Original article

The impact of a needleminer (*Epinotia subsequana*) outbreak on radial growth of silver fir (*Abies alba*) in the Aragón Pyrenees: A dendrochronological assessment

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Summary

We report the first dendrochronological assessment on the effects of the *Epinotia subsequana* (*Lepidoptera: Tortricidae*) needleminer on *Abies alba* forests in the Aragón Pyrenees (northeastern Spain), near the southwestern distribution limit of *A. alba*. We built local residual ring-width chronologies, in fifteen *A. alba* stands, using dendrochronological techniques. We found a strong decrease in radial growth in the 20th century, during the 1996–98 period, only at the sites AS (Paco Asieso, 42° 39′ N, 00° 17′ W) and DI (Diazas, 42° 38′ N, 00° 06′ W). There were previous surveys of *E. subsequana* outbreaks and fir defoliation, in the studied sites area, in 1995–96. They showed that the radial-growth suppression was caused by *E. subsequana*. We compared radial growth in the non-defoliated stands with mean regional chronology. The greatest decline in radial growth was in 1996–97. Thus, there was a 1–2 year lag in radial growth suppression following the defoliation. The recovery of radial growth occurred in 1998–99.

Keywords: *Abies alba*, *Epinotia subsequana*, defoliation, dendroecology, silver-fir decline

Introduction

In the 1980s, a high mortality of silver fir (*Abies alba* Mill.) was observed in the central-western Spanish Pyrenees (Aragón-Navarra). This episode of fir decline has been related to an increased climate variability and severe summer droughts (Camarero 2001). Some of the affected stands were locally attacked by borer beetles of the *Pityokteines* genus (*Coleoptera: Scolytidae*) (Martín, Cobos 1986). In spite of controversial silvicultural treatments, such as the intense logging of affected trees, the decline has continued in some Pyrenees stands until now. This motivated extensive dendroecological studies to determine which climatic and biotic

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factors (insects, fungi) were involved. Similar studies were also carried out in NE France (Bert 1993). The potential role of climate as a limiting factor was reinforced by the fact that the studied populations form the southwestern limit of silver fir in Europe (Vigo, Ninot 1987).

Within this spatiotemporal context (increased climate variability, sensitive fir populations), an intense *Epinotia subsequana* (Hw.) (*Lepidoptera: Tortricidae*) outbreak caused severe defoliation in 1995–96 in the Aragón Pyrenees (Sánchez Peña et al. 2000). Several *Epinotia* species affect *Abies* and *Picea* species in the temperate forests of Europe (Abgrall, Soutrenon 1991) and Northern America (Washburn, McGregor 1974). *E. subsequana* is mainly found in Northern and Central Europe forests of *A. alba* being considered as a generalist feeder (Strouts, Winter 2000). However, this was the first report of *E. subsequana* in Spain (Vives Moreno 1995), where its biological cycle was described in 1997 (Sánchez Peña et al. 2000).

The attacked firs showed brown reddish crowns in July–August, with their top third of the crown heavily affected (Sánchez Peña et al. 2000). The main injury symptom was the mined current-year needles which appeared dry at least in their two thirds distal parts. According to Sánchez Peña et al. (2000), the *E. subsequana* attacks were geographically located between Biescas (the Paco Asieso site – hereafter AS) and Torla (the Diazas site – hereafter DI; Fig. 1, Tab. 1). Hence, we regard these two stands as examples of defoliated stands. According to Sánchez Peña et al. (2000), the intensity of the attacks was high in 1995–96 and intermediate in 1997. These authors reported that many branches showed the 1995–97 internodes clearly defoliated, whereas in 1998 the longitudinal growth of the affected firs had recovered after the outbreak.

The use of dendroecological techniques has enabled researchers to date with annual resolution, and to quantify precisely the effects of insects and other herbivores on radial tree growth (Schweingruber 1996). There is a characteristic tree-ring signature related to infestation by defoliating insects. The destruction of current-year and older needles induces abrupt radial-growth decrease whose magnitude is proportional to the intensity and duration of the defoliation (Swetnam et al. 1985). The main objective of this study was to describe the effects of a recent *E. subsequana* outbreak on *A. alba* radial growth in the Aragón Pyrenees. To our knowledge, there has been no research as to the effects of *E. subsequana* defoliation on *A. alba* growth in natural stands near its Southern distribution limit.

