009	1890–2009	1718–2009
PC1 (%)	42.16	45.89	46.77	49.58

^a Different letters indicate significant ($p < 0.05$) differences between age groups (a,b) and within each site for age group (c,d) (Mann-Whitney *U* test; Quinn and Keough 2002).

^b Variables abbreviations: raw ring-width data: SD, standard deviation; AR1, first-order autocorrelation; residual chronologies: MS, mean sensitivity; r_{bt}, mean correlation among trees; EPS, expressed population signal; PC1, variance in first eigenvector.

^c Chronology segments with EPS > 0.85 were considered as well replicated following Wigley *et al.* (1984).

chronologies were developed using the ARSTAN program (Cook and Holmes 1984), which removes the biological trends in radial growth as trees thicken. Tree-ring widths were converted into growth indices with stable mean and variance, by dividing observed values by expected values, estimated using a spline curve of 50 years to keep 50% of the variability (Cook and Peters 1981). Autoregressive modeling was performed to remove temporal autocorrelation and to generate residual indices at the individual tree level, which were used in further analyses. Finally, a biweight robust mean was used to compute mean residual chronologies for each age group and study site. Among the developed individual tree chronologies, we considered only those that covered the common time period 1917–2009. As a first step in the analysis, we used rotated principal components analysis (PCA) to display the major sources of variation in the tree-ring indices and to test for groups of trees with similar age and year-to-year variation in growth (see Supplementary Material).

The following dendrochronological statistics (see Table 2) were also calculated for the common interval 1917–2009 to compare growth features between the two age groups in both study sites (Fritts 2001): mean and standard deviation (SD) of the raw tree-ring width data, first-order

autocorrelation of tree-ring width raw data (AR1), the mean sensitivity (MS) of residual series, the mean between-tree correlation (r_{bt}) of residual series, the expressed population signal (EPS) of residual width series (chronology segments with EPS over 0.85 were considered reliable and used in growth-climate analyses following Wigley *et al.* 1984), and the percentage of variance explained by the first principal component (PC1).

Climate Data

We used local climatic data taken from the meteorological stations located nearest to the study sites provided by the Spanish Meteorological Service (AEMET 2011). These climatic data were used to quantify trends and analyze annual and monthly climatic variables (mean, maximum and minimum temperatures, precipitation, and drought severity) and to assess the climate-growth relationships in each study site and for each age group. We obtained two climatic datasets covering the period 1948–2006 using data from 13 and 6 local meteorological stations for the Mágina and María study sites, respectively (Supplementary Material). The mean distance between sampled stands and meteorological stations was *ca.* 10 km (Figure 1). Given the scarcity of local meteorological

stations with long and robust climatic records in the sampled areas, two regional series were created by using linear regressions based on local interpolations of the nearest stations (Fernández Cancio and Manrique Menéndez 1997). The stations of Huelma (Mágina, 1084 m) and María (María, 1190 m) were considered as reference stations (Supplementary Material).

Finally, we calculated a local drought index (DRI, in mm) using monthly mean temperatures and precipitation for each site (Sánchez-Salguero *et al.* 2012a). The DRI index was defined as the difference between the cumulative precipitation and the estimated potential evapotranspiration (estimated as a function of monthly mean temperatures and geographical latitude, following the formulation of Thornthwaite) (Thornthwaite and Mather 1957) from August of the previous year until September of the year of tree-ring formation, because water availability during this 14-month period determines radial growth of the studied species (Richter *et al.* 1991). Lower (higher) DRI values indicate dry (wet) conditions (Bigler *et al.* 2006).

Climate-Growth Relationships

To quantify the growth responses to climate we calculated correlation and bootstrapped response functions using residual chronologies as dependent variables and local monthly climatic variables as independent ones. Growth indices and monthly climatic series were correlated from the previous May up to October of the year of tree-ring formation following Richter *et al.* (1991). Growth-climate relationships were quantified using Pearson correlation coefficients and bootstrapped response function coefficients (Fritts 2001). To assess the temporal stability of growth-climate associations, moving correlations were also obtained for the residual chronologies based on only monthly selected mean maximum temperatures and DRI. We calculated 25-year moving correlations for the period 1901–2005 considering climatic variables highly related to growth. Correlation and response functions were calculated using the program Dendroclim 2002 (Biondi and Waikul 2004).

