

Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*

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Summary

1. Long-term basal area increment (BAI) in *Abies pinsapo* was studied to investigate the way density-dependent factors modulate the responses of radial growth to climatic stresses in relict stands of a drought-sensitive Mediterranean fir.

2. First, we verified that spatially explicit competition predicts mean *A. pinsapo* BAI at our study site; i.e. it modulates the degree to which the average climate-driven potential for growth is expressed. Second, we verified that the long-term pattern of temperature predicts the long-term pattern of BAI, estimated as the main trend over a time period of *c.* 40 years. Finally, we assessed whether the intensity of tree-to-tree competition restrains the potential improvements achieved by our model of BAI when a short-term, high-frequency stressor such as drought (inter-annual precipitation variability) is introduced.

3. We applied Dynamic Factor Analysis (DFA) to characterize regional climatic trends and to test the hypothesis that trees subjected to contrasting competition intensity may differ in their growth pattern. Significant long-term climate trends obtained by DFA were used as predictors of long-term BAI.

4. The mean BAI was mainly determined by competition, whereas growth trends obtained by DFA did not differ among dominant, suppressed and dying trees. Common trends of growth decline were strongly related to long-term, late-winter to summer temperatures, while the residuals were related to total annual precipitation, although with decreasing significance as competition increased. Our results support the contention that the reported patterns of *A. pinsapo* growth decline and death occur as a result of the interacting effects of both competition and climate stressors acting at long- and short-term time scales.

5. *Synthesis.* Long-term climatic drought stress was the main driving factor of growth decline in *A. pinsapo*. Moreover, trees already suffering from competition (a long-term stress) were predisposed to decline given an additional short-term stress, such as a severe drought.

Key-words: *Abies pinsapo*, adaptive capacity, basal area increment, climatic change, competition, drought, Dynamic Factor Analysis, global warming, linear mixed models, vulnerability

Introduction

Both drought and stand structural changes have the potential to profoundly alter the growth and vigour of tree populations (Saxe *et al.* 2001; Sarris, Christodoulakis & Körner 2007;

Thuiller *et al.* 2008). Trees of different sizes and crown classes compete differently for light, water and other resources within a stand (Peet & Christensen 1987; Orwig & Abrams 1997). Thus, depending on stand structural attributes, a same type of forest community might exhibit different ecological thresholds and regime shifts in the face of changing climatic conditions (Andersen *et al.* 2008). Nevertheless, the interacting effects of

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these two factors have rarely been assessed, perhaps because they are likely to operate simultaneously, making it difficult to disentangle their separate impacts.

Individual tree growth decline and death often occur as a result of the combined effects of many different long- and short-term stressors (Manion 1991; Pedersen 1998a). However, many studies attempting to decipher the causes of tree decline and death in undisturbed stands have traditionally viewed suppression as a primary cause of mortality rather than as a predisposing factor. Such a biased view comes from studies in which observations of mortality events linked to high competition either mainly concerned small trees (He, Zhang & Bazzaz 2005; Martin-Benito *et al.* 2007) or discarded interacting effects of competition with long- and short-term climatic stressors (Pedersen 1998b; Dobbertin 2005). Consequently, an assessment of the effects of drought stress and changes in stand structure on forest growth must define the spatial and temporal scales that are suitable according to the specific traits of the studied species, such as life span, drought-stress tolerance and competitive ability.

The dendrochronological assessment of radial-growth trends may be useful to identify trees with high probabilities of decline and death (Ogle, Whitham & Cobb 2000; Bigler *et al.* 2004). Several studies have shown that mortality rates are inversely related to radial-growth rates (Wyckoff & Clark 2000; Bigler 2003; van Mantgem *et al.* 2003). Usually, reduced wood formation occurs prior to visual symptoms of decline (e.g. crown defoliation) and tree death. This highlights the usefulness of dendrochronology to investigate the ecological implication of tree-to-tree competition under a warmer future climate and to forecast the impending decline of particular forests (Bigler *et al.* 2004).

Contrasting growth responses to water stress among trees in different crown classes might be particularly relevant for understanding the dynamics of forests dominated by species that are highly sensitive to drought stress (Adams & Kolb 2004). Previous works have suggested that tree-to-tree competition, as a long-term predisposing stressor, may be an additional risk factor for drought-induced mortality in water-stressed areas (Bigler *et al.* 2007; Greenwood & Weisberg 2008). Because soil-water availability is a key limiting resource in Mediterranean ecosystems, drought spells are a common short-term disturbance in these forests (Peñuelas, Lloret & Montoya 2001). To assess the contributing effects on forest decline of competition and drought, as long- and short-term stressors, respectively, we focused on declining Spanish stands of *Abies pinsapo* Boiss. (Linares, Camarero & Carreira 2009), a relict fir species endemic to coastal mountains near the strait of Gibraltar.

In Spain, current climatic warming has severely affected the growth of drought-sensitive conifer species (Macias *et al.* 2006; Andreu *et al.* 2007). Recently, Linares, Camarero & Carreira (2009) pointed out that, in addition to climate stress, endogenous factors such as stand structural changes promoted by shifts in land use can also be important contributors to forest decline processes. They reported that the likelihood of high-mortality plots in *A. pinsapo* forests increased downwards

(drier conditions), where mortality showed no overall preference for smaller size classes, and was linked to closed overstorey stands with homogeneous structure exhibiting long-term trends of little tree radial-growth. Conversely, low-mortality plots were equally likely at both low and high elevations and corresponded to more diversified and open-canopy stands (Linares, Camarero & Carreira 2009). In Spain, the strict protection measures applied since the 1950s to protect the remnants of *A. pinsapo* forests have eliminated their traditional uses (logging, fuel extraction, grazing) leading to a remarkable increase in tree cover and density (Linares & Carreira 2009).

In this study, we assess whether the performance of statistical models of tree growth and decline can be improved significantly by combining climatic and density-dependent stressors as predictor variables operating at different time scales. Our approach provides an original way to analyse the effects of both climatic stress and tree-to-tree competition on radial growth using Dynamic Factor Analysis (DFA) to quantify common trends in climatic variables and to provide climatic predictors of growth (basal area increment, BAI) at the individual level. We hypothesize that any structural changes that increase tree-to-tree competition reduce the average adaptive capacity of the trees to drier climatic conditions, thus enhancing their vulnerability. Our specific aims were to (i) quantify the growth patterns of *A. pinsapo* trees subjected to contrasting competition intensities, (ii) use long-term regional climate trends of temperature and precipitation for predicting tree growth, and (iii) discuss the effects of climatic trends and stand structure modifications on ecological thresholds and regime shifts of tree populations. The results are interpreted within a conceptual framework of vulnerability, sensitivity and adaptive capacity to change.

Materials and methods

We used ring-width data as the response variable, the intensity of competition and smoothed climatic trends as long-term stressors, and precipitation as a short-term stressor. First, we assessed whether competition may be a reliable predictor of *A. pinsapo* radial growth. Second, we examined whether long-term climatic trends predict long-term growth patterns. Third, we evaluated whether the introduction of inter-annual precipitation variability as a short-term stressor improves our growth model, and how it depends on competition intensity.

