

RESEARCH
PAPER



Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests

Juan Carlos Linares¹, J. Julio Camarero² and José Antonio Carreira^{3*}

¹Área de Ecología, Universidad Pablo de Olavide, Carretera de Utrera, Km. 1, 41002 Sevilla, Spain, ²Aragón I+D, Instituto Pirenaico de Ecología, CSIC, Avda. Montañana 1005, 50192 Zaragoza, Spain, ³Área de Ecología, Universidad de Jaén, Campus Las Lagunillas, 23071 Jaén, Spain

ABSTRACT

Aims The combined effects of changes in climate and land use on tree mortality and growth patterns have rarely been addressed. Relict tree species from the Mediterranean Basin serve as appropriate models to investigate these effects, since they grow in climatically stressed areas which have undergone intense cover changes. The aim is to use climate, aerial photographs, stand structure and radial-growth data to explain the mortality and historical patterns of growth of *Abies pinsapo* in the area where this relict species was first protected.

Location Sierra de las Nieves, West Baetic Range, southern Spain.

Methods We assessed variations of tree cover in *A. pinsapo* forests through image analyses of aerial photographs spanning the last 50 years. We sampled 31 stands to assess current altitudinal patterns of forest structure and mortality. We evaluated the relationships between radial growth and regional climate using linear models in three sites at different elevations.

Results Regional warming and a decrease in precipitation were detected. Forest tree cover increased at all elevations from 1957 until 1991, but it afterwards decreased below 1100 m. Currently, the likelihood of tree mortality increases downwards and is associated with dense, closed stands with a low living basal area. In contrast to previous droughts, a sharp synchronized reduction in tree growth, not fully accounted for in linear climate–growth models, occurred at low elevations in 1994–95, but not upwards. It was preceded by a weakening of the negative association between low-elevation growth and water deficit since the late 1970s.

Conclusions The intense densification of *A. pinsapo* forests following strict protection measures in the late 1950s enhanced the vulnerability of climate-sensitive *A. pinsapo* forests to recent drier conditions. Such abrupt land-use changes help to explain recent patterns of mortality and growth decline in low-elevation *A. pinsapo* forests.

Keywords

Abies pinsapo, aerial photographs, climate warming, dendroecology, drought, forest decline, relict species, Spain.

*Correspondence: José Antonio Carreira, Área de Ecología, Universidad de Jaén, Campus Las Lagunillas, 23071 Jaén, Spain.
E-mail: jafuente@ujaen.es

INTRODUCTION

Climatic warming and land-use modifications, two of the most conspicuous components of current global change (Vitousek, 1994), have the potential to profoundly change the distribution and growth of tree populations (Brubaker, 1986). These two components are likely to operate as concomitant stressors on forest ecosystems, making it difficult to disentangle their separate

impacts. Both components influence the distribution of mountain forests in the Mediterranean Basin, since land-use changes during the last century have shaped forest structure and climatic warming is severely affecting the growth of tree species, especially those that are highly sensitive to water stress (Grove & Rackham, 2001; Andreu *et al.*, 2007). The southernmost European mountain forests in Andalusia (southern Spain) might be some of the most vulnerable areas for the loss of tree species due to climatic warming

(Bakkenes *et al.*, 2002). Indeed, most studies reporting on growth changes or shifts in species distribution in Iberian Mediterranean mountains attribute the majority of observed changes to either climate change or land-use alterations, or alternatively cannot disentangle their contributions (Jump *et al.*, 2006).

An important consideration in the analysis of the interactions between changes in climate and land use is that many species ranges are not in equilibrium with the climate because their current distribution was shaped by additional factors such as historical disturbances (Davis, 1984). Disturbances may alter tree cover and stand density, which in turn could affect the responses of trees to climatic stress (Kulakowski *et al.*, 2006). A moderate decrease in logging may lead to an increase in tree cover, stand density and basal area, while maintaining size-class heterogeneity, and lead to gradual self-thinning. However, conservation measures that suddenly exclude any forestry use in the case of over-exploited relict tree populations will significantly enhance tree cover and stand density with poor size-class differentiation. Such a drastic process of forest densification may cause a reduction in the soil-water availability per tree in water-stressed areas, which could predispose those trees to subsequent drought-induced growth decline and cause severe mortality episodes (Bigler *et al.*, 2006).

Relict tree species may serve as a model case for assessing the modulating effects of tree cover and density-dependent factors on the responses of forests to climatic stress. Relict tree species usually form isolated and marginal populations, and are regarded as very vulnerable in the face of climatic oscillations (Davis & Shaw, 2001). On the other hand, they are often selected as target species in conservation politics. However, the long life span of trees somewhat complicates efforts to investigate the dynamics of relict Mediterranean tree populations, which are required to make reliable inferences about their future distribution changes (Camarero *et al.*, 2005). In the case of Mediterranean relict tree species, this conservation effort has resulted in an elimination of traditional uses (e.g. logging, fuel extraction, grazing) with subsequent increases in tree cover within protected areas (Ruiz de la Torre *et al.*, 1994).

To develop the idea that changes in climate and land use interact to affect forest ecosystems, we apply a conceptual framework considering vulnerability to change as a function of the system's sensitivity and its adaptive capacity (IPCC, 2007). We assume that the sensitivity of a forest to a given climate change is mainly determined by its species composition and adaptation to local conditions, and that the correlation between the radial growth of dominant trees and climatic variables can be used as a surrogate of the species intrinsic sensitivity. To consider the interacting effect of land-use change, we propose it can modulate the adaptive capacity of the trees to climate stress, through density-dependent factors related to stand structure. Here we use the term 'adaptive capacity' to mean the ability of a system to adjust to environmental change (including variability and extremes) or to moderate potential damage (IPCC, 2007).

As a preliminary assessment of this model, we focus on the local context of recent symptoms of decline observed in some Spanish *Abies pinsapo* forests. This fir is a Tertiary-relict species, endemic from south-west Spain and northern Morocco. Previous

dendrochronological studies indicate that *A. pinsapo* shows a high sensitivity to water availability in summer (Génova, 2007), which is one of the main growth constraints in the Mediterranean Basin. As a starting point, we hypothesized that current climatic warming might amplify the intensity of such a main stressor. To test this, we calculated long-term climatic regional trends related to water deficit (temperature, precipitation and evapotranspiration). However, the absence of symptoms of decline in historically managed, North African *A. pinsapo* populations led us to consider that changes in land use might be a factor contributing to the explanation of such processes of decline in their Spanish counterparts (Linares, 2008).

In Spain, strict protection measures have been applied since the 1950s to protect the remnants of *A. pinsapo* forests (Ruiz de la Torre *et al.*, 1994). We therefore hypothesized that: (1) this land-use change led to an increase of forest cover and stand density with poor size-class differentiation and, eventually, to stand stagnation; (2) such structural changes in the canopy reduced the average adaptive capacity of the trees; and (3) this increased the vulnerability of the forest to drier climatic conditions, exacerbating recent patterns of mortality and growth decline in low-elevation *A. pinsapo* forests. To test (1) we quantified the historical changes in tree cover in the first-protected areas of *A. pinsapo* forests, described their current stand structure and compared local tree-ring width chronologies, along an altitudinal gradient. As a first approach to evaluate (2) and (3) we report here on temporal trends in non-climatic residuals of radial growth, and on spatial patterns of density and mortality. The main application of this study is the assessment and reconsideration of the effects of current protection measures on the long-term conservation of relict Mediterranean tree species. A description of recent mortality patterns and historical growth trends should provide a reliable evaluation of the effectiveness of conservation measures to protect relict Mediterranean tree species in water-stressed areas under the context of current climate change.

MATERIALS AND METHODS

Tree species

Abies pinsapo (Boiss.) is a relict species belonging to the group of circum-Mediterranean firs mostly restricted to small populations located in coastal Mediterranean mountains (Barbero & Quézel, 1975). At present, *A. pinsapo* is just locally distributed in the Baetic Range (southern Spain) and the Rif Mountains (northern Morocco), mainly on north-facing slopes, 1000 m a.s.l. and higher. In southern Spain, fragmented populations of *A. pinsapo* experienced an expansion following the implementation of conservation measures in the 1950s, such as the cessation of logging and grazing. In this area, *A. pinsapo* occupied c. 724 ha in 1936, c. 1500 ha in 1957, 3027 ha in 1993, and 3956 ha in 2002 (Linares, 2008).

