

Growth Loss of Lebanon Cedar (*Cedrus libani*) Stands as Related to Periodic Outbreaks of the Cedar Shoot Moth (*Dichelia cedricola*)

Serdar Carus¹ and Mustafa Avcı²

An outbreak of *Dichelia cedricola* (Diakonoff) (Lep.: Tortricidae), the cedar shoot moth (CSM), began in spring 1998 and lasted 3 years. This was the first monitored outbreak of the CSM in Isparta, Turkey. Tree crowns recovered to near normal condition by the middle of each growing season (in early June) during the outbreak. Tree volume and volume element increments were examined throughout the outbreak cycle from 1954 to 2001. In the past, CSM activity in stands of Lebanon cedar (*Cedrus libani* A. Rich.) was assessed through radial increment analyses. Cedar tree ring chronologies were analyzed for evidence of the CSM. Tree-ring chronologies from nonhost cedar (nondefoliated sample trees) were used to estimate potential growth in the host cedar (defoliated sample trees) during current and past outbreaks; all trees selected were the same subspecies and varieties. Regional outbreaks of the CSM were identified by synchronous and sustained growth periods of the trees. In 2001, increment cores were collected from 17 host and 16 nonhost dominant or codominant trees and annual radial growth indices from 1954–2001 were calculated for each of two host and two nonhost sample plots. Growth functions were defined as the cumulative sum of radial, height, and volume increment, and were graphically compared between CSM host cedar and nonhost cedar trees. Tree ring evidence suggests that a large-scale outbreak occurred in 1955 (from 1955 to 1966) and a small outbreak occurred in 1985 (1985–1990) and in 1998 (1998–continued) in the study area. The average diameter growth reductions around 1955, 1985 and 1998 were 40%, 46% and 7% of potential, respectively. It was concluded that a narrow latewood band is significant indicator of defoliation by the CSM and the outbreaks appear to be associated with dry winter and spring weather prior to the autumn and winter in which wood feeding occurred.

KEY WORDS: Lebanon cedar; *Dichelia cedricola*; growth loss; tree ring analysis; dendrochronology.

INTRODUCTION

The widest natural distribution of cedar (*Cedrus libani* A. Rich.), one of the most important forest trees of Turkey, is in the Taurus Mountains of Turkey, with a total area of approximately 336,000 ha. Cedar is significant from the historical, cultural, aesthetic, scientific and economic aspects (2,3,9). It grows in Mediterranean mountain climates,

Received Oct. 12, 2003; revised ms. received May 2, 2004; accepted July 28, 2004; <http://www.phytoparasitica.org> posting Nov. 24, 2004.

¹Forest Management Department, Faculty of Forestry, Süleyman Demirel University, Isparta, Turkey. *Corresponding author [Fax: +90-246-2371810; e-mail: scarus@orman.sdu.edu.tr].

²Forest Entomology and Protection Department, Faculty of Forestry, Süleyman Demirel University, Isparta, Turkey [e-mail: avci@orman.sdu.edu.tr].

generally between 800 and 2100 m elevation (9), and has distinct ring boundaries. Its age is known to reach up to 500 years.

Insect outbreaks are one of the major disturbances affecting the forests. Defoliation of host species by insects has a significant influence on forest stand dynamics by reducing tree growth, increasing tree mortality, and altering species composition (5). Insect damage causes a 3% reduction in annual wood growth (2). The amount of insect damage was determined to average 221,909 m³ during the years 1997 to 2000 in Turkish forests.

Outbreaks of *Dichelia cedricola* (Diakonoff) (Lep.: Tortricidae), the cedar shoot moth (CSM), in cedar forests were first detected in this part of the western Mediterranean region of Turkey in 1998 (3). The insect has a one-year life cycle. Eggs hatch in August and new larvae feed until cold weather begins in late autumn. The CSM overwinters as young larvae, which in late spring resume feeding on the needles at the tips of branches, reaching up to 1.2 cm in length by summer. The heaviest defoliation occurs from March to June. The larvae spin cottonlike webs when they are active, and the damaged parts of the tree with dead agglutinated needles remain long after the feeding period (3).