CLIMATIC DATA

To estimate robust and long-term regional climatic records, local data from six nearby meteorological stations were combined into a regional mean for the period of 1920–2005 (Table S1 in Supporting Information). 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. To combine the data from each station, we used the MET routine from the Dendrochronology Program Library (Holmes 1992). In the study area, the estimated mean annual temperature is 11.6 °C, and the total annual precipitation is 1089 mm. Because of the Mediterranean-type seasonality at our study sites, annual means were based on data from September of

the previous year to the current August (see also Linares, Camarero & Carreira 2009).

Field sampling and dendrochronological methods

Abies pinsapo Boiss. is a relict species belonging to the group of circum-Mediterranean firs that have been mostly restricted to small populations located in coastal Mediterranean mountain areas (Linares & Carreira 2009). At present, *A. pinsapo* is just locally distributed in the Baetic Range (S Spain) and the Rifain Range (N Morocco), mainly on north-facing slopes above 1000 m a.s.l. (Linares, Camarero & Carreira 2009).

The study was carried out in 2004 at natural stands of *A. pinsapo* located near the lower elevation limit (36°43' N, 4°57' W, 1200 m a.s.l., aspect NW, slope *c.* 40%) of the species' altitudinal range. In four plots (size *c.* 0.1 ha; located *c.* 100 m apart), all trees with more than 3 cm diameter at 1.3 m (d.b.h.) were identified, tagged and mapped, and their d.b.h. was measured (see the structural characteristics of the four study plots in Table 1). A total of 184 stem d.b.h. cross-sections (42, 32, 52 and 58 trees from plots 1, 2, 3 and 4, respectively) from dominant, co-dominant and suppressed trees, which were all randomly selected and felled in an ongoing thinning experiment, were studied for age determination at 1.3 m and radial-growth analyses. Selection of the trees was performed with the consideration of two criteria: (i) achieving a data set covering the whole diameter class distribution and (ii) selecting randomly located trees (once the number of trees to be felled in each size-class was fixed, the specific target individuals were selected by a random procedure). Only alive and apparently healthy trees were sampled to avoid, as much as possible, other factors affecting growth. Further information about the age distribution of sampled trees can be found in Fig. S1.

Cross-sections taken at 1.3 m were sanded until tree rings were clearly visible under a binocular microscope. All samples were visually cross-dated. Tree-ring widths (TRWs) were measured to the nearest 0.01 mm on two radii per cross-section using a LINTAB measuring device (F. Rinntech, Heidelberg, Germany), and cross-dating quality was checked using COFECHA (Holmes 1983). The trend of decreasing ring-width with increasing tree age and size was removed by converting TRWs into BAI. Relative radial-growth reduction (GR) was estimated using the method developed by Nowacki & Abrams (1997) to identify suppressions, i.e. abrupt and sustained decreases in radial growth. We first calculated the ring-width means of subsequent 10-year periods over all growth series. Then, we 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 means, respectively. We considered a sustained or a severe growth reduction when GR was greater than 50% or 100%, respectively, in at least half the trees.

COMPETITION INDEX

We estimated the tree-to-tree competition intensity (CI) that each focal tree was subjected to by calculating a distance-dependent competition index, which takes into account the number, size and distance to the neighbouring competitors (Linares *et al.* 2009). The degree of competition experienced by the focal *i* tree was calculated as the sum of the quotients, for all *j* neighbouring trees surrounding it within a radius *R*, between the ratio d.b.h._{*j*}/d.b.h._{*i*} and the distance between the *i* and the corresponding *j* trees (dist_{*ij*}):

$$CI = \sum_{j=1}^{N(R)} (d.b.h._j/d.b.h._i)/dist_{ij} \quad \text{eqn 1}$$

The threshold radius above which neighbours were regarded as not competing was estimated by comparing the CI data sets that were obtained using *R* values ranging from 1 to 10 m with the mean BAI. The mean BAI–CI relationship was calculated over the entire time span of each TRW series, and only in the case of trees older than 60 years the period 1945–2004 was used. The highest correlations between CI and mean BAI were obtained for values of *R* = 8 m and this threshold radius was selected for further calculations. Then, we fitted an exponential-decay function between the competition index and BAI. We used the CI value in which the slope of the exponential function changes to classify trees as dominant or suppressed individuals. Additionally, trees with stable, very low secondary growth or inactive cambial activity over the past 5 years were classified as dying trees (Bigler *et al.* 2004).

DATA ANALYSES AND MODELLING

Dynamic factor analysis

DFA (see Zuur *et al.* 2003) was used to estimate underlying common patterns in both the climate and tree-ring data. In DFA, the time series are modelled as a linear combination of stochastic nonlinear trends, which describe trends better than traditional models. In the present study, DFA was applied independently to (i) obtain a climate dynamic factor model and (ii) test differences of BAI trends from trees subjected to contrasting competition strength.

CLIMATE DFA

First, DFA was applied on monthly mean temperature and total precipitation regional series as a dimension reduction technique to obtain latent smoothing functions over the time of the annual and seasonal climatic trends. The analysis was based on the so-called structural time series models (Harvey 1989) that allow a description

Table 1. Structural characteristics of the study plots. Values are means ± SE. Significant (*P* < 0.05) differences between plots based on Mann–Whitney tests are indicated by different letters: D, dominant trees; S, suppressed trees; dy, dying trees

Plot	Surface (m ²)	d.b.h. (cm)	Age (years)*	Density (trees ha ⁻¹)	Basal area (m ² ha ⁻¹)	Basal area of D/S/dy trees (%)
1	982	17.18 ± 0.76a	50 ± 2.4	1314	37.64	80.5/16.4/3.1
2	905	17.25 ± 1.02a	48 ± 1.6	1425	46.93	79.3/18.9/1.8
3	850	14.84 ± 0.81a	49 ± 1.9	1682	38.78	87.3/10.0/2.7
4	852	12.31 ± 0.56b	52 ± 1.3	2535	39.90	69.2/23.1/7.7

*Age estimated at 1.3 m.

of the N response variables (i.e. each monthly climatic series) with a Dynamic Factor Model (DFM) given by:

$$s_n(t) = \sum_{m=1}^M \gamma_{m,n} z_m(t) + \mu_n(t) + \varepsilon_n(t) \quad \text{eqn 2}$$

$$a_m(t) = a_m(t-1) + \eta_m(t) \quad \text{eqn 3}$$

where $s_n(t)$ is the value of the n th response variable at time t (with $1 \leq n \leq N$); $z_m(t)$ is the m th unknown trend (with $1 \leq m \leq M$) at time t ; $\gamma_{m,n}$ represents the unknown factor loadings; μ_n is the n th constant level parameter for displacing up and down each linear combination of common trends (i.e. the intercept term in the regression DFM); and $\varepsilon_n(t)$ and $\eta_m(t)$ are error components that are assumed to be independent of each other and normally distributed with zero mean and unknown covariance matrix. Factor loadings $\gamma_{m,n}$ indicate the weight of a particular common trend in the response time series s_n . In addition, the comparison of factor loadings of different time series (i.e. precipitation or temperature for different months) allows for the detection of interactions between the different s_n . The annual DFM was obtained including the monthly series as response variables ($n = 12$), whereas seasonal DFM was obtained using a 3-month moving window (i.e. September–October–November, then October–November–December, and so on). Results from the DFA were interpreted in terms of the estimated parameters $\gamma_{m,n}$; the goodness-of-fit of the model was assessed by Akaike's (1974) Information Criterion (AIC), which combines the measure of fit with a penalty term based on the number of parameters used in the model. Based on this, the two most significant seasonal common trends of temperature and precipitation were used afterwards as the potential explanatory variables of the BAI [see below, Linear Mixed-Effect Model (LMEM) design].