Study sites and field survey

The study was carried out in the eastern distribution limit of *A. pinsapo* (Sierra de las Nieves Natural Park, West Baetic Range,

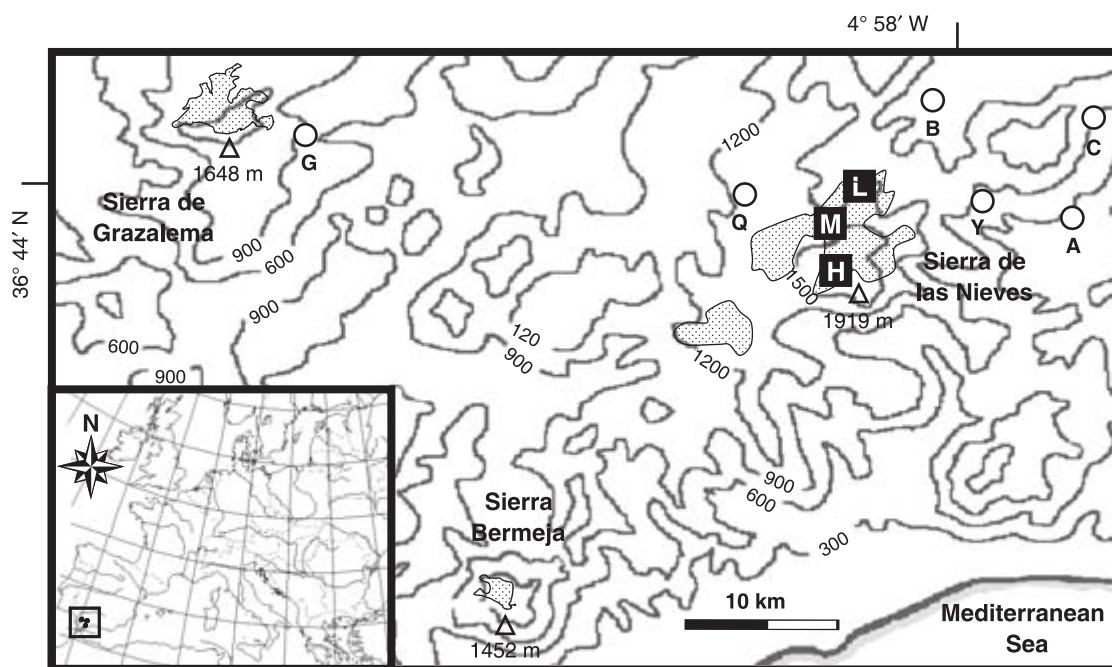


Figure 1 Distribution of *Abies pinsapo* forests in Europe (inset; based on Jalas *et al.*, 1999) and study sites along the altitudinal gradient in Sierra de las Nieves Natural Park, south-east Spain (H, high-elevation site; M, mid-elevation site; L, low-elevation site). The grey areas indicate the approximate *A. pinsapo* distribution area in south-east Spain, and the circles correspond to meteorological stations from which data were collected to compute regional climatic series (site codes are explained in Table 3).

southern Spain), near the Mediterranean coast (36°40'–36°44' N, 04°55'–05°01' W; Fig. 1). We chose this location because: (1) it contained most of the current *A. pinsapo* populations; (2) it was the first where conservation measures were adopted because of public ownership of some forests; and (3) several episodes of decline have been observed there since 1994 (Linares & Carreira, 2006). The study area was defined as the terrain within the perimeter delineated by the presence of *A. pinsapo* along the altitudinal gradient from 1000 to 1700 m that crosses over the Yunquera and Ronda Pinsapo fir forests. The mean annual temperature is 14.7 °C and the annual precipitation ranges from 800 mm in the lower sites to c. 2000 mm in the upper study sites. Rainfall patterns are distinctly Mediterranean, with c. 80% of all the precipitation falling between October and May, followed by a long summer drought.

We recorded tree diameter [considering only trees with diameter at breast height (d.b.h.) > 3 cm], stand density and basal area and recent mortality, using an extensive, stratified random sampling, in equi-frequent classes every 200 m in elevation. We sampled 31 *A. pinsapo* stands in 150-m² plots to estimate several environmental (elevation, aspect, soil type, topography, structure, overstorey and understorey types) and biotic (density and basal area of *A. pinsapo* stumps, living and dead trees) variables. Data on dead trees refer to trees that had died recently, i.e. since the late 1990s according to dendrochronological estimates.

Correlations between stand elevation and total or percentage basal area of dead trees were assessed using the nonparametric Spearman correlation coefficient (r_s). The relationship between elevation and mortality was highly heteroscedastic, and we were

specifically interested in testing whether the likelihood of extreme events (high and low mortality) was related to elevation. Thus, we calculated quantile regressions to extend the inference of the slope to any part of the response variable, independently of the change and variability experienced by the rest of the distribution (Koenker, 2005). This method is able to detect opposite trends in statistical extremes hidden in non-significant mean effects, or to detect changes in median conditions despite the existence of extreme events, which are often misleadingly considered as outliers under a parametric perspective (Cade & Noon, 2003). The statistical analyses were conducted using the R QUANTREG package (<http://www.econ.uiuc.edu/~roger/research/rq/rq.html>; R Development Core Team, 2008).

To describe the relationships between environmental and forest variables (e.g. mortality) we used an indirect ordination method. Variable data were both quantitative and semi-quantitative, and in the last type we assigned a class representing a logical increase in value. Soil depth class, for example, ranged from 1 (shallow soils) to 3 (deep soils) (Table 1). We chose correspondence analysis (CA), assuming that most of the relationships among variables were not linear (Benzécri, 1992).

Based on the extensive field survey, we selected three representative sites along the altitudinal gradient to quantify changes in radial growth (Table 2). In the lower plots, *A. pinsapo* co-occurs with Mediterranean tree species (*Pinus halepensis* Mill., *Quercus rotundifolia* Lam.), whereas sub-Mediterranean species appear at middle elevations (*Crataegus monogyna* Jacq.) and are more important upwards (*Quercus alpestris* Boiss., *Taxus baccata* L.). The studied forests have not been disturbed by intense logging or

Table 1 Study variables analysed using correspondence analysis.

Variable	Type	Units	No. of classes	Comments
Elevation	Q	m	–	–
Aspect	S	–	3	Humid (N–NW–NE), mesic (W–SW) and dry microclimates (E–SE)
Topography	S	–	2	Steep (ridge) and flat (valley bottom) slope
Soil depth	S	–	3	Shallow-rocky (rocky outcrops > 75% surface, soil depth < 10 cm), intermediate (rocky outcrops 20–75%, soil depth = 5–15 cm) and deep soils (rocky outcrops < 20%, soil depth > 15 cm)
Structure	S	–	3	Homogeneous (few d.b.h. classes, very few old trees and seedlings), heterogeneous (few old trees and regeneration) and mature stands (high size variability, old trees and abundant regeneration)
Overstorey	S	–	3	Open, intermediate and closed overstorey
Understorey	S	–	3	Open, intermediate and closed understorey
Density	Q	individuals ha ⁻¹	–	Calculated for stumps, living and recently dead trees
Basal area	Q	m ² ha ⁻¹	–	Calculated for stumps, living and recently dead trees

Q, quantitative; S, semi-quantitative; d.b.h., diameter at breast height.

Table 2 Characteristics of *Abies pinsapo* stands along the altitudinal gradient.