A ring produced in a particular year is a function of several interrelated biological, physical, stand, and climatic factors. Because our main objective was to understand or evaluate the effect of defoliation on growth, factors that affected the width of an annual ring produced in a given year and that were not related to defoliation, were removed from the ring width series. Dendroecological methods (10) allow one to account for abiotic and biotic conditions that affect annual radial growth in trees, such as climate and tree age, and then isolate the contribution of a single factor, such as insect defoliation, to radial growth. Several recent North American studies have used dendroecological analysis to investigate the effects of defoliating insects on radial growth (6,14,16,17,20-22).

The cedar stand in the study area is divided into two equal sections by the Karuçan stream. The current severe CSM outbreak that began in the spring of 1998 was absent on the eastern side of the Karuçan stream. According to forestry officials, periodic outbreaks have been permanently present in the western part of the region since 1985. Furthermore, personal communication with old residents in this region indicated that periodic outbreaks of CSM occurred repeatedly before 1985 and the redwood ant (*Formica rufa* L.) (Hym.:Formicidae) has existed for long periods. This result may be related to the occurrence of the redwood ant in the eastern part of the study area (nonhost cedar sample plots 2 and 4). CSM density was surprisingly changed by the redwood ant. Two and three nests of redwood ants were found in the nonhost cedar plots no. 2 and 4, respectively. *F. rufa* feeds especially on CSM larvae, eggs and pupae (3). An average sized colony of *Formica polyctena* has been found to consume about 6.1 million insects in a season (18).

In order to analyze the impact of CSM outbreaks, we determined that sample trees in the eastern section were not host trees in the years 1985 and 1998 and that the western section of Karuçan stream contained host trees. Among trees selected as host and nonhost cedar in the sample plots, it was determined that they were not a different subspecies or variety. Sample plots 1 and 3 (host) and 2 and 4 (nonhost) consisted of pole and small-saw log-sized trees when this current outbreak was detected. The four plots, symmetrically located to the Karuçan stream in ~6-ha stands, were selected as baseline in order to ensure similar stand, edaphic, climatic and physiographic characteristics.

Our assumption is that host and nonhost cedar trees within an uncut stand have similar radial growth patterns (growth curves) in the absence of CSM defoliation. The radial

growth pattern of cedar trees known to have been previously defoliated by the CSM are different from undefoliated cedars that are in the same region. However, past CSM activity would cause different radial growth patterns, and therefore the period of activity can be detected and measured. This paper describes a method to estimate the occurrence, intensity and potential hazard of past CSM outbreaks in this region dominated by cedar forest (~70 years of age) of the western Mediterranean region of Turkey. Our first objective was to analyze the impact of CSM on the radial, height and stem volume growth of the host cedar that survived the last outbreak. Our second objective was to detect periodicity of the CSM outbreaks.

MATERIALS AND METHODS

Study area The study area was located in the western Mediterranean region of Turkey, which is approximately 40 km from Isparta. It is at 38°05'N, 30°42'E, average slope 23°, predominantly north-facing aspect, ~ 1575 m altitude, and ~ 1223 ha in size. The study area is found on calcareous formations of Eocene age. The soil varies from shallow to medium to medium-deep, and is generally stony. However, many cracks between limestone blocks contain fine soil and create a physiologically deep soil (9).

Climate data Mean monthly and annual temperature and rainfall data for the period 1929–2001 were obtained from the Isparta Meteorological Station. In the study area, the 685 mm (mean annual) precipitation falls mainly from October through May. There was great deviation in the distribution and amount of precipitation during the investigation period. This region is in the transitional zone between the Mediterranean climate and the continental climate with colder winters and hotter summers. Mean annual temperature is 9.1°C. In accordance with De Martonne's dryness coefficient ($I=25.87$), the study area is defined as humid.

