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ORIGINAL PAPER

Dendroecological analysis of relict pine forests in the centre of the Iberian Peninsula

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Abstract *Pinus nigra* subsp. *salzmannii* is found in the east and centre of the Iberian Peninsula, in the south of France and in North Africa. This subspecies occupies the westernmost position of the species' general range. The persistence on the Iberian Peninsula of very long-lived specimens of *Pinus nigra* subsp. *salzmannii*, along with their sensitivity to climate, has drawn the attention of many researchers, but to date the importance of dendroecological studies relating to conservation of biodiversity or the genetic resources of this taxon had not been stressed. In the present paper we use dendroecological methods to analyse the relict pine forest in Navalacruz, an interesting and endangered genetic forestry resource on the northern slopes of the Gredos mountains (in Spain's Central System Range) at the subspecies' south-western global limit. This forest provides a prime example for demonstrating the potential application of dendroecology for studying the origin, dynamics, local variability, relationships with climate and anthropogenic disturbances of relict forest populations. We dated 93 growth sequences from 47 trees ranging from 1809 to 2006 and we have determined that interspecific competition is the most relevant factor as regards differences in the diameter growth of these trees. Moreover, we detected great variability and numerous common growth disturbances unrelated to climatic oscillations. These quasi-periodic disturbances alternate between suppression and release suggesting continuous management cycles of different intensities. Despite its high level of disturbance, the pine forest presents a certain degree of climatic sensitivity. Comparing with others *Pinus nigra* subsp. *salzmannii* populations, we denoted a temporal grading of the growth response to precipitation that is indicative of differences in the start and length of the vegetative period. Furthermore, we compiled different dendroecological and palaeobiogeographical data to demonstrate that this dense, homogeneous and relatively younger *P. nigra* population is of an indigenous nature. This study aims to

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provide data for improved management and conservation of this exceptional and highly endangered bastion of biodiversity.

Keywords *Pinus nigra* subsp. *salzmannii* · Dendrochronology · Spain · Relict · Genetic resource · Conservation

Introduction

Pinus nigra originally occupied a large area throughout the Mediterranean region. This area was likely fragmented during the succession of glacial and interglacial periods in the Quaternary, which led to microspeciation which resulted in a series of very closely-related taxa (Regato et al. 1991; Price et al. 1998; Shankhar and Lebreton 2010). Among these taxa, *Pinus nigra* subsp. *salzmannii* is found in the east and centre of the Iberian Peninsula, southern France and North Africa, where it constitutes the taxon occupying the westernmost position of the species general range. In Spain it constitutes a borderline element lying between typically Mediterranean and Eurosiberian species (Costa et al. 1997). The bio-geographic amplitude of this species range makes it strategic with regard to analysing recent global changes.

Particularly interesting are the relict populations of *Pinus nigra* subsp. *salzmannii* located on slopes of Spain's Central System where, growing on granites and gneisses (unusual substrates for this subspecies), they represent marginal populations at the species' south-western global limit. The populations comprise small woods or stands, generally at altitudes between 1,400 and 1,600 m; sometimes they form mixed forest together with *Pinus sylvestris*, *Pinus pinaster* or *Quercus pyrenaica*. They present morphological features that differentiate them from other Iberian populations, such as long needles, measuring up to 20 cm, similar to those of the subspecies *laricio*, which also develops upon siliceous substrates (Regato et al. 1992). These relict nuclei are mainly located in two zones in the Central System: in the westernmost area of the Guadarrama mountains and the eastern sector of the Gredos mountains on both the southern and northern slopes (Fig. 1). Many authors consider that these populations have been introduced or simply ignore them (Rivas-Martínez 1963; Sánchez Mata 1989; Sardinero 2004; Tíscar and Linares 2011). Over the last few decades, however, numerous research projects have demonstrated the indigenous nature of these stands of *Pinus nigra* subsp. *salzmannii*, as well as their interest as regards both biogeography and biodiversity conservation. Authors have analysed historical, toponymic, floristic, geobotanic, palynological and dendroecological data, and recently fossil macroremains (Génova et al. 1988; Regato et al. 1992; Rubiales et al. 2007; Génova et al. 2009a). In many cases, these stands comprise old trees, regeneration is limited and fires that continually sweep through the region constitute a constant hazard (Gómez Manzaneque et al. 2005).

Scientific research aimed at protecting marginal populations, particularly relevant for the long-term conservation of genetic diversity and the evolutionary potential of species, has been highlighted as a top-priority issue by Hampe and Petit (2005). On the northern slope of the Gredos mountains the Navalacruz relict pine forest can clearly be differentiated from other populations in the area by its high density and degree of homogeneity (Gandía et al. 2005), as well as the fact that it is the northernmost forest at the lowest altitude in the region. In the historical documentation, this stand was cited for the first time as a "Pine Forest" in 1859 (Icona 1990; García 2009), although the particular species is not mentioned. It was not until half-way through the XX century that this pine forest was