Plot	Latitude (N)	Longitude (W)	Elevation		Aspect	Area (m ²)	Annual precipitation		Age (years)‡	Density of living/dead trees (individuals ha ⁻¹)
			(m a.s.l.)	Slope (%)			(mm)*	d.b.h. (cm)†		
Low	36°43'19"	04°57'54"	1226	36	NE	540	1115	12.7 ± 0.8a	45 ± 1.4a	2016/90
Middle	36°42'38"	04°59'01"	1557	42	NE	468	1306	12.2 ± 0.9a	34 ± 1.2b	1965/58
High	36°41'33"	05°01'10"	1749	21	N	2500	1531	20.7 ± 1.7b	33 ± 1.6b	294/10

*Estimated using local precipitation data (Pílonas station, 36°41' N, 05°01' W, 1713 m, 1971–2005).

†Significant ($P < 0.05$) differences among plots, calculated using Mann–Whitney tests, are indicated by different letters.

‡Age estimated at 1.3 m based on cross-dated cores with pith of sampled trees.

d.b.h., diameter at breast height.

fires during the last 50 years. Soils in the study area are mainly calcic haploxerepts at low- and mid-elevation sites and calcixerolls at upper sites (Linares, 2008).

Climatic data

To estimate robust and long-term regional climatic records, local data from six nearby meteorological stations were combined into a low-elevation regional mean for the period of 1920–2005 (Table 3). These stations represent the best available data for this portion of southern Spain. To estimate the missing data for each station, and to combine them, we used the MET program from the Dendrochronology Program Library (Holmes, 1992). For each station, monthly variables (mean temperature, total precipitation) were transformed into normalized standard deviations to give each station the same weight in calculating the average values for each month and year. Because of the Mediterranean-type seasonality in our study sites, annual means were based on 'hydrologic' (September of the previous year to current August) rather than calendar years. To provide a more mechanistic evaluation of climatic control on growth, an annual water budget was

obtained as the sum of monthly differences between precipitation data and potential evapotranspiration estimates following a modified version of the Thornthwaite method (Willmott *et al.*, 1985).

To compare and investigate the long-term trends in temperature, we used data from the San Fernando (36°29' N, 06°13' W, 80 m, c. 150 km west-south-west of the study area, 1870–2005, 1.0% missing data) and Gibraltar stations (36°02' N, 05°04' W, 3 m, c. 100 km south-west of the study area, 1852–2005, 1.2% missing data) which have the longest and best-quality instrumental series in southern Spain (Wheeler, 1992). The regional temperature data showed significant relationships between both series for all monthly data sets ($r = 0.47–0.83$, $P < 0.01$).

Historical and aerial photographs

To evaluate the temporal trends in *A. pinsapo* forest coverage, we used historical and aerial photographs. Historical land-use changes in *A. pinsapo* forests were qualitatively assessed by comparing photographs taken in and out of the study area throughout the 20th century (e.g. Fig. 2). To quantify the recent historical changes in *A. pinsapo* forest coverage, we used digital panchromatic aerial

Table 3 Data from the meteorological stations used to compute subregional climate series.

Station (code)	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Distance* (km)	Years for precipitation data	Mean annual precipitation (mm)	Missing values (%)	Years for temperature data	Mean annual temperature (°C)	Missing values (%)
Alozaina (A)	36°43'40"	04°51'24"	386	11	1955–2003	602	11.8	1977–2003	18.6	2.8
Casarabonela (C)	36°47'00"	04°50'24"	480	12	1954–2003	808	6.1	1966–1981	16.7	7.8
El Burgo (B)	36°47'20"	04°56'43"	591	9	1949–2003	615	0.6	1966–2003	15.2	7.2
Yunquera (Y)	36°43'56"	04°55'13"	681	5	1966–84	640	6.0	–	–	–
Grazalema (G)	36°45'34"	05°22'01"	823	35	1913–2003	2011	1.2	1964–2003	15.4	2.7
Quejigales (Q)	36°41'20"	05°02'51"	1100	6	1983–2001	1167	6.6	1983–2001	10.8	7.0

*Distance from the meteorological station to the nearest sampling site.

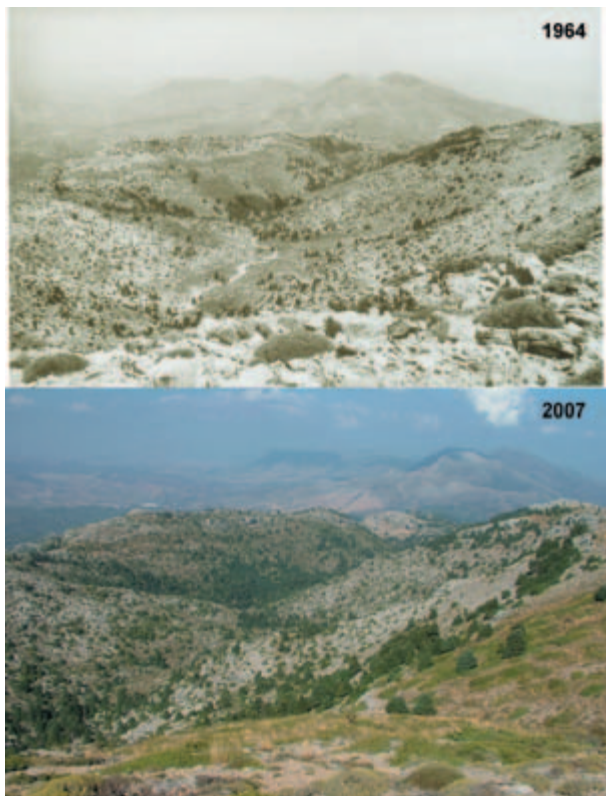


Figure 2 Photographs from 1964 (upper figure, photograph taken by M. A. Calvente) and 2007 (lower figure, photograph taken by J. C. Linares) at Sierra de las Nieves (south-east Spain) showing an increase in *Abies pinsapo* forest cover and stand density.

ortho-photographs of the study area taken in 1957, 1991 and 2001. The study area was subsampled using ArcGIS (ESRI, 2002). In each aerial photograph, unclear zones, due to topographical features, were removed. We then selected 30 randomly located plots (550 m × 325 m), 500 m apart, within the extensive survey area previously described. Simultaneously, digital maps (scale 1:10,000) and field data were used to check the plot location and its characteristics (elevation, aspect and slope). Images were exported as bitmap files and processed through a supervised digital classification scheme (Chuvieco, 1990). *Abies pinsapo* crowns

show a high contrast in the images (see Appendix S1 in Supporting Information). To also include a shape component in the criteria to assign pixels to one of two classes (tree cover and non-tree cover), we applied a fractal dimension spectrum analysis using the HarFA software package (<http://www.fch.vutbr.cz/lectures/imagesci>). This approach had previously been cross-validated for *A. pinsapo* forests against conventional (visual, maximum likelihood) thresholding approaches (Linares *et al.*, 2006). The area fraction of *A. pinsapo* tree cover was quantified on classified images using the IMAGEJ image-analysis software (<http://rsbweb.nih.gov/ij/>).

Dendrochronological methods

To estimate long-term changes in radial growth we used dendrochronological methods. At each site, two or three cores were taken from at least 10 dominant and co-dominant trees at 1.3 m using an increment borer. Cores were mounted and sanded with up to 600-grit paper until tree rings were clearly visible under a binocular microscope. All samples were visually cross-dated. Tree-ring widths were measured to 0.01 mm using a LINTAB measuring device (Rinntech, Germany) and cross-dating quality was checked using COFECHA (Holmes, 1983). Four series showing portions of low correlation to the reference site chronology were discarded.

The trend of decreasing ring width with increasing tree size was removed by converting radial increment into tree basal-area increment (BAI), which has been used to assess long-term declines in radial growth (Phipps & Whiton, 1988). The percentage growth change filter of Nowacki & Abrams (1997) based on changes in mean growth rates was applied to identify abrupt growth reductions (GR), i.e. sustained decreases in radial growth. We first calculated the ring-width medians of subsequent 10-year periods along all the growth series. We then defined the percentage of growth reduction as $GR = [(M1 - M2)/M2 \times 100]$, where M1 and M2 are the preceding, and subsequent, 10-year ring-width medians, respectively. Annual suppressions were defined as those years with $GR > 100\%$ in all radii of all trees, which we assumed were mostly caused by extreme climatic events (e.g. droughts). We calculated changes in growth rates of the medians since medians are more robust estimators of central tendency than means (Rubino & McCarthy, 2004).

