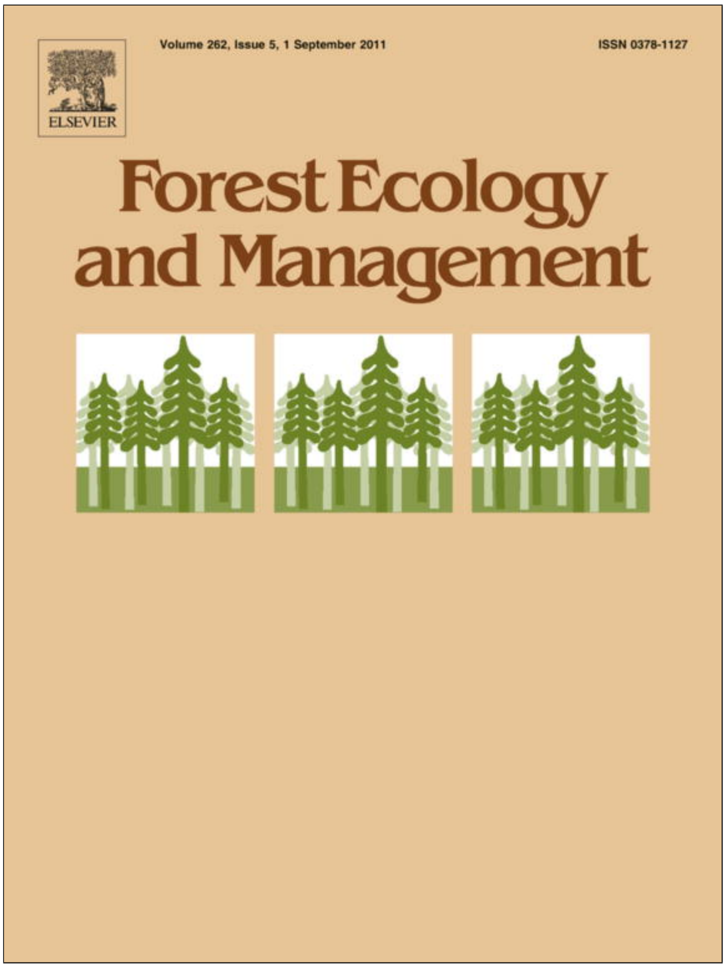
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Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests

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ABSTRACT

The causal factors and effects of forest declines are not well understood in temperate conifer forests. Most studies have focused on climatic and environmental stressors and have obviated the potential role of historical forest management as a predisposing factor of decline. Here, we assess if the recent silver fir (*Abies alba*) decline observed in the Spanish Pyrenees was predisposed by historical logging and incited by warming-induced drought stress. We analysed a dataset of environmental, structural, and historical variables at the tree and stand level including 32 sites with contrasting degrees of defoliation distributed over 5600 km^2. We followed a dendroecological approach to reconstruct historical logging and to infer the effects of warming-induced drought stress on growth. The silver fir decline was more severe and widespread in western low-elevation mixed forests dominated by trees of small size and slow growth. These sites were subject to higher water deficits than eastern sites, where late-summer rainfall as the key climatic variable controlling silver fir growth was higher. Declining sites showed more frequent growth releases induced by historical logging than non-declining sites. Historical logging and warming-induced drought acted as long-term predisposing and short-term inciting factors of silver fir decline in the Pyrenees, respectively. We suggest that biomass increases caused by past intense logging affected the vulnerability of silver fir against late-summer water deficit. Future research in declining temperate conifer forests should consider the interacting role of predisposing historical management and inducing climatic stressors such as droughts.

1. Introduction

Forests store approximately 45% of terrestrial carbon, but huge carbon emissions may occur rapidly from sudden mortality episodes linked to forest decline (Breshears and Allen, 2002). Recently, numerous cases of forest decline have been reported worldwide and related to warming-linked drought stress (Allen et al., 2010). Warming-induced forest decline in drought-stressed environments is linked to rapid defoliation and selective mortality of overstory trees (McDowell et al., 2008). Nevertheless, in temperate conifer forests, the environmental factors causing forest decline are not as well studied as in dry woodlands (van Mantgem and Stephenson, 2007).

Forest decline is still poorly understood because of the interaction of several stress factors acting at different spatio-temporal scales, which complicates the disentangling of lagged cause-effect relationships (Manion, 2003). In addition, few long-term assessments of the potential stressors involved have been carried out. Many decline episodes have been studied following Manion's (1981) conceptual model, which includes predisposing, inciting, and contributing stress factors causing a decline in tree vigor. Predisposing factors such as site conditions reduce a tree's vigor over the long term (Suarez et al., 2004), whereas inciting factors such as drought lead to a strong and short-term reduction in tree vigor (Bigler et al., 2006). Contributing factors such as mistletoe, insects, and fungi may lead to tree death acting as secondary stress factors. Historical land-use factors such as past logging may predispose forests to decline (Linares et al., 2009). However, few studies have assessed the role of historical logging on the decline of temperate conifer forests despite most of them have been intensively managed (Frelich, 2002).

The different natures of interacting factors such as land-use legacies (e.g., historical logging) and climatic extremes (e.g., severe droughts) have precluded considering the interactions between them. For instance, historical effects have persisted for decades and centuries shaping the current structure of most temperate conifer forests in Europe (Kirby and Watkins, 1998). Therefore,

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any link between the historical management and warming-induced drought stress may be highly relevant for understanding past and current episodes of forest decline (Foster et al., 2006). A retrospective approach based on long-term tree growth data may provide historical information to infer the links between past forest use, drought stress, and forest decline.

Decline episodes of silver fir forests (*Abies alba* Mill.) in central Europe were systematically reported in the 1970s (Skelly and Innes, 1994). In the 1980s, silver fir decline was also observed in the Central Spanish Pyrenees (Aragón Pyrenees, Fig. 1), being more severe in western stands where up to 50% of trees showed severe defoliation (Camarero et al., 2002). Therefore, it may be hypothesized that drought stress has recently increased due to climate warming and a regime shift in precipitation causing silver fir decline. In addition, most of these forests were logged to extract timber up to the 1970s when their management ceased due to rural migration to cities (Cabrera, 2001). In this study, we addressed the following questions: (1) How did silver fir growth change in the Aragón Pyrenees during the twentieth century, and how was this growth variability related to the recent pattern of defoliation and decline? (2) Did historical logging, reconstructed using historical information and dendrochronological dating of growth releases, and warming-induced drought synergistically act as predisposing and inducing factors of the recent silver fir decline? To answer these questions we analysed a detailed dataset of environmental, structural, and historical variables at the tree and stand level, including sites subjected to contrasting climatic conditions, combined with tree-ring data and assessments of crown defoliation.

