Ann. For. Sci. 63 (2006) 293– 300
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DOI: 10.1051/forest:2006008

Original article

Radial-growth and wood anatomical changes in *Abies alba* infected by *Melampsorella caryophyllacearum*: a dendroecological assessment of fungal damage

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(Received 5 May 2005; accepted 18 August 2005)

Abstract – The fungus *Melampsorella caryophyllacearum* causes serious damage on *Abies alba*. However, radial-growth loss caused by the fungal infection has not been quantified before. In the Spanish Pyrenees, three stands were sampled (dasometry, incidence, intensity), and cores were taken from asymptomatic and symptomatic trees for dendroecological analyses. Climate-growth correlations were assessed through correlation functions relating monthly mean temperature and total precipitation with radial growth. The incidence of the disease significantly increased with tree dominance. The maximum reduction of radial growth (20%) in symptomatic trees was observed during 1983–2002, when xylem showed frequent traumatic resin ducts. During the year before growth, the radial-growth loss was positively correlated to a wet December. In the year of tree-ring formation, growth loss was negatively correlated with minimum temperatures in February, March and April. The climatic effects on radial-growth of asymptomatic and symptomatic trees are discussed.

dendroecology / fungal infection / silver fir / tree-ring width

Résumé – Croissance radiale et changements anatomiques du bois chez *Abies alba* infecté par *Melampsorarella caryophyllacearum* : une évaluation dendrochronologique des dommages fongiques. Le champignon *Melampsorarella caryophyllacearum* cause de sérieux dommages chez *Abies alba*. Cependant, les pertes causées par cette infection fongique n'ont pas encore été quantifiées. Dans les Pyrénées espagnoles, trois stations ont été étudiées et des carottes de sondages ont été prises chez des arbres sans symptôme et chez des arbres présentant des symptômes pour des analyses dendrochronologies. Les corrélations croissance/climat ont été évaluées par des fonctions de corrélations reliant la température mensuelle moyenne et les précipitations totales et la croissance radiale. L'incidence de la maladie s'accroît significativement avec la dominance de l'arbre. La réduction maximale de croissance radiale (20 %) chez les arbres présentant des symptômes a été observée pendant la période 1983–2002, quand le xylème montre des traumatismes fréquents des conduits résinifères. L'année précédant la croissance, la perte de croissance radiale était positivement corrélée avec un mois de décembre humide. Dans l'année de formation du cerne, la perte de croissance était négativement corrélée avec les minima de températures en février, mars et avril. Les effets climatiques sur la croissance radiale des arbres asymptomatiques et symptomatiques sont discutés.

dendroécologie / infection fongique / sapin pectiné / largeur de cerne

1. INTRODUCTION

The decline of *Abies alba* Mill. has been the subject of great concern in Central Europe and North America since the early 1970s [32, 35]. Among the main proposed causes of fir decline were air pollutants, and climatic and biotic factors. In the 1980s, a high mortality of *A. alba* was observed in the western Spanish Pyrenees (Aragón-Navarra) [9, 22], which motivated extensive dendroecological studies to determine which climatic and biotic factors were involved [11]. Similar studies were also carried out previously in France [5, 6]. The use of dendroecological techniques has enabled researchers to date with annual resolution, and to quantify precisely the effects of fungal pathogens on radial growth [12].

The fungus *Melampsorella caryophyllacearum* Schroet. (= *M. cerastii* (Pers.)), also called fir broom rust, has been reported to cause serious damage on *Abies* species [2, 25, 34, 37]. The fungus causes the production by the tree of witches' brooms, and hypertrophied ring growths on the trunk or branches resulting in spherical swellings [1, 34, 40]. Of greater concern, *M. caryophyllacearum* may contribute to a tree's death by weakening it such that wind breaks the tree at the site of the

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Table I. Site descriptions of the sampled plots.

	Plot 1	Plot 2	Plot 3
Latitude (N)	42º 59'	43º 00'	42º 58'
Longitude (W)	1º 03'	1º 04'	1º 03'
Elevation (m a.s.l.)	1030	1005	1010
Aspect	N	N	S
Slope (º)	32	37	31
Abies alba density (stems ha^{-1})	716	584	595
A. alba average height (m)	21.0	22.3	22.9
A. alba basal area (m^2 ha^{-1})	47.8	66.4	58.1
Fagus sylvatica basal area (m^2 ha^{-1})	3.6	4.8	2.8
Pinus sylvestris basal area (m^2 ha^{-1})	1.4	0.0	3.6
Mean presence of *Viscum album* (%)	13.8	20.7	3.7
Mean tree condition[1] ± SD	0.6 ± 1.1	0.8 ± 1.2	0.5 ± 0.9