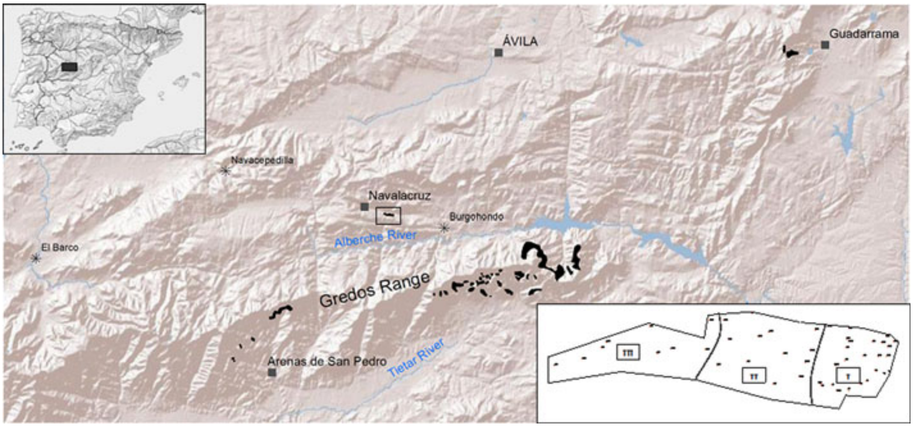


Fig. 1 Location on the Iberian Peninsula of the relict pine forests of *Pinus nigra* subsp. *salzmannii* in the Central System (Guadarrama and Gredos mountain ranges), modified from Regato et al. (1992) and Gómez Manzaneque (2009). *Bottom right box* ecological zones defined in the Navalacruz pine forest (see Table 3) and georeferenced position of each of the trees studied. *Asterisks* location of meteorological stations used; *black squares* significant villages/cities

mapped and defined as a natural formation of *Pinus nigra* (Ceballos 1966) and its recent use as a seed source (Arias 2010) makes it one of the most unique stands in Spain's Central System, as well as an element of great interest for conservation of the taxon's genetic resources. In order to support the forest's use in this sense, however, there is a need for accurate information on its origin and dynamics and the changes it has undergone over the last few centuries; there is also a need to interpret this taxon's potential future in new climatic and environmental scenarios.

In this paper, we address some of the objectives already proposed in previous studies that pioneered the use of dendroecological techniques to show the indigenous nature of relict forest populations (Génova et al. 1988; Génova 1998). Furthermore, we analyse the forest structure, growth oscillations, main events and climatic variables affecting the forest over time. Our overall aim is to assist the management and conservation of this exceptional and highly endangered bastion of biodiversity. Thus, we attempt to add to the few studies using dendroecological techniques to support conservation of relict or endangered forests (Gareca et al. 2010).

Materials and methods

The Navalacruz pine forest

The Navalacruz pine forest (Fig. 1), presenting an area of approximately 40 ha (with 80 trees/ha and a total of 4,000 trees, according to Gandía et al. 2005), forms part of Spanish Public Wildlands, number 44; it is bordered by a plantation of *Pinus sylvestris* dating from the 1960s. The substrate comprises granites and the local climate presents characteristics typical of Mediterranean mountains with continental features.

The pine forest is situated at an altitude of between 1,050 and 1,250 m and almost exclusively comprises adult trees, there being very little natural regeneration. The *cascalbo* pine (regional denomination of the taxon referring to its light-coloured bark) is found together with other tree species such as *Pinus pinaster*, which are found at lower altitudes at the foot of the slope; *Quercus pyrenaica*, dispersed throughout clearings in the pine forest and *Fraxinus angustifolia* in ravines. In some areas there are dense formations of certain shrub species such as *Cytisus scoparius*, *C. multiflorus*, *Rubus* spp., *Crataegus monogyna* or *Juniperus oxycedrus*, whereas in others there is a noteworthy presence of the perennial grass *Festuca elegans*. Although the neighbouring *Pinus sylvestris* plantations have been logged for wood, the *Pinus nigra* forest has remained uncut for the last 20 years. Moreover, there has been a notable decline in traditional grazing in the last few decades, as witnessed by the high density and volume of the herbaceous and shrub strata (Moya 2008).

Climatic records

In the region there are a number of meteorological stations with these generally presenting short, incomplete records. We created a single monthly record from the available data to represent the climate at the sampling site (see Table 1). We compiled the temperature series from the El Barco (1933–1973) and Navacepedilla stations (1974–2006) having checked the homogeneity of both datasets. The precipitation record was mainly based upon data from the Burgohondo station (this was closest to the Navalacruz pine forest, although it lacked temperature data). This station also lacked data from the 40, 50 and 60s of the last century and from the year 2000. In order to reconstruct the missing data, we used specific regression functions for each month based on the record from El Barco station, with this verified by the high r^2 coefficient: 0.78 (Moya 2008); whereas, for 2000, we used the data from the Navacepedilla station. Thus, we constructed a monthly continuous climatic record of over 70 years.

Dendroecological analysis

The dendroecological sampling method chosen involved randomly selecting healthy adult trees representing the ecological diversity of the area previously identified by means of cartography, satellite images and field trips. Using a 40-cm-long standard Pressler borer, we extracted 94 samples from 47 trees (2 per tree, in opposite directions) during the month of July 2007. The samples were taken at normal height (approximately 1.30 m from the ground) and we noted the principal dendrometric and ecological data from each selected and georeferenced tree.

Once the samples were dried and prepared in transverse sections, we measured the rings (with an accuracy of 1/100 mm) with the LINTAB measuring system and associated TSAP software (Rinn 2005). Tree age was estimated directly when any of the extracted samples contained the pith and indirectly when the samples were incomplete, with the techniques described by Rozas (2004). We conducted the synchronisation and subsequent dating of

Table 1 General characteristics of the meteorological records employed in our study

Meteorological stations	Latitude/longitude	Altitude (m)	Temperature	Precipitation
El Barco	40°21′N 5°31′W	1,007	1933–1983	1931–1983
Navacepedilla	40°29′N 5°11′W	1,250	1974–2006	1965–2006
Burgohondo	40°25′N 4°47′W	928	–	1931–2000
Reconstructed	–	–	1933–2006	1931–2006

the growth series obtained by means of several visual, graphic and statistical techniques (Cook and Kairiukstis 1990) and checked these using COFECHA software, a program for crossdating and measurement quality control (Holmes 1992a). We obtained the local chronology by standardising the individual sequences with spline models and applying the robust mean with the programme ARSTAN (Cook and Holmes 1996).