Materials and methods

Study area

The main characteristics of the two defoliated silver-fir stands are summarized in Tab. 1. These stands are located at opposite extremes of the area affected by *E. subsequana* in the 1990s (Fig. 1). They can be regarded as representative of the fir forests in the Aragón Pyrenees. At site DI, a rocky ridge separates two contrasting slopes dominated by *A. alba* (N-NW aspect) and *Pinus sylvestris* L. (W-SW aspect), respectively. This ecotonal structure was not so evident at the AS site. At both sites, the bedrock is calcareous generating basic and stony soils. The DI site is located on a lateral glaciar moraine. The dominant tree and shrub species are: *P. sylvestris*, *Sorbus aucuparia* L., *S. aria* (L.) Crantz, *Ilex aquifolium* L., *Corylus avellana* L., and *Buxus sempervirens* L. The main understorey plant species are *Vaccinium myrtillus* L. and *Daphne laureola* L. The last logging activities in both stands date from at least 20 years ago, so no recent radial-growth release has been observed in the tree-ring series.

According to meteorological data from nearby stations (Broto, 42°36′ N, 00°07′ W, 1005 m a.s.l., 1949–99; Torla, 42°38′ N, 00°07′ W, 1053 m, 1954–99; Canfranc-Los Arañones, 42°45′ N, 00°31′ W, 1160 m, 1910–99; Yésero, 42° 37′ N, 00°15′ W, 1132 m, 1970–99), the climate in the area can be described as continental with Mediterranean influence. Mean annual temperature and total annual precipitation are 8–12 °C and 1161–1321 mm, respectively. Maximum mean temperature (17–21 °C) and minimum total precipitation (59–69 mm) are recorded in July.

Field sampling and dendrochronological methods

In each stand, several dominant and codominant *A. alba* trees from an area ca. 1 ha were selected for dendrochronological sampling. Their size (DBH and total height) was measured. To estimate stem density and basal area of *A. alba* and *P. sylvestris* (Tab. 1), the number and DBH of all neighbors found within

a circle of 7.62 m radius around each sampled tree were recorded (Holmes, Reed 1991).

Dendrochronological sampling was carried out following standard methodology (Fritts 1976; Cook, Kairiukstis 1990). We took 2–3 cores per tree at 1.3 m. The cores were dried and polished using sand-paper of progressively finer grain. Then, they were cross dated using skeleton plots and noting nar-
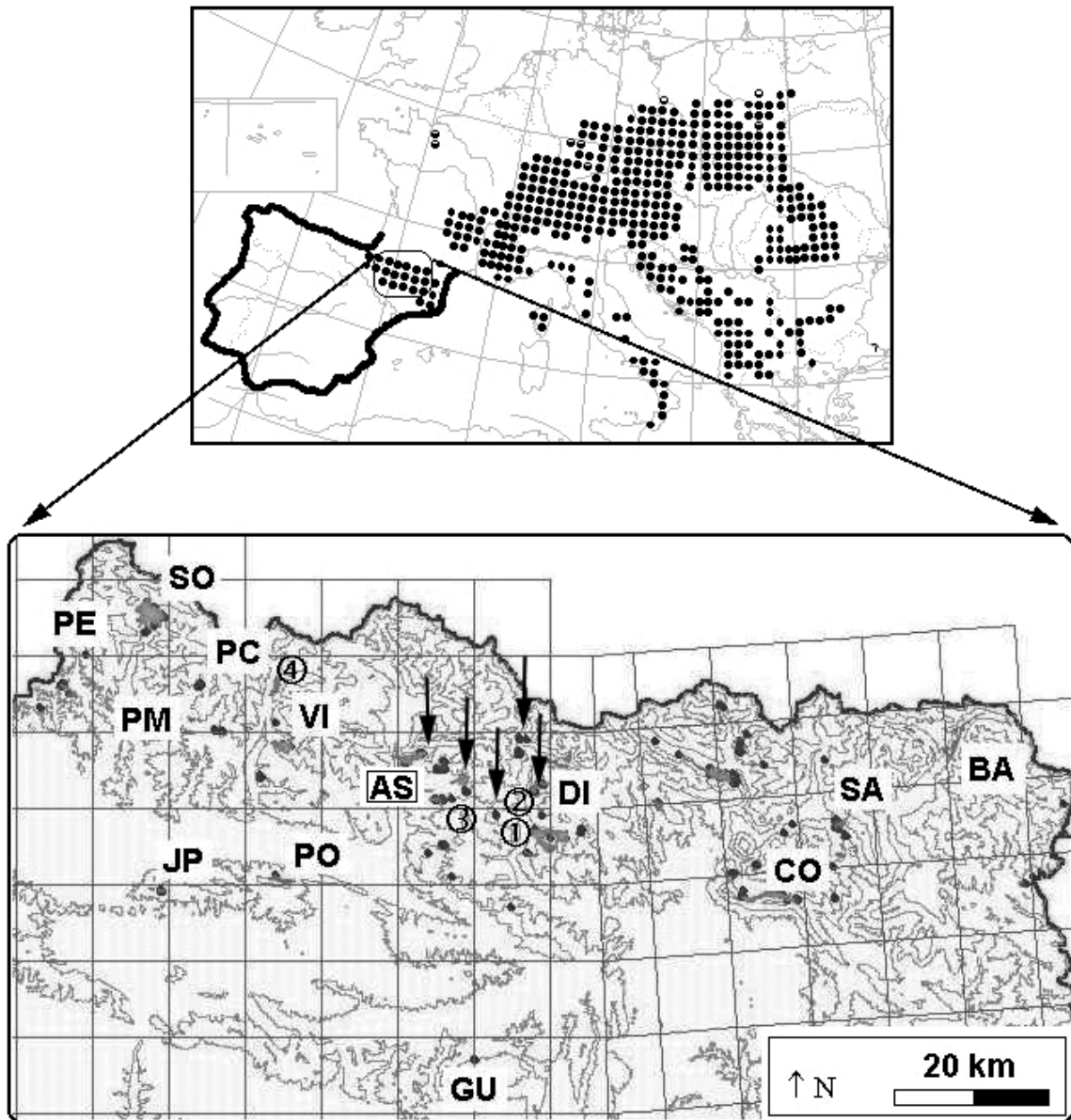