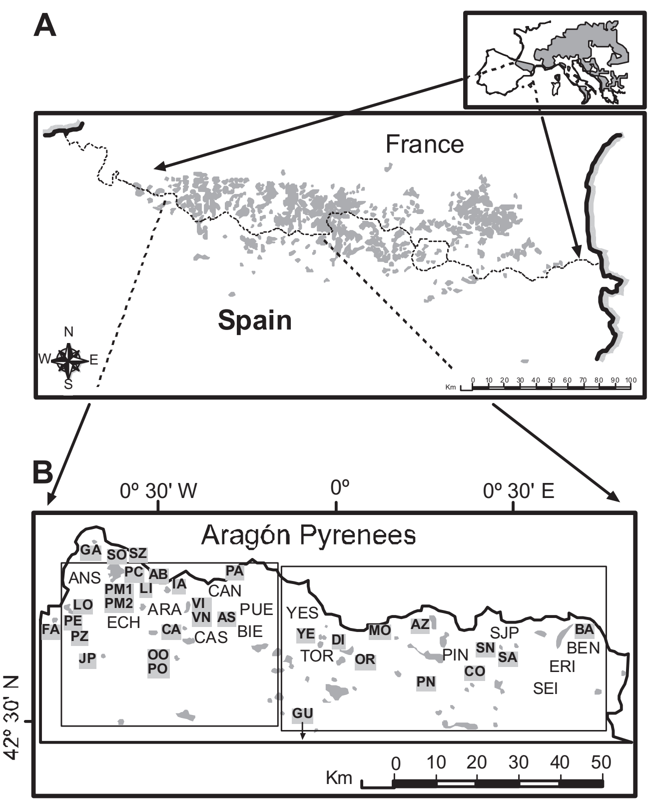

Fig. 1. Distribution of *A. alba* in Europe (A) and study sites in the Aragón Pyrenees (B), northeastern Spain (site codes with bold letters, see Table 1). The two rectangles in the lower figure delineate the two homogeneous climatic sub-regions based on local data from the displayed climatic stations (3 letter codes): Western (WAP) and Eastern (EAP) Aragón Pyrenees (see Supplementary data S1).

2. Material and methods

2.1. Study area

The Pyrenees constitute a transitional area between more humid conditions in their northern margin and drier conditions southwards (Vigo and Ninot, 1987). This gradient overlaps with a longitudinal gradient caused by the location of the range between the Atlantic Ocean and the Mediterranean Sea. According to meteorological data from nearby stations, the climate in the study area is continental with oceanic (western sites) or Mediterranean (eastern and southern sites) influences (Supplementary data S1). The westward oceanic influence leads to greater precipitation in winter and a smaller temperature range than eastwards, where the Mediterranean influence prevails being characterized by higher precipitation in summer, as expressed in percentage relative to the annual precipitation, than westwards.

The studied silver fir populations are located in the Aragón Pyrenees, NE Spain (Fig. 1). The main geographic and topographic characteristics of the 32 sampled stands appear in Table 1. In the Aragón Pyrenees, silver fir stands are usually found at humid sites on north-facing slopes, where they form pure or mixed stands with *Fagus sylvatica* L. or *Pinus sylvestris* L. Silver fir forests in the study area may experience summer-drought stress in August despite a total annual precipitation between 900 and 2000 mm, which usually increases with elevation. Most studied stands are located on marls and limestones, which generate basic soils, or on moraine deposits with rocky but deep soils. The most frequently used method of timber harvesting in the study area was diameter limit cutting, which mostly affected fast-growing and big trees (Aunós and Blanco, 2006). According to historical data (Cabrera, 2001), logging intensity during the 20th century in the Pyrenees was greatest in the 1950s but no data are available on how widespread logging in this region was and how it affected the current structure and dynamics of different stands.

2.2. Climate data

Because local climatic records are inadequate to study the spatiotemporal variation of mountain climates, we created regional climatic records averaging the longest and most complete local climate records available from the study area (see methods in Supplementary data S1). We used monthly climatic data (mean temperature, total precipitation) to delineate two relatively homogeneous climatic areas within the Aragón Pyrenees, hereafter abbreviated as WAP (western Aragón Pyrenees) and EAP (eastern Aragón Pyrenees) sub-regions. We preferred to use local climate data instead of gridded or interpolated climatic datasets because local data captured more climatic variability among sites than gridded data. We obtained mean temperature and precipitation data for each sub-region for the period 1940–1999. Finally, we calculated annual and cumulative monthly water deficits for both climatic sub-regions using a modified Thornthwaite water-budget procedure (Supplementary data S2).

2.3. Field sampling

Sampling was conducted beween 1999 and 2001. We sampled at least one silver fir stand (forests with at least 10 ha of area and silver fir cover >50%) in each 10-km^2 grid in the Aragón Pyrenees (Fig. 1). The sampled stand in those grids with multiple stands was selected randomly. More stands in those 10-km^2 grids with more defoliated trees were sampled because we were mainly interested in discerning the causes of forest decline. We sampled 21 and 11 sites within the WAP and EAP sub-regions, respectively. At each

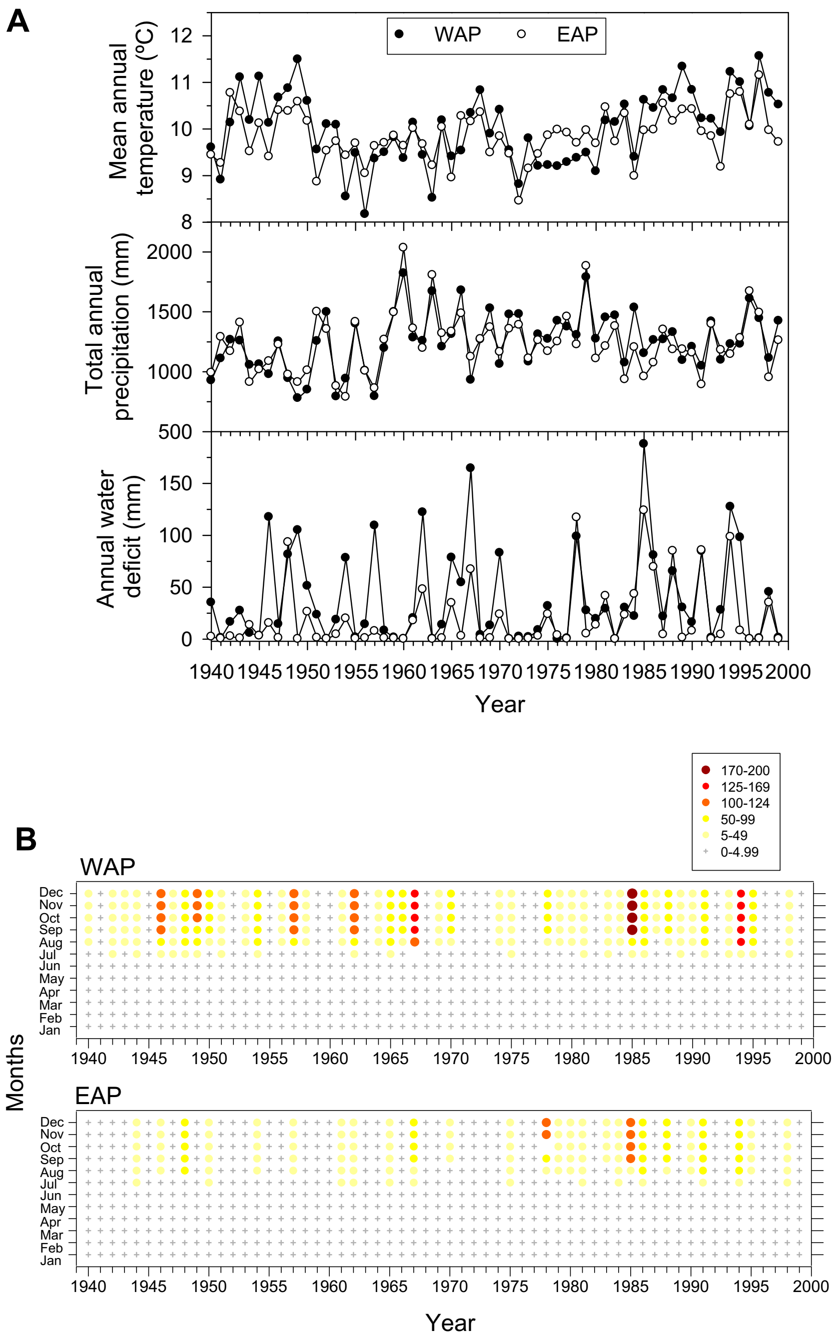

Fig. 2. Climatic variability during the 1940–1999 period for the two homogeneous climatic sub-regions: western (WAP) and eastern (EAP) Aragón Pyrenees. (A) Mean annual temperature, total annual precipitation, and annual water deficit. (B) Cumulative monthly water deficits (the scale is in mm).

site, 10–15 dominant trees (diameter at 1.3 m, dbh > 20 cm; stem height > 10 m) were randomly selected for sampling within a 500-m long and 20-m wide transect randomly located within the stand giving a total of 378 sampled trees. Several topographical variables were obtained for each site and tree. Elevation, aspect, and slope steepness were measured in the field at the tree level. In addition, slope was estimated for each site using the tangential curvature of the terrain (continuous variable with values <0 = concave and >0 = convex) based on a 20-m digital elevation model.