Study measurements and analysis The study stands are the result of natural regeneration in 1930. In 1998, the outbreak began in the cedar stand, and partial defoliation occurred in 2001. Four sample plots located in natural, undisturbed, middle-aged (of even age) stands of cedar were selected for study during the autumn months of 2001. Increment cores were collected from trees at four locations (plots) in the study area. Two of these plots (nos. 1 and 3) had been heavily defoliated since 1955 and two (nos. 2 and 4) had no previous record of CSM activity (3). Habitat characteristics of these four baseline sampling plots were assumed to be similar. The chosen approach was based on the assumption that, if nonhost and host trees responded in a similar manner to climatic variations, then the differences between standardized ring chronologies of nonhost and host trees would primarily reflect nonclimatic environmental variations, such as the effects of the CSM (4,5,15,22).

All trees within the plots were identified, height and diameter were measured, and defoliations were evaluated. The age of 25–30 sample trees also was recorded to allow an estimation of site quality (productivity). Tree diameter and information on the presence or absence of CSM attacks, crown form, defects, and diseases were recorded. Trees in the sample plot provided the growth information and were the basis for basal area and diameter growth statements for the 0.1-ha plot. Tree volume was calculated using a double-entry volume table of cedar (9).

Collection and measurement of increment cores In the autumn of 2001, increment cores were taken from 17 dominant and codominant host cedars and from 16 dominant and codominant nonhost cedar trees. Increment cores were extracted at breast height from opposite sides of each sample tree parallel to the topographic contour. Cores were inserted into labeled plastic straws that were thermally sealed to prevent moisture loss and kept frozen until they were measured (Table 1). Using a stereomicroscope, annual increment was cross-dated (10) and measured in mm (0.01 mm precision) on each core for the period 1944–2001. The age of the tree (at breast height) was also recorded.

TABLE 1. Site description and characteristics of increment cores

Plot no. and type	Altitude (m)	Slope (°)	Increment cores (no.)	Mean (range) age of rings (years)	Standard deviation (age)
1, Host	1550	28	9	48 (33-63)	10.2
2, Nonhost	1610	18	8	42 (30-59)	11.3
3, Host	1570	29	8	49 (32-59)	10.3
4, Nonhost	1570	20	8	39 (26-51)	9.3

All sites are north-facing.

TABLE 2. Results obtained with the ARSTAN and COFECHA programs

Cedar Groups	Nonhost	Host
Chronology type	Standard	Standard
Mean	1.0000	1.0000
Median	0.9979	1.0250
Mean sensitivity	0.1025	0.1194
Standard deviation	0.1964	0.2098
Skewness	-0.7060	-1.8761
Kurtosis	0.0362	3.1510
Autocorrelation order 1	0.8183***	0.8093***
Partial autocorr. order 2	0.1202	-0.2577
Partial autocorr. order 3	-0.2235	-0.4149
Series intercorrelation	0.6373***	0.6267***
Average mean sensitivity	0.1082	0.1354

*** Significance at 99% confidence level.

Two dominant cedar host trees in plots 1 (T1) and 3 (T3) and one nonhost cedar in plot 2 (T2) were cut. Stem disks were taken 0 m, 0.3 m, 1.3 m and at every meter starting 1 m from the top of the trees. After sanding, ring widths of the stem disks were measured with a precision of 0.01 mm along four radii (cardinal points). The total stem height of the trees was divided into three equal sections: lower, middle and upper. The lower and upper sections of the tree stem are presented, to demonstrate the outbreak better (12,13,19).

