

Growth patterns and sensitivity to climate predict silver fir decline in the Spanish Pyrenees

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Abstract Patterns in radial growth have often been used to predict forest decline since they are regarded as indicators of the tree responses to long-term stressors. However, the sensitivity of tree growth to climate, as a proxy of the trees' adaptive capacity to short-term climatic stress, has received less attention. Here, we used retrospective tree-ring analyses to determine whether growth patterns and sensitivity to climate are related to *Abies alba* (silver fir) decline in the Spanish Pyrenees. We used regional climatic data to calculate normalised temperatures and drought indexes. Basal-area increment (BAI) was measured for declining (defoliation >50%) and non-declining (defoliation <50%) silver firs in four stands with contrasting decline levels. A dynamic factor analysis (DFA) was applied to test the hypothesis that declining and non-declining trees have experienced different long-term growth trends. Growth sensitivity to climate was computed as the average change in BAI per unit of change in a given

climate variable. Declining trees showed a negative growth trend during the last 20 years. Trees with lower relative BAI and negative BAI trends showed stronger growth sensitivity to climate and higher defoliation than trees with the opposite characteristics. Our findings underscore the idea that long-term climatic warming seems to be a major driving factor of growth decline in Pyrenean silver fir forests. Ongoing growth reduction and enhanced growth sensitivity to climate may promote vegetation shifts in these declining forests located near the xeric edge of the species distribution area.

Keywords *Abies alba* · Basal-area increment · Climate warming · Drought · Dynamic factor analysis · Tree decline

Introduction

Pronounced temperature rises and variations in rainfall patterns have the potential to profoundly alter the growth dynamics of tree species (Macías et al. 2006; Andreu et al. 2007; Sarris et al. 2007). Past climate-warming events seem to have promoted shifts in plant species and biomes towards the poles or upwards in the case of mountains ecosystems (Taberlet and Cheddadi 2002). However, the extent of current forest vulnerability to recent climate change near the climatic distribution limits of most tree species presents large uncertainties, mainly because the intra-specific responses to regional warming and extreme drought events remain poorly understood (Peñuelas et al. 2007; Linares et al. 2011; Linares and Camarero 2011). Here, we aimed at testing the interacting effects among tree growth patterns and growth sensitivity to climate.

The understanding of contrasting growth responses to climate stress, accounted among different individuals and

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stands of the same tree species, might be particularly relevant for understanding forest dynamics in a warmer world (Linares et al. 2011; Rathgeber et al. 2011). Previous works have suggested that declining trends of radial growth may be considered as reliable indicators of long-term stress and represent an additional risk factor for drought-induced tree decline (Dobbertin 2005; Bigler et al. 2007; Greenwood and Weisberg 2008). Because soil–water availability is a key limiting resource in drought-prone Mediterranean forests, the interacting effects of tree growth patterns and growth sensitivity to climate could be affecting the persistence of tree populations near the xeric limit of the species distribution area (Peñuelas et al. 2007; Linares and Tísar 2010; Linares and Camarero 2011).

Individual tree decline and death often occur as a result of the combined effects of different long- and short-term stressors (Manion 1991; Pedersen 1998a). Dendrochronological assessments of changing trends of radial growth may be useful to understand decline processes (Ogle et al. 2000; Bigler et al. 2004). Moreover, tree decline is also linked to crown defoliation (see for instance Carnicer et al. 2011). Thus, the combination of defoliation and growth estimates may provide a retrospective assessment of the changes of tree vitality in response to climatic stressors since growth decline usually precedes needle loss, and tree defoliation may be also used as an indicator of recent tree decline (Solberg 2004; Dobbertin 2005).

Radial growth, used here as a proxy of whole plant carbon gain (Litton et al. 2007), may be used to identify those trees with the highest probabilities of severe defoliation, decline and death (Wunder et al. 2008; Vieilledent et al. 2010; Carnicer et al. 2011). Several studies have shown that tree defoliation, mean radial growth and radial growth trends are, to some extent, inversely related (Buchman et al. 1983; Kobe and Coates 1997; Wyckoff and Clark 2000; van Mantgem et al. 2003). However, the potential interacting effects of long-term growth patterns and short-term growth sensitivity to climate on decline probability, and their use as surrogates for evaluating the vulnerability of tree species to climate change, have received less attention (Pedersen 1998b; Das et al. 2007).

Usually, reduced wood formation occurs prior to visual symptoms of decline such as crown defoliation. Thus, dendrochronology may be useful to forecast the impending decline of particular trees and forests (Dobbertin 2005). Moreover, if tree decline is the result of the combined effects of several types of stressors acting at different time scales on growth, information from both long-term growth patterns and short-term growth sensitivity to climate should improve our knowledge of decline mechanisms based also on the specific traits of tree species (e.g. drought tolerance).

To evaluate the contributing effects of long-term growth patterns (rates and trends) and short-term growth sensitivity

to climate on tree decline, we used retrospective tree-ring and climate analyses and crown defoliation as a surrogate of tree vitality. We focused on declining silver fir (*Abies alba* Mill.) stands from the Spanish Pyrenees (Camarero et al. 2011; Linares and Camarero 2011). We hypothesised that silver fir decline, here estimated by assessing tree defoliation, is related to tree growth patterns and could be explained as a response to climatic stressors. Our specific aims were (i) to test whether declining and non-declining trees have experienced different long-term growth trends and (ii) to evaluate whether growth patterns and their sensitivity to climate at the tree level are useful predictors of silver fir decline.