[1] 0 = healthy tree (0–10% defoliation); 1 = few symptoms (11–25%); 2 = moderate symptoms (26–60%); 3 = dying tree (61–90%); and 4 = dead tree.

swelling. It has been reported that the disappearance of *A. alba* from Alpine stands in Italy may be partially caused by *M. caryophyllacearum* [25]. Moreover, this pathogen has been proposed as the main factor involved in the *A. sibirica* decline forests in Siberia [2]. The disease is common wherever firs grow, being present in North America [20, 27, 34, 42], Europe [16, 25, 33], and Asia [2, 28, 37]. The first report of the disease in Spain, where *A. alba* reaches its SW distribution limit in Europe, was in 2002 [22].

Previous research on the disease is scarce, and basic information concerning the intensity, incidence and effects of this disease on tree growth is necessary. Some evidence suggests that broom rust on branches can reduce tree volume growth [34], but this is not universally accepted [37]. The first purpose of this study is to test the hypothesis that infection of *A. alba* by *M. caryophyllacearum* causes reduction of radial growth in *A. alba*. A second objective is to quantify the influence of climate (temperature, precipitation) on radial growth in symptomatic and asymptomatic trees in order to assess the combined role of climate and fungal infection on radial-growth. To fulfil both objectives, we used dendrochronological methods, which to our knowledge have not been used before to study the effects of *M. caryophyllacearum* infection on radial growth.

2. MATERIALS AND METHODS

2.1. Study area

The study area belongs to the Irati forest in the western Pyrenees (Navarra), NE Spain. It has well-drained Eutric Podzoluvisols, and bedrock of Paleocene chalkstone. According to meteorological data from nearby stations (Abaurrea Alta, 42º 54' N, 1º 12' W, 1050 m a.s.l., 1986–2002; Aribe, 42º 57' N, 1º 16' W, 701 m, 1973–2002; and Yesa, 42º 37' N, 1º 11' W, 487 m, 1940–2002), the climate in the area can be described as Atlantic with continental influence, with a summer-drought period of ca. 2 months (Fig. 1). The mean distance between the study site and the meteorological stations was 15 km. Maximum temperatures occur from July to September, while minimum temperatures are observed from December to February, with a mean annual temperature of 13.1 ºC. Rainfall has a summer minimum from June to August, and a maximum from October to December, with a mean annual precipitation of 777 mm (Fig. 1). During the 1960–2002 period, the lowest daily temperatures in February, March and April occurred in 1986 (–10 ºC), 1971 (–9 ºC) and 1986 (–2 ºC), respectively.

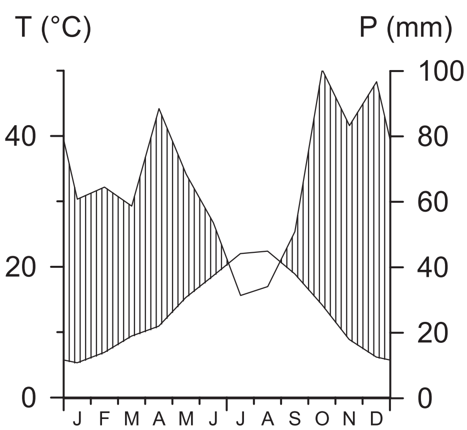

Figure 1. Climatic description of the study area based on climatic data from the Yesa meteorological (Navarra, Spain, period 1960–2002).

The community type in Irati forest is mostly defined as *Festuco altisima-Abieteto albae sigmetum*, which is basophile and ombrophile [39]. Within the studied area, *A. alba* is the dominant tree species, although *Fagus sylvatica* L. and *Pinus sylvestris* L. are also present. The main understorey plant species are *Pteridium aquilinum* (L.) Kuhn, *Vaccinium myrtillus* L., and *Daphne laureola* L.

2.2. Field sampling and estimation of incidence, intensity and rot wood

Extensive surveys of *M. caryophyllacearum* were conducted throughout the entire forest since 1996 to select intensive sampling sites. Detailed examination of the symptoms, and damage caused by the disease was studied in three plots located within a central area of the forest (Tab. I). This area was selected because of great abundance

Table II. Characteristics of the asymptomatic (A, $n = 5$) and symptomatic (S, $n = 5$, with trunk swellings) cored trees in the three sampled plots. Mean values are given with standard deviation.