To study the climate–growth relationships, elementary tree-ring width chronologies were standardized applying a spline function with a 50% frequency response of 20 years using ARSTAN (Cook, 1985). The tree-ring widths were converted into indices by dividing the observed values by the expected values that were estimated using the spline function. Autoregressive modelling was performed to remove the first-order temporal autocorrelation. Finally, a bi-weight mean was computed to average the standardized individual series and produce three site residual ring-width chronologies. For each site, the chronology segment with EPS > 0.85 was regarded as reliable, following Wigley *et al.* (1984), where EPS is the expressed population signal, which measures the tree-to-tree common growth variance.

We related the ring-width site chronologies to regional 1970–2005 climate data using correlation (Pearson r) and response functions. Response function coefficients are based on bootstrapped stepwise multiple regressions computed on the principal components of climatic variables to remove the dependence between climatic variables (Fritts, 1976). The bootstrapped response function provides a robust approach to test the stability and significance of the regression coefficients within a specific time period. Mean regression coefficients were regarded as significant ($P < 0.05$) if they were at least twice their standard deviation after 999 bootstrapped iterations. Climate–growth relationships were analysed from July of the previous year to August of the year of tree-ring formation based on previous analyses of radial growth phenology and growth–climate relationships in *A. pinsapo* (Génova, 2007; Linares, 2008). We calculated the non-climatic growth residuals in each site after subtracting the estimated growth indices based on the climate model (response function) from the actual indices. Correlation and bootstrap response functions were calculated with PRECON version 5.17 (Fritts *et al.*, 1991). Finally, to evaluate temporal trends in the degree of proximate control of water stress on growth, we also computed moving correlations for 20-year periods between the low-elevation chronology (ring-width indices) and cumulative water deficit of 1 up to 4 years. Water deficit was calculated from January to June, when the study species achieves most of its growth (Linares, 2008). Soil water balance for the study site is modelled on a monthly basis and assuming an available water capacity of 102 mm, by estimating soil-water withdrawal (actual evapotranspiration), recharge and surplus (Willmott *et al.*, 1985). Calculations were done by using the AET software developed by D. G. Gavin (<http://geography.uoregon.edu/gavin/software.html>).

RESULTS

Climatic trends

The regional annual series showed significant and opposite trends for annual air temperature (increasing) and precipitation (decreasing) since 1920 (Fig. 3a,b). The latter was mainly due to the long-term decrease in spring rainfall. Accordingly, the annual water surplus declined significantly ($P < 0.05$) since 1920 at a mean rate of 4 mm year⁻¹ (Fig. 3c). Warm and dry conditions were detected during the 1980s and 1990s, whereas low temperatures

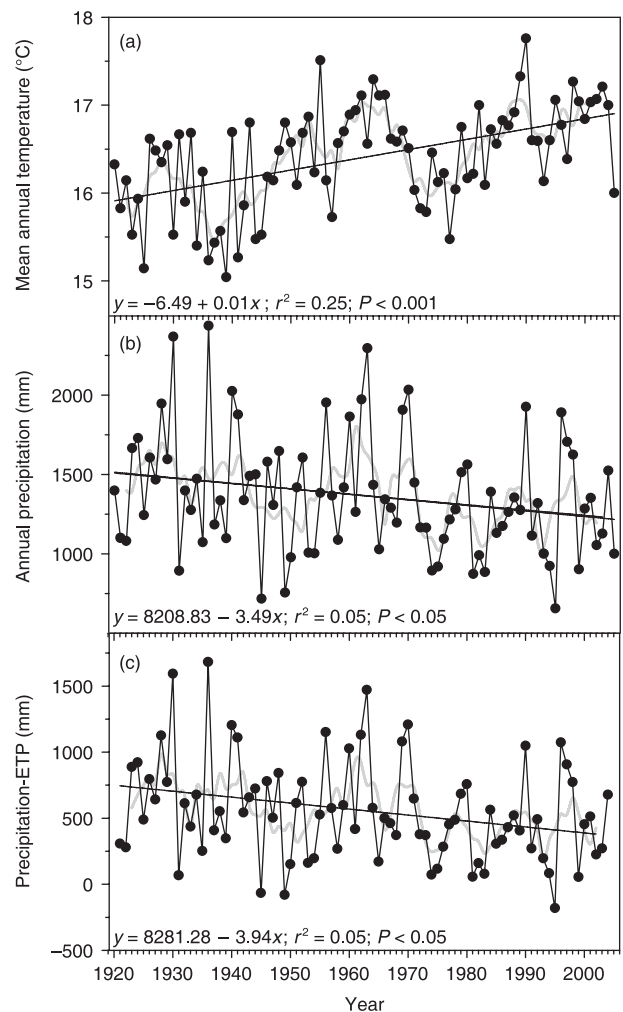


Figure 3 Long-term regional trends in mean annual temperature (a), total annual precipitation (b) and potential annual water surplus (precipitation minus evapotranspiration, EPT) (c). Annual values in (c) correspond to ‘hydrologic’ years from the previous September to the current August. The grey lines indicate the 5-year running average.

prevailed in the 1970s. Minimum annual precipitation was detected in the period 1994–95, but similar low rainfall records also occurred before (e.g. 1945–46, 1954–55, 1973–75, 1981–82). The annual water budget was negative in the 1994–95 hydrologic year, indicating water deficit. Seven out of the ten lowest values of the annual water surplus recorded since 1920 occurred in the last 30 years.

Patterns of *A. pinsapo* size frequency distributions, basal area and mortality

Stand size-class distributions were inequitable along the whole altitudinal gradient, with small (d.b.h. < 20 cm) and big (d.b.h. > 40 cm) trees comprising nearly 80% and less than 5% of the individuals, respectively (Fig. 4a). The highest frequency of very small trees (d.b.h. < 10 cm) was found upwards. The altitudinal