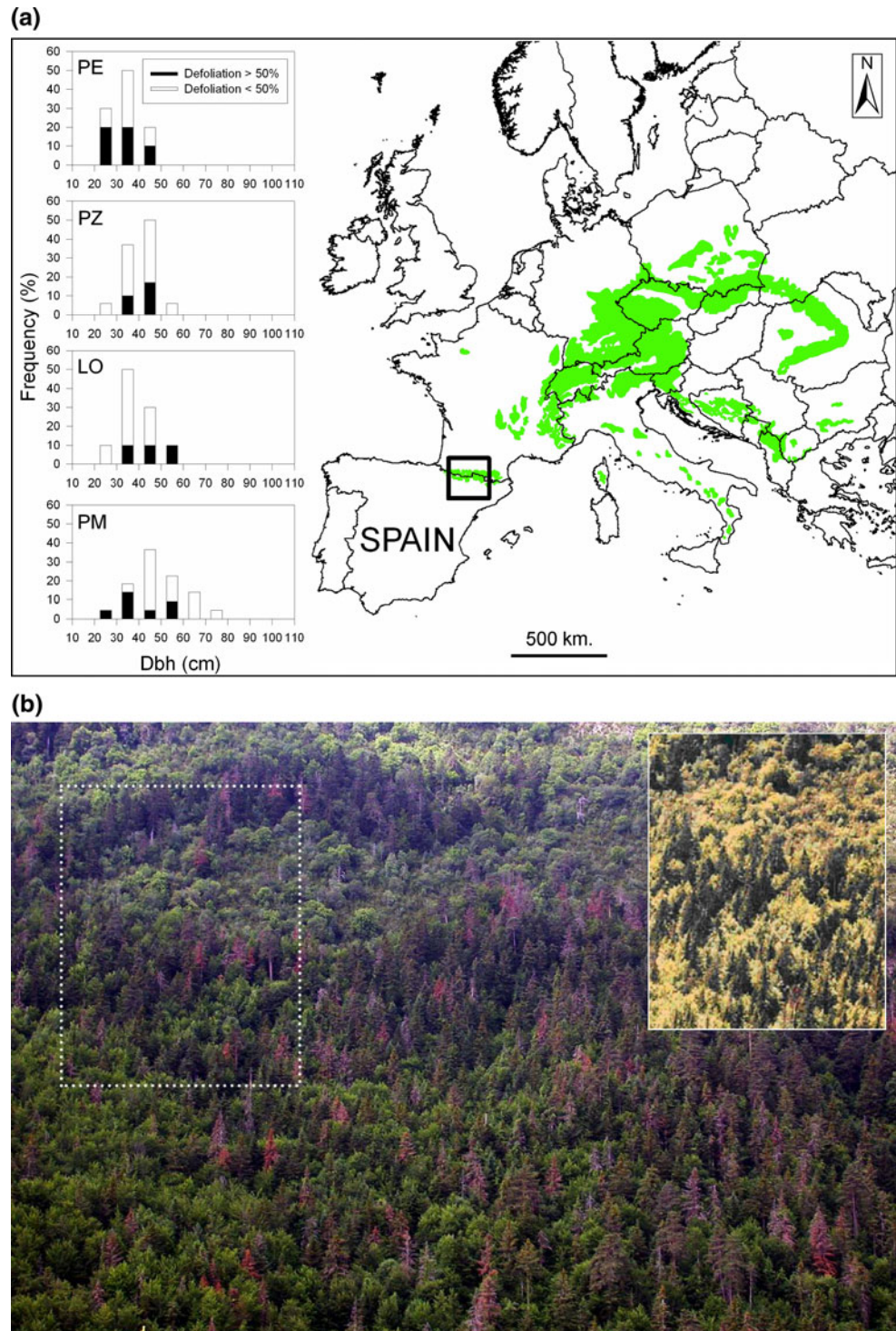
Materials and methods

Study species and field sampling

The Pyrenees constitute a transitional area between more humid conditions in their northern margin and drier conditions southwards where Mediterranean vegetation becomes dominant. The studied *A. alba* populations are located in the Aragón Pyrenees, north-eastern Spain (Fig. 1), where silver fir stands are usually found at humid sites on north-facing slopes forming pure or mixed stands with *Fagus sylvatica* L. or *Pinus sylvestris* L. Most studied stands are located on marls and limestones, which generate basic soils, or on moraine deposits with rocky but deep soils. The most used method of timber harvesting in the study area was diameter limit cutting, which mostly affected fast-growing and big trees. According to historical data, logging intensity during the twentieth century in the Pyrenees was greatest in the 1950s but no data are available on how widespread was in this region (Cabrera 2001).

In the Aragón Pyrenees, silver fir growth decline was characterised by high defoliation levels and increased mortality rates and it mostly affected low-elevation sites since the 1980s (Camarero et al. 2002, 2011; Linares and Camarero 2011). Since we were interested in comparing *A. alba* stands with different decline symptoms, we performed an extensive field survey, visiting at least one site in all 10-km² grids where silver fir formed forests across the study area. Based on this extensive field survey, we selected four representative stands with abundant declining and defoliated trees (see below the definition of declining and non-declining trees; Table 1). At each site, ten to twenty dominant trees were selected for sampling within a 500-m long and 20-m wide transect randomly located within the stand. Several topographical variables were obtained for each site and tree. We measured the size of all trees located within the transect (diameter at 1.3 m, dbh; stem height)

Fig. 1 Distribution of *A. alba* in Europe and study sites in the Aragón Pyrenees, north-eastern Spain (a) and view of a declining silver fir stand in the Paco Ezpela (site PE) (b). In the upper graph, the *inset* shows the size structure (dbh) of sampled declining (defoliation >50%) (black) and non-declining (defoliation <50%) (white) silver fir individuals. Sites codes are as in Table 1. In the lower image red and defoliated trees are declining silver firs, whereas the dark- and light-green trees are healthy firs or pines (*P. sylvestris*) and beeches (*F. sylvatica*), respectively. The photograph was taken in June 2006, and the *upper-inset* photograph corresponding to the area outlined by the dashed line was taken in August 2001. Tree defoliation and high mortality levels have been widespread in this site since at least 1986



and assessed their vigour using a semi-quantitative scale based on the percentage of crown defoliation (Müller and Stierlin 1990): class 0, 0–10% defoliation (healthy tree); 1, 11–25% (slightly damaged tree); 2, 26–50% (moderately damaged tree); 3, 51–75% (severely damaged tree); 4, 76–90% (dying tree); 5, standing dead trees with >90% defoliation or only retaining red needles. Since estimates of

per cent crown defoliation may vary among observers and places, we used as a reference a tree with the maximum amount of foliage at each site (Dobbertin 2005). Defoliation was based on the visual assessment of the loss of foliage, which may be considered to be an estimate of crown transparency (Solberg 2004). Declining trees were considered as those with crown defoliation greater than 50%, and

Table 1 Geographical, topographical, structural and vigour characteristics of the four sampled sites

Site (code)	Latitude (N)	Longitude (W)	Aspect	Elevation (m)	Slope (°)	Dbh (cm)	Height (m)	Basal area (m ² ha ⁻¹)	Declining trees with defoliation > 50% (%)	Standing dead trees (%)
Paco Ezpela-high (PE)	42°45'	0°52'	NE	1,232	27	35.0 ± 2.3	18.2 ± 0.9	10.1	35.0	14.3
Paco Ezpela-low (PZ)	42°45'	0°52'	NE	1,073	26	43.0 ± 1.2	21.4 ± 0.6	24.7	33.3	8.3
Lopetón (LO)	42°46'	0°52'	NW	1,009	32	38.1 ± 2.7	20.8 ± 0.8	24.8	30.0	12.0
Paco Mayor (PM)	42°42'	0°38'	N	1,333	30	49.8 ± 3.3	24.0 ± 0.6	32.9	31.8	9.6

Values are means ± SE. Declining trees had crown defoliation >50%, and standing dead trees had defoliation higher than 90% or retained only red needles

declining sites were regarded as those with more than 25% trees with such degree of defoliation decline.