TREE-GROWTH DFA

Second, we applied DFA to identify underlying common trends or latent effects in the tree-ring data series in order to test differences among contrasting tree-competition classes. We applied the DFA model on normalized BAI series of trees of the above defined tree classes (i.e. dominant, suppressed and dying trees). We analysed the BAI series for the 1970–2004 period, when sample size was maximum and BAI had stabilized. Iterative selection of trees with the higher loading factors was performed in order to obtain robust underlying trends. Trees with loading factors lower than 0.1 were discarded from further analyses, because a loading value close to zero indicates that such trees do not follow the common pattern. This procedure yielded a set of 17 dominant, 25 suppressed and 28 dying trees. Several combinations of trend numbers and error covariance matrices were investigated. The results were interpreted in terms of the estimated parameter $\gamma_{m,n}$ (i.e. weight of the common trend in each tree) and the visual agreement between model estimates for the different competition classes.

For both approximations, the optimal number of common trends was based on AIC values. In addition, a symmetric, non-diagonal error covariance matrix was used for the noise term that was also based on the AIC values. The model used was Data = Sum of the M common trends + noise. We performed a maximum number of 1500 iterations with a stop criterion Epsilon (difference in likelihood) set to 0.00001 (Zuur *et al.* 2003). All analyses were applied on normalized time series, because this facilitates the interpretation of DFA factor loadings and the comparison of regression parameters. DFA was implemented using the Brodgar ver. 2.4.1 statistical package (High-

land Statistics Ltd., Newburgh, UK), which was linked to the R software (R Development Core Team 2010). Further details about DFA may be found in Zuur *et al.* (2010).

LINEAR MIXED-EFFECT MODEL

Significant temperature and precipitation trends, which were obtained by DFA, were used as potential long-term explanatory variables for BAI of dominant, suppressed and dying trees in each plot. To model BAI as a function of long-term climatic trends, we fitted LMEM using the nlme package in R software (R Development Core Team 2010). Common trends of seasonal temperature and precipitation were included as fixed effects, and each tree was included as a random effect. The covariance parameters were estimated using the restricted maximum-likelihood (REML) method, which obtains estimates of parameters by minimizing the likelihood of residuals from fitting the fixed-effects portion of the model (Zuur *et al.* 2009). We used an information-theoretic approach for multi-model selection based on the AIC corrected for small sample sizes (AICc). We considered models with substantial support to be those in which the ΔAIC (i.e. the difference of AICc between models) was < 2 (Burnham & Anderson 2002). The residuals of the model with the highest support were related to annual and seasonal precipitation data using simple linear regressions (Fortin *et al.* 2008).

Results

CLIMATE TRENDS

For all climatic variables, small AIC values indicated that just one common trend captured the main climatic trends in the study area. The DFA explained 55.17% of the observed variance on mean annual temperature (Fig. 1a), which has increased by 0.20 units of standard deviation per year over the period from 1970 to 2004, indicating a warming trend of $+0.74$ °C. Monthly temperature loadings were relatively large and positive for the period from spring to mid-summer (March to July; see Fig. 1c), which indicates congruent trends for these months. The fitted annual common trend allowed the recognition of two regional warming episodes from the late-1930s to the early 1960s and from the mid-1970s to the present. No long-term trends were detected by the DFA with regard to total annual precipitation (Fig. 1b). High positive loadings corresponded to February and November rainfall, whereas July showed a negative loading factor (Fig. 1c).

Seasonal DFAs over a 3-month running window revealed that the spring to mid-summer months present the most significant common temperature trend (Table 2). The June–July–August mean temperature ($T_{\text{Jn-Jl-Au}}$ in Table 2) showed the lower AIC followed by that of the February–March–April ($T_{\text{Fe-Mr-Ap}}$) seasonal span (see also Fig. 1a). The higher mean loading factor was obtained for March–April–May (Mr-Ap-My), because these 3 months showed similar warming trends. The first ranked precipitation (P) DFA loadings were obtained for the Fe-Mr-Ap and the Mr-Ap-My intervals (Table 2 and Fig. 1b), although these trends were less significant than those obtained for temperature. Subsequently, these four

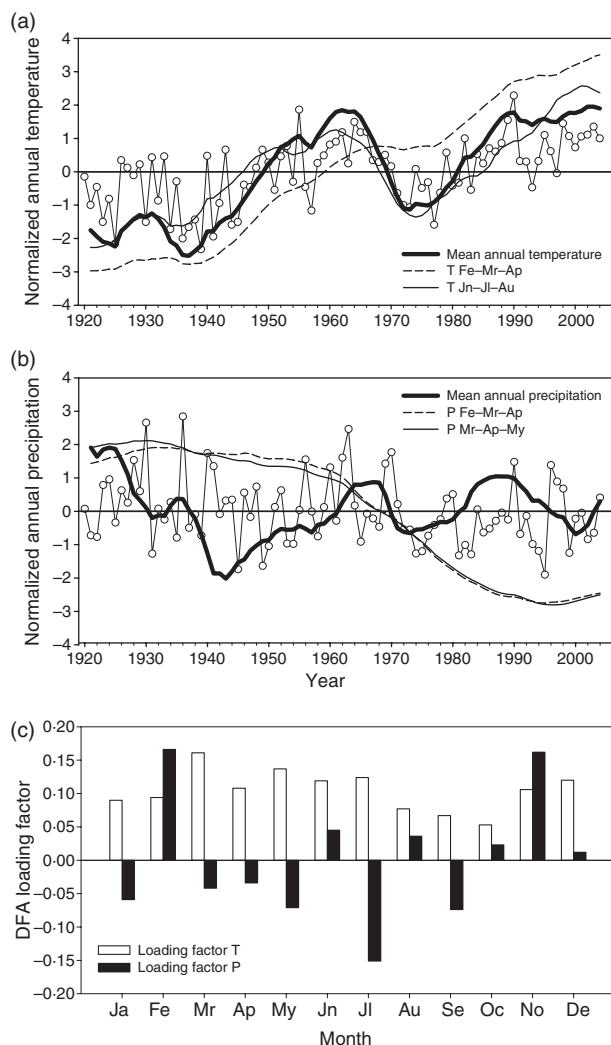


Fig. 1. Estimated trends (solid lines) and observed values (white dots) of annual (a) mean temperature (T) and (b) total precipitation (P) in the study area. The most significant seasonal trends (Fe–Mr–Ap, February–March–April; Jn–Jl–Au, June–July–August; Mr–Ap–My, March–April–May), based on normalized monthly data, are also displayed. The lower graph (c) shows the monthly dynamic factor analysis (DFA) loading factors.

fitted common trends (i.e. T Ju–Jl–Au, T Fe–Mr–Ap, P Fe–Mr–Ap and P Mr–Ap–My) were used as potential predictors of raw BAI.