We analysed the dated growth sequences using the programme JOLTS (Holmes 1999) to detect changes in tendency or brusque medium-frequency oscillations appearing synchronously in numerous trees and determined the occurrence, coincidence and characteristics of these changes in tree growth (release and suppression).

According to Schweingruber (1996), brusque medium-frequency changes in growth trends may be related to numerous disturbances: floods, avalanches, volcanic eruptions, mudslides and rock falls, pests or diseases, fires or changes in management. If changes affect a large number of trees and other factors cannot be identified, it is very likely that these changes are indicators of the effects of forestry treatments (Lorimer and Frelich 1989) involving past management and canopy history, as has been determined in some Spanish forests (e.g. Rozas 2004; Génova 2007).

We determined 'pointer' years using the LRM programme (Holmes 1992b). This programme selects the years in which the growth values of rings are differentiated from the immediately previous one in a proportion greater than, or equal to, 20 %. We only selected pointer years over 75 % of the series analysed.

Furthermore, the relationship between the standardized chronology and climatic data was determined by means of response-functions programs: RESPO (Holmes and Lough 1999) and DENDROCLIM2002 (Biondi and Waikul 2004). We chose to analyse the relationship between mean temperatures and total monthly precipitation in the period ranging from August of the previous year to October of the current one. This period is somewhat longer than the ones used in previous studies analysing the relationship between *Pinus nigra* subsp. *salzmannii* and climate in Spain's Central System (Génova and Fernández 1999), but it is similar to the one employed in other regions of Spain (Andreu et al. 2007; Linares and Tiscar 2010).

Results

Dendrometric structure of the pine forest and chronology

The maximum age, estimated according to the number of growth rings, is 198 years and the minimum age is 87 years. The central age classes contain the highest number of trees (91 % from 100 to 180 years of age and approximately 70 % from 120 to 160 years); since the extremes contain fewer trees, the age distribution model therefore approaches a normal distribution (Fig. 2a). Most trees presented a DBH (diameter at breast height) of 30–80 cm and only one individual exceeded 100 cm, forming an asymmetric distribution (Fig. 2b). We also analysed the relationship between age and DBH (Fig. 2c): the r^2 obtained shows that there is no close relationship between the variables.

We dated 93 growth sequences ranging from 1809 to 2006. Average tree-ring width is 1.72 ± 0.74 mm and we distinguished two well-differentiated growth stages: a young and middle growth stage lasting 100 years (with an average ring width of 1.96 mm) and a subsequent mature stage in which the average width falls to 1.22 mm (Fig. 3; Table 2). The dated sequences were standardized and averaged in a local chronology, the most interesting characteristics of which are shown in Table 2.

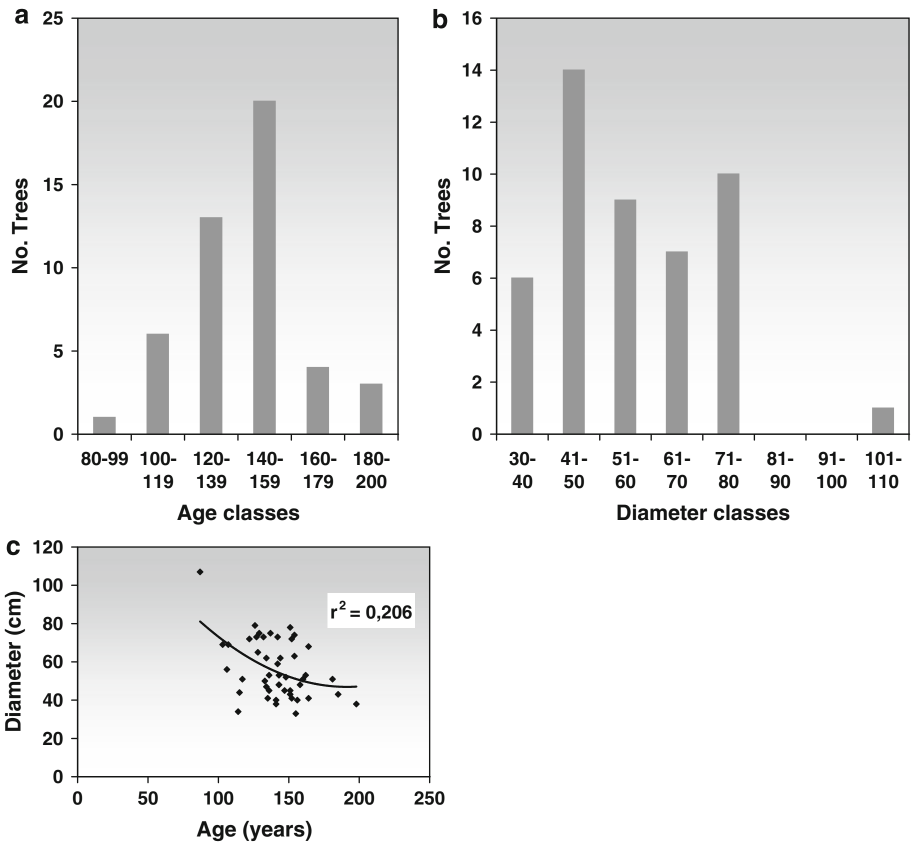


Fig. 2 **a** Age classes, **b** diametric classes and **c** regression between age and diametric classes defined for the Navalacruz pine forest

Spatial variability

We studied spatial variability by comparing the different ecological zones representing the diversity of the pine forest. We defined three zones with the use of cartography, satellite and field images, demarcated according to forest density (D), shrub and herbaceous-strata density (DSH) and stoniness (S) of the substrate (Table 3; Fig. 1). Figure 4 shows average tree growth in each zone.