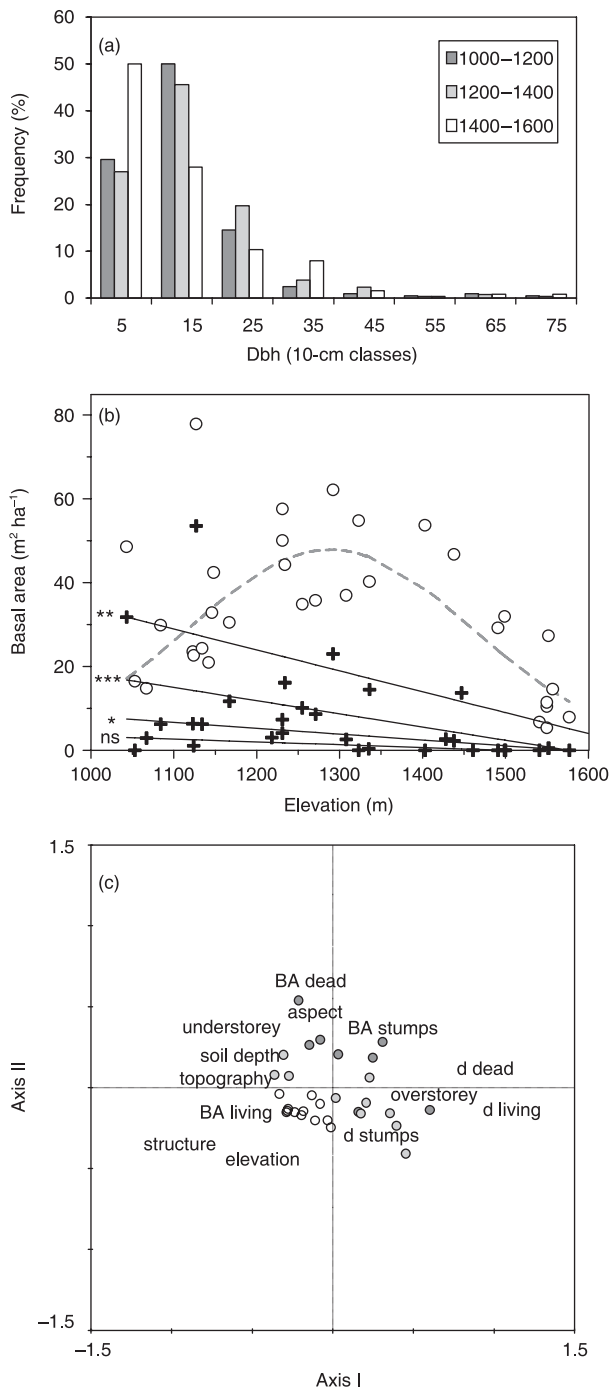


Figure 4 Changes in size, basal area and mortality of *Abies pinsapo* stands along the altitudinal gradient. The three graphs describe diameter at breast height (d.b.h.) distributions (a) in three 200-m elevation intervals (low elevation, 1000–1200 m; mid elevation, 1200–1400 m; high elevation 1400–1600 m), basal area and mortality (b), and relationships between environmental and forest variables (c). In (b), empty circles and crosses indicate total and dead basal area of trees per sampling plot, and model lines correspond to trends in total basal area (Gaussian function $y = 47.35 \exp\{-0.5 [(x - 1288.60)/171.33]^2\}$; $R^2 = 0.34$; $P < 0.01$), and in the 0.25th, 0.5th, 0.75th and 0.9th quantiles of the distribution of dead basal area (quantile linear regression fits; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns, not significant). The ordination diagram (c) shows

distribution of stand basal area was modelled using a Gaussian function ($P < 0.01$) with an estimated maximum value ($\sim 50 \text{ m}^2 \text{ ha}^{-1}$) near 1300 m (Fig. 4b). Stand basal area did not differ between plots located below and above that altitude ($P = 0.49$, Mann–Whitney U -test). However, stand density was significantly ($P = 0.001$) higher below ($1548 \text{ individuals ha}^{-1}$) than above 1300 m ($836 \text{ individuals ha}^{-1}$). Mean dead basal area was significantly ($P < 0.001$) higher below ($27.4 \pm 4.9\%$ of the total basal area) than above 1300 m ($6.8 \pm 3.1\%$).

The percentage of dead basal area showed a negative correlation with stand elevation ($r_s = -0.58$, $P < 0.001$). Quantile regression analyses revealed negative and highly significant relationships with elevation for the 0.9th and 0.75th quantiles of the frequency distribution of stand dead basal areas (Fig. 4b). Such a relationship was still significant ($P < 0.05$) for the 0.5th quantile, but there were no patterns regarding lower parts of the distribution. This indicates that stands with very low mortality are equally likely at both low and high elevations, whereas the likelihood of extreme mortality events increased downwards (eight out of the ten stands with the highest mortality were found below 1300 m). Moreover, below 1300 m, the basal area of dead trees was also correlated with the total basal area in the stand ($r_s = 0.54$, $P = 0.02$).

The first two axes of the CA accounted for 47.5% of the total variance. As evidenced by the first CA axis (Fig. 4c), high dead and living tree densities corresponded to closed overstorey stands with homogeneous structure and low living basal area, often on steep slopes, that were somewhat less abundant with increasing elevation. The second axis shows an increase of the basal area of dead trees at sites with an east–south–east aspect, particularly downwards.

Historical changes in *A. pinsapo* forest cover

Data from 1957, 1991 and 2001 clearly show an increase over time in the fraction of tree cover in the studied *A. pinsapo* forest areas (Fig. 5a). Visual interpretation of aerial images (see Appendix S1) and comparison of historical photographs (Fig. 2) suggest this was a widespread pattern in Spanish *A. pinsapo* populations. The forest densification process started in pre-existing scattered patches with open overstorey that experienced a local expansion. The maximum percentage cover increment from 25% in 1957 to 40% in 2001 occurred mainly at elevations between 1200 and 1300 m. The rate of change in area covered by *A. pinsapo* forests increased along the entire altitudinal range during the period 1957–91, especially in the 1000–1100 m and 1300–1400 m ranges (Fig. 5b). In contrast, this rate became negative, and significantly different from that in the previous period, at the lowest-elevation sites (1000–1100 m) between 1991 and 2001, but forest cover continued its increase at the highest elevations (1400–1600 m).

the position of sampling sites (symbol colours correspond to the elevation ranges described in Fig. 4a) and variables according to the first two axes of the correspondence analysis (CA). Axis I and Axis II of the CA accounted for 29.9% and 17.6% of the total variance, respectively. Variable abbreviations: d, density; BA, basal area (see also Table 1).

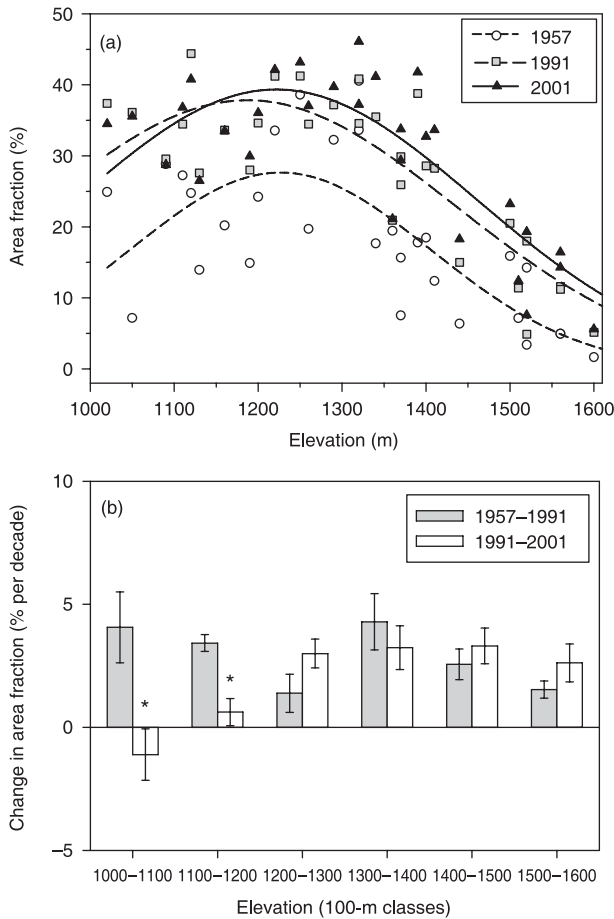


Figure 5 Spatio-temporal patterns of tree cover in *Abies pinsapo* forests (area fraction) along the altitudinal gradient (a) reconstructed using aerial photographs (1957, 1991, 2001), and comparison of the decadal changes in area fraction (b) between the 1957–91 and 1991–2001 periods (mean \pm SE; asterisks denote significant differences among the two periods, $P < 0.05$, Student's t -tests). The fitted curves in Fig. 5(a) are adjusted with the same type of Gaussian function used in Fig. 4(b).

Altitudinal differences in radial-growth trends

The mean BAI over the 1980–2005 period, when sample size was maximum and BAI was stable, was significantly greater in the high-elevation site than in the low- and mid-elevation sites (Fig. 6a; ANOVA and Student–Newman–Keuls (SNK) post-hoc test, $F_{2,75} = 85.36$, $P < 0.001$). Indeed, current BAI in the low- and mid-elevation sites is very low ($c. 3 \text{ cm}^2 \text{ year}^{-1}$) considering that the mean d.b.h. of trees in those sites ranges between 12 and 13 cm (Table 2). Radial growth was higher in the mid-elevation than in the low-elevation site during the 1970s, but a converging trend has occurred since the 1980s leading to no significant differences between the two sites, and current growth rates below 1 mm year^{-1} (data not shown). In contrast, maximum values of tree-ring width (2.5–3.8 mm) were found at the highest-elevation site since the early 1980s. Trees from the low-elevation sites produced very narrow rings in 1995 and 1998 (Fig. 6b), and such