RESULTS

Climatic Trends: Increased Aridity

We found significant increases (+1.6°C in Mágina and +1.72°C in María) in mean annual maximum temperature in both study sites, and a significant reduction of annual precipitation (−135 mm in Mágina and −44 mm in María), this trend in aridity being particularly pronounced in Mágina (Figure 2A, B). No long-term trend was detected in the drought index (DRI) but years with negative DRI values (*i.e.* dry years) were more frequent during the last half of the 20th Century as compared with the first one (Figure 2C).

Growth Patterns: Higher Common Growth Variability in Old than in Mature Trees

The longest series dated back to A.D. 1541 at María and the longest one reached the year 1613 in Mágina (Figure 3, Table 2). In both sites we found EPS values higher than 0.92. We found synchronous growth reductions in both study sites in the 1770s, 1800s, late 1940s, 1960s, 1980s, 1990s and 2000s, usually corresponding to droughts. The 20th Century presented a much higher frequency of both very wide and narrow rings as compared with the 19th Century (Figure 3).

In the two study sites the old trees showed higher first-order autocorrelations and a relatively higher common variance and mean correlation among trees than mature trees (Table 2). Mean sensitivity did not differ between age groups.

Age-Dependent Growth-Climate Associations

Low maximum temperatures and high precipitation levels in the previous September enhanced *P. nigra* growth in María, and higher growth in Mágina was linked to warm previous December, particularly in the case of old trees (Figure 4). Mágina old trees showed a stronger response to wet conditions in May of the year of growth than mature trees. Regarding the temperature effects on growth, old trees always exhibited a greater response than mature trees excepting the negative effect of the previous September maximum temperatures in the case of María. In this