RADIAL-GROWTH TRENDS

The four studied plots showed similar long-term TRW, BAI and GR trends (Fig. 2a–c, Table 1). The period before the 1980s was characterized by a generalized BAI increase, which was lower in plot 4 than elsewhere. Growth decline started in all studied plots between the late-1980s and early 1990s (Fig. 2c). A sharp growth reduction occurred in 1995. Indeed, between 1994 and 1995, more than half of all trees showed relative growth reductions greater than 100% (Fig. 2d). Since this date, BAI in the four plots has been very low ($c. 3 \text{ cm}^2 \text{ year}^{-1}$)

Table 2. Ranked strength (mean loading factor) of seasonal climatic trends (T , mean temperature; P , total precipitation) obtained by Dynamic Factor Analysis (DFA) over 1921–2004, based on their measure of fit (AICc, Akaike Information Criterion corrected for small sample; lower AICc values correspond to better DFA models). Linear slopes from normalized data over 1970–2004 are also shown. The models in bold typeface (lower values of AICc for temperature and precipitation) were selected as predictors of basal area increment (BAI). Months are abbreviated by two letters (when the first two are coincident, the third letter is used for the abbreviations instead of the second letter)

Season	AICc	Months loading factor			1970–2004 trend ($^{\circ}\text{C}$, mm)
T Jn–Jl–Au	679.35	0.06	0.07	0.05	2.12
T Fe–Mr–Ap	698.74	0.10	0.16	0.12	2.82
T My–Jn–Jl	698.88	0.14	0.10	0.14	1.29
T Mr–Ap–My	699.03	0.18	0.14	0.15	2.52
T Ap–My–Jn	704.45	0.10	0.11	0.10	2.34
T De–Ja–Fe	712.21	0.07	0.07	0.07	2.61
T No–De–Ja	712.49	0.05	0.05	0.06	2.26
T Oc–No–De	714.86	0.01	0.06	0.06	2.16
T Se–Oc–No	722.28	0.03	0.01	0.07	0.77
P Mr–Ap–My	732.39	0.05	0.03	0.02	–173.32
P Fe–Mr–Ap	734.19	0.01	0.05	0.03	–181.74
P Ja–Fe–Mr	737.04	0.01	0.01	0.04	–168.80
T Ja–Fe–Mr	737.04	0.10	0.10	0.13	2.73

considering that the mean d.b.h. of trees ranged between 12 and 17 cm and the mean age is $c. 50$ years (Table 1).

RELATIONSHIPS BETWEEN COMPETITION AND GROWTH

Low BAIs were clearly associated with high tree-to-tree competition in the four studied plots (Fig. 3, Table 3). The CI showed a high correlation with the growth of the focal tree for relatively small neighbourhoods (radii around the focal tree from 2 to 8 m). Considering the whole study period, all plots showed significant negative exponential relationships between CI and mean BAI of the trees, accounting for 30–40% of the growth variance (Fig. 3a). A similar BAI–CI relationship was found for the 1985–94 and for the 1995–2004 periods, which were characterized by high and low precipitation levels, respectively (Fig. 3b,c; see also Fig. 1b). Trees subjected to higher competition showed lower mean BAI values regardless of the considered period. But variations in mean annual precipitation determined the strength of the BAI–CI relationship (weaker in the dry period, see Table 4) and the range of BAI values, which was especially responsive for trees with CI figures lower than 7 (see maximum BAI values to the left of the inflection point of fitted curves in Fig. 3a–c). Thereafter, when CI surpassed a threshold of $c. 7$, BAI tended to be almost asymptotic. Finally, we defined three groups of trees based on the CI–BAI relationships: ‘dominant’ trees, which were characterized by $\text{CI} < 7$ and $\text{BAI} > 5 \text{ cm}^2 \text{ year}^{-1}$; ‘suppressed’ trees, with $\text{CI} > 7$ and $\text{BAI} < 5 \text{ cm}^2 \text{ year}^{-1}$; and ‘dying’ trees, which were characterized by $\text{CI} > 7$ and mean $\text{BAI} < 1 \text{ cm}^2 \text{ year}^{-1}$ since 1990 or by no secondary growth over the past 5 years.

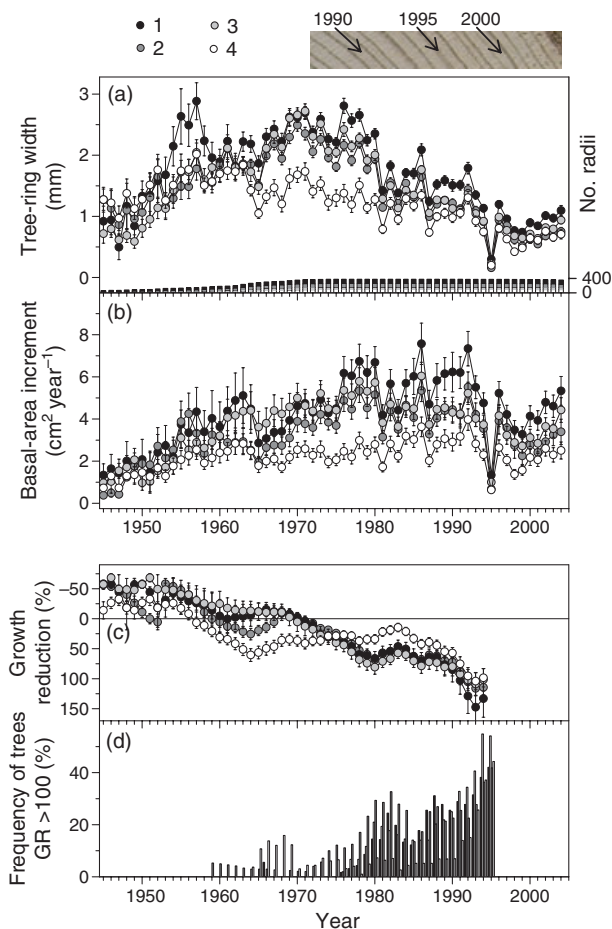


Fig. 2. Mean radial growth during the period 1940–2004 in the study plots expressed as tree-ring width (a) and basal area increment (b), and relative growth reduction (GR) quantified as the mean relative growth reduction (c) and the frequency of trees per year that show severe growth reductions (GR > 100%). Note the narrow 1995 tree-ring displayed in the upper image, which corresponds to a representative cross-section. Error bars represent the standard error. Sample size is displayed in the upper graph as bars of different shades (No. radii).