	Plot 1		Plot 2		Plot 3	
	A	S	A	S	A	S
DBH (cm)	33 ± 1	30 ± 1	32 ± 4	34 ± 2	30 ± 1	30 ± 4
Height (m)	24 ± 2	22 ± 3	23 ± 1	25 ± 3	23 ± 3	22 ± 2
Age (y)	96 ± 10	86 ± 0	86 ± 3	98 ± 18	75 ± 9	78 ± 8

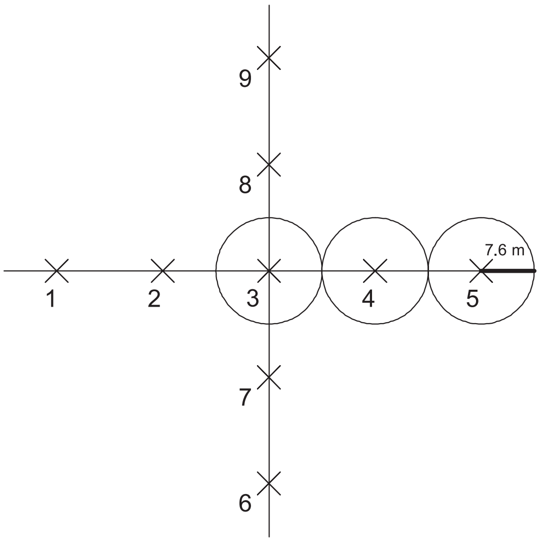

Figure 2. Intensive sampling scheme showing the location of the nine sample points along the two intersecting transects in a plot.

of *M. caryophyllacearum* symptoms and absence of symptoms and signs related to other fungal pathogens or insects. The identity of the fungus was confirmed by the symptoms and the characteristics of aeciospores produced on the infected needles [1, 42].

The intensive sampling was conducted in June 2003, because the witches' brooms are more noticeable in early summer [8]. Nine sampling points, 15.2 m apart, were marked along two intersecting transects (5 points on one transect and 4 points on the other) in each of the 3 plots (Fig. 2). The following data were recorded on all trees within a radius of 7.6 m from each sample point (309 trees for the whole study): height and diameter at breast height (DBH) of the tree, status of the tree (dominant, subdominant, dominated), number of swellings and brooms per tree, and height of each swelling and broom. Tree vigour was estimated according to the defoliation degree using the following semiquantitative scale: 0 = healthy tree (0–10% defoliation); 1 = tree with few symptoms (11–25% defoliation); 2 = tree with moderate symptoms (26–60%); 3 = dying tree (61–90%); and 4 = dead tree (91–100%) [23]. The presence of swellings, brooms and *Viscum album* L. on *A. alba* trees was recorded by carefully examining the canopy using binoculars. The frequency (%) of affected trees (incidence) and the average number of swellings and brooms per symptomatic tree (intensity) were calculated. The data were arcsine transformed to follow normality and analysed using multifactorial ANOVA, considering plot and status of the tree as factors. Tukey's multiple-range test was applied to compare mean values.

In plot 3, three dominant trees with pronounced spherical swellings on the trunk were felled. Their age and height ranged 77–85 years and 20.0–22.9 m, respectively. Their trunks were transversally sawed at the swelling level, and 60 cm upward and downward the swelling level. Transversal disks, were transported to the laboratory, polished carefully, examined with the help of a stereo binocular (Leica MZ 12.5, Germany) and cross-dated. Mean diameters (one measurement each 120º, bark excluded) and percentages of transversal rot area were also obtained for each disk.

2.3. Dendrochronological methods

The radial growth of trees was estimated taking increment cores from the same number of asymptomatic and symptomatic trees in each plot (Tab. II). Trees were selected based on their similar size (DBH, height) and age. Dendrochronological sampling was carried out using a Pressler increment borer, and following standard methodology [14]. Three cores per tree were taken, one near the ground and the two others at breast height (1.3 m) in opposite directions and perpendicular to the maximum slope in order to avoid the reaction wood. The basal core was used to estimate tree age, whereas the other two cores were used to quantify radial-growth changes. The cores were dried and polished using sand-paper of progressively finer grain. Then, they were cross-dated using characteristic tree-rings, mainly narrow (e.g., 1965, 1986) and light rings (e.g. 1963, 1972). In basal cores without pith, the number of missing rings was estimated using geometric methods based on a regression between the distance from the pith and the number of tree rings for cores with pith ($r^2 = 0.96$, $P < 0.05$). Tree-ring width was measured to the nearest 0.01 mm in the two cores taken at 1.3 m using a semiautomatic TSAP measurement system (Time Series Analysis and Presentation, Frank Rinn, Heidelberg, Germany). Tree-ring cross dating was checked using COFECHA software [19]. The individual series showed a decreasing trend relative to size and age, and they were averaged according to asymptomatic and symptomatic trees. No standardization was performed to compare the radial growth of asymptomatic vs. symptomatic trees since their mean ages did not differ significantly (Tab. II), and both groups showed similar age-related trends [31].