Figure 1. Distribution of *A. alba* in Europe (top map; filled circle, native occurrence; rest of symbols, status or record uncertain; see Jalas, Suominen 1994) and geographical location of some of the sampled silver-fir (*A. alba*) stands in the Aragón Pyrenees, northeastern Spain. Stands affected by *E. subsequana* outbreaks are also included (DI, Diazas; AS, Paco Asieso). Arrows point to areas affected by the 1995–97 insect outbreaks. The approximate location of the meteorological stations is also indicated (①, Broto; ②, Torla; ③, Yésero; ④, Canfranc-Los Arañones). Gray points and areas indicate the distribution of *A. alba* within the 10 km² grid. Abbreviations of the names of other sampled stands with no recent records of *E. subsequana* outbreaks (non-defoliated stands): PE, Paco Ezpela; SO, Selva de Oza; PM, Paco Mayor; PC, Puente de los Corralones; VI, Paco de Villanúa; JP, San Juan de la Peña; PO, Peña Oroel; GU, Guara; CO, Collado de Collubert; SA, Collado de Sahún; BA, Ballibierna.

row and light rings (Stokes, Smiley 1968; Yamaguchi 1991). The annual relative frequency (%) of narrow and missing tree rings was computed on the total amount of cores for the two defoliated stands.

Ring width was measured, to the nearest 0.01 mm, by a semiautomatic CATRAS measurement system (Aniol 1983). Tree-ring cross dating was checked using the COFECHA software (Holmes 1983). Segments showing anomalous radial growth (e. g. reaction wood) or a low correlation with the mean series were discarded (Blasing et al. 1983). Most ring-width series show evident trends because of the increase in age and diameter of growing trees (Fritts 1976). These series were detrended by a two-step process. Firstly, a negative linear or exponential function was fitted. Secondly, a cubic smoothing spline with a 50 % frequency response cutoff of 50 years was used. This spline adequately removes the variance of lower frequencies in closed-canopy

Table 1. Geographic, topographic, and structural characteristics of the affected silver-fir stands (AS, Paco Asieso; DI, Diazas). SE is the standard error.

	AS	DI
Latitude (N)	42° 39′ 25″	42° 37′ 50″
Longitude (W)	00° 17′ 30″	00° 05′ 40″
Elevation range (m a. s. l.)	1305–1335	1505–1550
Aspect	NW-N	NW-N
Mean slope (°)	33	22
A. alba density (stems · ha^{-1})	1129 ± 152	1302 ± 186
A. alba basal area (m^2 · ha^{-1})	37.2 ± 6.1	45.4 ± 2.2
P. sylvestris basal area (m^2 · ha^{-1})	3.1 ± 1.3	18.4 ± 4.9
Number of sampled trees	10	12
Mean DBH ± SE (cm)	60.6 ± 3.6	56.5 ± 2.2
Mean height ± SE (m)	25.2 ± 0.7	25.9 ± 0.6
Mean age at DBH ± SE (yrs.)[a]	110 ± 9	119 ± 10
Crown defoliation (%)	0	0

[a] Age estimated at breast height only considering those cores with pith and with inner rings near the missing pith. We applied a two-step correction for the latter group: *(i)* using a circle template to estimate the distance to the geometric pith, and *(ii)* calculating the number of missing rings. These were estimated by a regression based on cores with pith. In this regression, we regarded the distance from the pith as the independent variable and the number of rings as the dependent one.

forests (Cook, Peters 1981). In this study we were mainly interested in the high-frequency variability of radial growth, such as that related to insect outbreaks. Autoregressive modelling was performed on each detrended ring-width series. They were averaged using a biweight robust mean to obtain residual chronologies (Monserud 1986). This was done using the ARSTAN program (Cook 1985; Cook, Holmes 1986).