GROWTH TRENDS AS A FUNCTION OF CLIMATE BASED ON DFA AND LMEM

Common trends among individuals belonging to each one of these previously defined groups of trees were separately computed for the 1970–2004 BAI series (Fig. S2). The model containing one common trend and a non-diagonal error covariance matrix was the most suitable as judged by the AIC (data not shown). The common trend obtained for each one of the three tree groups was highly significant, and the three yielded similar shapes (Fig. S2). The mean loadings of the trees within the dominant, suppressed and dying groups were relatively large and positive and showed little variance (inset in Fig. S2). This indicates that the subset of studied trees followed a similar underlying growth trend independently of their competition class.

Therefore, the LMEM relating raw BAI data and climate trends was performed on the whole set of trees at each repli-

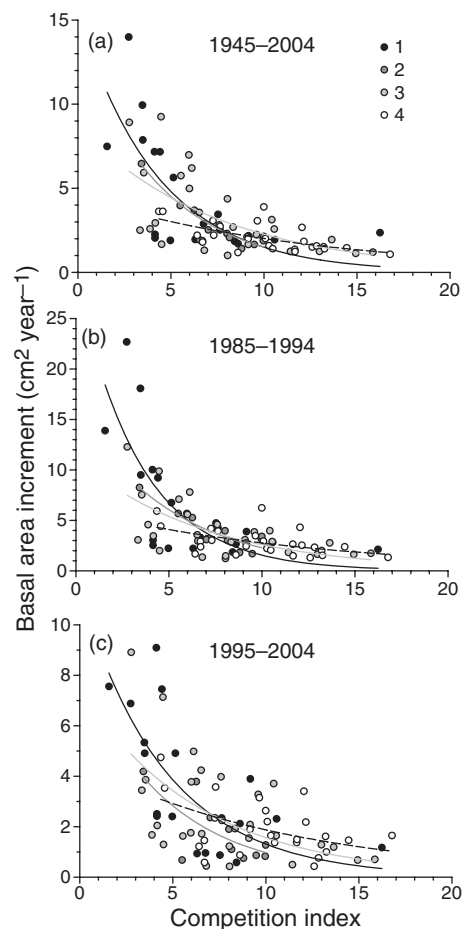


Fig. 3. Relationships between the competition index and the basal area increment of trees in the four study plots (noted as 1, 2, 3 and 4, respectively, in the inset) considering three time periods (1945–2004, 1985–94, 1995–2004). A subset of 80 trees was used because edge effects did not allow computing the competition index in the full data set of trees. The negative-exponential functions for each plot are represented with different symbol shades (data) and line types (sampling plot 1, black continuous line, $n = 17$; plot 2, dark grey line, $n = 11$; plot 3, light grey line, $n = 27$; plot 4, dashed black line, $n = 25$).

cated plot. The selected model explaining long-term BAI was based on the long-term trends of February–March–April and June–July–August temperatures (Fig. 4, see also Table 5). This single model appeared to fit the BAI data reasonably well in the four studied plots (67.8%, 61.4%, 72.1% and 45.7% of variance explained, respectively). Although the model was fitted without *a priori* discrimination among tree classes, the use of model intercepts from the corresponding individual trees allowed BAI predictions for each tree class separately (Fig. 4). Finally, simple linear regression performed on the residuals of the LMEM model showed that they were significantly related to total annual precipitation (see Fig. 5 and Fig. S3). The sharp growth decline recorded in 1995, which was not reflected by the BAI models based on long-term climatic trends, was now captured as BAI variation related to a short-term stressor such as a transient drought (Fig. 5). Moreover, the degree by which LMEM residuals responded to yearly rainfall patterns was inversely related to competition intensity (Table 6). In the case

Table 3. Mean radial growth (tree-ring width) for different periods in the four study plots. The year when sustained growth reduction (GR) started in each plot (GR > 50% in > 50% trees of each plot) and the slope of the linear growth trend since this year are also displayed. Values are mean \pm SE. Significant ($P < 0.05$) differences between plots based on Mann–Whitney tests are indicated by different letters

Plot	Tree-ring width 1945–2004 (mm)	Tree-ring width 1985–94 (mm)	Tree-ring width 1995–2004 (mm)	Year sustained GR	Slope of the linear growth-trend during sustained GR period (mm year ⁻¹)
1	1.74 \pm 0.07a	1.56 \pm 0.09a	0.86 \pm 0.07a	1972 \pm 1a	-0.07 \pm 0.005a
2	1.44 \pm 0.06b	1.22 \pm 0.07b	0.63 \pm 0.07b	1973 \pm 1a	-0.06 \pm 0.004a
3	1.50 \pm 0.06b	1.21 \pm 0.07b	0.70 \pm 0.06ab	1974 \pm 1a	-0.06 \pm 0.003a
4	1.19 \pm 0.03c	1.03 \pm 0.05b	0.58 \pm 0.03b	1966 \pm 1b	-0.03 \pm 0.002b

Table 4. Regression parameters based on exponential-decay functions ($y = ae^{-bx}$) and statistics of the relationship between radial growth (dependent variable, expressed either as mean tree-ring width, TRW, or as basal area increment, BAI) and the competition index (independent variable), considering different time periods

Plot	Parameters	TRW (1945–2004)	TRW (1985–94)	TRW (1995–2004)	BAI (1945–2004)	BAI (1985–94)	BAI (1995–2004)
1	<i>a</i>	2.51 \pm 0.35	2.54 \pm 0.46	1.13 \pm 0.30	15.45 \pm 4.02	29.17 \pm 8.21	11.35 \pm 2.86
	<i>b</i>	0.07 \pm 0.02	0.10 \pm 0.03	0.07 \pm 0.05	0.23 \pm 0.06	0.29 \pm 0.08	0.22 \pm 0.06
	<i>R</i> ² (adj)	0.36**	0.37**	0.14 ^{ns}	0.37**	0.41**	0.37**
2	<i>a</i>	2.15 \pm 0.27	2.04 \pm 0.42	1.66 \pm 0.68	13.58 \pm 1.41	16.06 \pm 2.82	8.21 \pm 3.49
	<i>b</i>	0.06 \pm 0.02	0.07 \pm 0.07	0.17 \pm 0.07	0.22 \pm 0.02	0.20 \pm 0.03	0.21 \pm 0.07
	<i>R</i> ² (adj)	0.40**	0.23*	0.23*	0.85**	0.65**	0.37*
3	<i>a</i>	2.28 \pm 0.37	1.59 \pm 0.42	1.06 \pm 0.35	8.72 \pm 2.18	11.23 \pm 2.68	7.51 \pm 2.26
	<i>b</i>	0.06 \pm 0.02	0.04 \pm 0.03	0.08 \pm 0.05	0.14 \pm 0.04	0.15 \pm 0.04	0.16 \pm 0.05
	<i>R</i> ² (adj)	0.28*	0.11 ^m	0.13 ^{ns}	0.40**	0.34**	0.29**
4	<i>a</i>	1.74 \pm 0.20	1.44 \pm 0.27	0.82 \pm 0.23	4.52 \pm 0.86	6.05 \pm 1.50	4.53 \pm 1.32
	<i>b</i>	0.04 \pm 0.01	0.04 \pm 0.02	0.04 \pm 0.03	0.08 \pm 0.02	0.08 \pm 0.03	0.09 \pm 0.03
	<i>R</i> ² (adj)	0.36**	0.15 ^m	0.06 ^{ns}	0.42**	0.29**	0.11*

^{ns} not significant; ^mmarginally significant $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

of dominant trees, the BAI variance accounted for annual precipitation increased from a mean of $8.5 \pm 3.3\%$ to $23.0 \pm 9.2\%$ between the periods 1965–84 and 1985–2004. Conversely, BAI residuals of trees subjected to higher competition lost responsiveness to yearly rainfall variability in the last two decades (Table 6).