2.4. Response of radial growth to monthly climate

To minimize the influence of size and age and to underscore the climatic influence on radial growth, the raw data of tree-ring widths were standardised and detrended using a two-step process. First, a negative exponential function was fitted. Second, a cubic smoothing spline with a 50% frequency response cut-off of 50 years was used to retain the high-frequency variability of radial growth, which may be related to *M. caryophyllacearum* damage. Autoregressive modelling was then performed on each detrended ring-width series. Finally, the detrended series were averaged to obtain residual chronologies using the ARSTAN program [13]. The statistics describing the chronologies of asymptomatic and symptomatic trees were based on the standard chronologies.

The role of climate (mean, minimum and maximum temperature, and precipitation) on *A. alba* growth was assessed through correlation analyses between monthly climatic data and tree-ring indices for the period 1960–2002 [17]. Since the radial-growth of *A. alba* is usually

Table III. Incidence (percentage of affected trees) and intensity (mean number of swellings and brooms per symptomatic tree) caused by *Melampsorella caryophyllacearum* on *Abies alba* trees in three sampled plots located in Irati forest (Navarra, Spain). Values within parenthesis correspond to the range.

		Plot 1	Plot 2	Plot 3	Mean ± SD
	Trees examined	117	95	97	103 ± 12
Incidence (%)	Swellings	39.3	45.3	43.3	42.6 ± 3.1
	Brooms	5.1	14.7	9.3	9.7 ± 4.8
Intensity	Swellings per tree	1.6 (1–5)	2.1 (0–5)	1.5 (0–4)	1.7 ± 0.3
	Brooms per tree	0.1 (0–1)	0.3 (0–2)	0.2 (0–1)	0.2 ± 0.1

Table IV. Mean incidence, intensity, position, and height of swellings and brooms (± SD) caused by *Melampsorella caryophyllacearum* on *Abies alba* trees located in Irati forest (Navarra, Spain) according to their competitive status (subdominant, codominant, and dominant). Values within parenthesis correspond to the range.

		Subdominant	Codominant	Dominant
	Trees examined	61	92	156
	Average height	17.5 ± 4.0	20.7 ± 2.6	24.6 ± 3.0
Incidence (%)	Trees with swellings	16.8 ± 14.6	40.9 ± 14.2	56.4 ± 2.0
	Trees with brooms	0.0 ± 0.0	5.1 ± 8.8	16.8 ± 6.2
Intensity	Swellings per tree	1.0 (1–1)	1.5 (0–5)	1.5 (0–5)
	Brooms per tree	0.0 (0–0)	0.1 (0–1)	0.3 (0–2)
Position (%)	Swellings on trunk	17	68	72
	Swellings on branches	83	32	28
	Brooms on trunk	–	100	79
	Brooms on branches	–	0	21
Height (m)	Swellings on trunk	6.0 (1–10)	7.6 (3–14)	7.5 (0.5–25)
	Swellings on branches	9.2 (5–7)	10.6 (2–15)	12.6 (4–21)
	Brooms on trunk	–	9.0 (7–11)	15.8 (7–22)
	Brooms on branches	–	–	12.5 (10–16)

related to climate of the year previous to tree-ring formation [5, 30], the correlation window included from September of the year prior to growth (*n*-1) up to September of the growth year (*n*). The following climatic data from the Yesa station were used: total monthly precipitation (*P*), mean maximum and minimum monthly temperature (T_{max} and T_{min}), and mean monthly temperature (*T*). Three statistical significance thresholds were used: $\alpha = 0.10, 0.05$, and 0.01 (coded 1, 2 and 3).

3. RESULTS

The incidence and intensity of *M. caryophyllacearum* varied among the three plots examined. Plot 2 was the most severely affected, with 45.3% of its trees with swellings and 14.7% of its trees with brooms (Tab. III). The maximum average number of swellings and brooms per symptomatic tree were also observed in plot 2, being 2.1 and 0.3, respectively. Trees with swellings in a position below 60 cm and, thus potentially infected in the first years after planting, showed an average height (24.9 m) similar to asymptomatic trees (22.3 m). Plot 2 was the unique in which trees with *M. caryophyllacearum* symptoms were significantly ($P = 0.001$) taller than asymptomatic trees (mean ± SD were 25.6 ± 2.0 and 21.0 ± 1.9 m, respectively). The mean DBH of symptomatic trees in plots 1, 2 and 3 were significantly higher than the mean DBH of asymptomatic trees ($P < 0.0001$). Although no mortality appeared to be directly associated with the disease, the percentages of trees broken by wind at their swelling height in plots 1, 2, and 3 were 3.0, 5.7, and 1.9, respectively.