Quantification of the defoliation effect on radial growth

The dendroecological analysis of the effects of defoliation is usually based on the comparison of radial growth in host *versus* non-host trees (Swetnam et al. 1985). Basically, this procedure consists in removing the environmental influence, common to host and non-host chronologies, from the host tree-ring chronology. The environmental effect is assumed not to be related to the insect outbreak. Some authors have defined thresholds of radial-growth decrease to reconstruct past insect outbreaks. For instance, Swetnam et al. (1985) defined a threshold equal to mean radial growth –1.28 SD (standard deviation). We used this threshold to detect possible past *E. subsequana* outbreaks.

To quantify the effect of the recent *E. subsequana* defoliation on radial growth, we modified the dendroecological analysis described above. In this study, we compared defoliated and non-defoliated host trees (*A. alba*) in nearby stands, because non-host species (e. g., *P. sylvestris*) respond very differently to climate in comparison with *A. alba* (Gutiérrez 1989; Rolland et al. 1999). This strategy is only appropriate for quantifying recent insect outbreaks, because the currently healthy host trees might have been affected during previous outbreaks (Swetnam et al. 1985). We developed a regional mean chronology (control) using 138 trees (310 cores) from close sites (Euclidean distance from affected area was less than 60 km) where there were no reports of previous outbreaks during the last 10 years (Fig. 1). The chronology at the Guara site (GU in Fig. 1) was excluded from the analyses because most of the trees at the site were too young (50 % cores contained less than 70 tree rings). All chronologies cross dated, which meant they were responding to the same regional climate. For instance, two residual chronologies from sites ca. 115 km apart were still signifi-

cantly related (1900–99 period, $r = 0.36$, $P < 0.001$). The control chronology was compared with chronologies from the two defoliated stands to remove other environmental factors from the latter series (e. g. climate). The host-tree chronologies were corrected by scaling the residuals ones from the control chronology to the same variance as the host-tree chronologies. The scaled residual ones were subtracted from the host-tree indices to obtain the "corrected indices" (p. 32, Swetnam et al. 1985). The corrected host-tree indices were used to quantify the radial-growth decrease induced by the needleminer. The decrease was expressed as a relative difference (%) of the annual corrected index with respect to 1.

Results

Within the biogeographic range of silver fir in the Aragón Pyrenees, the only structural peculiarity of both selected fir stands was the predominance of *P. sylvestris* as a secondary tree species, especially at the DI site (Tab. 1). The affected stands were also characterised by firs with dense crowns and no recent signs of past defoliation.