Discussion

Extreme climate events, such as successive and severe droughts, may cause abrupt growth declines and pulses of elevated tree mortality (Suarez, Ghermandi & Kitzberger 2004; Bigler *et al.* 2007). They are also expected to more severely affect tree populations growing near the species' climatic tolerance limit (Macias *et al.* 2006). In the past 25 years, severe droughts, which have been characterized by high temperatures and low precipitation, such as the 1994–95 period, caused intense forest-dieback episodes in Spain (Peñuelas, Lloret & Montoya 2001). In recent years, several studies have linked growth decline to increasing dryness in the Mediterranean Basin (e.g. Sarris, Christodoulakis & Körner 2007). In the Spanish Pyrenees, the growth decline of *Abies alba* has also been attributed to an increase in water stress due to a summer temperature rise (Macias *et al.* 2006). Other authors found that the climate–growth relationships of *A. alba* changed in the

second half of the 20th century (Tardif *et al.* 2003; Pinto *et al.* 2007). This temporal instability in growth–climate relationships might be linked to the negative relationship between precipitation variability and radial growth (Andreu *et al.* 2007). However, none of the mentioned studies explicitly took into account the possible role of stand structure and density changes, in addition to climate factors, to explain growth decline and forest dieback. Moreover, long-term processes, rather than just short-term extreme events, seem to be strongly related to tree decline too, as has recently been shown for several conifer species in Europe (Bigler & Bugmann 2004; Bigler *et al.* 2004; Rebetez & Dobbertin 2004) and North America (Waring 1987; van Mantgem & Stephenson 2007).

Our key finding is that competition operates as a strong modulator of the adaptation capacity of *A. pinsapo* growth both to long- and to short-term climatic stress. This result is significant because it provides an understanding of growth decline processes in regard not only to regional climatic trends but to recent land-use history, too. It also highlights that canopy structural and density-dependent factors should be incorporated into conceptual frameworks for the assessment of the vulnerability of forest ecosystems to climate change (Fig. 6). The presented results demonstrate how growth decline was related to long-term climate dryness, whereas mean growth (BAI) was reasonably well predicted by the competition inten-

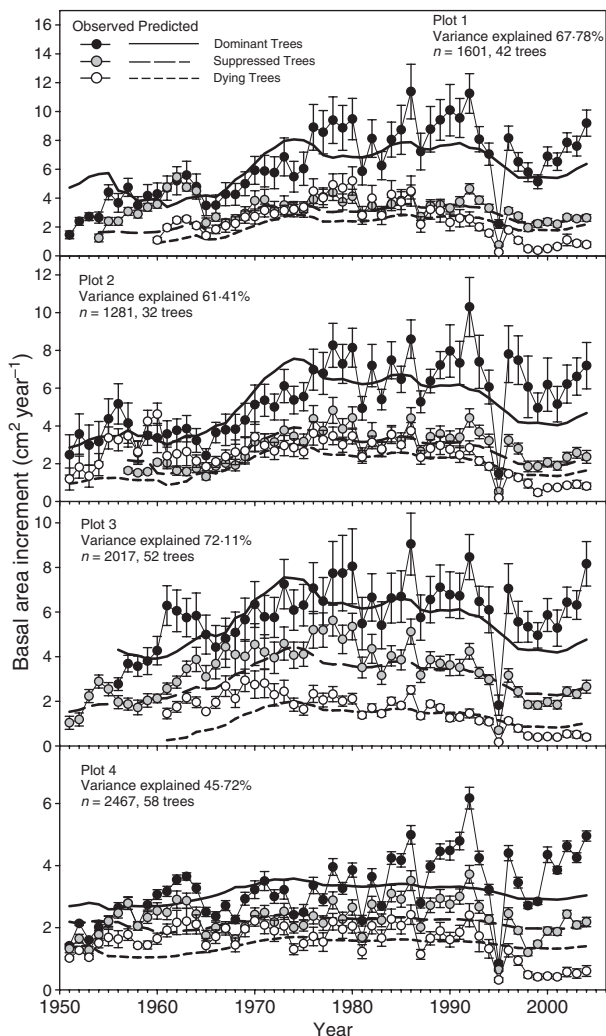


Fig. 4. Raw data of basal area increment for dominant, suppressed and dying trees (line and scatters) in the four studied plots, and linear mixed-effect model (LMEM, lines) fits based on long-term trends of temperature for the February–March–April and the June–July–August windows. The inset displays the amount of variance explained by the LMEM, the number of tree rings measured and the number of trees studied per plot. Error bars represent the standard error.

sity experienced by the trees. Finally, mortality might be understood in terms of short-term damage and loss of vigour caused by drought, which, in the case of trees subjected to high competition, is more likely to result in the surpassing of physiological thresholds (see also Linares *et al.* 2009).

Underlying growth trends were consistent and not fundamentally different among the four studied plots (Fig. 2c,d) and among dominant, suppressed and dying trees (Fig. S2 in Supporting Information). Such trends can thus be conceptually unified as a common response to long-term temperature increase and climate dryness. On the other hand, our demonstration that average growth rate at different time scales (see Fig. 2) is mainly related to stand structure provides information that is useful for predicting stand-level decline and drought-induced mortality. Specifically, our results imply that climate dryness is a widespread *A. pinsapo* stressor, but that

trees that are already experiencing long-term competition stress, as measured by narrow ranges and low means of radial growth, and, thus, are growing close to their lower survival threshold, have higher mortality probabilities when challenged with additional short-term drought stress (Linares *et al.* 2009). Although this model of tree growth decline and death is intuitive, empirical demonstrations of it are rare (but see Pedersen 1998b; van Mantgem *et al.* 2003). The role of competition as a predisposing stress factor has been evidenced comparing full-stocked and thinned stands since the negative effects of drought on tree growth and vigour may be mitigated through selective thinning (Manion 1991; Peet & Christensen 1987). An interesting implication of our findings is that various stressors could lead to increases in drought severity without corresponding increases in drought intensity. For example, if tree-to-tree competition caused a decline in growth rates in a significant proportion of a population of susceptible trees (Canham, LePage & Coates 2004), any given drought spell could be expected to severely damage or kill more trees than it would in a more heterogeneous stand structure with respect to species composition, structure, age and density (Pedersen 1998a).