Climate data

We used local climatic records to study the spatio-temporal variation of climatic conditions in the study area (Table 2). To estimate the missing data for each meteorological station and to obtain a regional climatic record, we used the programme MET from the *Dendrochronology Program Library* (Holmes 1992). The annual water budget (named as drought index thereafter; P-ETP) was obtained from the sum of the differences between monthly data of precipitation (P) and potential evapotranspiration (ETP), and the last variable was estimated by a modified version of the Thornthwaite method (Willmott et al. 1985).

To obtain the regional climatic means, local data were normalised to give each station the same relative weight. Mean temperature and P-ETP were normalised by subtracting the mean and dividing by the standard deviation:

$$Z_i = \frac{(x_i - \bar{x})}{\sigma} \quad (1)$$

where Z_i is the x_i score distance from the x average (\bar{x}) in standard deviation units (σ).

Dendrochronological methods

Dendrochronological sampling was performed in the 10–20 trees selected per site following standard methods (Fritts

1976). Two or three cores were taken from each tree at breast height (1.3 m) using an increment borer. The wood samples were air dried and polished with a series of successively finer sand-paper grits until tree rings were clearly visible. Then, the wood samples were visually cross-dated. Tree rings were measured to the nearest 0.001 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). The visual cross-dating of the tree rings was checked using the programme COFECHA (Holmes 1983). The trend due to the geometrical constraint of adding a volume of wood to a stem of increasing radius was corrected by converting tree-ring widths into basal-area increments, hereafter abbreviated as BAI (Biondi and Qaadan 2008). We also calculated BAI trends of each tree as the slopes of linear regressions over a given time period, and the relative basal-area increment (relBAI) calculated as BAI divided by BA (basal area). The BAI trend accounted for the change of the growth rate over a time, while relBAI was considered to take into account the current growth rate (BAI) as well as the size of the tree (BA).

Dynamic factor analyses of growth trends

Dynamic factor analysis (DFA) was used to estimate the common underlying trends in tree growth data (Zuur et al. 2003). DFA analyses were applied to normalised BAI time series, calculated by subtracting the mean and dividing by the standard deviation, because this facilitates the interpretation of factor loadings and the comparison of

Table 2 Characteristics of the meteorological stations used to describe climatic conditions in the studied *Abies alba* sites

Station	Latitude (N)	Longitude (W)	Elevation (m)	Years for precipitation data	Mean annual precipitation (mm)	Missing values (%)	Years for temperature data	Mean annual temperature (°C)	Missing values (%)
Ansó	42°45'	0°50'	820	1970–1999	1,184	6.9	1970–1999	9.8	9.7
Echo	42°44'	0°45'	860	1957–1999	1,196	8.5	1975–1996	10.5	8.3
Aragüés del Puerto	42°42'	0°40'	980	1970–1999	1,291	4.2	1970–1999	11.0	3.1
Castiello de Jaca	42°38'	0°33'	885	1970–1999	1,033	2.5	1970–1999	10.2	1.1
Canfranc	42°45'	0°31'	1,160	1910–1999	1,836	1.0	1910–1999	8.3	6.9

regression parameters (see also Biondi and Qaadan 2008; Linares et al. 2010). This method provides for each group of trees factor loadings, which indicate the weight of a particular trend in this time series. In addition, the comparison of factor loadings of different time series allows the detection of common BAI trends among different stands.

The model used was $\text{data} = \text{sum of the } M \text{ common trends} + \text{noise}$. The goodness of fit of the model was assessed by Akaike's information criterion (AIC, Akaike 1974), which combines the measure of fit with a penalty term based on the number of parameters used in the model. 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. DFA was implemented using the Brodgar statistical package version 2.4.1 (Highland Statistics, Newburgh, UK), which was linked to R software (R Development Core Team 2011). Further details about DFA may be found in the Electronic Supplementary Material (Appendix 1), and in Zuur et al. (2003).

Evaluation of growth sensitivity to climate

The differences (residuals) between measured and modelled growth can be used to estimate how climatic stressors constrain tree growth (Solberg 2004; Dobbertin 2005). Here, we estimated the long-term BAI trends by DFA and then obtained the differences between the observed and the modelled BAI (BAI residuals, thereafter BAIr). We aimed to evaluate the extent to that deviations from modelled common trends, which should be observed in declining trees (i.e. sudden growth decline or negative growth trends), are related to climate. Since the DFA main trends obtained for declining trees could be in theory strongly related to climate, we used the DFA main trends obtained for non-declining healthy trees as modelled BAI (see Electronic Supplementary Material Fig. S1). Then, we estimated the BAI residuals (BAIr) as the differences between measured (declining and non-declining trees) and modelled growth for non-declining trees. BAIr may be regarded as an estimate of high-frequency BAI variability. Thus, growth-climate relationship was estimated as the Pearson correlation coefficient between the BAIr calculated for each individual tree and the normalised climate variables. Using the same reasoning, the growth sensitivity to climate was estimated as the slope obtained by linear least squares regression between the BAIr calculated for each individual tree and the normalised climate variables. We assumed that, for a given tree, the growth-climate slope describes its responsiveness to climate variability, quantified as the change in BAI divided by the corresponding change in the climate variable, over the entire ranges of variance of both variables. Higher slope values should

indicate a steeper growth response to climatic variability and therefore higher growth sensitivity to climate.

Results

Normalised mean annual temperature yielded systematically above average values after 1981, with extreme warm years in the following periods 1937–1938, 1986–1990 and 1997–1998 (Fig. 2). The coldest periods recorded for the twentieth century in the study area were 1917, 1955–1956 and 1963. The normalised drought index (P-ETP) yielded extreme drought events with pronounced water deficit in 1933, 1937, 1949 and 1989, while years with high water availability were observed in the 1960s (1960, 1966) and 1970s (1977, 1979).

All the trees studied were of similar size (mean dbh = 40 cm, mean height = 21 m) and age (mean = 100 years; Tables 1, 3). Stand basal area ranged between 25 and 33 m² ha⁻¹, excepting for the PE stand, which yielded 10 m² ha⁻¹, as well as the highest percentages of severely defoliated and standing dead trees (Fig. 1 inset; Tables 1, 3). The first-order autocorrelation of raw ring-width chronologies, calculated for the period 1900–1999, ranged from 0.27 to 0.42; the mean sensitivity of residual indexed chronologies was about 0.24, which corresponds to a low high-frequency variability. The first principal component of residual indexed chronologies ranged between 46 and 53%, which indicates a high tree-to-tree common growth variance in all study sites (Table 3).