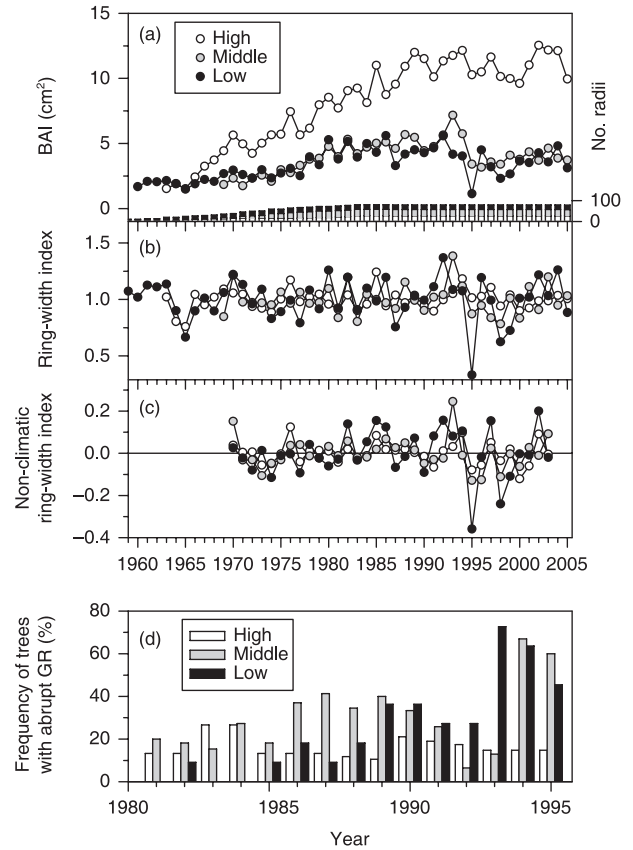


Figure 6 Growth changes in the high-elevation (H), mid-elevation (M) and low-elevation (L) *Abies pinsapo* forests as reflected by basal-area increment (BAI) (a), ring-width indices (b), non-climatic ring-width indices after extracting climatic influences (c), and the frequency of trees showing abrupt growth reductions (GR) (d). Stacked bars at the bottom of (a) indicate the annual sample size (number of radii) in each site.

growth reduction was observed after extracting most of the climatically driven growth variance (Fig. 6c). Non-climatic residuals of radial growth increased since the early 1980s for the low-elevation site, and during the 1990s for the mid-elevation site. These residuals showed strong negative departures from the climate-predicted indices in 1995 and 1998 at all sites, but the residuals were more negative at the low-elevation site than elsewhere. From 1994–95, more than half of all trees at the low- and mid-elevation sites showed abrupt growth reductions, whereas only 15% of the trees at the high-elevation site did so (Fig. 6d).

Climate-growth relationships

Analysis of the ring-width chronologies shows that, on average, recent radial growth was the highest in the uppermost stand (Table 4). The low-elevation site had the highest year-to-year variability in growth and the highest mean correlation of all series with the master chronology. This kind of feature is usually considered as indicative of a strong and among-trees consistent control of growth by climatic stress. However, the proportion of

Table 4 Descriptive statistics of the tree-ring width chronologies from the three sampling sites. The last column shows the months and climatic variables showing significant ($P < 0.05$) relationships with growth based on correlation and bootstrapped response function coefficients.

Site	No. trees/radii	Tree-ring width \pm SD (mm)	AR1*	MS†	r	Max r (period)	Period with EPS > 0.85	R^2	Climate-growth relationships*
Low	11/22	1.52 \pm 0.68	0.75	0.23	0.62	0.79 (1990–99)	1952–2005	0.41	POct _{$t-1$} (+), PJun _{t} (+)
Middle	15/30	1.99 \pm 1.07	0.83	0.21	0.39	0.55 (1990–99)	1969–2005	0.48	TDec _{$t-1$} (+), PJun _{t} (+)
High	14/28	3.08 \pm 0.88	0.58	0.13	0.26	0.44 (1980–89)	1963–2005	0.44	TDec _{$t-1$} (+), TJun _{t} (+)

Symbols and abbreviations: AR1, first-order autocorrelation; MS, year-to-year mean sensitivity, which is a measure of the relative difference from one ring-width index to the next (higher MS values correspond to greater high-frequency variability) and it is calculated by dividing the absolute value of the differences between each pair of ring-width indices by the mean of the paired index. r , mean correlation of all series with the master chronology; Max r , maximum running mean correlation and period calculated for 10-year periods with a 5-year overlap (1970–79, 1975–84, 1980–89, ..., 1995–2004); EPS, expressed population signal; R^2 : coefficient of determination, which indicates the proportion of growth variance accounted for by the climatic response-function model in each site.

*P and T refer to monthly total precipitation and mean temperature, respectively. The months are abbreviated with three letters. The subscripts indicate the years of growth (t) and previous to tree-ring formation. The + symbol indicates a positive relationship.

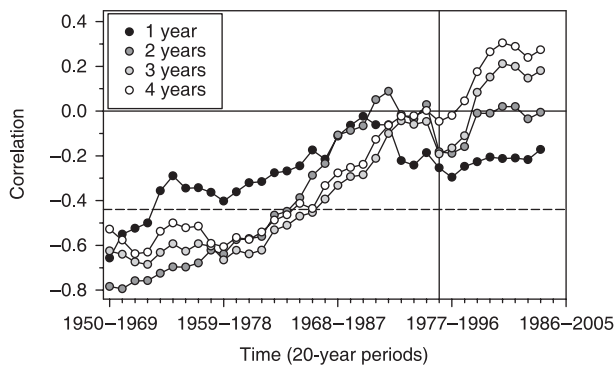


Figure 7 Moving correlations for 20-year periods between radial growth (ring-width indices) at the low-elevation site and cumulative water deficit of 1, 2, 3 and 4 years. The vertical line indicates the first 20-year period which included the year 1995, and the dashed horizontal line shows the significance level ($P < 0.01$).

growth variance explained by climate was similar along the altitudinal gradient (between 41 and 48%). In the low- and mid-elevation sites, we identified a positive relationship between growth and current June precipitation, which also holds for previous October precipitation at the lowest site (Table 4). Abundant rainfall in late spring (June) and early autumn (October) might alleviate the water stress caused by summer drought typical of the Mediterranean climate. In fact, the severe growth decrease in 1994–95 was preceded by a very low precipitation in the late autumn of 1994 and spring 1995. Previous December temperature was positively related to growth in the mid- and high-elevation sites, whereas current June temperature was positively associated with growth in the high-elevation site. The relationship between growth and water deficit was negative overall at the lowest site (Fig. 7). However, the moving correlations detected a shift from significant to non-significant values in the 1960s, and in the mid-1980s, for a cumulative water deficit of 1 year, and 2–4 years, respectively (Fig. 7).

DISCUSSION

Extreme climate events such as successive and intense droughts may cause sudden growth declines and pulses of elevated tree mortality (Bigler *et al.*, 2006). Consecutive severe droughts might be expected to more severely affect populations of relict trees growing near a species' climatic tolerance limit. In the last 25 years severe droughts characterized by high temperatures and low precipitation, such as the period 1994–95, caused several episodes of forest dieback in Spain (Peñuelas *et al.*, 2007). In the Spanish Pyrenees, the growth decline of *Abies alba* has been attributed to an increase in water stress due to a rise in summer temperature (Macias *et al.*, 2006). Other authors have also found that the climate-growth relationships of silver fir changed in the second half of the 20th century (Tardif *et al.*, 2003; Pinto *et al.*, 2007), and this change may be linked to the negative relationship between precipitation variability and radial growth (Andreu *et al.*, 2007). However, none of these studies explicitly took into account the possible role of changes in forest cover and stand density, in addition to climate factors, to explain growth reduction and dieback episodes. In Andalusia (southern Spain), the 1990s was one of the warmest decades of the past century (Giorgi, 2002), and coincided with an overall trend of decreasing precipitation (Rodrigo *et al.*, 1999, 2000). Nevertheless, past drought episodes in Andalusia during the 1970s and 1980s did not cause such episodes of decline in relict tree populations despite being as severe as the latest events. This difference raises a question about the existence of cumulative predisposing stress factors interacting with climatic stress.