Considering the results obtained, we have determined that interspecific competition is key to the development of these pines: zone III (with the lowest tree density) presents maximum mean growth rates (although the shrubs, herbaceous and stoniness density is greater here), in relation to the I and II more densely forested zones. Thus, greater competition (less spacing between trees) involves less diametric growth, whereas less competition (more spacing) is related to a higher growth rate. By contrast, competition with scrubland does not appear to significantly affect the trees' growth. We performed this analysis at three different altitudinal zones (results not shown), but we observed no divergence between the growth values measured in the different zones, which appears to indicate that altitude does not constitute a relevant factor for diameter growth.

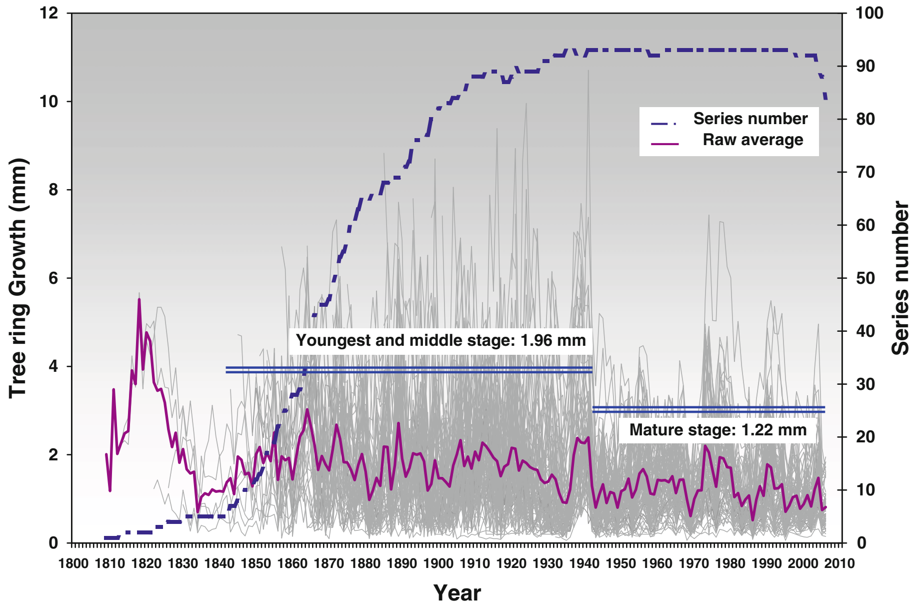


Fig. 3 Dated tree ring growth sequences, raw average chronology and number of samples replicating each year

Table 2 Characteristics of Navalacruz local chronology

Site name	Nt	Ns	M	SD	Ms	TS (1)	TS (2)	EPS	SNR	VFE (%)
Navalacruz	47	93	1.72	0.74	0.34	1809–2006	1860–2005	0.85	6.02	33.74

Nt number of trees, *Ns* number of sequences, *M* mean value of tree ring (mm), *SD* standard deviation, *Ms* mean sensitivity, *TS (1)* complete time span, *TS (2)* time span in which EPS > 0.85, *EPS* expressed population signal, *SNR* signal to noise ratio, *VFE* variance in first eigenvector

Temporal variability: releases, suppressions and pointer years

We detected a notably high number of common disturbances, both with regard to growth suppression, in situations of intense competition between trees associated with very dense forest formations, and to growth release corresponding to increased growth resulting from a decline in competition. Over the 1860–2005 period there were 12 periods of release and suppression represented by over 40 % of the individual series, twice the 20 % limit indicating generalised forestry treatment proposed by Lorimer and Frelich (1989). A total of 6 growth suppression periods (1873–1881, 1892–1897, 1914–1919, 1922–1930, 1940–1946, 1978–1983) and another 6 release periods (1883–1889, 1902–1909, 1933–1938, 1950–1954, 1970–1975, 1987–1990) succeeded each other in a quasi-cyclical fashion. Furthermore, in the decade 1935–1945, over 60 % of the sequences synchronously pay witness to a noteworthy release followed by a period of suppression and, in the 1970–1990 period, there was a consecutive period of release, suppression and finally release, with several extremes which can also be seen in over 60 % of the growth sequences (Fig. 5).

As for the pointer years, particularly negative values appear in 1881, 1897, 1943, 1969, 1986, 1995 and positive values in 1938, 1941, 1973 and 1977.