We measured the size of each of the 10–15 selected trees located within the transect (diameter at 1.3 m, dbh; stem height), and assessed their vigor 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% (slight damage); 2, 26–50% (moderate damage); 3, 51–75% (severe damage); 4, 76–90% (dying tree); 5, dead trees with >91% defoliation or only retaining red needles. Since estimates of percent crown defoliation may vary among observers and places, we used as a reference a tree with the maximum amount of foliage at each site. Declining trees were defined to have crown defoliation greater than 50%, and declining sites were defined to have more than 25% trees with such a degree of defoliation. Dead trees were regarded as those whose crown showed complete defoliation or only retained red needles. Dead trees were considered in further analyses (dendrochronological data, competition index) since preliminary observations indicated that they have recently died, i.e. from 1 to 15 years before sampling was performed. Several vigor variables were recorded for each sampled tree using binoculars. We used a semi-quantitative scale from low (0) to high abundance (3) to estimate: (i) the production of epicormic shoots along the main stem and (ii) abundance of mistletoe (*Viscum album* L.) in the crown. Furthermore, no interactions with recent and past insect outbreaks were detected in declining sites (Camarero et al., 2003).

To estimate the degree of competition for each sampled tree, we used the Daniels (1976) competition index (D_i). First, we measured the number and dbh of all neighboring trees found within a circular plot of 7.6 m in radius placed around each subject tree. We calculated the index as:

$$D_i = \mathrm{dbh}_i^2 \Big/ \left(\sum \mathrm{dbh}_j^2\right) \Big/ n \qquad (1)$$

where dbh_i and dbh_j are the diameters of the subject tree i and the competitor tree j, respectively; n is the number of neighboring trees. We assumed that these data reflect the current and past competitive environment of each tree since most trees had a dbh > 30 cm and were established during the early 20th century (Table 1). These data were also used to estimate the mean density (stems ha^{-1}), dbh, and basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$) of silver fir and coexisting species. Values are given as means ± standard errors throughout the text.

2.4. Dendrochronological methods

Dendrochronological sampling was performed following standard methods (Fritts, 1976). Two or three cores were taken from each tree at breast height (1.3 m) using an increment borer. In the field, we were able to estimate sapwood length for 92 trees from 22 sites. The wood samples were air-dried and polished with a series of successively finer sand-paper grits. The samples were visually cross-dated. Tree rings were measured to the nearest 0.01 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating of the tree rings was checked using the program COFECHA (Holmes, 1983).

To calculate tree age at 1.3 m for cores without pith, we used a geometric method based on the distance to the estimated pith according to the curvature of the innermost tree. Stem sections and cores with pith (n = 120) were used to calculate a regression between the distance to the pith and the number of tree rings (r = 0.98, P < 0.05).

The percentage growth change (GC) filter of Nowacki and Abrams (1997) was applied to identify abrupt and sustained increases or decreases in radial growth (i.e. releases or suppressions, respectively). First, we calculated the ring-width medians of subsequent 10-year periods along all growth series because medians are more robust estimators of central tendency than means. We defined M1 and M2 as the preceding and subsequent 10-year ring-width medians, respectively. The percentage of positive (PGC) and negative (NGC) growth changes were defined as:

$$\mathrm{PGC} = [(\mathrm{M2} - \mathrm{M1})/\mathrm{M1} \cdot 100] \qquad (2)$$

$$\mathrm{NGC} = [(\mathrm{M1} - \mathrm{M2})/\mathrm{M2} \cdot 100] \qquad (3)$$

Releases, which we assumed to result mostly from logging operations, were defined as periods with at least 5 consecutive years showing positive growth changes greater than 75%. This assumption was based on the concurrence between the inferred dates of most release events and periods of intense logging management in the study area (Cabrera, 2001). Previous analyses indicated that growth releases caused by natural disturbances and gap formation were less important (Camarero et al., 2002). Other causes of releases such as local-scale blowdowns were excluded by sampling trees located at least 100 m apart from canopy gaps and by avoiding uprooted trees or trees with stem breakage. To assess changes in relative growth reduction, we calculated mean curves of negative growth change for declining and non-declining sites.

Basal area increment (BAI, $\mathrm{cm}^2\ \mathrm{year}^{-1}$) is a more meaningful indicator of growth than ring width because it removes variation in growth attributable to increasing circumference. Therefore, ring widths were converted to BAI assuming a circular outline of stem cross-sections and using the formula:

$$\mathrm{BAI} = \pi(R_t^2 - R_{t-1}^2) \qquad (4)$$

where R is the radius of the tree, and t is the year of tree-ring formation. In healthy dominant trees, BAI series usually show an early phase of low growth followed by a rapid increase and a final stable phase (LeBlanc et al., 1992). Mean annual values of tree-ring width, growth change, and BAI were obtained for declining and non-declining sites throughout the twentieth century.

2.5. Dendroclimatic analyses

To assess the growth-climate relationships, a tree-ring width chronology was established for each site (see descriptive statistics of chronologies in Table 2). For each tree, its ring-width series was double-detrended using a negative linear or exponential function and a cubic smoothing spline with a 50% frequency response cutoff of 30 years to preserve high-frequency variability following Macias et al. (2006). Autoregressive modeling was performed on each detrended ring-width series, which were finally averaged using a biweight robust mean to obtain residual site chronologies using the program ARSTAN (Cook and Krusic, 2005). The spatial and temporal relationships among these site chronologies for the period 1900–1999 were summarized using Principal Component Analysis (PCA).

We calculated 32 correlation functions relating each site residual chronology to the corresponding sub-regional climate dataset for the period 1950–1999. Climate-growth relationships were performed using monthly mean temperature and total precipitation from the previous January up to September of the growth year. Finally, to summarize these results and to define the main climatic response of declining vs. non-declining sites, we performed a PCA on the matrix of all the correlation function coefficients. In the PCA biplot, the correlation between growth (residual site chronologies) and climatic variables is given by the cosine of the angle between two vectors (arrows) but sites' vectors were displayed as apices for visual clarity. Vectors pointing in similar (opposite) direction indicate a high positive (negative) correlation, whereas vectors crossing at right angles correspond to a near zero correlation. Climatic variables with the longest vectors are the most important.

2.6. Assessment of relative contribution of variables to decline

We conducted a partial redundancy analysis (pRDA; see Supplementary data S3) to assess the relative contribution of environmental, structural, and historical variables to explain forest decline (response variables), and the amount of residual variation (Zuur et al., 2007). The explanatory variables were divided into three groups: (i) environmental variables (elevation, slope, northness, eastness, soil type, summer rainfall); (ii) structural variables (age, dbh, height, mean dbh of neighboring trees, competition index, density, and basal area of *A. alba*, *F. sylvatica* and *P. sylvestris*); and (iii) one anthropogenic variable (frequency of releases) as an indicator of historical logging. The following variables were included as response variables: degree of defoliation, abundance of mistletoe, presence of epicormic resprouts, and the growth ratio between the mean BAI for 5-year periods after (1990–1994) and before (1980–1984) the decline. Based on preliminary analyses, we selected the mean BAI values for these two 5-year periods because they represent most of the relative growth changes after and before the sharp decline in BAI (Camarero et al., 2002). Associations between variables were also evaluated through Spearman correlation (r_s) analyses. We used R (version 2.12.1) for statistical analyses (R Development Core Team, 2010).