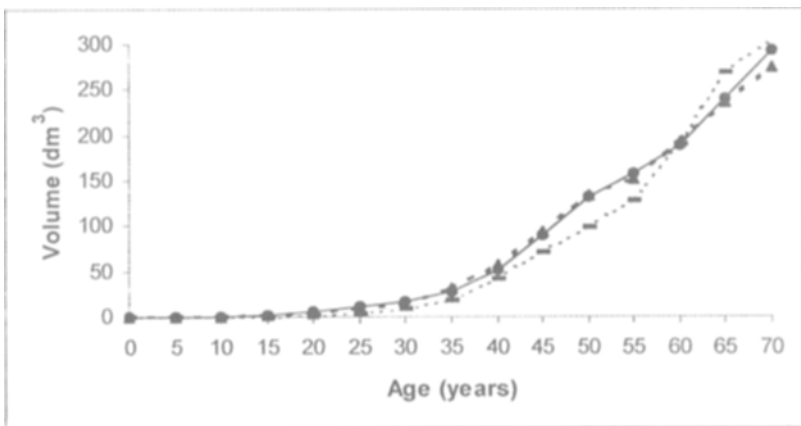
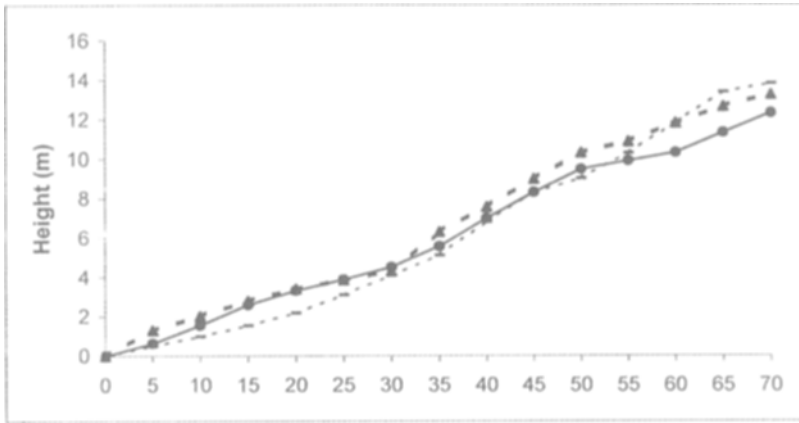
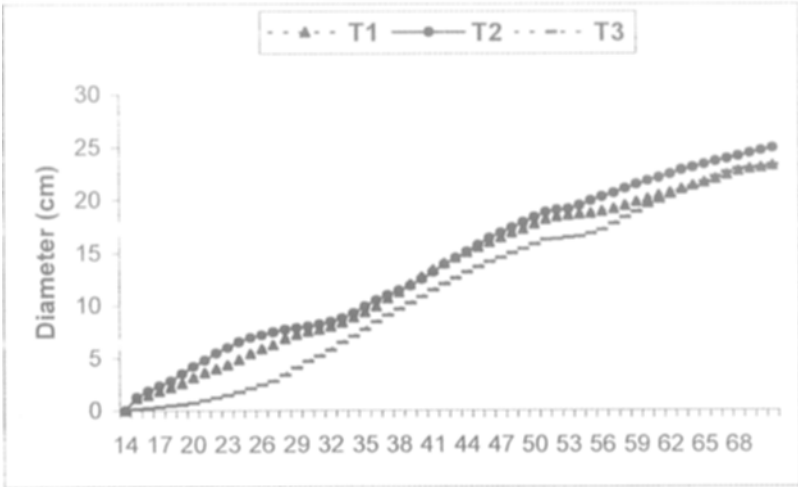


Fig. 1. Developmental trend of diameter, height and volume associated with the age of the host (plots 1 and 3) and nonhost (plot 2) cedar sample trees. T1, plot 1; T2, plot 2; T3, plot 3.

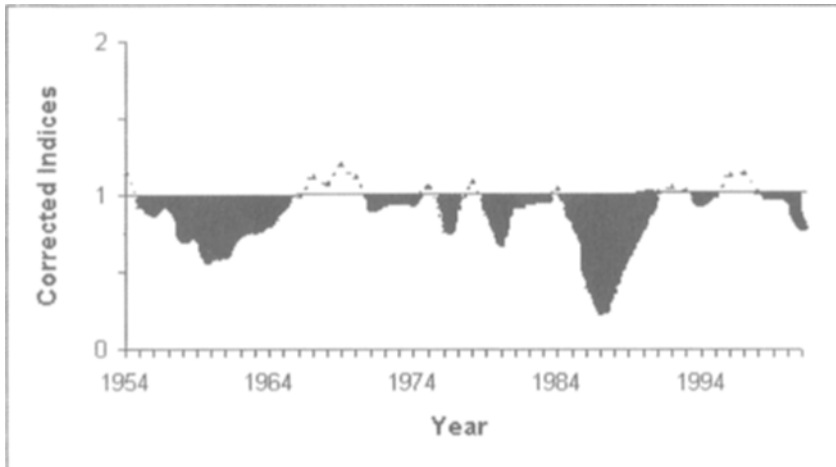
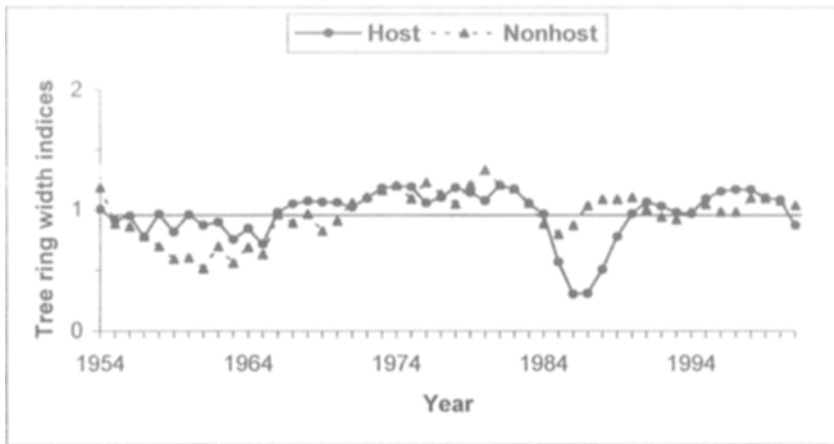