Table 3 Ecological zones defined in Navalacruz

Zones	D	DSH	S	N	Rm	Am	M
I	95	Low	Low	25	25 ± 5.7	145 ± 24	1.34 ± 0.46
II	32	Medium	Medium	13	28 ± 6.8	143 ± 13	1.50 ± 0.65
III	16	High	High	9	37 ± 6.4	128 ± 17	2.26 ± 0.80

D density (no. of trees/ha), *DSH* density of shrub and herbaceous strata, *S* stoniness, *N* number of trees studied, *Rm* mean radius, *Am* mean age, *M* mean value of tree ring (mm)

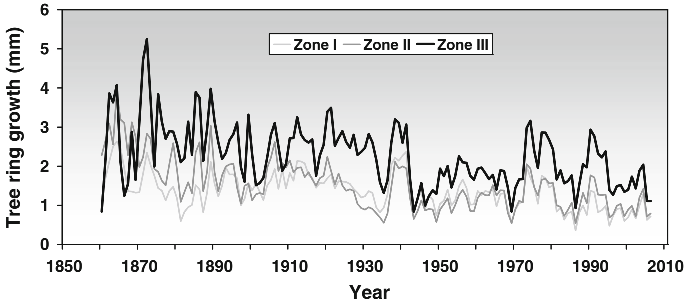


Fig. 4 Average tree ring width series in the three ecological zones determined. Table 3 shows the characteristics of each zone

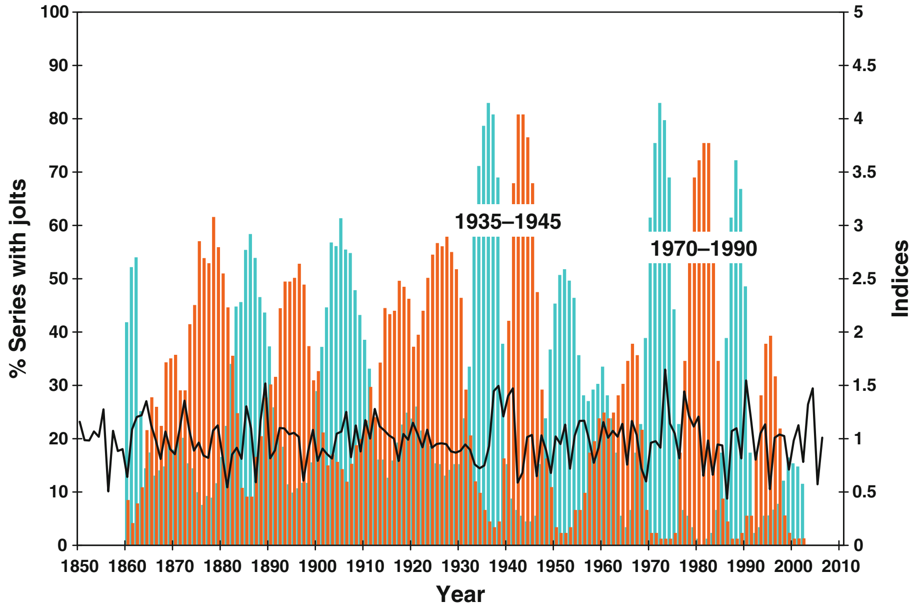


Fig. 5 Percentages of standardised tree-ring growth series indicating changes in medium-frequency trends (the *blue columns* represent suppressions and the *orange ones* represent release) and local residual chronology (*solid black line*). (Color figure online)

Climate and growth-climate relationship

The reconstructed climatic record for the zone supplied temperatures covering 74 years (1933–2006) and 76 years of precipitation (1931–2006). These data are indicative of a Mediterranean climate with continental features characterised by an average temperature of 11.5 °C, a mean annual precipitation of 554 mm with a 2-month period of hydric deficit (July and August).

Analysing the mean temperature variability throughout the analysis period, we delimited two periods (Fig. 6). From the start of the record to the end of the 1960s the mean annual temperature was more or less stable and homogeneous. Subsequently, mean annual temperature fell sharply during the first five-year period in the 1970s, with the most notable minimum values in 1971 and 1972 (lower than the mean value by over 2 SD—standard