3. Results

3.1. Climatic trends

Climatic data showed a strong warming trend in the WAP sub-region during the late 1940s and in the 1980s (Fig. 2A). Annual precipitation increased during the 1970s and 1990s, whereas it decreased in the 1940s and 1980s. The mean annual water deficit during the 1940–1999 period was significantly higher ($F = 9.13$, $P = 0.003$) in the WAP (82.3 ± 8.3 mm) than in the EAP (49.6 ± 7.0 mm) sub-region. The estimated annual water deficit reached maximum values in 1967 and 1985 in the WAP sub-region, and in 1978, 1985, and 1994 in the EAP sub-region. In most years, annual deficits were higher in the WAP sub-region than in the EAP sub-region (Fig. 2A and B).

3.2. Characteristics of declining sites

The sampled silver firs in the declining sites were on average 98 years old and their overall mean dbh and height were 53.5 cm and 23.0 m, respectively (Table 1). Most declining sites with severe defoliation were located in the WAP sub-region at a significantly ($F = 5.31$, $P = 0.03$) lower elevation (1196 ± 67 m) than the remaining sites (1391 ± 34 m) (Fig. 3, Tables 1 and 2). These silver fir stands showed mean dbh (43.3 ± 3.4 cm) and basal area (25.1 ± 4.2 m^2 ha^{-1}) values, which were significantly lower (diameter, $F = 5.56$, $P = 0.03$; basal area, $F = 4.53$, $P = 0.04$) than for non-declining sites (55.3 ± 2.1 cm, 40.4 ± 3.0 m^2 ha^{-1}) (Table 1). On average, there were more standing dead trees (Wilcoxon test, $W = 378$, $P < 0.001$) in declining (10.8 ± 1.1%) than in non-declining sites (1.2 ± 0.4%) (Table 2). The pRDA explained 70% of the variability of silver fir growth and vigor, and structural, environmental and anthropogenic variables accounted for 49%, 28% and 23% of this variability, respectively (Table 3). The explanatory variables selected by pRDA which showed a positive association with decline were basal area of *F. sylvatica* and *P. sylvestris* and number of releases detected during the period 1900–1980, whereas tree dbh was negatively related to decline.

At declining sites, there were more trees with releases ($\chi^2 = 15.39$, $P = 0.017$). Most of the defoliated trees from declining sites also tended to show less sapwood area (Spearman rank correlation between degree of defoliation and sapwood area; $r_s = -0.26$, $P = 0.03$). The mean number of releases per stand and the defoliation class were positively and significantly related ($r_s = 0.88$, $P < 0.001$).

3.3. Growth trends of declining sites

Tree-ring width was significantly lower ($F = 6.17$, $P = 0.02$) in declining (1.9 ± 0.2 mm) than in non-declining sites (2.7 ± 0.1 mm). In addition, the percentage of growth variability explained by climate was significantly higher ($F = 4.55$, $P = 0.04$) in declining (52.3 ± 1.6%) than in non-declining sites (45.9 ± 1.3%). The percentage was highest (57%) in the southernmost sites (e.g., GU), which experienced a greater drought stress than more northerly sites. However, no southern site showed signs of recent decline such as severe defoliation or reduced radial growth.

The mean sensitivity, a measure of the year-to-year changes in ring width, was positively and significantly related to the common growth variance explained by the first principal component (Table 4). The first two axes of a PCA based on site chronologies accounted for 51.8% and 6.8% of total growth variation and were negatively related to longitude and elevation, respectively (Table 4). Finally, defoliation was negatively associated with elevation, dbh, basal area and longitude (Table 4).

The basal area increment of declining sites diverged from that of non-declining sites since the 1940s (Fig. 4A). Nevertheless, both types of sites showed similar growth trends and short-term responses to climatic stress such as a very narrow ring in 1986 when the negative growth change reached very low values (Fig. 4B). Declining sites showed a greater frequency of trees with releases than non-declining sites during several decades (e.g., 1910s, 1950s, 1970s) before the onset of the decline (Fig. 4C).

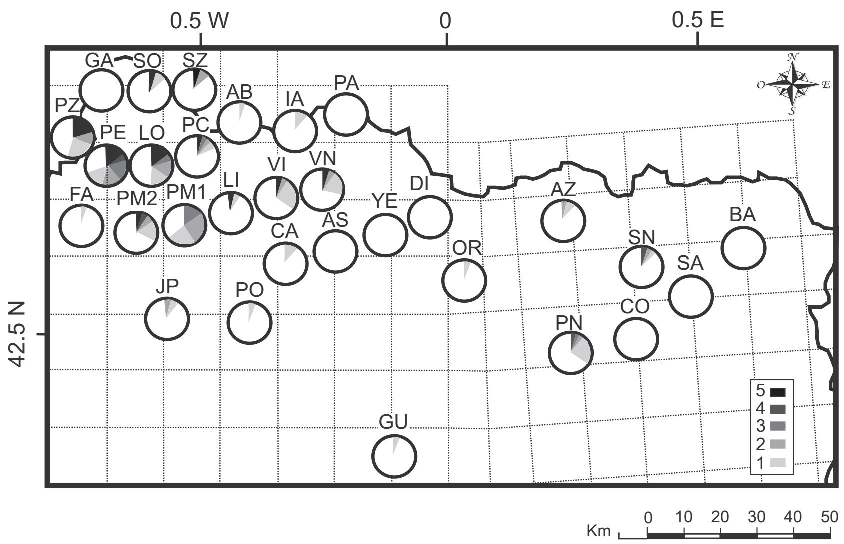

Fig. 3. Geographical patterns of crown defoliation in silver fir forests. The graph shows the percentage of trees in each stand with different defoliation levels (class 1, 11–25% crown defoliation; 2, 26–50%; 3, 51–75%; 4, 76–90%; 5, dead trees with >91% defoliation or retaining red needles). Site codes are as in Table 1. Underlined codes correspond to declining sites (sites with more than 25% trees with crown defoliation >50%). The grid corresponds to 10 × 10 km squares.

Table 1
Characteristics of the sampling sites (means ± SE). Declining sites are indicated with underlined abbreviations.