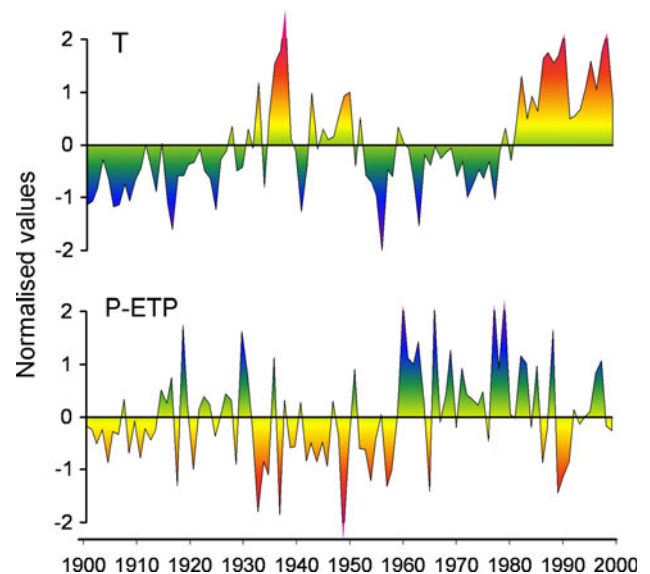


Fig. 2 Annual values of regional normalised mean temperature (T) and normalised total precipitation minus evapotranspiration (P-ETP; difference between precipitation—P and potential evapotranspiration—ETP)

Table 3 Growth features and dendrochronological statistics for the four sampling sites and considering the period 1900–1999

Site (code)	Age at 1.3 m (years)	No. trees/radii	Mean \pm SE tree-ring width (mm)	AR1	MSx	PC1 (%)
Paco Ezpela-high (PE)	88 \pm 5	15/39	1.70 \pm 0.09	0.28	0.24	45.77
Paco Ezpela-low (PZ)	114 \pm 7	15/30	1.67 \pm 0.10	0.42	0.19	49.09
Lopetón (LO)	104 \pm 6	12/24	1.48 \pm 0.11	0.32	0.30	53.40
Paco Mayor (PM)	100 \pm 5	20/43	1.80 \pm 0.17	0.27	0.22	50.20

The annual MSx measures the relative difference from one ring-width index to the next, 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. MSx ranges from 0 to 2 with larger values corresponding to greater high-frequency variability. The PC1 measures the tree-to-tree common growth variance within each site (Fritts 1976)

AR1 first-order autocorrelation of raw ring-width chronologies, MSx mean sensitivity of residual indexed chronologies, PC1 variance explained by the first principal component of residual indexed chronologies

The dynamic factor analyses (DFA) revealed that the model containing two common BAI trends and a non-diagonal error covariance matrix showed the highest fit and it was selected based on its lowest AIC (AIC = 296.01, for a non-diagonal error covariance matrix; AIC = 960.0, for a diagonal error covariance matrix). The DFA trend 1 showed a sustained rising BAI between 1900 and about 1980, and a steeply rising BAI from the mid 1980s onwards. The DFA trend 2 was characterised by a sustained rising BAI between 1960 and the late 1970s, which

was steeper than that observed for trend 1, and a sudden BAI decline from the mid 1980s forwards (Fig. 3a).

The variability in BAI was significantly explained by the first two DFA trends that accounted for about 71% of the overall variance (Table 4). Non-declining trees showed higher loading factors more related to the DFA trend 1, i.e. increasing BAI, whereas declining trees showed factors associated to the DFA trend 2, i.e. decreasing BAI (Fig. 3b; see also Electronic Supplementary Material, Table S1). These findings indicate that declining trees followed a similar long-term growth pattern two decades before observing decline symptoms (e.g. high defoliation) and tree death.

However, we also found deviations from the common growth pattern stated above. For instance, in the PE stand, declining trees yielded similar affinity to DFA trends 1 and 2, whereas declining trees from the other three stands showed a decreasing long-term BAI captured by the DFA trend 2 (see Figs. 3b, 4). The LO and PM stands showed the lowest couplings to the two DFA trends based on the amounts of BAI variance explained in both study sites (Table 4). This was mainly due to the sharp growth decline observed in 1986 (Fig. 4).

Correlations of BAI residuals (BAIr) with climatic variables were highly significant for August and November mean temperature of the year prior to tree-ring formation, as well as for January and July temperature of the year of growth (Fig. 5). Correlations between BAIr and P-ETP were on average lower than those obtained for mean temperature, but they were significant and positive for current March and June (Fig. 5). On average, the months showing significant temperature-BAIr correlations yielded a regression slope among temperatures and BAIr (i.e. temperature sensitivity) of about -0.50 , indicating that there was decrease of half unit of normalised BAI per unit of increase in the mean temperature of these months. March and June P-ETP yielded a regression slope (drought sensitivity) of about $+0.26$, indicating that an increase of 0.26 units of normalised BAI corresponded to an unit of increase in P-ETP of these months. However, both