We found a higher recent mortality in low-elevation *A. pinsapo* forests. This was preceded by a pattern of decline in radial growth since the 1980s at both low- and mid-elevation sites. Current spring-summer precipitation (mainly June rainfall) positively affected growth of *A. pinsapo* at the low site (Table 4), a relationship that has been observed in other Mediterranean firs (Akkemik,

2000). However, at upper elevations, late spring temperature was more influential for growth. Accordingly, a significant increase in basal-area increment, and maximum radial growth, was observed at the high-elevation site (Fig. 6, Table 4). This site is located at the top edge of the current altitudinal distribution of *A. pinsapo* in southern Spain. Such divergence in growth patterns along the altitudinal gradient seems to be linked to the 20th-century warming trend and the marked decrease in precipitation since the 1980s (Fig. 3). The diverging growth trends cannot be attributed to an age effect, since the mean tree age did not differ between the mid- and high-elevation sites (Table 2). However, stem density may have played a role since it was higher at the low- and mid-elevation sites than upwards. A link between growth suppression and mortality in *A. pinsapo* was previously noted (Arista, 1995).

Similar drought-induced growth declines related to recent warming have been detected in water-stressed forests in the eastern Mediterranean Basin (Sarris *et al.*, 2007). Indeed, the mortality events in low-elevation *A. pinsapo* forests were observed following extreme droughts (Linares & Carreira, 2006). This pattern suggests that if drought severity and water deficit increase in the future, chronic stress and concurrent mortality episodes will threaten low-elevation *A. pinsapo* populations, as has been observed with other tree species (Mueller *et al.*, 2005). Mortality of mature trees may promote a succession of species, leading to dominance by plants that are typical of more arid conditions (Aussenac, 2002). Indeed, colonization and replacement of *A. pinsapo* by *P. halepensis* have already been observed in the low-elevation sites. This replacement of tree species may represent a threat for Iberian *A. pinsapo* forests since the areas below 1300–1400 m comprise a disproportionate fraction (c. 70%) of the total surface currently covered by the species in Spain (Ruiz de la Torre *et al.*, 1994; Linares & Carreira, 2006).

The retreat of the current lower limit of distribution of this species may be viewed as a nonlinear process in response to low- and high-frequency climatic changes (Allen, 2007). The severe droughts recorded in the 1990s occurred in a context of climatic trends toward drier conditions. Such protracted climatic deterioration may explain the sharp and generalized growth decline and the synchronous and local mortality events in the low-elevation stands once physiological tolerance thresholds have been surpassed.

However, we found that mortality at low elevations showed a high among-plots spatial variability, with the likelihood of high-mortality plots increasing downwards. On the other hand, we observed a significant correlation between the percentage of dead basal area and total basal area for plots below 1300 m. These results, together with the ordination, point out that observed mortality at low elevations does not necessarily fit within a standard self-thinning process based on differential mortality of smaller size classes. They also indicate that spatial synchrony in mortality is an intra-plot (rather than among-plots) phenomenon, associated with closed and dense stands with homogeneous structure. This supports our idea that stand structure is interacting with climatic trends to cause the mortality patterns observed in Spanish *A. pinsapo* populations (i.e. it influences the ability to moderate potential damage).

Such findings contrast with the absence of similar mortality events in *A. pinsapo* populations from northern Morocco, where traditional land uses are still maintained under a low-intensity regime. Our comparison of historical and recent aerial photographs indicate that: (1) remnants of *A. pinsapo* forests in the 1950s mainly consisted of scattered individuals and low-density isolated patches, forming open stands dominated by mature trees; and (2) once strict conservation measures were adopted in that decade, tree cover in the studied areas increased across the entire altitudinal gradient, particularly at low elevations. Currently, *A. pinsapo* stands are characterized by relatively high mean basal areas reaching a maximum at mid-elevation, high tree-density values which increase downwards, and diameter distributions dominated by trees with small dbh (10–30 cm). Based on these results, we inferred that the reported increase in tree cover and subsequent canopy closure can be mainly attributed to a densification process of existing patches, and that this process was more intensive in the lower- than in the upper-elevation sites.

We further hypothesized that the consequences of conservation measures taken in the 1950s might have reduced the average adaptive capacity of the trees to climatic stress, thus increasing the vulnerability of *A. pinsapo* forests to climatic changes. The 1994–95 droughts would have acted as a threshold event, triggering mortality in low-elevation stands subjected to these predisposing effects. The predisposing effect of land-use changes might have acted to enhance a greater competition for soil water through the increase of tree density. Additionally, temporal trends in non-climatic residuals of radial growth appear to be congruent with the reported changes in forest-tree cover and current stand structure along the altitudinal gradient ('adaptive capacity' as the ability to adjust to environmental change, including variability and extremes). First, the climate–growth model based on the response functions did adequately capture the growth response to drought events that occurred before the 1970s, but did not fully capture the synchronized and sharp growth declines observed in the low- and mid-elevation sites during the more recent droughts of 1994–95 and 1998. In addition, the inverse correlation between radial growth at the lowest site and cumulative water deficit of 2–4 consecutive years was significant only until the early 1980s. In contrast, a shift in the growth response to cumulative water deficit from one to several years has been reported in other Mediterranean conifers during the late 20th century (Sarris *et al.*, 2007).

The interacting effects of changes in climate and land use are the basis of a plausible explanation for the observed mortality and historical growth patterns of *A. pinsapo*. However, several questions remain open. Isotopic analyses of tree-ring wood could help to ascertain long-term physiological responses to changing climatic conditions such as variations in water-use efficiency, as has been shown in other fir species (Bert *et al.*, 1997). Thinning treatments designed to enhance the structural diversity in low-elevation stands which are still not affected by high mortality, and the assessment of tree- and stand-based responses in growth, phenology and water and carbon use, will improve our mechanistic knowledge about the relationships between climatic stress, stand structure, competition for water and physiological thresholds of

A. pinsapo. Finally, the extension of our approach to the whole range of *A. pinsapo* forests, including both the other Spanish populations and the North African ones, and even other Mediterranean mountain fir forests, will serve to evaluate the generality of our hypotheses.

CONCLUSIONS

We reported on three lines of evidences to test the hypothesis that changes in climate and land use are interacting to explain mortality patterns in Spanish *A. pinsapo* populations. First, observed climatic trends, together with tree-ring width chronologies and climate–growth relationships along an altitudinal gradient, indicate that water stress increased at low to mid elevations while conditions for *A. pinsapo* growth improved at the highest elevation. Second, current mortality patterns show that high-mortality stands are more likely to be found at lower elevations; that high mortality is associated with dense and close stands with poor canopy structure; and that mortality shows no overall preference for smaller size classes at low elevations. Third, past strict conservation measures taken in the 1950s to protect remnants of *A. pinsapo* forests have led to substantial increases in tree cover in the entire altitudinal gradient. From multi-temporal comparisons of historical and aerial photographs, and *in situ* forest measurements, we inferred that these cover changes resulted in the current predominance of stands with a dense and poorly diversified structure, especially at low elevations. Four, at such elevations, we also found a reduction in the average adaptive capacity of the trees to drought, as indicated by temporal trends in non-climatic residuals of radial growth. These results are consistent with our proposition that the reported land-use changes have reduced the average adaptive capacity of the trees to climatic stress, thus increasing the vulnerability of climate-sensitive, relict *Abies pinsapo*–fir forests to drier conditions. Conservation policies for relict threatened tree species in the Mediterranean Basin and similar water-stressed areas should take into account the overlapping effects of stand dynamics and climate change.

ACKNOWLEDGEMENTS

This study was supported by projects PP06-RNM-02183 (Consejería de Innovación y Ciencia, Junta de Andalucía) and REN2002-2003-09509 (Spanish Ministry of Science). J.C.L. acknowledges a MEC-FPU grant. J.J.C. is grateful for the support of Fundación ‘Aragón I+D’ and Globimed network. We thank M Sykes and two anonymous referees for improving a previous version of this manuscript.

REFERENCES

Akkemik, U. (2000) Tree-ring chronology of *Abies cilicica* Carr. in the western Mediterranean region of Turkey and its response to climate. *Dendrochronologia*, **18**, 73–81.

Allen, C.D. (2007) Cross-scale interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems*, **10**, 797–808.