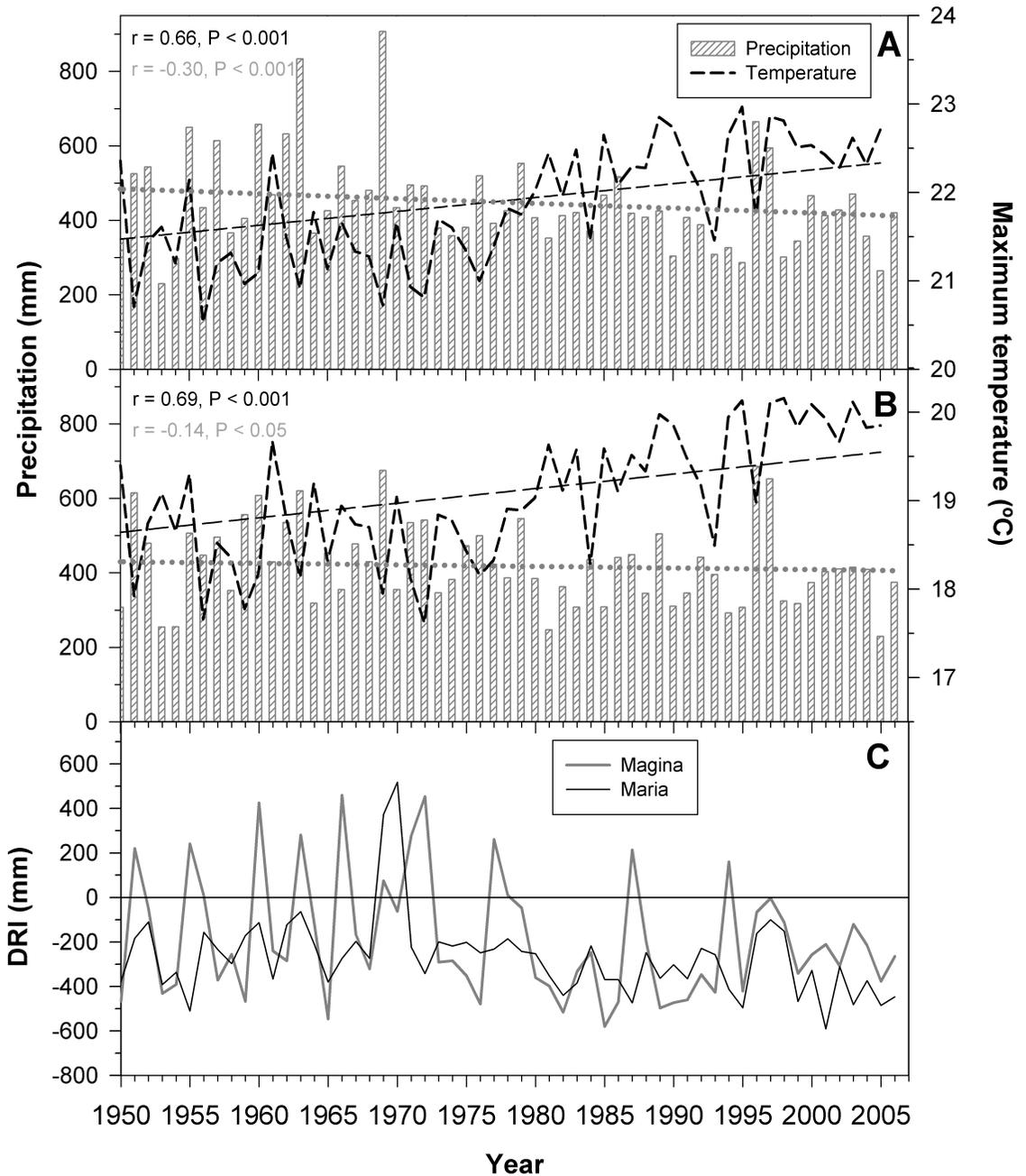


Figure 2. Climate trends in the two study sites (A, Mágina; B, María) for the period 1950–2006 for total annual precipitation, mean annual maximum temperature and drought severity (C) based on a drought index (DRI; positive and negative values correspond to wet and dry conditions, respectively). Climatic data were based on the local meteorological stations from Spanish National Meteorological Agency (see Supplementary Material). Correlation coefficients of the linear trends of each variable are also displayed in graphs A and B (temperatures = black lines and letters = precipitation, grey lines and letters).

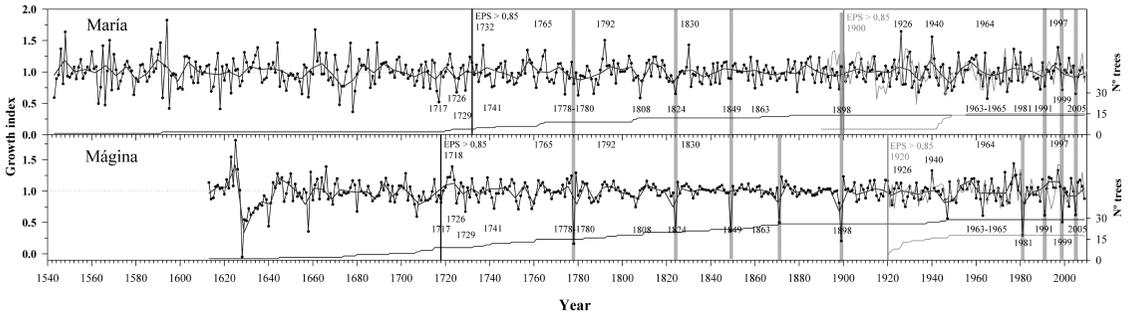


Figure 3. Residual tree-ring width chronologies (old trees = black lines; mature trees = grey lines) of the María and Mágina *P. nigra* study sites and corresponding sample size (number of trees, right y-axis). A five-year mean moving average is displayed over the old-tree chronology to illustrate low-frequency variability in growth. Abrupt and synchronous growth declines can be observed in both chronologies and they are illustrated using vertical blue bars. The intervals when the chronologies were reliable for each age group (EPS > 0.85) are also indicated.

site, tree growth responded positively and more strongly to the previous autumn and current spring drought severity than in Mágina, irrespective of tree age (Table 3).

Temporal Instability in Growth-Climate Relationships

The positive influence of the mean maximum March temperature on growth declined in both study sites during the second half of the 20th Century, whereas the relevance of February maximum temperature as a growth driver has either remained stable in Mágina or has increased in María, particularly affecting the old trees (Figure 5). The importance of water availability during the previous autumn (María) or the current spring (Mágina) as a driver of growth has steadily risen during the past half century, particularly in the case of mature trees from María.