Site	Code	Sub-region[a]	Latitude (N)	Longitude (W/E)	Aspect	Elevation (m)	Slope (°)	Soil[b]	dbh (cm)	Height (m)	Basal area ($m^2\ ha^{-1}$)	Age at 1.3 m (year)	Plant species[c]
Fago	FA	WAP	42° 44′	0° 53′ W	NW	918 ± 3	30 ± 4	B	61.3 ± 1.6	27.5 ± 0.8	45.9	96 ± 3	*Fs, Ps, Ca, Ia*
Paco Ezpela-high	PE	WAP	42° 45′	0° 52′ W	N–NE	1232 ± 1	27 ± 3	B	35.0 ± 2.3	18.2 ± 0.9	10.1	88 ± 5	Fs, Ia, Ca, Bs
Paco Ezpela-low	PZ	WAP	42° 45′	0° 52′ W	N–NE	1073 ± 3	26 ± 1	B	43.0 ± 1.2	21.4 ± 0.6	24.7	114 ± 7	*Fs, Ia, Ca, Bs*
Lopetón	LO	WAP	42° 46′	0° 52′ W	N–NW	1009 ± 3	32 ± 1	B	38.1 ± 2.7	20.8 ± 0.8	24.8	104 ± 6	Fs, Ps, Ia, *Bs*
Gamueta	GA	WAP	42° 53′	0° 48′ W	N–NW	1400 ± 10	23 ± 1	B	64.2 ± 2.2	30.1 ± 1.1	55.8	129 ± 8	*Fs, Dl, Sa, Sr*
Selva de Oza-high	SZ	WAP	42° 50′	0° 42′ W	N–NW	1272 ± 5	22 ± 2	B	58.2 ± 3.1	22.1 ± 0.7	38.3	115 ± 9	*Fs, Ps, Ia, Vm*
Selva de Oza-low	SO	WAP	42° 50′	0° 43′ W	N–NE	1195 ± 6	34 ± 3	B	66.6 ± 3.0	27.2 ± 0.9	51.7	152 ± 14	*Fs, Ps, Bs, Cm*
S. Juan de la Peña	JP	WAP	42° 31′	0° 41′ W	N–NE	1393 ± 33	22 ± 2	B	46.0 ± 2.3	16.4 ± 1.3	17.9	95 ± 9	*Ps, Fs, Ia, Bs*
Paco Mayor-high	PM1	WAP	42° 42′	0° 38′ W	N	1353 ± 2	22 ± 0	B	45.8 ± 2.3	24.0 ± 0.5	31.7	97 ± 3	*Ps, Fs, Cm, Bs*
Paco Mayor-low	PM2	WAP	42° 42′	0° 38′ W	N	1313 ± 13	39 ± 4	B	54.8 ± 4.1	24.1 ± 0.6	34.2	104 ± 8	*Fs, Ps, Ia, Bs*
Puente Corralones	PC	WAP	42° 46′	0° 38′ W	NW	1248 ± 3	32 ± 5	A	47.5 ± 3.0	21.6 ± 1.1	43.3	64 ± 5	Fs, Ps, Sa, Ia
Lierde	LI	WAP	42° 42′	0° 33′ W	N–NE	1222 ± 3	21 ± 3	B	74.1 ± 4.1	27.5 ± 0.6	87.1	96 ± 6	*Fs, Ps, Ia, Ca*
Peña Oroel-high	OO	WAP	42° 31′	0° 32′ W	N–NW	1604 ± 15	25 ± 10	B	59.1 ± 2.8	22.1 ± 0.6	43.8	95 ± 4	*Ps, Jc, Bs, Oa*
Peña Oroel-low	PO	WAP	42° 31′	0° 32′W	N	1587 ± 17	36 ± 3	B	46.5 ± 3.9	19.6 ± 0.9	34.6	77 ± 6	*Ps, Bs, Jc, Oa*
Los Abetazos	AB	WAP	42° 43′	0° 32′ W	N–NE	1403 ± 9	20 ± 4	B	75.0 ± 4.4	22.2 ± 0.9	63.8	65 ± 6	*Ps, Fs, Sa, Bs*
Castiello de Jaca	CA	WAP	42° 39′	0° 31′ W	N–NW	1175 ± 15	25 ± 2	B	41.2 ± 2.0	19.1 ± 0.7	30.5	131 ± 9	*Ps, Ca, Pt, Ao*
Izquierda del Aragón	IA	WAP	42° 45′	0° 31′ W	W–SW	1478 ± 5	27 ± 2	B	69.0 ± 5.6	24.9 ± 0.9	56.0	103 ± 15	*Ps, Sa, Fs, Tb*
Paco de Villanúa-high	VN	WAP	42° 41′	0° 30′ W	N	1270 ± 2	24 ± 1	B	37.4 ± 3.0	25.5 ± 1.4	20.2	100 ± 7	*Ps, Ia, Cm, Bs*
Paco de Villanúa-low	VI	WAP	42° 41′	0° 30′ W	N–NW	1234 ± 4	22 ± 2	B	42.7 ± 2.5	24.1 ± 1.2	41.6	96 ± 4	*Ps, Ia, Cm, Fs*
Paco Asieso	AS	WAP	42° 39′	0° 18′ W	N–NW	1327 ± 3	33 ± 2	B	60.6 ± 3.6	25.3 ± 0.7	37.2	87 ± 7	*Ps, Fs, Sa, Ia*
Panticosa	PA	WAP	42° 44′	0° 18′ W	N–NW	1280 ± 4	27 ± 3	B	71.0 ± 2.7	24.7 ± 1.0	56.3	117 ± 9	*Ps, Sa, Fs, Sr*
Yésero	YE	EAP	42° 39′	0° 13′ W	NW	1399 ± 4	30 ± 2	B	48.1 ± 3.1	20.0 ± 0.5	31.7	64 ± 4	*Ps, Ia, Bs, Dl*
Guara	GU	EAP	42° 18′	0° 12′ W	N–NW	1428 ± 9	26 ± 1	B	52.5 ± 2.6	20.0 ± 0.7	13.5	80 ± 9	*Ps, Tb, Bs, Jc*
Diazas	DI	EAP	42° 38′	0° 06′ W	N–NW	1528 ± 4	22 ± 2	A	56.5 ± 2.2	25.9 ± 0.6	45.4	98 ± 6	*Ps, Fs, Sa, Ia*
Orús	OR	EAP	42° 34′	0° 06′ E	N–NW	1370 ± 5	25 ± 2	B	42.3 ± 1.5	24.6 ± 0.6	39.5	108 ± 4	*Ps, Fs, Pt, Ao*
Montinier	MO	EAP	42° 39′	0° 07′ E	N	1400 ± 30	30 ± 2	B	46.1 ± 1.6	25.5 ± 0.8	29.6	117 ± 9	*Ps, Sa, Sr, Ia*
Azirón	AZ	EAP	42° 39′	0° 13′ E	N–NW	1613 ± 17	25 ± 2	A	68.0 ± 3.6	25.2 ± 0.5	33.3	90 ± 5	*Ps, Pu, Ao, Oa*
Peña Montañesa	PN	EAP	42° 27′	0° 14′ E	N–NE	1519 ± 22	21 ± 3	B	45.1 ± 2.2	18.7 ± 0.7	28.5	78 ± 5	*Ps, Bs, Ia, Jc*
Collubert	CO	EAP	42° 28′	0° 18′ E	N–NE	1474 ± 10	22 ± 12	B	56.0 ± 4.4	21.7 ± 0.4	29.9	83 ± 10	*Fs, Ps, Ia, Ao*
Selva Negra	SN	EAP	42° 34′	0° 20′ E	N–NE	1431 ± 7	24 ± 4	B	49.5 ± 3.5	23.2 ± 0.6	29.1	74 ± 3	*Ps, Fs, Sa, Pt*
Collado de Sahún	SA	EAP	42° 33′	0° 23′ E	N–NW	1789 ± 5	15 ± 9	A	60.1 ± 2.8	22.7 ± 0.8	36.5	117 ± 24	Pu, Ps, Vm, Rf
Ballibierna	BA	EAP	42° 38′	0° 35′ E	W–NW	1600 ± 4	30 ± 6	A	49.6 ± 2.3	21.3 ± 0.9	48.6	107 ± 5	*Fs, Vm, Ca, Rf*

[a] Climatic sub-regions (see Supplementary data S1): western (WAP) and eastern (EAP) Aragón Pyrenees.
[b] Soil types: basic (B) or acid (A) soil.
[c] Tree, shrub and main understory plant species are displayed in order of decreasing importance. Species abbreviations: *Ao* = *Acer opalus* Mill.; *Bs* = *Buxus sempervirens* L.; *Ca* = *Corylus avellana* L.; *Ca* = *Crataegus monogyna* Jacq.; *Dl* = *Daphne laureola* L.; *Fs* = *Fagus sylvatica* L.; *Ia* = *Ilex aquifolium* L.; *Jc* = *Juniperus communis* L.; *Oa* = *Oxalis acetosella* L.; *Ps* = *Pinus sylvestris* L.; *Pt* = *Populus tremula* L.; *Pu* = *Pinus uncinata* Ram.; *Rf* = *Rhododendron ferrugineum* L.; *Sa* = *Sorbus aucuparia* L.; *Sr* = *Sorbus aria* (L.) Crantz; *Tb* = *Taxus baccata* L.; *Vm* = *Vaccinium myrtillus* L. No vigor data were taken at site MO where growth was studied using stem sections from recently felled trees.