The incidence of the disease increased with tree dominance (Tab. IV). The mean percentages of trees with swellings according to the tree competitive status differed significantly ($P \leq 0.05$) between subdominant (16.8 ± 14.6), codominant (40.9 ± 14.2), and dominant trees (56.4 ± 2.0). The mean intensity was significantly lower for subdominant trees ($P < 0.05$), and similar for dominant and codominant trees (Tab. IV). In subdominant trees, more swellings were observed on branches than on the trunk, but the contrary occurred in codominant and dominant trees (Tab. IV). No brooms were observed in subdominant trees. All brooms in codominant trees were observed on the trunk, and 79% of the brooms in dominant trees were observed on the trunk. Mean height values of swellings on trunk and on branches were 7 and 10 m, respectively, not significantly different among tree classes according to their competitive status.

Mean diameters (± SD) of disks of the felled trees were significantly ($P \leq 0.05$) higher at the swelling level (31.9 ± 1.6 cm),

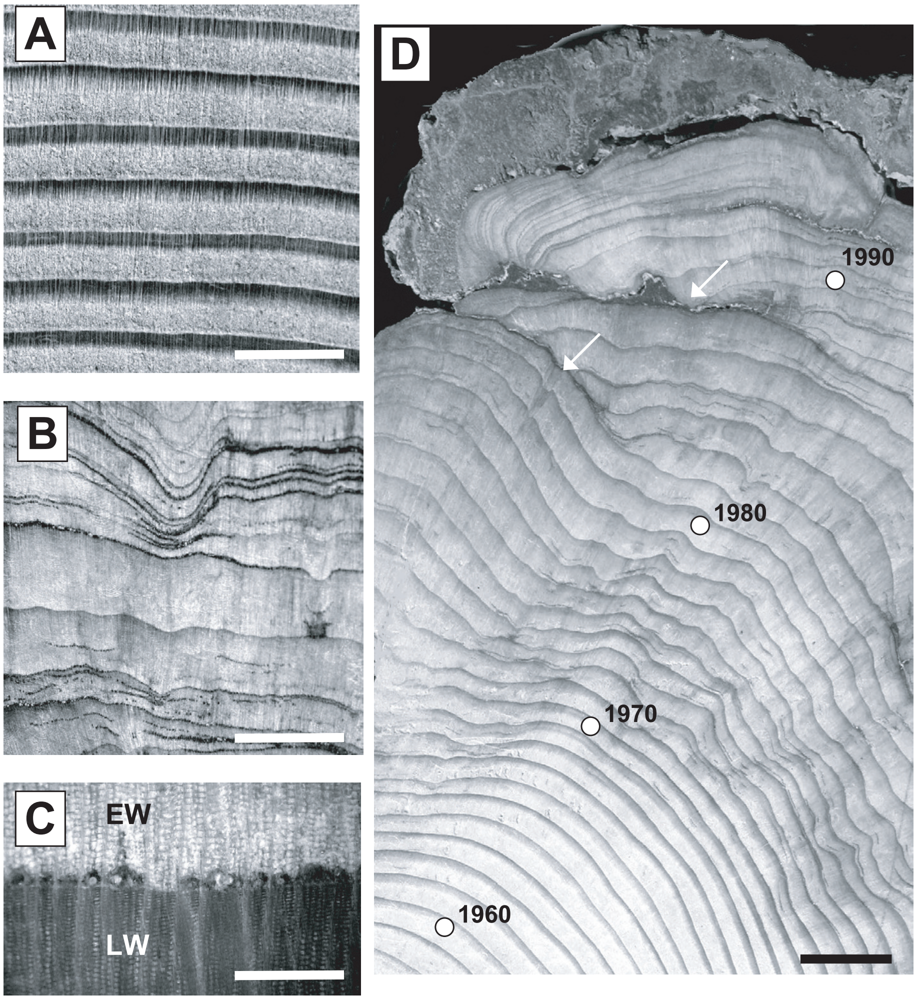

Figure 3. Transversal wood sections of an *Abies alba* tree infected by *Melampsorella caryophyllacearum*. (**A**) Concentric growth increments formed before 1960 compared with (**B**) eccentric growth increments formed from 1965 onwards. (**C**) Detail from a symptomatic tree showing axial traumatic resin ducts in the earlywood (EW) of the 1984 tree ring just after the end of the latewood (LW) of the 1983 tree-ring. (**D**) Discontinuous growth increments and wounds formed in 1982 and 1986 (arrows). Scale bars in **A**, **B**, **C** and **D** are 4, 4, 0.1 and 6 mm, respectively.