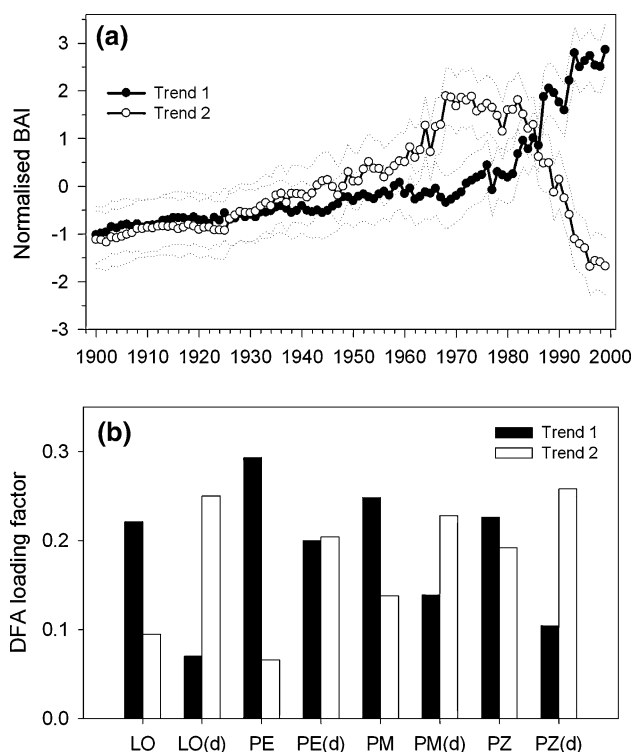


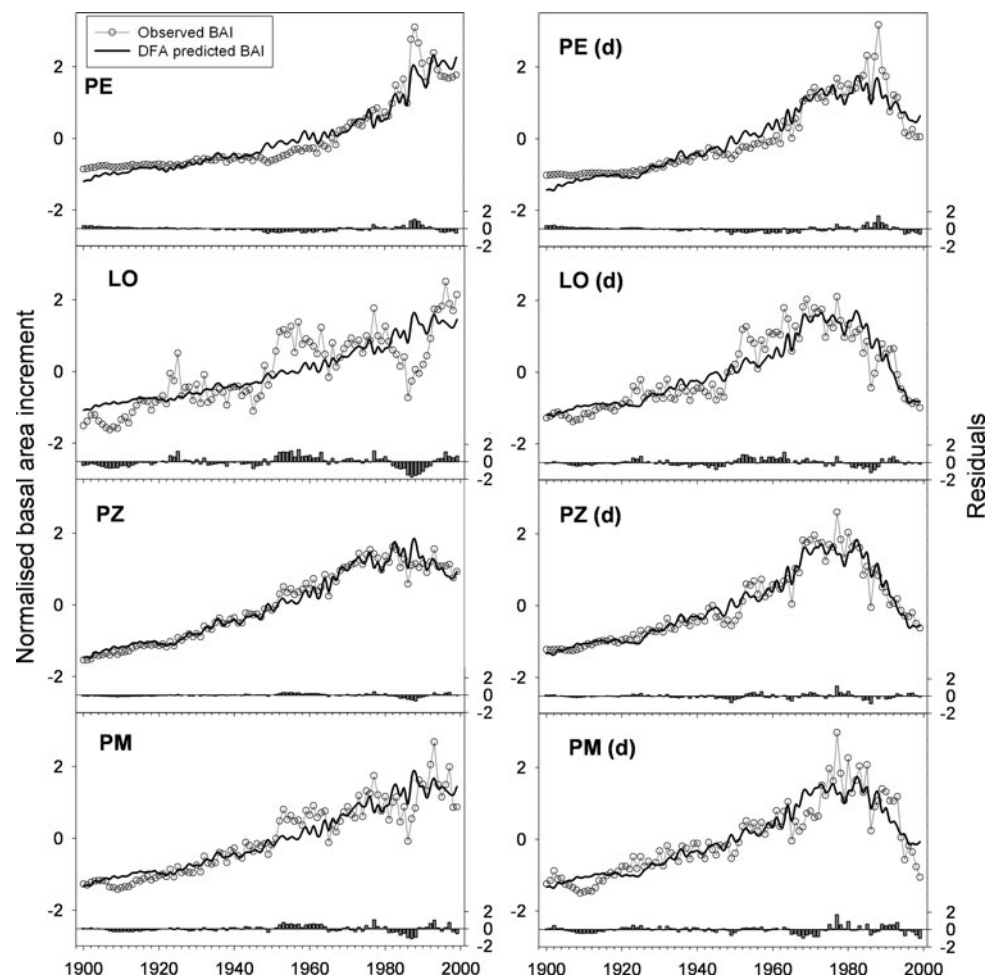
Fig. 3 Estimated common basal-area increment trends (a) established by dynamic factor analysis (DFA) in the studied *A. alba* trees. Dotted lines represent the 95% confidence interval. Loading factors (b) are displayed for DFA trends 1 (increasing BAI; black bars) and trend 2 (decreasing BAI; white bars) considering declining (d) and non-declining trees (indicated only by the site code) in the four study sites

Table 4 Variance in basal-area increment (BAI) explained by the two modelled common growth trends obtained through dynamic factor analysis (DFA) in declining (d) and non-declining (nd) *A. alba* trees

Site	Tree type	DFA common trend 1 (increasing BAI) Variance explained (%)	DFA common trend 2 (decreasing BAI) Variance explained (%)	DFA full model Variance explained (%)
PE	nd	87.19***	5.06*	88.48
PE	d	41.53***	48.40***	66.62
PZ	nd	51.71***	46.58***	74.55
PZ	d	11.23**	82.43***	86.42
LO	nd	46.91***	14.98***	40.90
LO	d	4.90*	79.10***	77.82
PM	nd	61.34***	25.39***	65.50
PM	d	19.81***	63.67***	65.66

See sites' codes in Table 1. Significance levels: * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

Fig. 4 Normalised basal-area increment (*thin lines with symbols*) and dynamic factor analysis trends (*thick lines*) fitted to declining (d) and non-declining trees. The bottom diagram represents the residuals (*bars*) of the DFA model (BAIr), expressed as the difference between observed minus predicted BAI values. These residuals were thereafter used as the high-frequency BAI pattern



temperature and drought sensitivity showed high variability among trees.

This variability among trees for temperature and drought sensitivity was significantly related to relative tree basal-area increment (relBAI, Fig. 6) and basal-area increment

trends (Fig. 7). On average, trees with lower relBAI and negative BAI trends showed high growth sensitivity to climate, i.e. an elevated growth responsiveness to changes in a given climate variable, and presented high defoliation levels (see Electronic Supplementary Material Fig. S2).

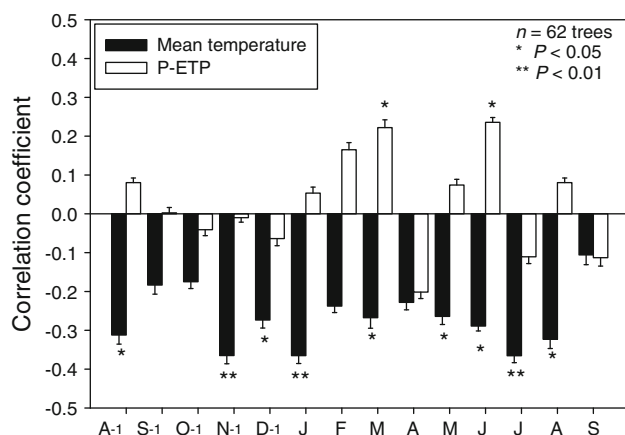


Fig. 5 Pearson correlation coefficients (means \pm SE) for the relationships between basal-area increment (BAIr) residuals of the individual tree chronologies ($n = 62$ trees) and the monthly series of normalised mean temperature and the difference between precipitation and evapotranspiration (P-ETP). Climatic variables corresponding to the year previous to tree-ring formation are indicated by (-1). Significance levels: * $P < 0.05$; ** $P < 0.01$

Discussion

We hypothesised that lower growth rate and declining growth trends reduce the average adaptive capacity of trees to drier climatic conditions by increasing their growth sensitivity to climate, thus enhancing their vulnerability. We found that declining trees followed similar diminishing growth trends up two decades before presenting external decline symptoms as abundant needle loss. Our results agree with those of other studies suggesting that responses of trees to climatic stress including decline and defoliation change among individuals (Galiano et al. 2010; Miyamoto et al. 2010; Linares et al. 2011; Linares and Camarero 2011). Our findings confirm that these responses can be predicted through the description and classification of characteristic growth patterns (Pedersen 1998a; Bigler and Bugmann 2004; Bigler et al. 2006), as well as throughout inherent tree growth sensitivity to climate.