Table 2
Frequency of dead trees and descriptive statistics of the ring-width chronologies. Site codes are as in Table 1 and Fig. 1.

Site[a]	Dead trees (%)[b]	No. trees	No. radii	Tree-ring width (mm)	SD[c]	AR1	MS	Period with EPS > 0.85	SNR	PC 1 (%)	Climate-R^2 (%)
FA	0.0	12	24	2.90 ± 0.12	0.15	0.09	0.24	1925–2000	14.61	58.34	49.14
PE	14.3	15	39	1.70 ± 0.09	0.18	0.28	0.24	1916–1999	6.07	45.77	50.83
PZ	8.3	11	25	1.67 ± 0.10	0.18	0.42	0.19	1917–1999	8.89	49.09	47.84
LO	12.0	10	23	1.48 ± 0.11	0.22	0.32	0.30	1916–1999	7.12	53.40	51.82
GA	0.0	15	26	2.19 ± 0.20	0.14	0.16	0.22	1883–2000	7.70	40.41	41.96
SZ	4.7	13	26	2.57 ± 0.25	0.14	0.43	0.23	1925–1999	5.36	36.88	41.13
SO	5.0	12	25	2.31 ± 0.20	0.16	0.39	0.15	1901–1999	5.60	39.50	43.92
JP	0.0	13	28	2.37 ± 0.19	0.15	0.13	0.25	1931–1999	6.39	34.17	55.52
PM1	10.0	10	22	2.01 ± 0.13	0.19	0.24	0.21	1925–1999	11.40	57.26	49.29
PM2	9.3	10	21	2.50 ± 0.22	0.15	0.30	0.24	1935–1999	6.17	43.68	58.64
PC	5.0	13	27	3.67 ± 0.24	0.14	0.41	0.13	1936–1999	7.46	43.97	47.34
LI	0.0	11	22	3.08 ± 0.23	0.11	0.23	0.21	1934–1999	7.38	44.58	43.63
OO	0.0	10	24	2.88 ± 0.18	0.16	0.22	0.22	1931–1999	11.45	57.07	53.73
PO	0.0	11	23	2.62 ± 0.11	0.15	0.09	0.20	1933–1999	6.96	52.45	54.39
AB	0.0	12	24	4.70 ± 0.20	0.16	0.58	0.18	1931–2000	5.24	36.31	41.76
CA	0.0	10	20	1.31 ± 0.11	0.19	0.46	0.27	1889–2000	5.81	47.85	52.72
IA	4.7	13	25	3.23 ± 0.25	0.16	0.37	0.19	1910–2000	7.83	43.18	40.28
VN	2.0	10	12	1.88 ± 0.16	0.15	0.42	0.20	1929–2000	4.90	47.70	34.78
VI	0.0	14	30	2.08 ± 0.13	0.10	−0.12	0.19	1926–2000	7.96	40.08	47.04
AS	5.0	10	20	3.26 ± 0.22	0.18	0.44	0.24	1939–2000	8.63	56.78	41.42
PA	0.0	12	23	2.50 ± 0.13	0.22	0.07	0.30	1924–2000	17.63	64.53	43.15
YE	0.0	12	24	3.52 ± 0.15	0.15	0.31	0.22	1930–2000	11.91	53.76	49.18
GU	0.0	10	23	3.11 ± 0.16	0.28	0.37	0.22	1931–1999	13.13	63.57	65.08
DI	0.0	12	24	2.75 ± 0.13	0.19	0.31	0.23	1931–2000	20.08	65.06	47.14
OR	0.0	11	22	1.73 ± 0.03	0.16	0.33	0.22	1906–2000	10.15	54.18	46.80
MO	0.0	15	30	1.61 ± 0.09	0.19	0.43	0.20	1912–1999	6.62	36.70	42.04
AZ	0.0	11	22	3.41 ± 0.17	0.11	0.26	0.17	1933–2000	6.55	41.85	42.51
PN	2.0	11	22	2.77 ± 0.18	0.11	−0.06	0.20	1936–2000	4.00	39.14	45.01
CO	0.0	12	27	3.01 ± 0.21	0.21	0.61	0.19	1930–2000	4.70	36.12	47.50
SN	5.0	14	29	2.90 ± 0.14	0.11	0.14	0.18	1934–2000	5.60	41.36	48.27
SA	0.0	12	29	2.38 ± 0.25	0.14	0.43	0.17	1930–2000	5.41	40.22	33.16
BA	0.0	11	29	2.12 ± 0.09	0.10	0.20	0.17	1923–2000	6.91	43.13	48.60

[a] Declining sites are indicated with underlined abbreviations.
[b] Dead trees were regarded as those which have shown complete defoliation or only retained red needles.
[c] Variables in columns 5–7 and 8–12 are referred to standard and residual chronologies, respectively. Variables abbreviations are: SD, standard deviation; AR1, first-order autocorrelation; MS: mean sensitivity; EPS: expressed population signal; SNR: signal-to-noise ratio; PC 1: variance explained by the first principal component; Climate-R^2: percentage of growth variance of the 1950–1999 residual chronologies explained by climate. The annual MS 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. MS ranges from 0 to 2 with larger values corresponding to greater high-frequency variability. EPS measures the tree-to-tree common growth variance, and a threshold value greater than 0.85 is mostly used for considering well-replicated chronologies.

Table 3
Effects of environmental (*X*), structural (*Z*), and anthropogenic variables (*W*) on silver fir growth and vigor. We used as response variables degree of defoliation, abundance of mistletoe and apical epicormic resprouts, and the growth ratio between the mean tree-ring width for the 1990–1994 and 1980–1984 periods. The *F* and *P* values are shown, and variables with $P < 0.1$ are indicated in bold.

Group	Variable	Eigenvalue using only one explanatory variable	Eigenvalue as % of sum of all eigenvalues using only one explanatory variable	*F*	*P*
Environmental variables (*X*)	Elevation	0.05	6.04	0.71	0.55
	Slope	0.03	3.23	1.00	0.61
	Northness	0.04	5.03	1.04	0.40
	Eastness	0.02	2.02	0.37	0.76
	Soil type	0.03	2.23	1.32	0.84
	Summer rainfall	0.06	9.45	1.57	0.19
Structural variables (*Z*)	Age	0.01	1.41	1.16	0.33
	dbh	**0.10**	**12.08**	**3.08**	**0.01**
	Height	0.02	2.82	1.58	0.21
	A. alba basal area	0.07	5.36	1.14	0.32
	***F. sylvatica* basal area**	**0.05**	**7.04**	**2.03**	**0.07**
	***P. sylvestris* basal area**	**0.03**	**4.23**	**2.61**	**0.05**
	Neighborhood dbh	0.03	4.23	0.70	0.57
	Daniels competition index	0.04	5.93	1.20	0.30
	Density	0.04	5.83	1.59	0.17
Anthropogenic variables (W)	**Releases**	**0.09**	**23.08**	**2.89**	**0.03**

Table 4
Relationships among the scores of the first two axes of the PCA based on the ring-width residual chronologies (axes 1 and 2) and the main ecological variables based on site-level data (Pearson correlation coefficients except those related to defoliation, which are Spearman coefficients). Defoliation refers to the percentage of trees in each stand with more than 50% crown defoliation during the 1999–2001 period. Abbreviations and variables are as in Tables 1 and 2.