than at 60 cm above and below the swelling level (23.5 ± 1.7 and 25.2 ± 2.9 cm, respectively). Only the oldest tree showed rot xylem, with percentages of transversal rot area at the swelling level, 60 cm above, and 60 cm below of 37, 22, and 18%, respectively. In this tree, the outermost radial growth was eccentric and xylem rings contained numerous axial traumatic resin ducts (Figs. 3A, 3B and 3C). Traumatic axial resin ducts were frequently observed in the earlywood of tree-rings formed during the 1980s (e.g., 1982, 1984, 1986). Most eccentric radial growths started in the early 1960s. Additionally, wounds and incomplete tree-ring formation occurred in 1971, 1982 and 1986 (Fig. 3D).

From 1930 to 1960, the mean radial growth of asymptomatic and symptomatic trees did not differ significantly (2.40 mm, $P = 0.99$). In contrast, from 1960 to 2002, mean annual radial growths of asymptomatic and symptomatic *A. alba* trees were 1.46 and 1.28 mm, respectively, and they differed significantly ($P = 0.001$). The most remarkable growth loss (ca. 20%) occurred in the period 1983–2002 (Fig. 4). The smallest growth loss occurred in plot 3. The *A. alba* chronology based on asymptomatic trees showed a lower year-to-year variation in ring width, and a higher mean correlation between trees than the chronology based on symptomatic trees (Tab. V).

Radial growth of *A. alba* in the Irati forest was positively related to maximum April temperatures in the year of growth and to December precipitation in the year prior to growth (Tab. VI). Higher precipitation in current March and warmer previous September were negatively related to tree-ring width. Mean minimum and maximum temperatures in August-September reached the highest values of the record in the Yesa station during the 1960s (e.g., 1962, 1964, 1967) and 1980s (e.g., 1985, 1987). The radial-growth differences between asymptomatic and symptomatic trees were negatively related to minimum temperatures in late winter (February) and early spring (April) during the year of tree-ring formation, and also positively related to previous December precipitation.

4. DISCUSSION

The pathogen *M. caryophyllacearum* caused a mean 20% reduction of radial growth in symptomatic *A. alba* trees during the period 1980–2002. This finding highlights the importance of this fungal damage for the appropriate management of silver-fir forests as wood supply. The radial growth loss observed is in agreement with the results reported for *A. balsamea* infected