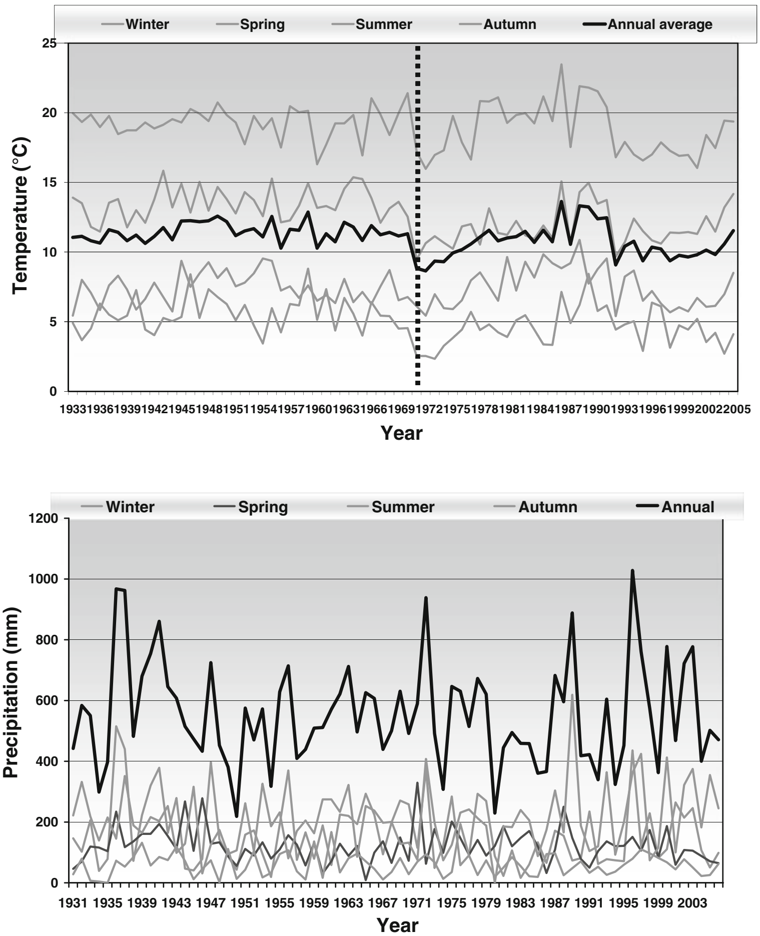
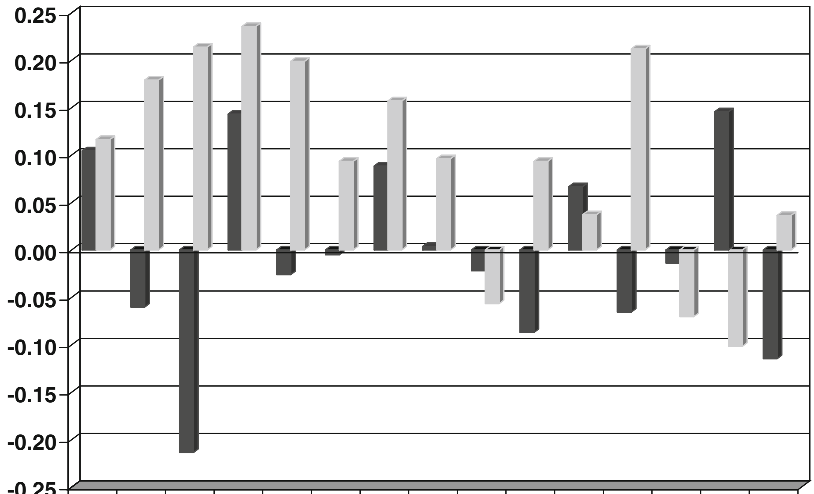


Fig. 6 *Top* temporal variability of seasonal and annual mean temperature in the Navalacruz reconstructed record. The *broken line* delimits the two periods determined for temperatures by their different characteristics. *Bottom* temporal variability of seasonal and annual precipitation in the Navalacruz reconstructed record



	Ago	Sep	Oct	Nov	Dic	Ene	Feb	Mar	Abr	May	Jun	Jul	Ago	Sep	Oct
Temperature	0.1	-0.1	-0.2	0.14	-0	-0	0.09	0	-0	-0.1	0.07	-0.1	-0	0.15	-0.1
Precipitation	0.12	0.18	0.21	0.24	0.2	0.09	0.16	0.1	-0.1	0.09	0.04	0.21	-0.1	-0.1	0.04

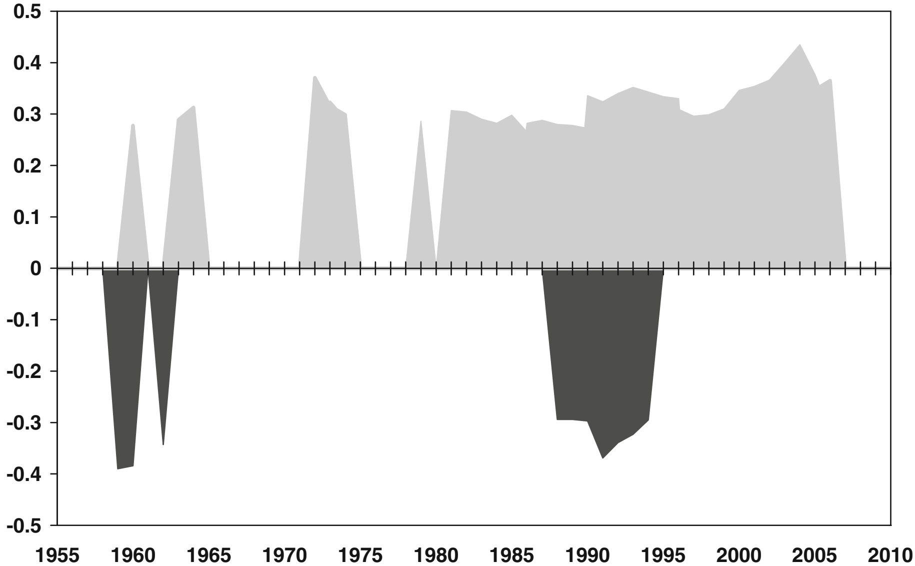


Fig. 7 *Top* response function of the Navalacruz chronology to monthly precipitation and temperature. *Bottom* moving response functions of the main significant factors: Autumn precipitation (*light grey*) and October temperature (*dark grey*)

deviations). This was followed by hot years in the second five-year period in the 1980s and the first years of the 1990s, with values higher than the mean by over 2 SD in the years 1987, 1989 and 1990. Finally the last decades present values generally lower than the mean.

Both annual and seasonal precipitation are generally more variable than temperatures, and can be divided into two wet periods: 1936–1943 (with maxima in 1936 and 1937) and 1996–2003 (with the maximum of the whole record in 1996), together with an additional pluviometric maximum in 1972. The driest periods were: 1944–1960 (with a minimum in 1950) and 1980–1986 (with a minimum in 1980), together with other minima in 1934 and 1974 (Fig. 6).