Fig. 2. Comparison of tree ring width indices and corrected indices with the host and nonhost cedar sample plot groups.

Dendrochronological analysis Ring widths were measured at the Faculty of Forestry of Süleyman Demirel University soon after the cores were extracted. All cores consisted of approximately 50 annual growth rings, the most reliable chronologies existing for the years from 1944 to 2001. We graphically cross-dated each series and eliminated series that may have had missing rings. The program COFECHA was used to verify the cross-dating (11) and corrections were made when necessary. The raw tree ring series were standardized using ARSTAN to correct for age-related growth trend and to produce the final index chronologies (8). We chose to use a negative exponential or a straight line with a 50% cutoff wavelength to standardize the series. This calculation transforms ring width into dimensionless index values. The standard chronology was used as a response variable in the analysis of growth in relation to defoliation. A standard chronology is most commonly used

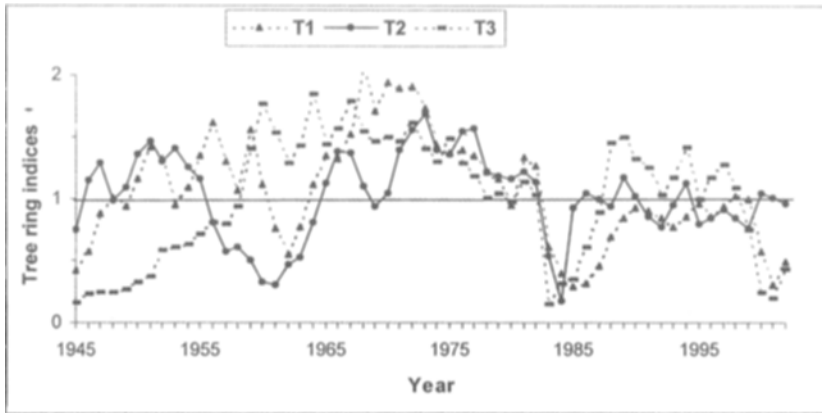


Fig. 3. Average standardized radial increment for the host (plots 1 and 3) and nonhost (plot 2) cedar sample trees. T1, plot 1; T2, plot 2; T3, plot 3.

in tree ring research (6,14,16,17,21). This kind of transformation is called standardization, and its purpose is to remove long-term trends or low-frequency variance from the tree ring series. Standardization eliminated the effect of individual tree age (position within the stem) and resulted in a series that represented the relative amount of growth for each year. Two cedar chronology groups were created: the host group and the nonhost group. Standardized ring widths were used for analysis of defoliation effects; averages were used in each sample plot. The results of the programs ARSTAN and COFECHA are presented in Table 2. These results indicated that the standard chronologies were found to be statistically significant in the nonhost and host cedar groups, and therefore it can be concluded that the results are reliable for comparison between plots.