	Axis 1	Axis 2	Latitude	Longitude[a]	Elevation	Slope	Defoliation	dbh	Height	Basal area	Age	Tree-ring width	AR1	MS	PC 1
Axis 2	0.53**														
Latitude	0.01	0.26													
Longitude	−0.45*	−0.41*	−0.57**												
Elevation	−0.48*	−0.62**	−0.53**	0.69**											
Slope	0.12	0.09	0.20	−0.26	−0.30										
Defoliation	0.30	0.40*	0.42*	−0.43*	−0.52**										
dbh	−0.30	−0.43*	0.20	0.04	0.20	−0.13	−0.48*								
Height	−0.07	−0.20	0.48*	−0.06	−0.13	0.03	−0.15	0.54**							
Basal area	−0.11	−0.27	0.39*	−0.06	0.01	−0.10	−0.37*	0.76**	0.60**						
Age	0.06**	0.08	0.43*	−0.17	−0.20	0.02	−0.02	0.10	0.40*	0.16					
Tree-ring width	−0.36*	−0.48*	−0.14	0.13	0.29	−0.06	−0.33	0.63**	0.06	0.39*	−0.65**				
AR1	−0.36*	−0.08	0.09	0.02	−0.01	0.00	−0.06	0.11	0.00	−0.06	0.08	0.14			
MS	0.45*	0.49**	0.04	−0.33	−0.38*	0.11	−0.03	−0.14	−0.14	−0.16	0.18	−0.36*	−0.16		
PC 1	0.18	0.31	−0.15	−0.13	−0.15	0.22	−0.15	−0.04	0.10	−0.04	−0.08	−0.04	−0.13	0.47*	
Climate R^2	0.43*	0.27	−0.42*	−0.20	−0.14	0.39*	0.13	−0.33	−0.49**	−0.38*	−0.24	−0.08	−0.20	0.31	0.33

[a] Negative and positive longitude values correspond to western and eastern sites, respectively.
* $0.01 < P \leqslant 0.05$ significance level.
** $P \leqslant 0.01$ significance level.

3.4. Growth responses to climate

The first two axes of the PCA based on the correlation coefficients between climatic variables and site chronologies accounted for 26.7% and 17.0% of the total variance, respectively (Fig. 5). Current June precipitation was positively associated with growth in western and declining sites, whereas previous September precipitation was positively associated with growth in non-declining sites. Previous February temperature was negatively related to growth in declining sites. The cumulative water deficits of the previous April and the current August were also negatively related to growth in declining sites. Warmer previous September and current April were negatively and positively associated with silver fir growth, respectively. The magnitude of the latter two associations decreased westwards. Lastly, previous May and current January precipitation showed a positive but minor association with growth in some sites.

4. Discussion

We found that several of the evaluated factors act synergistically and at different scales (region, stand, tree) on silver fir decline (Fig. 6). Furthermore, these factors may be connected within a mechanistic framework of tree decline and will be discussed below following Manion's (1981) conceptual model.

4.1. Induction of silver fir decline by drought at regional scales

The maximum growth reduction of silver fir occurred in 1986, which was preceded by the highest cumulative late-summer water deficit in the Aragón Pyrenees during the second half of the twentieth century. Defoliation and growth reduction were widespread in western low-elevation sites related to the outstanding water deficit in 1985, which was higher than in the eastern study area. The detected increase in drought stress was not only due to a decrease in precipitation, since similar dry periods occurred in the 1940s, but it is probably linked to the rise in temperature since the 1980s. Thus, warming-induced drought stress and late-summer water deficit seem to be the key climatic variables controlling silver fir decline since water reserves are usually low at the end of the growing season (Bert, 1993; Macias et al., 2006). Soil type was not a predisposing factor of decline as in other studies (Thomas et al., 2002; Pinto et al., 2007), probably because of the relatively homogenous soil types in the studied forests. Several studies in the Alps and Italy found a consistent response of silver fir growth with previous August temperature and precipitation (Rolland et al., 1999; Carrer et al., 2010), whereas in the Spanish Pyrenees this species was more sensitive to previous September conditions. Such difference may be due to genetic or phenological differences between these populations. In addition, extensive dendrochronological networks at European scales can help to interpret if this pattern is caused by climatic differences since the influence of previous September climate on silver fir growth increased eastwards.

The negative response of silver fir growth to the cumulative water deficit in the growing season was more marked in declining than in non-declining sites. Thus, declining and southern sites showed a greater responsiveness to climatic stress than the rest of the sites. Radial growth in declining sites was also enhanced by current June precipitation, whose effect increased as summer precipitation decreased westwards, and was also negatively affected by previous February temperature. This suggests that growth of declining trees was more vulnerable against late-summer drought, spring frosts or longer snow accumulation, which may delay growth onset, than non-declining trees (Rolland et al., 1999; Tardif et al., 2003). Consequently, drought-induced decline may also be exacerbated by water shortage during June when radial growth rates are highest. This response might be related to a poor stomatal regulation or to an increased consumption of carbohydrates linked to enhanced respiration (Aussenac, 2002).

4.2. Historical predisposition to silver fir decline at the stand and tree levels

The silver fir decline in Pyrenean forests was likely predisposed by past logging. However, historical factors have been rarely considered when explaining the causes of forest decline perhaps because these processes act at longer time scales than short-term droughts. In this study, tree competition was not a significant factor of decline (Table 3). This findings contrasts with those of Becker

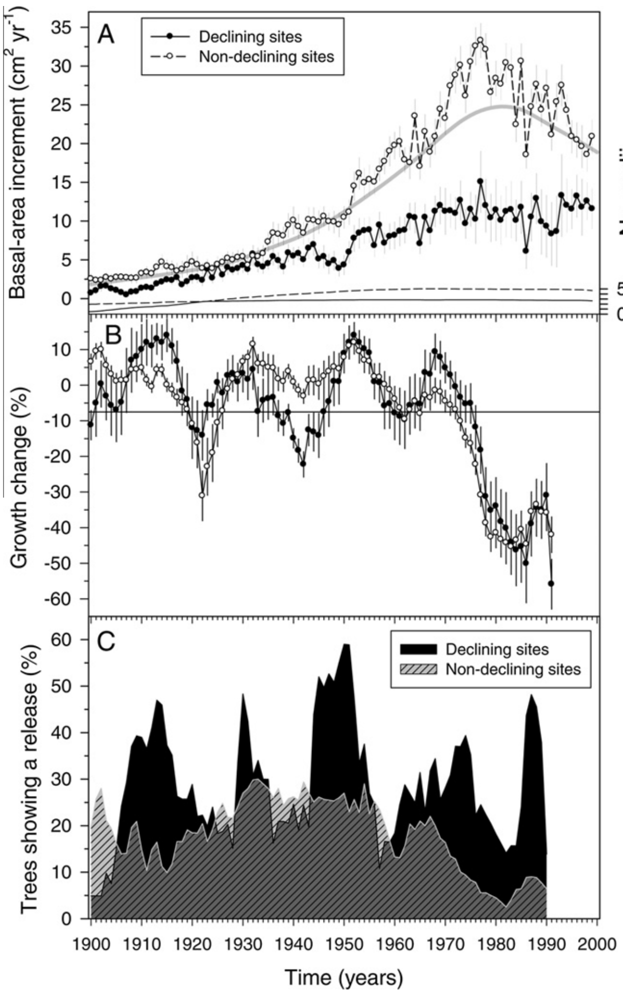

Fig. 4. Trends in basal area increment of declining and non-declining silver fir sites (A), changes in mean growth (B), and frequency of trees showing releases (i.e. positive growth changes greater than 75%) (C). Sample size is displayed in the upper graph. The smoothed curve in the upper graph (gray line) shows the long-term trend of basal area increment for all trees and was obtained using a loess function with a 0.1 span. The dark-gray area in the lower graph shows the common percentage of trees showing releases in both types of sites.