Radial growth was very high (> mean + SD) in 1954–65 and 1964–78 at the DI and AS sites, respectively (Fig. 2). These radial-growth releases corresponded to probable logging episodes dated approximately in 1952–53 (DI) and 1963 (AS). In addition, radial growth at these sites was greater than the regional mean in the 1940s and the first half of the 1980s. Mean radial growth in the rest of the non-defoliated
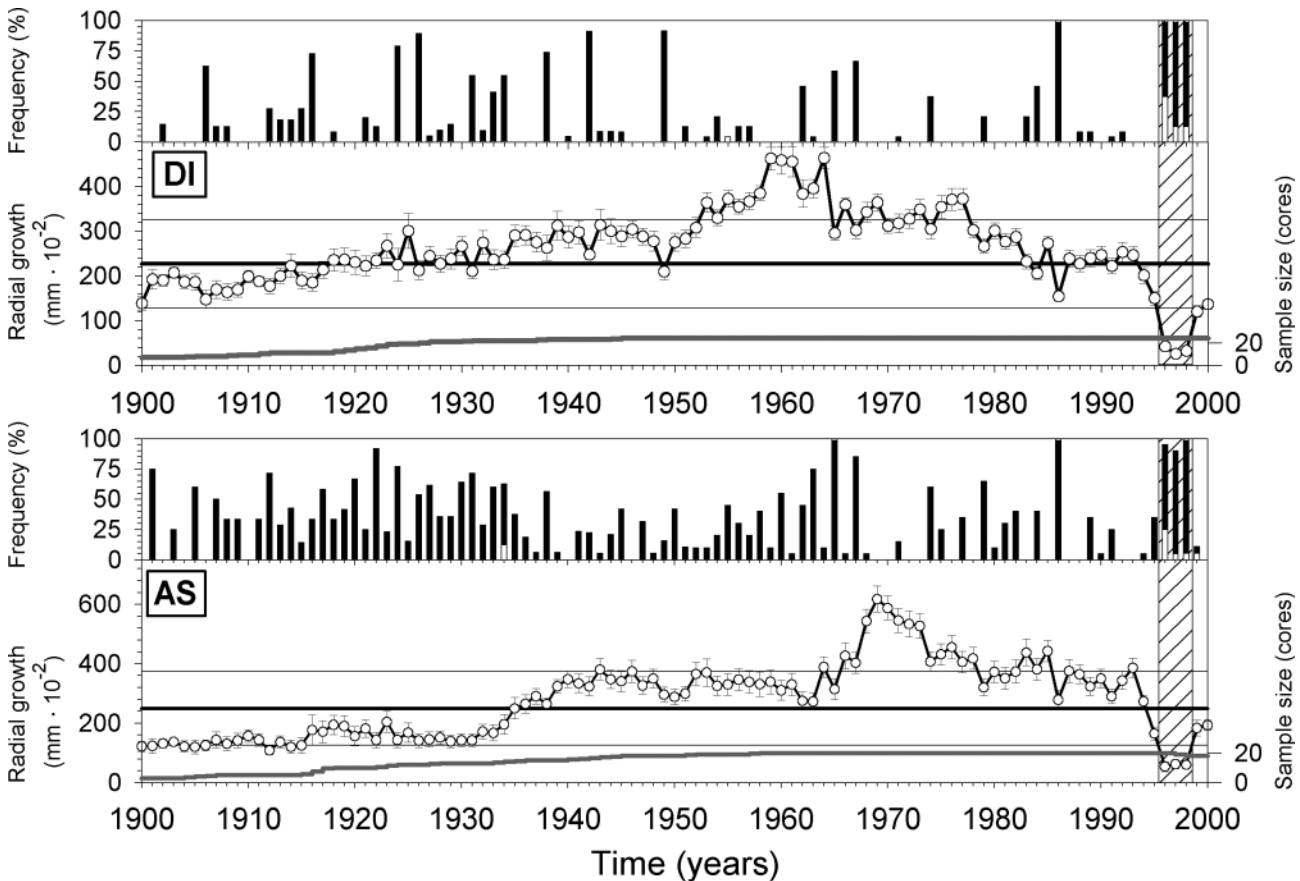

Figure 2. Mean radial growth in the two *A. alba* stands (AS, DI) affected by *E. subsequana* outbreaks (1996–98, hatched box). Each yearly value is the mean ±SD. Bars represent the relative frequency (%) of narrow (solid bars) and missing (open bars) rings. The black horizontal lines represent the mean (thick line) ±SD (thin lines) for the 20th century. Sample size (number of cores) is displayed as a gray line.

silver-fir stands peaked around 1965 and was high in the 1950–80 period (Fig. 3). The most remarkable radial-growth suppression in both affected stands occurred in 1996–98 (Fig. 2), and it was not observed in the non-defoliated stands (Figs. 3–4). Contrastingly, several narrow rings were found at all sites (e. g., 1965, 1986). Missing rings were very rare in the non-defoliated stands. However, they were very frequent in the affected stands during the insect outbreak. At the DI site ca. 40 % of all the sampled trees ($n = 12$) showed a missing ring in 1996 (Fig. 2). During the insect outbreak, mean radial growth in the defoliated stands was lower than mean growth –1SD of all individual trees at all sites (Fig. 4). This result was consistent either considering measured ring-widths or indexed values. In addition, mean radial growth in both defoliated stands during these three years reached lower values than the 20th century mean –1.28 SD. Considering the measured ring-width data, this is equivalent to a decrease of 1.45 mm · yr^{-1} dur-

ing the 1996–98 period in relation to the mean in the non-defoliated stands.

In both defoliated stands, the only period with three consecutive years during which radial growth was below the "–1.28SD" threshold was 1996–98 (Fig. 5). Radial-growth recovery started in 1998, reaching values close or even above the regional average in 1999 (Fig. 3). Radial-growth decline in the defoliated stands with respect to the non-defoliated ones was highest in 1997 (79 %, DI; 70 %, AS) and 1996 (59 %, DI; 66 %, AS). In these stands, the interannual radial-growth difference reached minimum values in 1995–96 (60–70 %) and peaked in 1998–99 (62–73 %).