The percent reduction in the tree-ring index associated with CSM outbreaks was calculated for host cedar trees. CSM outbreaks cause growth loss and sometimes mortality to cedar trees (3). Spring 1998 was the beginning of a CSM outbreak. The extreme drought that year weakened and placed the cedar trees under stress. In 1998, De Martonne's dryness coefficient and total monthly precipitation were 15.38 (semi-humid) and 312 mm, respectively.

RESULTS

Stand growth Sample plot averages indicated that defoliation negatively influenced growth of cedar (Table 3). The quadratic mean diameter for host and nonhost sample plots was 195.72 mm and 190.96 mm, respectively, in spring 1998. Mean diameter growth of host sample plots was 1.05 cm for 3 years, whereas mean diameters in the nonhost sample plots grew 1.08 cm (Table 3). Mean diameter increased in host sample plots, even those with CSM-caused tree mortality. Average growth values of host percentage for basal area, stem volume and top height were -8%, -15% and -10%, respectively. Average growth increment values for basal area and volume were -31% and -26%, respectively. Average top heights (H_{dom}) for host and nonhost sample plot groups were 13.28 m and 14.82 m, respectively. Basal areas for host and nonhost sample plot groups were $30.95 \text{ m}^2 \text{ ha}^{-1}$ and $33.50 \text{ m}^2 \text{ ha}^{-1}$, respectively. Stand volumes for host and nonhost sample plot groups were $183.30 \text{ m}^3 \text{ ha}^{-1}$ and $215.49 \text{ m}^3 \text{ ha}^{-1}$, respectively (Table 3).

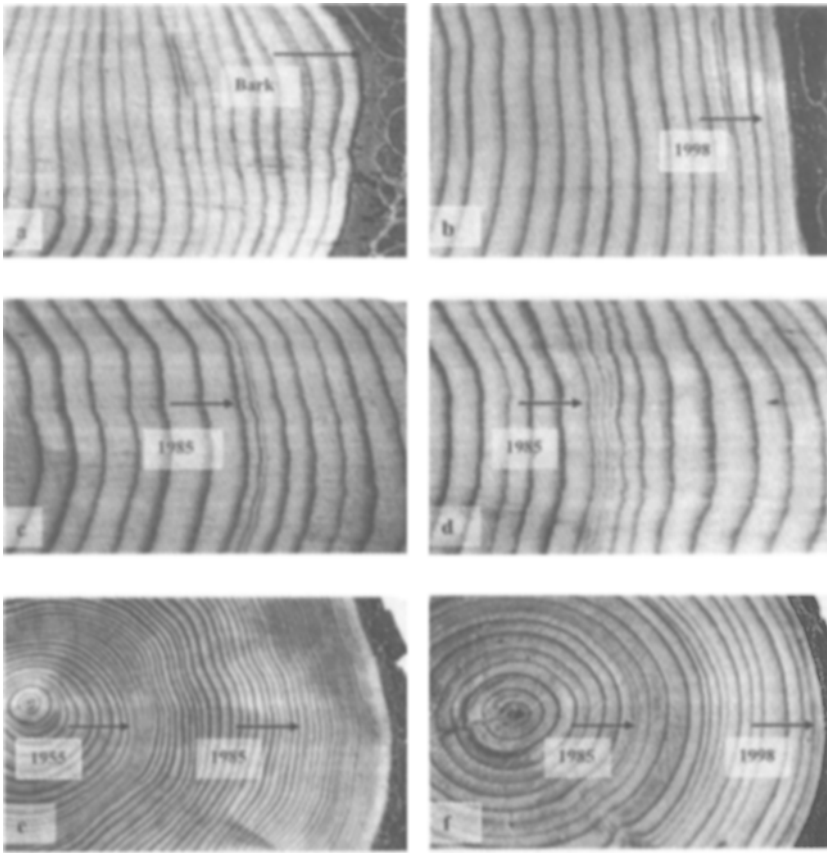


Fig. 4. Photographs of thin latewood during the initial year of defoliation for the most recent outbreak (1998, a and b); thin latewood (1985) and subsequent reduced growth (arrows) in the 1985 outbreak (c and d); and in the first severe outbreak (1955; e, nonhost since 1966, and f). One year after defoliation, the reaction at crown level (disc at 9.3 m height of host trees in plot 3) was more intensive than at the stem base. Left-hand photos, nonhost cedar; right-hand photos, host cedar.