DISCUSSION

The viability of relict southern drought-stressed pine populations at the southern limit of their geographical distribution is determined primarily by regional precipitation, but this response to water supply is also contingent on local factors, such as site conditions, and tree age (Camarero *et al.* 2013; Sánchez-Salguero *et al.* 2013). We detected an increasing sensitivity of relict *P. nigra* trees to drought regardless their age (Linares *et al.* 2013).

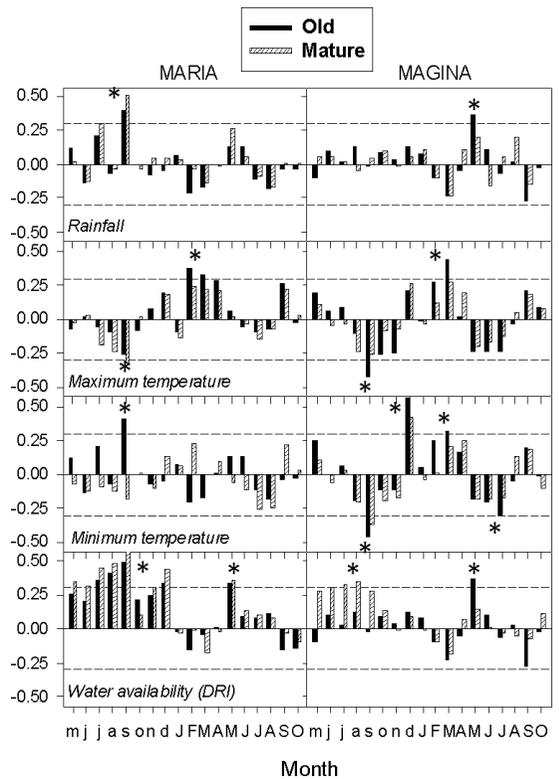


Figure 4. Pearson correlation coefficients calculated between *P. nigra* radial growth (ring-width indexes) and the monthly climate variables (mean maximum and minimum temperatures, total precipitation, drought index) for the 1950–2006 period in María and Mágina study sites. Growth is related with climate data from the previous (months abbreviated by lowercase letters) and current (months abbreviated by uppercase letters) years, the current year being that of tree-ring formation. The significance levels ($p < 0.05$) of correlation coefficients are indicated by dashed horizontal lines, whereas significant bootstrapped regression coefficients are indicated by asterisks.

Table 3. Comparisons of climate-growth relationships (r , Pearson correlation coefficients; levels of significance (ns = not significant; $*0.05 < p \leq 0.10$; $**0.01 < p \leq 0.05$) between old and mature trees calculated for the two study sites. Individual correlations (mean \pm SE are presented) were calculated between ring-width indices and annual climatic variables (T_{\max} = mean maximum temperature; T_{\min} = mean minimum temperature; DRI = drought index). The individual correlations were then compared between age groups within each site, and between sites irrespective of tree age, using one-way ANOVAs (F and p statistics are reported). The last column indicates the comparisons between sites irrespective of tree age (F and p values are reported in the same column).

Climatic Variable	Site	Age Group	r	Age Groups		Sites	
				F	p	F	p
T _{max}	María	Mature trees	0.12 \pm 0.02*	0.82	0.04	5.21	0.03
		Old trees	0.21 \pm 0.01*				
	Mágina	Mature trees	-0.15 \pm 0.02*				
		Old trees	-0.40 \pm 0.01**				
T _{min}	María	Mature trees	0.13 \pm 0.01*	4.19	0.04	7.20	0.02
		Old trees	0.21 \pm 0.02*				
	Mágina	Mature trees	0.08 \pm 0.03 ^{ns}				
		Old trees	0.12 \pm 0.01*				
DRI	María	Mature trees	0.28 \pm 0.02**	0.84	0.02	14.15	0.01
		Old trees	0.20 \pm 0.03*				
	Mágina	Mature trees	0.18 \pm 0.03*				
		Old trees	0.09 \pm 0.02 ^{ns}				

The dendroclimatic potential of *P. nigra* in Spain has been illustrated before (e.g. Creus 1998; Fernández *et al.* 1996; Andreu *et al.* 2007). However, the *P. nigra* chronologies presented in this study are new for the area studied in southeastern Spain and represent a new contribution helpful to the future

use of this species for dendroclimatological reconstructions of drought in the Western Mediterranean Basin. Our climate-growth analyses are consistent with other Iberian *P. nigra* chronologies (Martín-Benito *et al.* 2008). Further, most of the periods of growth reduction described here correspond to