Thus, stressors may interact, with competition predisposing trees to being killed by drought. Our results supported this hypothesis (see the growth trend of dying trees after 1995 in Fig. 4). Although very low annual precipitation was detected in the period 1994–95, similar low rainfall records also occurred before during the periods of 1945–46, 1954–55, 1973–75 and 1981–82 (Fig. 1b). However, none of these periods was linked to any decline episodes in *A. pinsapo* populations (Fig. 2), despite them being as severe as the 1990s event (Rodrigo *et al.* 1999). This different response raises questions about the existence of cumulative predisposing stress factors interacting with climatic stress. Alternately, other stressors, such as an increased post-drought pathogen load, may have supplied additional stress to the trees beyond what was estimated through the competition–growth relationships (Greenwood & Weisberg 2008). Moreover, low genetic variability within this relict species (Terrab *et al.* 2007) may also be a predisposing decline factor *sensu* Manion (1991), who suggested that factors such as previous droughts or insect attacks may lead to symptoms of decline, including partial crown dieback, and insect and hemiparasite infestations. In any case, age-related growth decline may be discarded because all studied plots showed intense crowding by trees with a mean age of 50 years (Table 1, see also Linares & Carreira 2009).

Tree-to-tree competition, brought about by the capture of resources by neighbours, is a long-term stress that affects the carbon and water balances of individual trees. It has thus the potential to modulate the responsiveness of tree growth to climatic variability. Stress causes distinctive changes in carbohydrate allocation patterns as well as unusual morphological characteristics (e.g. reduced foliage growth) and may indicate a tree is likely to die in the near future (Waring 1987). As discussed above, droughts may have altered the relationship between competition and growth (or mortality). Under high competition, trees became increasingly vulnerable because of a loss of adaptive capacity, as reflected by the low growth values

Table 5. Model selection criteria for *Abies pinsapo* growth expressed as basal area increment in the four studied plots. The most significant Dynamic Factor Analysis (DFA) climatic common-trends models, shown in Table 2, were tested. A null model (BAI = constant) was also included. ΔAIC , difference of AICc (Akaike information criterion corrected for small samples) with respect to the best model; $L(g_i/x)$, Likelihood of a model g_i given the data x ; W_i , relative probability that the model i is the best model given the observed data. Values in bold correspond to models with substantial support. T , mean monthly temperature; P , total monthly precipitation. Months are abbreviated by two letters (when the first two are coincident, the third letter is used for the abbreviations instead of the second letter)

Plot	Model	AICc	ΔAIC	$L(g_i/x)$	W_i
1 42 trees ($n = 1601$)	T Fe-Ma-Ap + T Jn-Jl-Au	-1198.07	0.00	1.00	1.00
	T Fe-Ma-Ap + P Fe-Ma-Ap	-1184.82	13.24	0.00	0.00
	P Ma-Ap-My	-905.33	292.74	0.00	0.00
	P Fe-Ma-Ap	-880.47	317.60	0.00	0.00
	T Fe-Ma-Ap	-847.56	350.51	0.00	0.00
	Null model	-802.08	395.98	0.00	0.00
	T Jn-Jl-Au	-796.40	401.67	0.00	0.00
Sum				1.00	
2 32 trees ($n = 1281$)	T Fe-Ma-Ap + P Fe-Ma-Ap	-1131.69	0.00	1.00	0.73
	T Fe-Ma-Ap + T Jn-Jl-Au	-1129.73	1.96	0.38	0.27
	T Fe-Ma-Ap	-893.30	238.39	0.00	0.00
	P Ma-Ap-My	-735.33	396.36	0.00	0.00
	P Fe-Ma-Ap	-723.47	408.22	0.00	0.00
	Null model	-716.12	415.58	0.00	0.00
	T Jn-Jl-Au	-712.71	418.98	0.00	0.00
Sum				1.38	
3 52 trees ($n = 2017$)	T Fe-Ma-Ap + T Jn-Jl-Au	-1694.43	0.00	1.00	1.00
	T Fe-Ma-Ap + P Fe-Ma-Ap	-1665.49	28.94	0.00	0.00
	T Fe-Ma-Ap	-1433.70	260.72	0.00	0.00
	P Ma-Ap-My	-1201.21	493.22	0.00	0.00
	T Jn-Jl-Au	-1197.89	496.54	0.00	0.00
	Null model	-1191.57	502.86	0.00	0.00
	P Fe-Ma-Ap	-1189.45	504.98	0.00	0.00
Sum				1.00	
4 58 trees ($n = 2467$)	T Fe-Ma-Ap + T Jn-Jl-Au	-2856.36	0.00	1.00	1.00
	T Fe-Ma-Ap + P Fe-Ma-Ap	-2824.79	31.57	0.00	0.00
	T Fe-Ma-Ap	-2781.99	74.37	0.00	0.00
	P Ma-Ap-My	-2750.69	105.67	0.00	0.00
	Null model	-2745.73	110.63	0.00	0.00
	P Fe-Ma-Ap	-2744.70	111.66	0.00	0.00
	T Jn-Jl-Au	-2733.62	122.74	0.00	0.00
Sum				1.00	

(Fig. 3, Table 3 and Fig. 4) and their weakened correlation with rainfall variability during drier periods (Table 6, Figs 5 and S3). Long-term competition could lead to further challenges in overcoming drought events, for instance, a requirement for superior carbon balance when faced with the need to recover from drought-induced crown loss (Franklin, Shugart & Harmon 1987). Because of their size, trees have large storage capacities and may thus accumulate considerable nutrients,

carbohydrates and water. These resources can often be mobilized during periods of stress, enabling a canopy or root system to continue to function or to be re-established following a stressful period (Waring 1987). Therefore, the relationships between competition, growth rate and the probability of post-drought death may be at least partly mediated by the size of the tree crown and, hence, the tree's ability to fix carbon (Pedersen 1998b; Dobbertin 2005). For a given tree size,

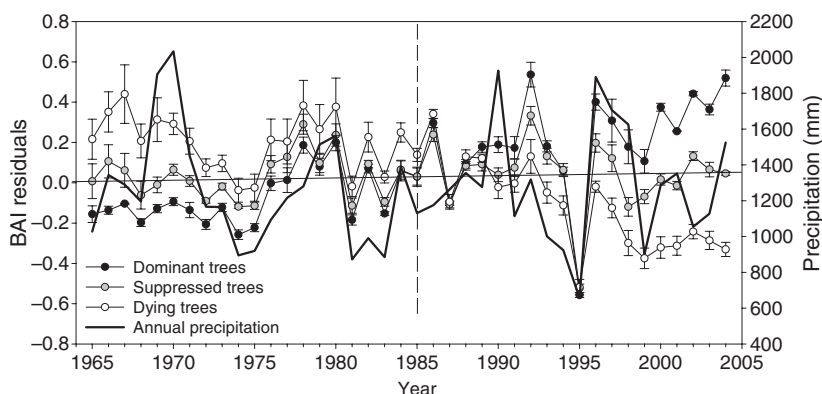


Fig. 5. Graphical comparison between total annual precipitation and the mean LMEM residuals of the three social classes (dominant, suppressed and dying trees). The dotted line separates two consecutive periods of twenty years (1965–84 and 1985–2004, see Table 6).