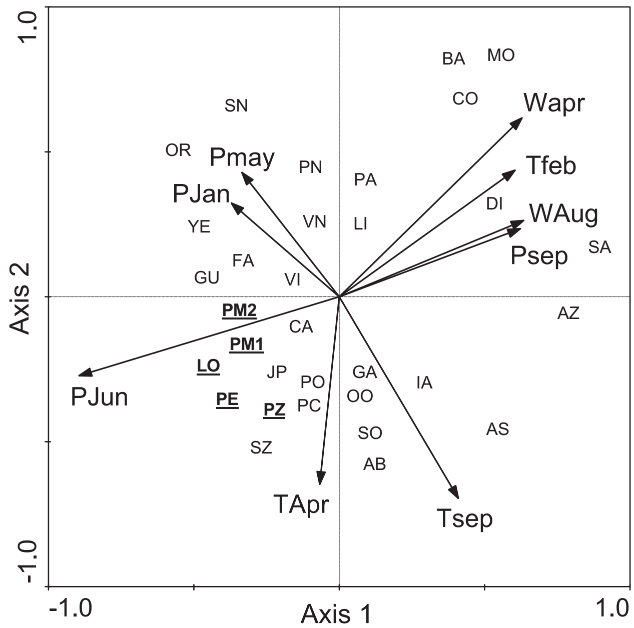

Fig. 5. Relative positions of silver fir correlation functions based on the first two components of a Principal Component Analysis. Correlations were calculated between monthly climatic data (*T*, mean temperature; *P*, total precipitation) and the residual chronologies for the period 1950–1999. Only the most significant ($P < 0.05$) climatic variables (arrows) are represented and they are abbreviated using a three-letter code. Climatic variables starting with "W" refer to cumulative monthly water deficit (e.g., WAug, cumulative water deficit from January up to August of the year of growth). The months studied go from previous January to current September (months abbreviated by lower/uppercase letters correspond to the previous/current year of tree-ring formation; e.g., TApr stands for April temperature of the year of tree-ring formation). The climatic data were calculated for the two climatic sub-regions (Western and Eastern Aragón Pyrenees). Declining sites are shown as underlined bold codes. See site codes in Table 1.

et al. (1989) and Linares et al. (2009) who found that tree competition for water caused the decline of *Abies* species in xeric sites. We suggest that competition in our study sites was not high enough for having acted as a decline factor because sampled sites were not dense forests dominated by big individuals. For instance the late 1980s releases found only in the declining sites were caused by the felling of dying trees but many of the surviving trees died later, although the basal area of those sites was low and water availability after thinning was probably improved (Camarero et al., 2002).

Our results confirm that formerly and intensively logged stands showed a greater response to the severe 1985 drought. Declining sites showed a greater frequency of trees with releases than non-declining sites during the 1950s and 1970s when logging was more widespread in the Pyrenees than currently (Cabrera, 2001). Thus, historical logging seems to have been more intense in declining sites than in non-declining sites. Reams and Huso (1990) also noted that declining red spruce stands in Maine were released one to three decades before decline started. In the Aragón Pyrenees, the most frequently used method of timber harvesting was diameter limit cutting which mostly affected fast-growing and big trees, thus promoting the persistence of small-diameter, slow-growing trees (Cabrera, 2001). In agreement with this, tree diameter and growth were consistently lower in declining than in non-declining sites (Tables 1 and 2). These even-aged stands overcome sudden changes in their growth dynamics due to a reduction in competition, and later they might have shown a greater response to the increased atmospheric moisture demand caused by the severe droughts in the 1980s.

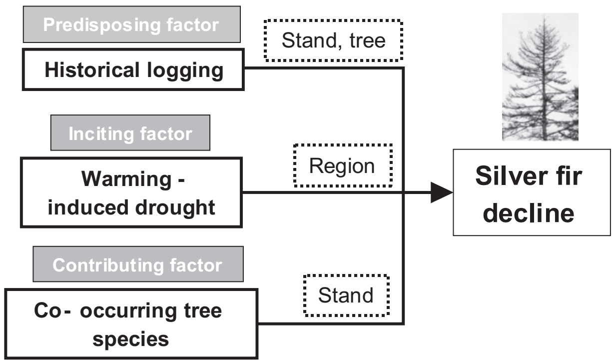

Fig. 6. Holistic view connecting the evaluated factors and their synergistic effects on silver fir decline (see Discussion). Gray-filled boxes include factors following Manion's (1981) conceptual model of decline, which includes predisposing, inciting, and contributing stress factors causing a decline in tree vigor. White boxes surrounded by continuous lines show factors implicated in the assessed silver fir decline. Finally, white boxes with discontinuous lines indicate the main scales at which the evaluated factors potentially act on silver fir decline.

The post-logging reduction of competition may have induced recurrent processes of sharp biomass gain, which differ from natural dynamics whose regime and spatial extent in the Pyrenees were less important during the 20th century than historical logging (Oliva and Colinas, 2007). Such sudden increase in biomass may alter the carbon balance in trees subjected to frequent logging of neighboring competitors (Waring, 1987). If water availability is greatly reduced these trees might show a sudden growth decline and increasing defoliation (Peguero-Pina et al., 2007), but respiration cost wills be increased by drought stress, likely affecting tree carbon balance in a negative way (McDowell et al., 2008). Experimental tests might evaluate if carbon and water use interact in episodes of forest decline through long-term (e.g., historical logging) and short-term (e.g., drought) constraints of growth.

Our findings have also implications for silver fir persistence in the south-western distribution limit of the species because ongoing decline of low-elevation silver fir stands favor their replacement by *F. sylvatica* and *P. sylvestris* in mesic and xeric sites, respectively (Camarero et al., 2002). We found that the basal area of beech and Scots pine were marginally significant predictors of decline (Table 3) indicating potential vegetation shifts from declining silver fir stands towards mixed forests and changing competition intensity in mixed forest as compared with pure silver fir stands.

4.3. Conclusions

Silver fir decline was more severe and widespread in xeric forests dominated by trees of small size showing frequent growth releases, i.e. subjected to intensive historical logging. Our results indicate that less intensive logging practices, which focus on silver fir trees of several sizes and ages, may be more desirable for the long-term management of these forests in the context of a forecasted warmer and drier climate in the Spanish Pyrenees. Finally, we partly concur with Manion (2003) and Auclair (2005) that some forest declines might be regarded as an additional disturbance factor of forest dynamics. However, both historical management and warming-induced drought stress may alter these dynamics acting synergistically, but at different time scales, on tree growth. First, historical management might set the stage for forest decline through selection and logging of big and fast-growing trees, thus leaving small and slow-growing trees in the stand, which are highly vulnerable to climatic stress. Second, short-term inciting climatic stressors as droughts may trigger forest decline. Therefore, the recurrence of forest decline episodes may be exacerbated in a warmer world thus challenging the persistence of formerly disturbed temperate conifer forests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.05.009.

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