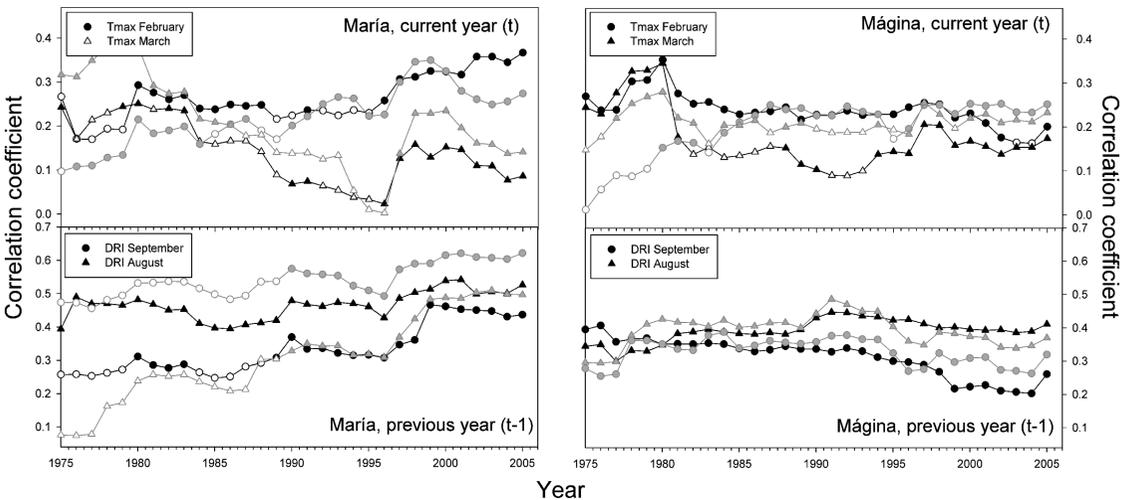


Figure 5. Moving correlations (Pearson coefficients) calculated between residual tree-ring width indexes for mature (grey lines and symbols) and old (black lines and symbols) trees of María and Mágina *P. nigra* sites and selected monthly climate variables (T_{\max} = mean maximum temperature, DRI = drought index) of the previous year ($t-1$) and the year of tree-ring formation (t). The coefficients were calculated for 25-year periods and the ticks in the horizontal axis show the last year of each period (e.g. the tick placed in 1975 corresponds to the 1951–1975 period). The filled symbols correspond to significant ($p < 0.05$) correlation coefficients.

droughts historically documented in southern Spain by Rodrigo *et al.* (1999).

The water availability and temperature conditions during the previous autumn and winter and also during early spring of the year of tree-ring formation were the main climatic drivers of *P. nigra* radial growth, though these factors did not have equal importance at the two sites and were age-dependent. This observation is consistent with other dendroclimatological studies of nearby *P. nigra* populations showing response to prior autumn and winter temperatures (Camarero *et al.* 2013; Sánchez-Salguero *et al.* 2012a, 2013). 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 that 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 (Pasho *et al.* 2011; Camarero *et al.* 2013).

This pattern is in agreement with similar positive influences of spring temperature on growth observed in southern Europe (Lebourgeois 2000; Linares and Tiscar 2011). Conifers are able to photosynthesize during winter, thus mild temperatures in late winter may enhance availability of carbohydrates synthesis that can be allocated for cambial growth in spring (Gimeno *et al.* 2012). Further, wet and mild conditions in spring may stimulate cambial dynamics or induce an earlier cambial reactivation, thereby resulting in increased production of earlywood and enhanced hydraulic conductivity (Camarero *et al.* 2010). 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 (Ritcher *et al.* 1991). Recharging 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 (Camarero *et al.* 2013).