Discussion

The main effects of defoliation on any conifer are: a decrease in photosynthetic area, a depletion of carbohydrate reserves which are primarily stored in the
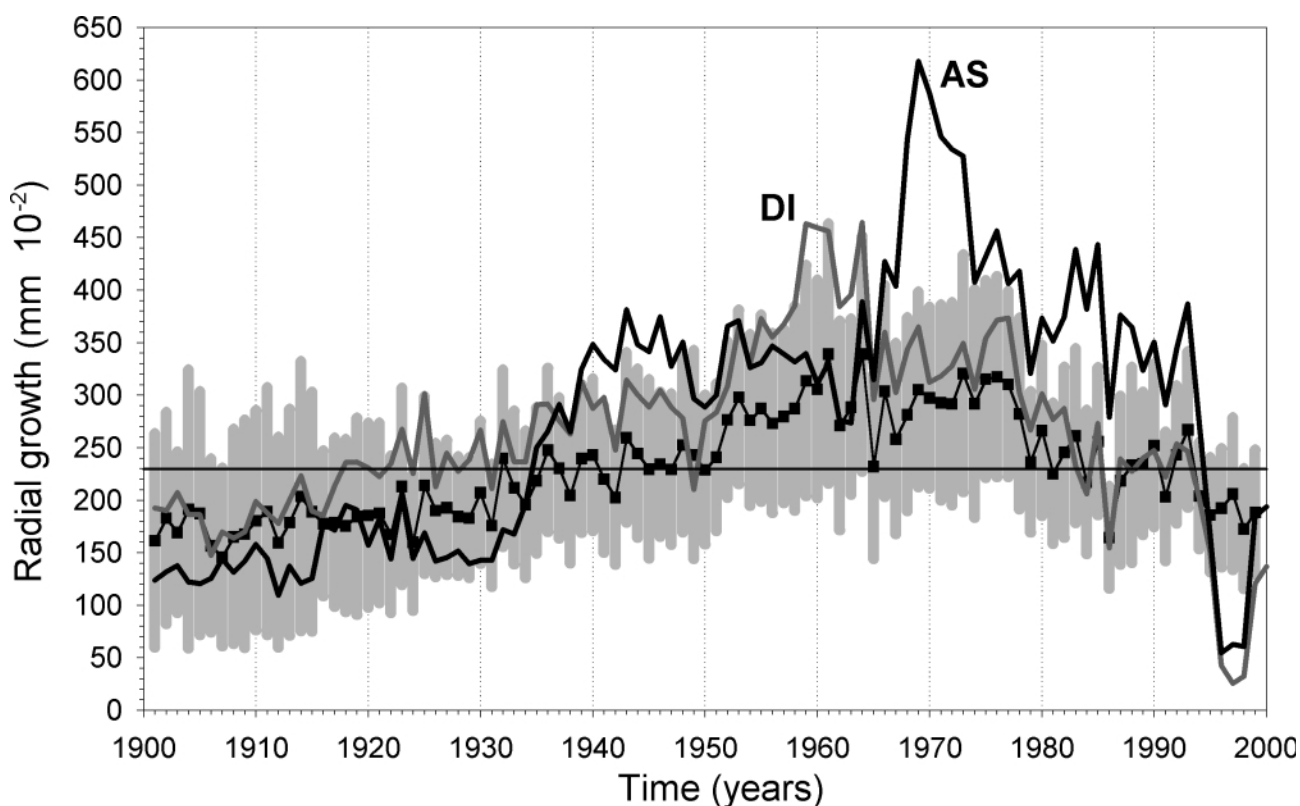

Figure 3. Comparison of radial growth in the two *A. alba* stands (AS, DI) affected by *E. subsequana* and the mean ±SD (black boxes and vertical gray lines) in the rest of the non-defoliated fir stands ($n = 10$) in the 20th century. The horizontal line shows the overall mean radial growth over the 20th century in the non-defoliated fir stands.

needles, a decline in tree growth, and a decrease in latewood production (Kulman 1971; Krause, Morin 1995; Muzika, Liebhold 1999; Speer et al. 2001). Decline in tree-growth vigor can lead to death if the host tree is very weakened. Radial-growth decrease may lag behind the onset of defoliation by 1–3 years and continue 1–2 years after the defoliation (Brubaker, Greene 1979; Mason et al. 1997). There is a minimum defoliation threshold which causes an evident radial-growth decrease (Kulman 1971). This restricts dendrochronological reconstruction of insect outbreaks because only moderate to severe infestations are detected in the corrected tree-ring series (e.g. Swetnam, Lynch 1993).

This study is the first report of the effects of an *E. subsequana* outbreak on *A. alba* radial growth in the Aragón Pyrenees. The strong decrease in radial growth observed in 1996–98 was only found at the AS and DI sites (Figs. 3–4). Therefore, some local factor, such as the defoliation produced by *E. subse-*

quana outbreaks, caused this growth decline. The greatest decline in radial growth was found in 1996–97 (Figs. 2–3 and 5). This means that there was a minimal time lag (1–2 years) between the intense defoliation episodes recorded in 1995–96 and the subsequent radial-growth decline at 1.3 m. Even after the *E. subsequana* outbreaks ended in the spring of 1997, radial growth was still low in 1998. In dendroecology, the "memory effect", i.e. the time autocorrelation of ring-width series, is well established. Both radial growth and climate in the year prior to ring formation greatly affect radial growth in the year when the tree ring is formed (Fritts 1976). In conifers, this is related to the large amounts of carbohydrates stored in needles of different ages (Kozlowski 1992).