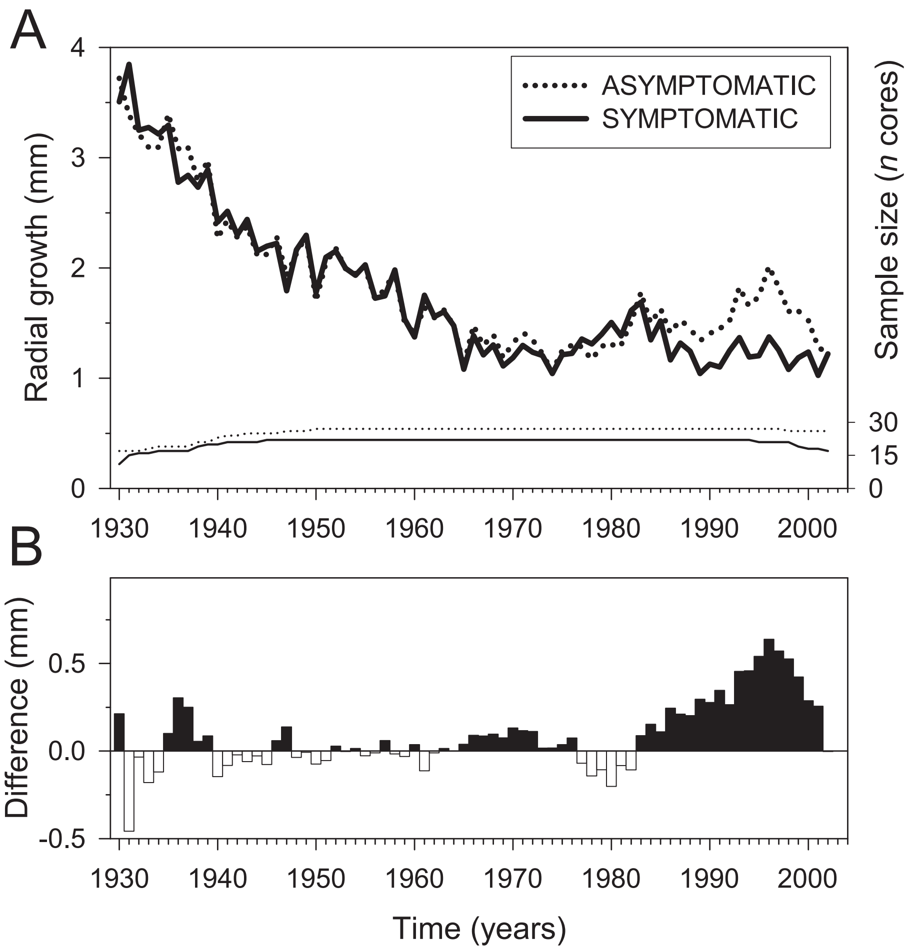

Figure 4. Mean annual radial growth of asymptomatic and *Melampsorella caryophyllacearum* symptomatic *Abies alba* trees for the period 1930–2002. (**A**) The lower horizontal lines are sample sizes for asymptomatic (dotted line) and symptomatic (continuous line) trees. (**B**) Differences between radial growth of asymptomatic and symptomatic trees. Positive and negative differences are represented with filled and empty bars, respectively.

by *M. caryophyllacearum* [34], which also caused a decrease in height growth. In Irati, the presence of swellings or brooms on *A. alba* trees did not seem to reduce tree height. If *M. caryophyllacearum* infected more frequently more vigorous trees, we ignore how this fact could obscure the growth-loss estimation using between-tree differences. On *A. sibirica*, neither diameter nor height growth loss due to *M. caryophyllacearum* were observed [37].

The presence of swellings on the trunk may play an important role in the radial growth loss observed. At the swelling level, incomplete and abnormal tree rings would alter the normal conductivity of sap flow and the translocation of photosynthates. The disorganization of xylem cells and the lack of phloem in *M. caryophyllacearum* infected twigs has been reported before [40]. Moreover, the tree will probably spend additional energy in peridermis restoration and in compartmentalising the fungus, whose mycelium is perennial [26], unlike that of most rusts. We report here for the first time the formation of tangential bands of traumatic resin ducts on *A. alba* in response to *M. caryophyllacearum*. The formation of traumatic resin ducts after injury from pathogenic fungi occurs in conifer xylem tissues to afford protection [7]. Traumatic resin ducts in *Abies* and other conifers develop in response to pathogen infection or wounding [4, 24] because resin acids display direct antifungal activity against pathogens [41].

The relationships shown in Table VI suggest that *A. alba* radial growth in Irati, near the SW distribution limit of the species, is mainly limited by a warmer September in the year prior to growth, as was also found in the Alps [30]. This might be explained by higher respiration rates or a more intense water stress in late summer driving to lower rates of photosynthate accumulation and reduced growth during the next year [3]. On the contrary, warmer April enhances radial growth probably through an earlier start of the growing season [10]. Precipitation exerted a lower influence on radial growth than temperature, which might be explained by the Atlantic climate of the study site. *A. alba* forests in the southern Pyrenees under a transitional Mediterranean climate showed a stronger rainfall signal on radial growth [9]. The negative effect of March precipitation was also observed in these southern stands, and it may be related to a delay in the start of cambial activity.

The climatic effects on radial-growth loss are probably related to the conditions of optimal development of the fungus, and the limitation of the host to react or to compartmentalise the disease. Both a high previous December precipitation and a low minimum temperature during the current late winter and early spring enhanced radial-growth loss. High December rainfall would provide the fungus with optimal moist conditions for development, thus causing radial-growth loss. The dependence of *M. caryophyllacearum* on humid conditions has been

Table V. Descriptive statistics of the *A. alba* detrended chronologies for asymptomatic and symptomatic trees. All statistics refer to the residual chronologies excepting the order of the autoregressive model width and the mean sensitivity, which are based on the raw data and the standard chronologies, respectively.