We found no relationship between the oscillations of these climatic variables and growth release and suppression periods in the Navalacruz pine forest. As regards response functions, the amount of variance explained by the model is 34 % with precipitation explaining more of the variance (27 %) than temperature. The significant meteorological variables (according to the Bootstrap Response, 95 % Percentile Range) and therefore those most affecting the tree-ring widths are, jointly, autumn precipitation from the previous year (from September to December) and precipitation during the months of February and July. As for temperatures, only those in October of the previous year show a negative and significant correlation (Fig. 7).

The moving response functions (Fig. 7), relating to the main climatic factors (Autumn precipitation and October temperature), highlight the temporal characteristics of these relationships. The relation with autumn precipitation starts to be roughly constant after 1980, perhaps because precipitation is somewhat higher from 1980 than in previous periods. As for October temperatures, their negative correlation with radial growth was significant only in 1958–1960, 1962 and 1988–1994.

Discussion

The persistence on the Iberian Peninsula of very long-lived specimens of *Pinus nigra* subsp. *salzmannii*, up to 1,000 years, along with their sensitivity to climate, has attracted the attention of many researchers in the last few decades and it is therefore one of the most studied taxa in Spain from the dendrochronological and dendroecological point of view (Génova et al. 2005; Andreu et al. 2007; Fulé et al. 2008; Martín-Benito et al. 2008; Linares and Tiscar 2010). Relict populations in southern France have also been studied (Amodei et al. 2012) quite recently. Some research has highlighted the biogeographic interest of these relict populations (Amodei et al. 2012; Fulé et al. 2008; Génova 2009), but to date the importance of dendroecological studies relating to conservation of biodiversity or the genetic resources of this taxon had not been stressed.

Origin and structure of the Navalacruz pine forest

The Navalacruz pine forest is of special interest from several points of view. This relict pine forest forms part of the westernmost forests of the global range of *Pinus nigra* and its subspecies *salzmannii*, occupying the northernmost position at the lowest altitude in Spain's Gredos mountains and almost exclusively comprises adult trees with no regeneration. Dendroecological analysis shows that it mainly comprises a dominant cohort of 120–160 year-old trees, the maximum longevity of which is approximately 200 years. Despite their apparent homogeneity, it has been demonstrated that age is not correlated with DBH; trees reaching a thickness of over 70 cm DBH can vary by over 60 years and the ones presenting a DBH of 30–40 cm by over 80 years, with this group including the most long-lived specimens. The general lack of correlation between tree age and DBH is common in old-growth natural forests (Parish et al. 1999; Harper et al. 2003; McCarthy and Weetman 2006).

Furthermore, the likelihood of this being an indigenous forest is supported by studies based upon subfossil macro-remains from an area close to the Navalacruz forest in the

Gredos massif. Here, 75 wood macro-remains corresponding to the group *Pinus* gr. *sylvestris/nigra* have been collected, analysed and identified, with one sample coming from the same municipality (Rubiales et al. 2007; Rubiales and Génova 2012). This sample, found on the banks of the Astillero seasonal stream, a tributary of Navalacruz Gorge, has been radiocarbon dated at 860 ± 20 years BP (Rubiales et al. 2007); this macro-remain consisting of 58 rings is the most recent of all fossil remains dated until now in the Gredos mountains. Moreover, a pine cone from a deposit close to the pine forest corresponds exactly with the morphological characteristics of the taxon *Pinus nigra* and has been dated. This pine cone constitutes the first accurate fossil evidence of *Pinus nigra* in the Central System and its age has been estimated at 1,756 ± 25 years BP (Rubiales and Génova 2012). These studies, together with the historical information compiled by García (2009), unequivocally show that the Navalacruz pine forest is a relict fragment, all that now remains of vast pine forests that likely covered the whole region. In addition, the predictive models developed by Benito Garzón et al. (2007) for the Gredos Mountains provide consistency to the existence of this species in nearby areas, both at present and 6 kyr BP.

Study of the differences between the three ecological zones defined in this forest, each fundamentally different with regard to density of forest formation, shows that interspecific competition is the most relevant factor as regards differences in the diameter growth of trees, with this echoing the results found by Piutti and Cescatti (1997) for beech trees in Europe. By contrast, competition with scrubland does not appear to significantly affect tree growth, although it might be affecting regeneration in the last few decades since forestry activities were abandoned (Moya 2008). Similar conclusions were reached in plantations of this taxon of different ages in south-eastern Spain, where it was seen that competition with the dominant scrubland was irrelevant when the trees were over 20 years of age (De Luis et al. 1998).

Disturbances and cycles of use

But why are there no long-lived trees in the Navalacruz pine forest like those existing in other relict populations in Spain's Central System (Génova et al. 2005) or in other Spanish relict multi-aged forests (Fulé et al. 2008)? Figure 8 shows the contrast between the dense, homogeneous forest in Navalacruz, comprising relatively young trees and a nearby relict formation (on the southern slopes of the Gredos mountains), where there are more heterogeneous and longer-lived specimens.

The proximity of the Navalacruz forest to villages inhabited for centuries, along with good accessibility (Fig. 1), enabled us to attribute its tree-age structure to management history. Moreover, our results referring to disturbances in this relict pine forest provide new information on its population dynamics, as well as data on former intensive use. Indeed, during the period in which the number of growth sequences is representative of the population (1860–2005), we detected great variability and numerous common growth disturbances unrelated to climatic oscillations. These quasi-periodic disturbances, alternating suppressions and releases, are suggestive of continuous management cycles of different intensities. Among these, we can highlight the most recent (for which more information exists) such as the release-suppression cycle of 1935–1945 and that of the 1970–1990 period, which involved very intense use.