The relationship between climate stress (e.g. drought) and tree susceptibility to insect attacks can be regarded as a normal curve where there is an optimal stress value for the insect concerned (Clancy
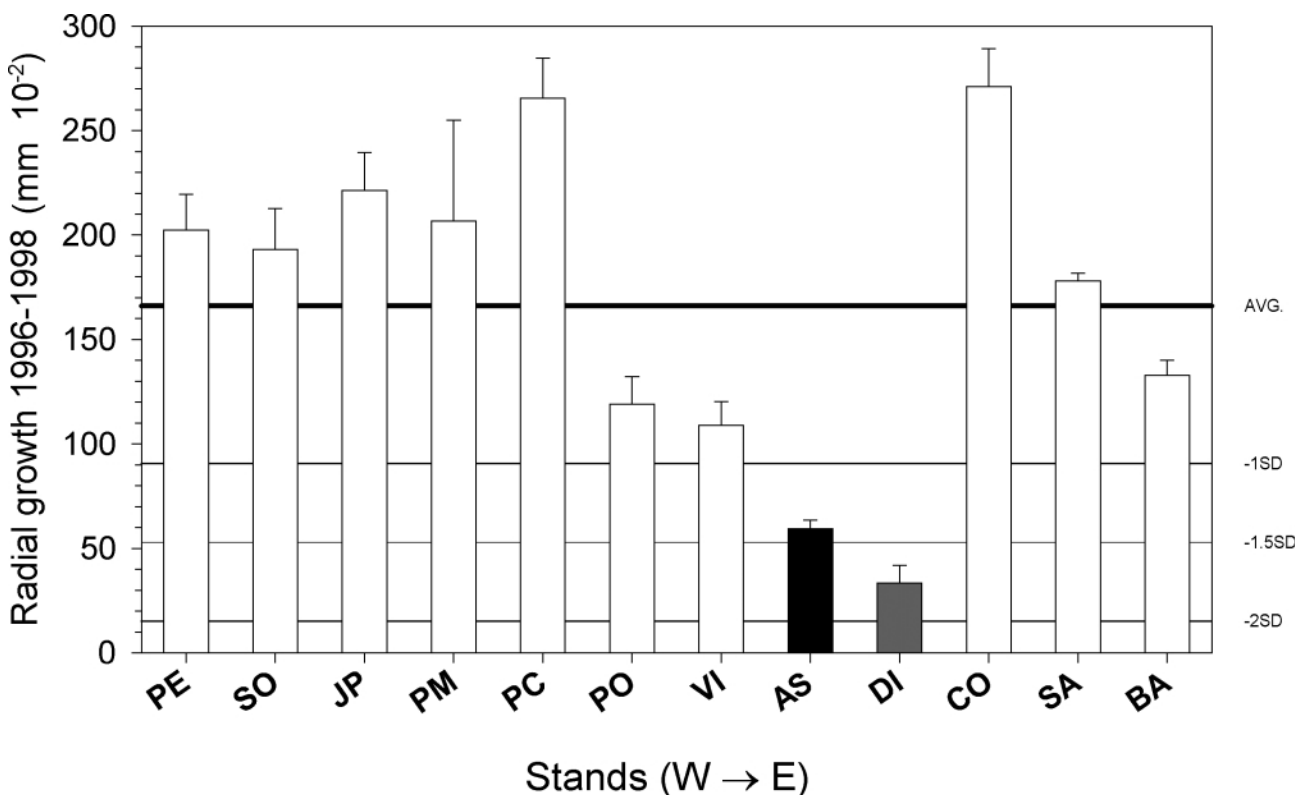
Figure 4. Comparison of radial growth during the insect outbreak (1996–98) in the two *A. alba* stands (AS, DI – colored bars) affected by *E. subsequana* and some of the non-defoliated stands (abbreviations like in Fig. 1). The sites are arranged from W (left) to E (right) along the Pyrenees. Each bar is the mean radial growth ±SD. The horizontal lines show the average radial growth (thick line) −1 SD, −1.5 SD, −2 SD (thin lines) in the 1996–98 period for all individual trees at the displayed sites.

et al. 1995). Conifers are usually more susceptible to herbivores when water-stressed (Waring, Cobb 1992). This might have been the case of the AS and DI sites in the first half of the 1990s. In comparison with the non-defoliated silver-fir stands, the only peculiar structural feature of the affected stands is the presence of *P. sylvestris* as the second main tree species. The presence of Scots pine indicates suboptimal or xeric conditions for silver-fir growth in the Pyrenees (Ceballos, Ruiz de la Torre 1979). The radial growth of *A. alba* is greater at mesic/humid sites than at xeric sites (Rolland et al. 1999). Based on this dendroecological approach, future studies should quantify the spatial pattern of previous outbreaks in the Pyrenees during the last century, which was characterised by regional warming (Bücher, Dessens 1991). Our analysis could also serve as an insight for monitoring silver-fir decline. It is still to be determined if the southward migration of *E. subsequana* might have been favored by dry and hot springs in the 1990s.