	Asymptomatic	Symptomatic
Chronology time span	1912–2003	1893–2003
No. of trees (radii)	15 (29)	13 (23)
Mean sensitivity[1]	0.12	0.16
VA (%)[2]	16.30	4.40
AR model[3]	1	1
Common interval time span[4]	1944–2003	1944–2003
No. of trees (radii)	15 (25)	13 (20)
Mean ring width ± SD (mm)	1.58 ± 0.69	1.48 ± 0.73
VFE (%)[5]	39.20	35.71
Between-tree correlation	0.35	0.31
SNR[6]	7.91	5.80
EPS[7]	0.89	0.85

[1] Mean sensitivity is a measure of the year-to-year change in ring width.
[2] VA, variance resulting from autocorrelation.
[3] AR, order of the autoregressive model.
[4] The interval containing the maximum number of radial index series.
[5] VFE, variance of the first eigenvector.
[6] SNR, signal-to-noise ratio is the measurement of the degree to which the chronology signal is expressed when tree-ring series are averaged.
[7] EPS, expressed population signal represents the degree to which a finite-sample chronology portrays the hypothetical infinite-sample chronology.

previously reported [25, 28], and further information on this subject is available [36]. This dependence is consistent with the lower radial-growth loss observed in plot 3, the only plot oriented to the south. More research is needed to clarify these relationships, but infected trees seem to be highly sensible to late frosts, as shown in the wounds formed in 1971 and 1986 at the swelling level.

In previous studies on *A. balsamea*, the incidence of *M. caryophyllacearum* varied with tree size, being up to 62% on stands with trees with DBH greater than 15 cm [34]. On *A. sibirica*, *M. caryophyllacearum* incidence was up to 30% [28]. Concerning intensity, the maximum mean number of brooms per *A. balsamea* tree was 4.3 within a 1 to 8 range [34]. According to our results, dominant *A. alba* trees are more symptomatic than suppressed trees. Similar observations have been made on *Pseudotsuga menziesii* and on *Tsuga mertensiana* affected by the root rot pathogen *Phellinus weirii* [18]. It seems that taller trees are more readily exposed to fungal propagules, a finding that is consistent with the distribution of *Nectria ditissima* cankers on beech trunks [21]. Swellings in the lower stem may have been initiated quite early, and swellings in upper parts must have developed later, when the trees had reached the respective height.

Considering radial growth loss, rot wood, and wind break at the swelling height, we estimate that *M. caryophyllacearum* infecting approximately 30% of mature *A. alba* trees could reduce timber volumes by as much as 10%, indicating that this disease has a significant impact on timber productivity of Irati *A. alba* stands. To prevent looses by *M. caryophyllacearum*, the disease may be removed by pruning or by felling the affected trees, including the destruction of infected branches [1, 28]. Our data indicate that the study site is overstocked as a result of a sub-exploitation, with basal area values notably over those (25–40 m^2 ha^{-1}) proposed for fir forests in equilibrium [38]. This situation is common among *A. alba* forests in Spain [15, 29].

Table VI. Significant simple correlations between indexed values of *Abies alba* radial growth and monthly climatic variables (T_{min}, minimum temperature; T_{max}, maximum temperature; T, mean temperature; and P, total precipitation) for the years of tree-ring formation (*n*) and the previous year (*n*-1). Climatic data are from Yesa station, period 1960–2002. Significance levels are presented as 1, 2 and 3 corresponding to $\alpha = 0.1$, 0.05 and 0.01, respectively. The signs + and - indicate positive and negative relationships, respectively.

Year	Month	Radial growth of asymptomatic trees				Radial-growth loss[1]			
		T_{min}	T_{max}	T	P	T_{min}	T_{max}	T	P
n-1	S	–1	–1	–2	+1	·	·	·	·
	O	·	·	·	·	·	·	·	·
	N	·	·	·	·	·	·	·	·
	D	·	·	·	+2	·	·	·	+2
n	J	·	·	·	·	·	·	·	·
	F	·	·	·	·	–2	·	–1	·
	M	–1	·	·	–2	–1	·	·	·
	A	·	+2	·	·	–2	·	·	·
	M	·	·	·	·	·	·	·	·
	J	·	·	·	·	·	·	·	·
	J	·	·	·	·	·	·	·	·
	A	·	·	·	·	·	·	·	·
	S	·	·	·	·	·	·	·	·

[1] Differences between radial growth of asymptomatic and symptomatic trees.

Thus, it may be convenient the opening of small gaps by the removal of symptomatic trees, as those trees will be damaged by the disease and they may transmit their susceptibility to descendants. Since *A. alba* is a shade-tolerant species, single tree-selection cutting will also benefit natural regeneration.

Acknowledgments: We thank Sergio Ahumada and Mabel Martín for technical help. Gobierno de Navarra, and Junta General del Valle de Salazar are acknowledged to allow the study to be initiated. J.J. Camarero thanks the support of an INIA-Gob. Aragón postdoctoral contract.

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