Decreasing growth trends are among the most obvious growth-related characteristics of declining and dying trees (Waring 1987). In healthy trees, BAI series usually show an early phase of low growth followed by a rapid juvenile increase and a final stable phase of maturation (Biondi and Qaedan 2008). We were able to detect a significant difference between long-term growth trends of healthy and severely defoliated silver firs by applying dynamic factor analyses (Fig. 3). Moreover, in many cases, declining trees showed the lowest growth rates, negative growth trends and high growth sensitivity to climate (Figs. 6, 7). Abrupt declines in growth or strongly negative growth trends may indicate a rapid physiological adaptation to changing environmental conditions (Dobbertin 2005; Linares and

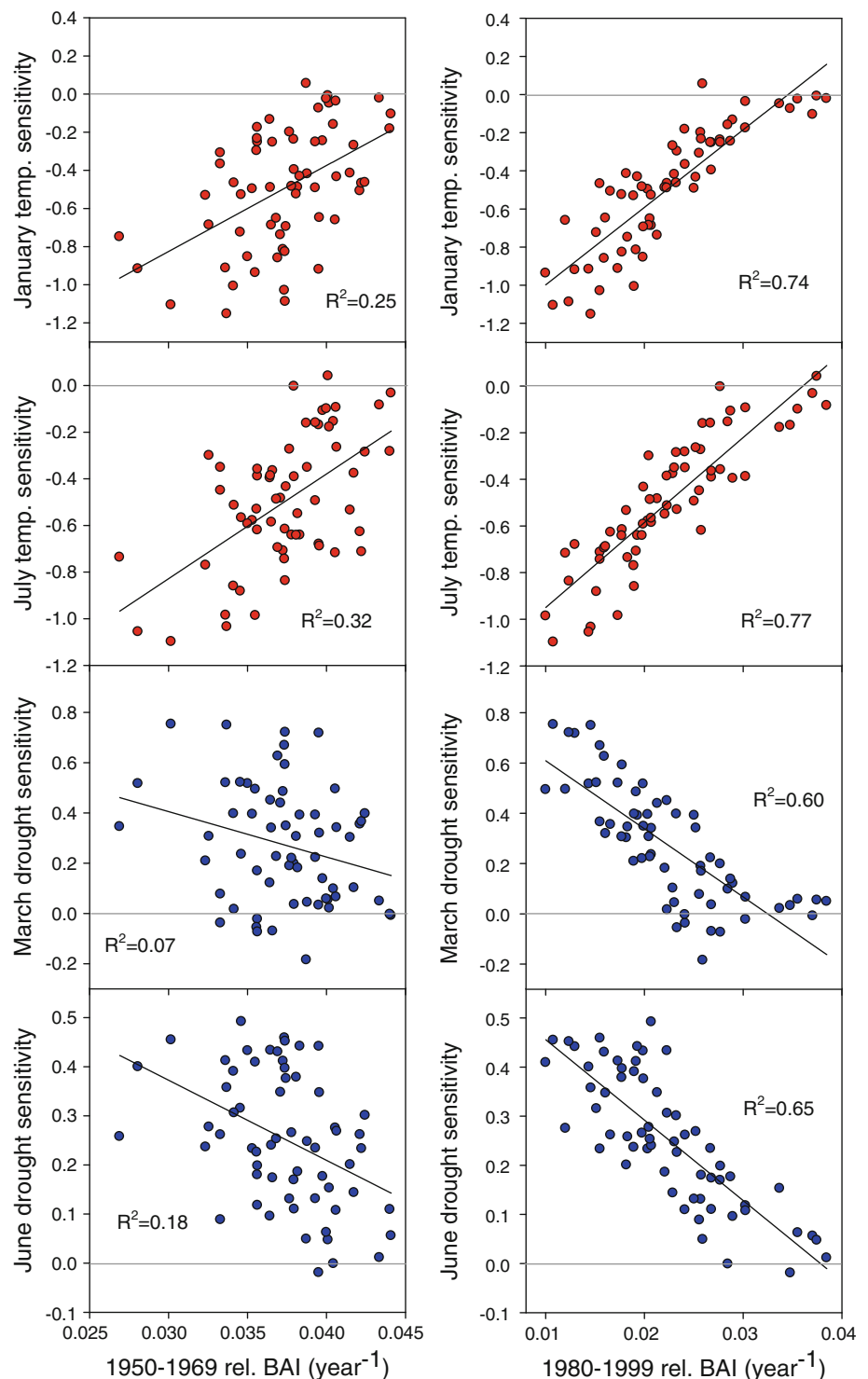
Camarero 2011). Our results suggest that silver firs reacted mainly to warming in the 1980s by reducing their carbon allocation to stem growth (note the abrupt growth reduction in 1986), while needle production and retention may not have been so affected by this stressing event. However, allocation to shoot formation and perhaps root growth had likely been lowering thereafter, following an increasing tree sensitivity to climate, until the temperature rise in 1997 and 1998, which resulted in increased crown defoliation, massive decline and enhanced tree decline since 1999 (Fig. 1b).

The process of tree dying may take decades (Villalba and Veblen 1998; Linares et al. 2010), and it is driven by a sequence of multiple stress factors (Franklin et al. 1987; Manion 1991; Dobbertin 2005; van Mantgem et al. 2009). Growth decline generally started several decades before tree death in Swiss Norway Spruce stands from the Alps as those studied by Bigler and Bugmann (2004). The growth trends of old *Pinus nigra* subsp. *salzmannii* trees, subjected to xeric conditions in south-eastern Spain forests, were mostly negative over the past century (Linares and Tíscar 2010). Declining Slovenian silver firs showed also decreasing growth trends for about 50 years (Torelli et al. 1999; Bigler et al. 2004). The growth curves of dead and living Scots pine trees at three different sites in the Swiss Valais started to diverge between 10 and 20 years prior to death (Bigler et al. 2006). Similar results were obtained for dying and living *Abies pinsapo* trees at low-elevation sites in southern Spain (Linares et al. 2010).

It is well established that silver fir growth is very sensitive to water deficit (Pinto and Gegout 2005; Pinto et al. 2008) being negatively affected by high temperature conditions and related drought stress along the growing season and the previous fall (see Fig. 5; Tardif et al. 2003; Macias et al. 2006; Carrer et al. 2010; Linares and Camarero 2011). In addition, *Abies* species are more susceptible to drought stress than other co-existing species such as Scots pine and beech under over-stocking conditions that impose a strong competition for soil water (Becker et al. 1989). Therefore, warming-induced drought stress is likely more related to silver fir decline than changes in precipitation, since no year with extremely low precipitation was recorded in our study area since 1960 excepting 1965 and, to a lower extent, 1989 (Fig. 2). By opposite, annual temperature yielded systematically above average values since 1981.