Conclusion

We report the first dendrochronological assessment on the effects of *Epinotia subsequana* outbreaks on the radial growth of *Abies alba* stands in the Aragón Pyrenees (northeastern Spain). We found a strong decrease in radial growth in the 1996–98 period at two sites (AS, DI). The greatest decline in radial growth occurred in 1996–97, 1–2 years following the most intense defoliation episodes. The recovery of radial growth occurred in 1998–99.
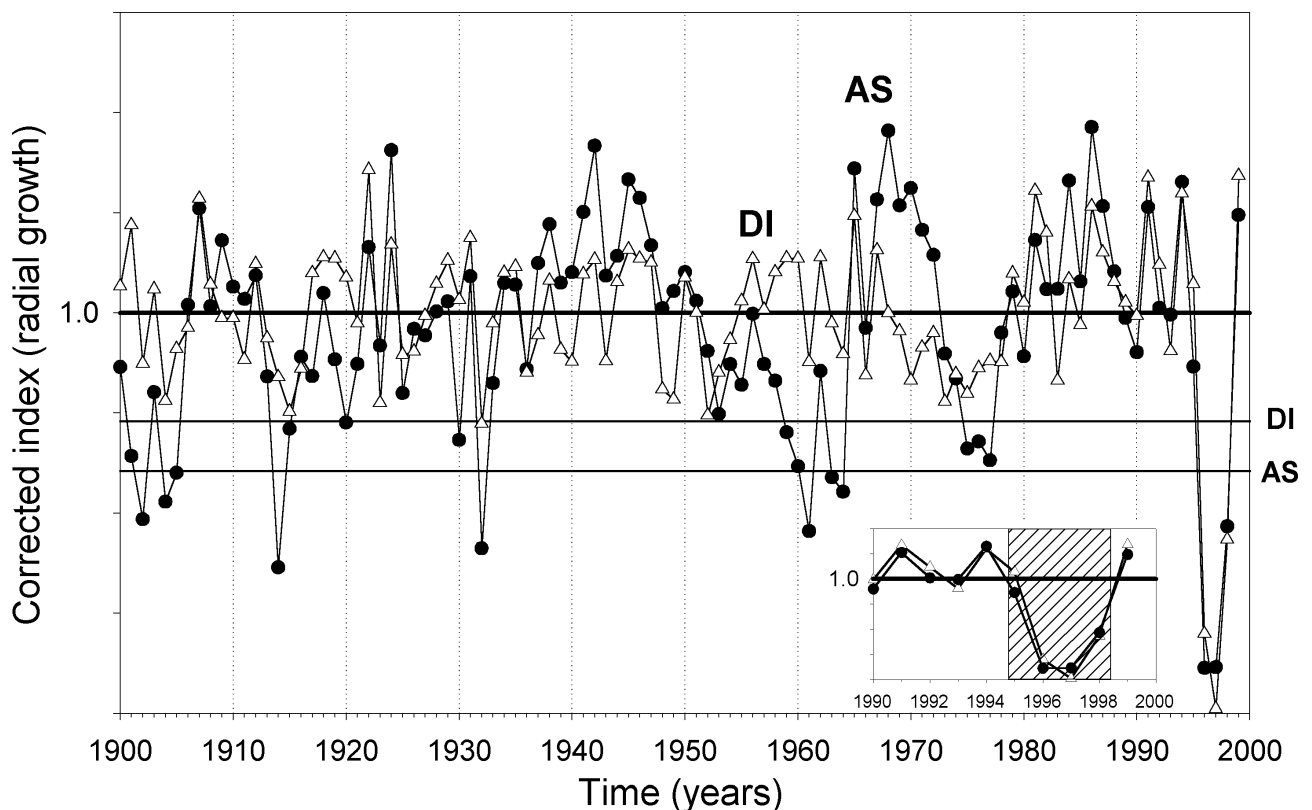
Acknowledgements

Figure 5. Corrected radial-growth indices for the *A. alba* stands (AS, circles; DI, triangles) affected by *E. subsequana*. The inset shows the indices for the 1990s (the hatched box represents the 1996–98 insect outbreak). The horizontal lines show the mean for both sites (index = 1, thick horizontal line) and the lower thresholds (mean −1.28 SD) for each stand.

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