Andreu, L., Gutiérrez, E., Macías, M., Ribas, M., Bosch, O. & Camarero, J.J. (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Global Change Biology*, **13**, 1–12.

Arista, M. (1995) The structure and dynamics of an *Abies pinsapo* forest in Southern Spain. *Forest Ecology and Management*, **74**, 81–89.

Aussenac, G. (2002) Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. *Annals of Forest Science*, **59**, 823–832.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, J.B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390–407.

Barbero, M., & Quézel, P. (1975) Les forêts de Sapin sur le pourtour méditerranéen. *Anales del Instituto Botánico Cavanilles*, **32**, 1245–1289.

Benzécri, J.P. (1992) *Correspondence analysis handbook*. Dekker, New York.

Bert, D., Leavitt, S.W. & Dupouey, J.L. (1997) Variations of wood $\delta^{13}C$ and water-use efficiency of *Abies alba* during the last century. *Ecology*, **78**, 1588–1596.

Bigler, C.J., Bräker, O.U., Bugmann, H., Dobbertin, M. & Rigling, D. (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems*, **9**, 330–343.

Brubaker, L.B. (1986) Responses of tree populations to climatic change. *Vegetatio*, **67**, 119–130.

Cade, B.S., & Noon, B. R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420.

Camarero, J.J., Gutiérrez, E., Fortin, M.-J. & Ribbens, E. (2005) Spatial patterns of tree recruitment in a relict population of *Pinus uncinata*: forest expansion through stratified diffusion. *Journal of Biogeography*, **32**, 1979–1992.

Chuvieco, E. (1990) *Fundamentos de teledetección espacial*. Rialp, Madrid.

Cook, E.R. (1985) *A time series analysis approach to tree-ring standardization*. PhD thesis, Department of Geosciences, University of Arizona, Tucson.

Davis, M.B. (1984) Climatic instability, time lags, and community disequilibrium. *Community ecology* (ed. by J. Diamond and T.J. Case), pp. 269–284. Harper, New York.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.

ESRI (2002) *ArcGIS 8.2*. Environmental Systems Research Institute, Redlands, CA.

Fritts, H.C. (1976) *Tree rings and climate*. Academic Press, New York.

Fritts, H.C., Vaganov, E.A., Sviderskaya, I.V. & Shashkin, A.V. (1991) Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width, number of cells, cell-size, cell-wall thickness and wood density. *Climate Research*, **1**, 97–116.

Génova, M. (2007) El crecimiento de *Abies pinsapo* y el clima de Grazalema: aportaciones dendroecológicas. *Investigación Agraria: Sistemas y Recursos Forestales*, **16**, 145–157.

- Giorgi, F. (2002) Variability and trends of sub-continental scale surface climate in the twentieth century. Part I: observations. *Climate Dynamics*, **18**, 675–791.
- Grove, A.T. & Rackham, O. (2001) *The nature of mediterranean Europe: an ecological history*. Yale University Press, New Haven.
- Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 68–78.
- Holmes, R.L. (1992) *Dendrochronology program library*. Laboratory of Tree-Ring Research, University of Arizona, Tucson.
- IPCC (2007) *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Jalas, J., Suominen, J. & Lampinen, R. (eds) (1999) *Atlas Florae Europaeae*. Cambridge University Press, Cambridge. Available at: <http://www.fmnh.helsinki.fi/english/botany/afe/index.htm>.
- Jump, A.S., Hunt, J.M. & Peñuelas, J. (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.
- Koenker, R. (2005) *Quantile regression*. Cambridge University Press, Cambridge.
- Kulakowski, D., Rixen, C. & Bebi, P. (2006) Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. *Forest Ecology and Management*, **223**, 66–74.
- Linares, J.C. (2008) Efectos del cambio global sobre la dinámica poblacional y la ecofisiología de bosques relictos de *Abies pinsapo* Boiss. PhD Thesis, Universidad Jaén, Jaén, Spain.
- Linares, J.C. & Carreira, J.A. (2006) El pinsapo, abeto endémico andaluz. O, ¿qué hace un tipo como tú en un sitio como éste? *Ecosistemas*, **3**, 171–191.
- Linares, J.C., Esteban, F.J., Viñebla, B. & Carreira, J.A. (2006) A computational analysis of multi-temporal vegetation changes using the fractal dimension spectrum. *HarFA – Harmonic and Fractal Image Analysis*, **1**, 97–100. Available at: <http://www.fch.vutbr.cz/lectures/imagesci>.
- Macías, M., Andreu, L., Bosch, O., Camarero, J.J. & Gutiérrez, E. (2006) Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its southwestern distribution limit. *Climatic Change*, **79**, 289–313.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A. & Whitham, T.G. (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*, **93**, 1085–1093.
- Nowacki, G.J. & Abrams, M.D. (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, **67**, 225–249.
- Peñuelas, J., Ogaya, R., Boada, R. & Jump, A.S. (2007) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography*, **30**, 829–837.
- Phipps, R.L. & Whiton, J.C. (1988) Decline in long-term growth trends of white oak. *Canadian Journal of Forestry Research*, **18**, 24–32.
- Pinto, P.P., Gégout, J.-C., Hervé, J.-C. & Dhôte, J.-F. (2007) Changes in environmental controls on the growth of *Abies alba* Mill. in the Vosges Mountains, north-eastern France, during the 20th century. *Global Ecology and Biogeography*, **16**, 472–484.
- R Development Core Team (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org/>.
- Rodrigo, F.S., Esteban-Parra, M.J., Pozo-Vázquez, D. & Castro-Díez, Y. (1999) A 500-year precipitation record in Southern Spain. *International Journal of Climatology*, **19**, 1233–1253.
- Rodrigo, F.S., Esteban-Parra, M.J., Pozo-Vázquez, D. & Castro-Díez, Y. (2000) Rainfall variability in Southern Spain on decadal to centennial time scales. *International Journal of Climatology*, **20**, 721–732.
- Rubino, D.L. & McCarthy, B.C. (2004) Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia*, **21**, 97–115.
- Ruiz de la Torre, J., García, J.I., Oria de Rueda, J.A., Cobos, J.M., Neva, J.C., Navarro Cerrillo, R.M., Catalina, M.A., López-Quintanilla, J., Álvarez Caliente, M., Arista, M., Talavera, S. & Herrera, J. (1994) *Gestión y Conservación de los Pinsapares Andaluces*. AFA, Sevilla, Spain.
- Sarris, D., Christodoulakis, D. & Körner, C.H. (2007) Recent decline in precipitation and tree growth in the eastern Mediterranean. *Global Change Biology*, **13**, 1187–1200.
- Tardif, J., Camarero, J.J., Ribas, M. & Gutiérrez, E. (2003) Spatio-temporal variability in radial growth of trees in the Central Pyrenees: climatic and site influences. *Ecological Monographs*, **73**, 241–257.
- Vitousek, P.M. (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.
- Wheeler, D. (1992) The temperature record of the San Fernando Observatory, Cádiz: 1871–88. *Journal of Meteorology*, **17**, 257–265.
- Wigley, T.M.L., Briffa, K.R. & Jones, P.D. (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, **23**, 201–213.
- Willmott, C.J., Rowe, C.M. & Mintz, Y. (1985) Climatology of the terrestrial seasonal water cycle. *Journal of Climatology*, **5**, 589–606.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Analysed aerial photographs

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCHES

Juan Carlos Linares is currently a researcher in the University Pablo de Olavide (Seville, Spain). His research is focused on the population structure and dynamics of relict trees species from Mediterranean mountains, involving responses to global change at several scales from the landscape to the individual (ecophysiology).

Jesús Julio Camarero is a forest ecologist currently working in the Instituto Pirenaico de Ecología (CSIC). His research deals with the climatic factors controlling forest growth and regeneration using tools such as dendroecology, wood anatomy and spatial statistics.

José A. Carreira is lecturer in ecology at University of Jaén. His research is focused on the effects of perturbations (climate and land-use changes, nitrogen atmospheric deposition inputs, fires) on the biogeochemistry and dynamics of Mediterranean forests and shrublands, with emphasis on study cases which are unique in terms of their particular combination of state factors.

Editor: Martin Sykes