Rising temperatures increase the vapour-pressure deficit and evaporation, resulting in greater water loss through transpiration (Aussenac 2002; Linares and Camarero 2011). Moreover, temperature rises may affect negatively carbon storage in silver fir because both the rates of carbohydrate consumption and respiration are strongly linked to temperature (Atkin et al. 2005). This hypothesis could be supported by the marked growth decline and subsequent tree mortality observed after extremely hot growing

Fig. 6 Correlations between tree growth sensitivity to climate and relative basal-area increment averaged for 1950–1969 and 1980–1999. The growth sensitivity to climate is estimated as the slope of the linear regression obtained between the residuals of basal-area increment (BAIr) and the monthly series of climate (each point represent the slope obtained for a tree; $n = 62$ trees); the value of growth sensitivity to climate indicates the units of BAI increase (or decrease if the value is negative) per unit of change in the climate variable. Only the significant regressions ($P < 0.05$) are drawn. R^2 values are also noted

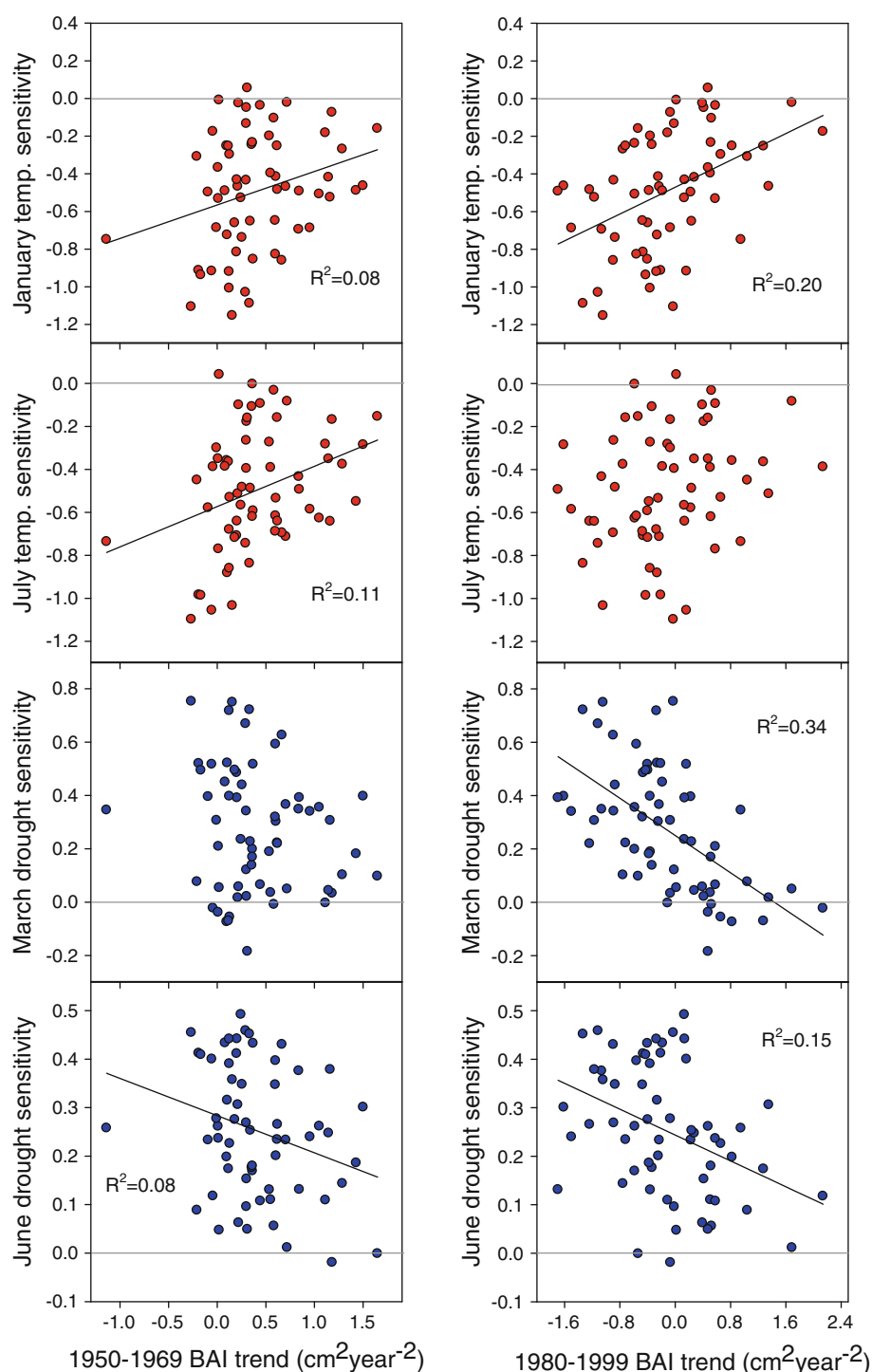


seasons in the periods 1986–1990 and 1997–1998 (Camarero 2000), which were more severe than those induced by the 1965 drought when lower temperatures might have alleviated drought stress.

Bigler et al. (2006) demonstrated that recurring droughts correlated well with modelled tree decline and death probability for Scots pines (*Pinus sylvestris*) in a

dry inner-alpine Swiss valley. Furthermore, these authors concluded that a variable describing the most recent growth trend is needed to adequately predict tree mortality risk. Based on dynamic factor analyses, we have found that non-declining and declining trees follow contrasting underlying growth trends, characterised by steady-to-rising and declining basal-area increment in the

Fig. 7 Correlations between tree growth sensitivity to climate and basal-area increment trends computed for the periods 1950–1969 and 1980–1999 (see also caption of the Fig. 6 for further explanations). Only the significant regressions ($P < 0.05$) are drawn. Significant R^2 values are also noted



former and in the later trees, respectively. Moreover, our results support the contention that *A. alba* is a tree species highly vulnerable to increased warming-induced drought stress.

Our findings underscore that tree decline is driven by the individual growth sensitivity. Such intra-specific variability may have deep consequences for tree growth

and survival leading to the selective mortality of the most sensitive trees (Clark 2003) as has been evidenced in silver fir (Vieilledent et al. 2010; Rathgeber et al. 2011). Future studies on forest decline should deal with the consideration and quantification of intra-specific variability at the tree level considering both local and regional scales.

Concluding remarks

The uncertainty on predicting forest vulnerability to climate warming depends on the different individual growth responses to climatic stress, which may selectively alter species dynamics in sites with contrasting conditions or past successional trajectories. These differences between co-existing trees of the same species should be further investigated, and they may be related to contrasting tree susceptibility to insects, pathogenic fungi or mistletoes (Solberg 2004; Jactel et al. 2005), genetics factors or micro-environmental conditions (for instance, topography or soil conditions; see Camarero et al. 2002). Our findings emphasise the links between tree defoliation, long-term growth patterns and growth sensitivity to climate in water-limited populations near the southern distribution limit of *Abies alba* in the Spanish Pyrenees. We suggest that increasing growth sensitivity to rising air temperatures will likely portray widespread and severe, in terms of defoliation and mortality, decline episodes in drought-prone areas under a warmer climatic scenario.