In autumn, growth in the most xeric María site may be favored by the combination of wet (late summer storms) and warmer conditions through an extended growing season. The annual precipitation in this site is far below (354 mm) the amount of precipitation in the Spain distribution

core of *P. nigra* (ca. 550 mm), and it may represent the lowermost limit of drought tolerance for the species in the Iberian Peninsula (Martín-Benito *et al.* 2010; Sánchez-Salguero *et al.* 2012a). The fact that our dendroclimatic analyses did not reveal a strong radial growth response to summer precipitation may be explained by the very scarce or even absent summer precipitation at those locations. However, hot and dry summers may also increase drought stress indirectly in autumn and constrain radial growth (Figure 4).

The unstable relationships observed between growth and February–March temperatures indicate divergent responses, particularly during the late 20th Century. These trends reflect the observed climatic differences between the least xeric site (Mágina) and the driest one (María). In the Vienna Basin, Leal *et al.* (2008) also observed that *P. nigra* decreased its responsiveness to spring conditions. In short, our study suggests that current-year winter and spring temperatures and precipitation, as well as drought severity, were particularly important factors for determining radial growth of relict black pine populations in southern Spain (Camarero *et al.* 2013).

The radial growth of mature *P. nigra* trees was more sensitive to precipitation and drought stress (DRI) during the previous autumn and current spring than that of old trees, showing that growth–climate associations were age-dependent in these relict stands, and not size-dependent as suggested by other studies (Mérian and Lebourgeois 2011), but in contrast to Linares *et al.* (2013). The effect of age *per se* on growth has been previously discussed (Mencuccini *et al.* 2005). Mature trees may have less well-established root systems and more restricted access to the deeper mineral soil layers and water reserves than old trees, making the former more sensitive to drought stress than the latter (Rozas *et al.* 2009). In addition, old trees may show more water storage capacity in their stems than mature trees, which may imply a lower vulnerability to water shortage in old trees. These results are consistent with the significant link between spring climatic conditions and tree-ring growth rates observed in *P. nigra* populations (Richter *et al.* 1991; Linares and Tiscar 2011), which may result in a longer growing season providing a comparative

advantage for old trees. Another potential age-dependent growth difference in *P. nigra* was the fewer significant correlations obtained between temperatures and growth in the old trees compared to the mature trees. Old trees may show a strong positive response to temperature caused by an earlier age-dependent response of growth to warmer spring conditions (Rossi *et al.* 2008).

Relict *P. nigra* populations in Southern Spain are probably experiencing an increasing warming-induced drought stress in recent decades, which has proved to be forcing recent decline episodes (Sánchez-Salguero *et al.* 2012b, 2013). One of the potential physiological causes for age-related growth decline in trees is associated with water limitations caused by potential hydraulic restrictions. Our results show site- and age-related differences in the growth responses of relict *P. nigra* forests to regional climate, which locally may modulate the persistence of these populations and their responses to additional stressors.

CONCLUSIONS

Relict *P. nigra* populations dominated by mature individuals (age ≤ 100 years) and subjected to dry conditions would likely respond negatively to decreased precipitation, whereas those dominated by old trees (age > 100 years) would respond more to rising temperatures. We showed that age is an important modulating factor of tree growth responsiveness to climate and should be included in models attempting to predict how relict tree populations will react to climate warming at local and regional scales. A way to forecast drought-induced growth decline in *P. nigra* would be to monitor relict populations subjected to xeric conditions as compared with others growing under mesic conditions in the core of the distribution area. However, local contingent factors such as site (*e.g.* topography, soil type) and tree features (*e.g.* competition, stand structure) may greatly modify these responses. To solve such questions is particularly important for managing the circum-Mediterranean mountain pine woodlands because they are expected to be more vulnerable to rising temperatures and increasing aridity than in temperate areas.

ACKNOWLEDGMENTS

This project was funded through DIVERBOS (CGL2011-30285-C02-02) and INIA-RTA (RTA2010-00065-00-00). R. Sánchez-Salguero acknowledges a FPU (Formación de Profesorado Universitario) grant (AP2007-04747) (Ministerio de Educación, Spain). We also acknowledge the financial support from University of Córdoba-Campus de Excelencia CEIA₃ and AEMET (Agencia Estatal de Meteorología) for providing meteorological data. We thank Francisca de la Hoz and Angela Merino for their support during field works, and R. Arias for his assistance in the laboratory. J. J. Camarero thanks the support of ARAID and Globimed.

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Received 2 April 2013; accepted 9 April 2014.

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