Table 6. Variance explained (%) by simple linear regressions between annual precipitation and the LMEM residuals. Data have been analysed separately, in the four studied plots, for the three social classes (dominant, suppressed and dying trees) and two consecutive periods of 20 years (1965–84 and 1985–2004)

	Plot	1	2	3	4
1965–84	Dominant	6.49*	5.02*	10.94*	11.60*
	Suppressed	16.03**	10.46*	13.71**	12.95**
	Dying	11.28*	23.04***	27.40***	44.91***
1985–2004	Dominant	26.85***	33.94***	17.78**	13.52**
	Suppressed	11.85*	15.41**	14.34**	4.48*
	Dying	2.67*	10.37*	6.14*	1.27 ^m

^mmarginal significance $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

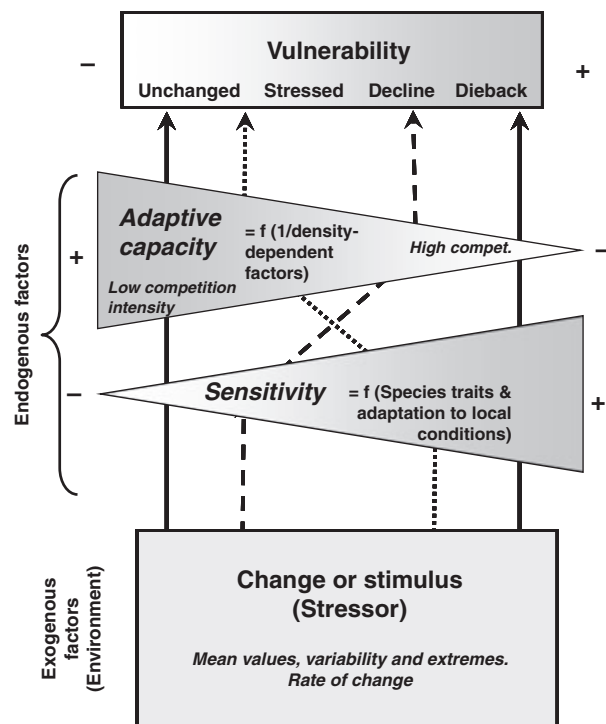


Fig. 6. Conceptual framework for the assessment of the vulnerability of a forest ecosystem to environmental change in terms of its intrinsic sensitivity and the modulation of its adaptive capacity as an inverse function of density-dependent factors such as competition.

individuals subjected to high competition are more likely to have a sparser crown and lower total leaf area than dominant trees (Linares *et al.* 2009). Thus, a given amount of crown defoliation induced by drought on a suppressed growing tree would cause the tree to have much less total photosynthetic leaf area than the same relative defoliation of crown in a dominant growing tree would do (Dobbertin & Brang 2001). Conversely, trees not experiencing such intense long-term stress due to competition would be better able to resist the effects of short-term, drought-induced stress (Figs 4 and 5).

Given the interactions between stand structure and growth, the predictive power provided by climate-focused models that

neglect tree-to-tree competition is unlikely to be matched in the future. More fundamentally, we suggest that the challenges of managing and maintaining structurally complex stands require a shift from empirical, non-spatial models that emphasize prediction to more mechanistic, spatially explicit models that can incorporate the consequences of changing physical and competitive environments within stands (Canham, LePage & Coates 2004; Das *et al.* 2008). Information concerning stand structure and tree growth are also useful in the context of proactive conservation management, for instance, to support decision options on partial harvesting measures aimed to reduce average tree-to-tree competition and to achieve a more diversified forest structure (Franklin *et al.* 2002; Carreira, Quintanilla & Linares 2009). It is difficult, however, to generalize the results of these models, because few attempts to describe the process of post-drought mortality in a comprehensive manner exist. A more mechanistic description of drought-induced mortality would include measures of the trees' physiological status and an account of the effects of the damage on post-drought carbon gain and water use on trees that are subjected to contrasting competition (Linares *et al.* 2009).

We have reported herein on three lines of evidences to test the hypothesis that short- and long-term stressors are interacting to explain growth decline patterns in Spanish *A. pinsapo* populations. First, climatic trends, together with tree-ring width chronologies, indicate increasing water stress and growth decline in *A. pinsapo* populations. Second, growth decline was related to long-term climate dryness (late-winter to summer temperature increases), whereas mean growth was well predicted by tree-to-tree competition (also a long-term stressor), because trees that are subjected to lower competition show higher growth values. Third, mortality in trees subjected to high competition was related to recent drought spells (a short-term stressor).

Our findings that climate and tree-to-tree competition interact over short- and long-term scales to impact tree growth suggest that poorly asymmetric and highly competitive neighbourhoods reduce the adaptive capacity of the trees to environmental stressors, thus increasing forest vulnerability. This highlights the importance of considering forest structure, beyond just species composition and site quality, when assessing the vulnerability (*sensu* IPCC 2007; see also Lindner *et al.* 2009) of forest ecosystems to climate change (Fig. 6). Our analytical approach for the partitioning of growth variance among contributing factors showed how trees that were subjected to high competition are growing near their lower survival threshold. Thus, their ability to adjust to environmental change, including trends, variability and extremes, is strongly limited. The main application of this study is the assessment and reconsideration of no-management, strict protection measures currently applied to the conservation of relict tree species in water-stressed areas, such as Mediterranean ecosystems, which previously had a long history of human use. At least for the reported *A. pinsapo* case, such policy seems to be detrimental in the long-term, because the resulting enhancement of density-dependent factors and

competition leads to a reduction in the intrinsic adaptive capacity of tree growth to both long- and short-term climatic variability. The assessment of stand structure effects on tree vulnerability to climate dryness should aid to better protect tree populations growing near the species' climatic tolerance limit under the context of current climate warming.

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Supporting Information

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

Table S1. Characteristics of the meteorological stations used to compute the regional mean climatic series.

Figure S1. Age (estimated at 1.3 m) distribution for sampled trees.

Figure S2. Estimated trends obtained by DFA of the normalized basal area increment for dominant (Dom, black symbols, $n = 17$), suppressed (Supp, grey symbols, $n = 25$), and dying trees (white symbols, $n = 28$).

Figure S3. (a) Graphical comparison between total annual precipitation and the stand-level residuals of BAI not accounted for by the linear mixed effect model (LMEM) based on the long-term trends of temperature for the February–March–April and the June–July–August windows, and (b) linear regressions between annual precipitation and the LMEM residuals in the four studied plots.

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