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References

- Akaike H (1974) A new look at statistical model identification. *IEEE Trans Autom Control* 19:716–722
- Andreu L, Gutiérrez E, Macías M, Ribas M, Bosch O, Camarero JJ (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Glob Chang Biol* 13:1–12
- Atkin OK, Bruhn D, Hurry VM, Tjoelker MG (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. *Funct Plant Biol* 32:87–105
- Aussenac G (2002) Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. *Ann For Sci* 59:823–832
- Becker M, Landmann G, Lévy G (1989) Silver fir decline in the Vosges mountains (France): role of climate and silviculture. *Water Air Soil Poll* 48:77–86
- Bigler CJ, Bugmann H (2004) Predicting the time of tree death using dendrochronological data. *Ecol Appl* 14:902–914
- Bigler CJ, Grisar J, Bugmann H, Cufar K (2004) Growth patterns as indicators of impending tree death in silver fir. *For Ecol Manag* 199:183–190
- Bigler CJ, Bräker OU, 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
- Bigler CJ, Gavin DG, Gunning C, Veblen TT (2007) Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos* 116:1983–1994
- Biondi F, Qaadan F (2008) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res* 64:81–96
- Buchman RG, Pederson SP, Walters NR (1983) A tree survival model with application to species of the Great Lakes region. *Can J For Res* 13:601–608
- Cabrera M (2001) Evolución de abetares del Pirineo aragonés. *Cuadernos de la Sociedad Española de Ciencias Forestales* 11:43–52
- Camarero JJ (2000) El decaimiento del abeto en los Pirineos. *Medio Ambiente Aragón* 4:18–20
- Camarero JJ, Padró A, Martín-Bernal E, Gil-Pelegrín E (2002) Aproximación dendroecológica al decaimiento del abeto (*Abies alba* Mill.) en el pirineo Aragonés. *Montes* 70:26–33
- Camarero JJ, Bigler CJ, Linares JC, Gil-Pelegrín E (2011) Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *For Ecol Manag* 262:759–769
- Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *PNAS* 119:1515–1525
- Carrer M, Nola P, Motta R, Urbinati C (2010) Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. *Oikos* 119:1515–1525
- Clark JS (2003) Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology* 84:1370–1381
- Das AJ, Battles JJ, Stephenson NL, van Mantgem PJ (2007) The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. *Can J For Res* 37:580–597
- Dobbertin M (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur J For Res* 124:319–333
- Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecological process. *Bioscience* 37:550–556
- Fritts HC (1976) Tree rings and climate. Academic Press, London
- Galiano L, Martínez-Vilalta J, Lloret F (2010) Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems* 7:978–991
- Greenwood DL, Weisberg PJ (2008) Density-dependent tree mortality in pinyon-juniper woodlands. *For Ecol Manag* 255:2129–2137
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* 43:68–78
- Holmes RL (1992) Dendrochronology program library. Laboratory of Tree-Ring Research, University of Arizona, Tucson
- Jactel H, Brockerhoff E, Duelli P (2005) A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. *For Div Funct Temp Boreal Syst* 176:235–262
- Kobe RK, Coates KD (1997) Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can J For Res* 27:227–236
- Linares JC, Camarero JJ (2011) From pattern to process: linking intrinsic water-use efficiency to drought induced forest decline. *Glob Change Biol*. doi:10.1111/j.1365-2486.2011.02566.x
- Linares JC, Tiscar PA (2010) Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. *Tree Physiol* 30:795–806
- Linares JC, Camarero JJ, Carreira JA (2010) 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*. *J Ecol* 98:592–603

- Linares JC, Delgado-Huertas A, Carreira JA (2011) Climatic trends and different drought adaptive capacity and vulnerability in a mixed *Abies pinsapo*—*Pinus halepensis* forest. *Clim Chang* 105:67–90
- Litton C, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Glob Chang Biol* 13:2089–2109
- Macias M, Andreu L, Bosch O, Camarero JJ, Gutiérrez E (2006) Increasing aridity is enhancing silver fir *Abies alba* (Mill.) water stress in its south-western distribution limit. *Clim Chang* 79:289–313
- Manion PD (1991) Tree disease concepts. Prentice-Hall, Englewood Cliffs
- Miyamoto Y, Griesbauer HP, Green DS (2010) Growth responses of three coexisting conifer species to climate across wide geographic and climate ranges in Yukon and British Columbia. *For Ecol Manag* 259:514–523
- Müller EHR, Stierlin HR (1990) Sanasilva tree crown photos with percentages of foliage loss. WSL, Birmensdorf
- Ogle K, Whitham TG, Cobb NS (2000) Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81:3237–3243
- Pedersen BS (1998a) Modeling tree mortality in response to short and long-term environmental stresses. *Ecol Model* 105:347–351
- Pedersen BS (1998b) The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. *Ecology* 79:79–93
- Peñuelas J, Ogaya R, Boada M, Jump AS (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* 30:830–838
- Pinto PE, Gegout JC (2005) Assessing the nutritional and climatic response of temperate tree species in the Vosges mountains. *Ann For Sci* 62:761–770
- Pinto PE, Gegout JC, Herve JC, Dhote JF (2008) Respective importance of ecological conditions and stand composition on *Abies alba* Mill. dominant height growth. *For Ecol Manage* 255:619–629
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>
- Rathgeber CBK, Rossi S, Bontemps JD (2011) Cambial activity related to tree size in a mature silver-fir plantation. *Ann Bot* 108:429–438
- Sarris D, Christodoulakis D, Körner C (2007) Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob Chang Biol* 13:1–14
- Solberg S (2004) Summer drought: a driver for crown condition and mortality of Norway spruce in Norway. *For Pathol* 34:93–104
- Taberlet P, Cheddadi R (2002) Quaternary refugia and persistence of biodiversity. *Science* 297:2009–2010
- Tardif J, Camarero JJ, Ribas M, Gutiérrez E (2003) Spatiotemporal variability in tree ring growth in the Central Pyrenees: climatic and site influences. *Ecol Monogr* 73:241–257
- Torelli N, Shortle WC, Cufar K, Ferlin F, Smith KT (1999) Detecting changes in tree health and productivity of silver fir in Slovenia. *Eur J For Pathol* 29:189–197
- van Mantgem PJ, Stephenson NL, Mutch LS, Johnson VG, Esperanza AM, Parsons DJ (2003) Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands. *Can J For Res* 33:1029–1038
- van Mantgem PJ, Stephenson NL, Byrne JC et al (2009) Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524
- Vieilledent G, Courbaud B, Kunstler G, Dhôte J-F (2010) Mortality of silver fir and norway spruce in the western Alps—a semi-parametric approach combining size-dependent and growth-dependent mortality. *Ann For Sci* 67:305
- Villalba R, Veblen TT (1998) Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79:2624–2640
- Waring RH (1987) Characteristics of trees predisposed to die. *Bioscience* 37:569–574
- Willmott CJ, Rowe CM, Mintz Y (1985) Climatology of the terrestrial seasonal water cycle. *Int J Climatol* 5:589–606
- Wunder J, Reineking B, Bigler CJ, Bugmann H (2008) Predicting tree mortality from growth data: how virtual ecologists can help real ecologists. *J Ecol* 96:174–187
- Wyckoff PH, Clark JS (2000) Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. *Can J For Res* 30:156–167
- Zuur AF, Fryer RJ, Jolliffe IT, Dekker R, Beukema JJ (2003) Estimating common trends in multivariate time series using dynamic factor analysis. *Environmetrics* 14:665–685