Génova et al. (2009b) compared the disturbances in the Navalacruz forest with those that occurred in a *Pinus sylvestris* forest of a similar age in the Guadarrama mountains (which also forms part of Spain's Central System). Analysis of the disturbances detected in both forest populations shows very different scenarios with regard to growth dynamics;

Fig. 8 Contrast between two *Pinus nigra* subsp. *salzmannii* populations in Gredos mountains: *left* the dense and relatively homogeneous Navalacruz pine forest; *right* heterogeneous stand with long-lived trees affected by fire on the southern slopes of these mountains

these are much more stable and homogeneous in the *Pinus sylvestris* forest. The differences observed may be related to unregulated management in the Navalacruz pine forest (Moya 2008), compared with the other study case in which a Management Project, and successive revisions thereof, has been enforced for over 100 years (Benso 2007).

The Navalacruz relict pine forest has surely been severely reduced in the last two centuries, as can be seen in the Public Wildlands catalogue of 1859 (Icona 1990), in which it is given the name "Pine Forest" and is described as a population of 200 ha. Different interventions, such as unregulated logging for construction, firewood or *tea* extraction (splinters of very resinous wood extracted from the heartwood of living trees by means of the *desventrado* process—a traditional activity in the Gredos mountains according to García (2009) that eventually increases mortality), have reduced the area of these forests and modified their structure as a result of the demise of the bigger and longer-lived trees.

Growth-climate relationship

Despite its high level of disturbance, the Navalacruz pine forest presents a certain degree of climatic sensitivity which partly reflects the patterns seen in other populations of the same species. Furthermore, the climatic information contained in the trees of this marginal population of *Pinus nigra* subsp. *salzmannii* will prove to be valuable, as it represents a forest at the lowest altitude in the Central System range subject to a Mediterranean mountain climate with continental features.

We detected a high positive incidence of autumn precipitation on growth from the previous year, an infrequent reaction in this taxon. However, the negative effect of October t-1 temperatures is frequent, as has been described by several authors in eastern Spain (Andreu et al. 2007; Linares and Tiscar 2010; Martín-Benito et al. 2008). A prolonged growing season up to September and October likely induces late low-rate photosynthetic activity and respiration, thus reducing the amount of available carbohydrate resources for the following year (Andreu et al. 2007; Fritts 1976). The positive correlation with February precipitation has only previously been mentioned by Génova and Fernández (1999) in the central east of Spain.

The sensitivity of the Navalacruz pine forest to summer drought during the month of July in the year of growth is also significant. As for other relict populations in Spain's Central System (Génova and Fernández 1999), the effect of summer precipitation is brought forward one month, most likely because Navalacruz lies at a lower altitude. On the contrary, the effect of precipitation upon *Pinus nigra* subsp. *salzmannii* is one or two months later in southern France or south-eastern Spain, where tree growth is primarily influenced by May or June precipitation (Amodei et al. 2012; Martín-Benito et al. 2008; Linares and Tiscar 2010). This temporal grading of the growth response to precipitation is indicative of differences in the start and length of the vegetative period in different zones of the Iberian range of *Pinus nigra* subsp. *salzmannii*. Thus, the effects of drought stress are displaced according to altitude or longitude, as demonstrated by Leal et al. (2007) for *Pinus nigra* subsp. *nigra* in the Austrian Alps.

Implications for management

The relict populations of *Pinus nigra* subsp. *salzmannii* in the central region of the Iberian Peninsula face an uncertain future because of their negligible, if any, regeneration. The region's climate is so variable that it is rare to find all the necessary conditions, including rainfall and warm temperatures together with large numbers of pine kernels, vital for the germination of new shoots. In addition, goats have a particular liking for the needles of the *cascalbo* and fires are very frequent in the area (Gómez Manzaneque 2009).

Lack of regeneration appears to be widespread throughout the Iberian range of the species, a fact that for some authors is related to masting (Serrada 2005; Tíscar and Linares 2011). In our specific case, the Navalacruz pine forest in Spain's Central System constitutes a clear example of a low-altitude population that could provide a valuable genetic resource in a warming environment as defined by Hampe and Petit (2005). For this reason it is essential that management measures should be undertaken to increase protection of this enclave and there is vital need for actions aimed at protecting and conserving the area of this taxon. There is a pressing need for in-depth studies of the genetic characteristics of these relict populations and their relationship with other Iberian and western Mediterranean populations.

In order to conserve this autochthonous genetic heritage, it is essential to remove the allochthonous plantations with other subspecies of *P. nigra* near this forest (Gómez Manzaneque 2009). As regards adaptation to global change, forest management should be directed towards thinning of denser plots due to the positive effects on trees' response to climate (Piutti and Cescatti 1997; Martín-Benito et al. 2011). Less between-tree competition means that more resources are available for individual trees. The results of our study suggest that local conditions are very important for growth and regeneration and that a multivariate approach to conservation is desirable. Thus, despite the small size of the area, we propose that interventions be based upon ecological characteristics: in some cases, growth and regeneration may be favoured by selective tree thinning, whereas in other cases, regeneration might be favoured by elimination of some of the scrubland and perennial herbaceous species. A combination of the results of our research with information on regeneration patterns could help improve future efforts for the conservation of this relict forest.

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