Individual tree growth *Radial growth:* Cedar trees were relatively young, with fewer than 60 tree rings at coring height. There was an abrupt growth reduction starting at 25 (1955), 55 (1985) and 68 (1998) years of age, lasting between 12, 6 and 4 years, respectively (Fig. 1). The average annual ring width of cedar was less during the outbreak than before and after the outbreak, indicating a temporary decline in growth due to intensive CSM feeding (Table 4).

Diameter growth of host cedar was compared with that of nonhost cedar trees in the outbreak. Ratios of annual diameter increments for nonhost trees to host trees increased sharply after the outbreak. For example, for the 1998 outbreak, annual diameter increments of sample trees were reduced by 3% in the first growing season after defoliation (1999), 4% in the second year after defoliation (2000), and 21% after the second defoliation (2001).

Height and volume growth: After severe defoliation by the CSM, including bud destruction, host cedar trees react with prolific epicormic shoot production. Periods of moderate to severe CSM outbreaks may be detected (Fig. 1). The changed width growth

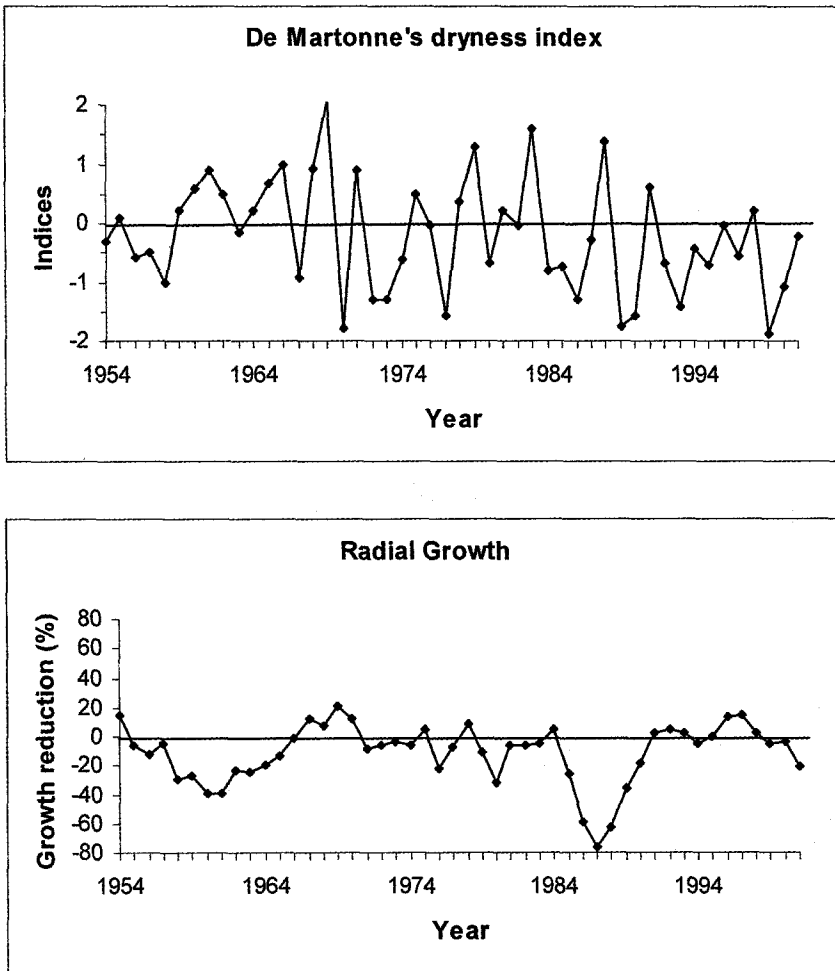


Fig. 5. Comparison of De Martonne's dryness index and radial growth reduction (%) for the host and nonhost cedar sample plot groups.

of the nonhost trees during periods of increment decline in hosts may be used as another indicator of a CSM outbreak. Defoliation of hosts in plots 1 and 3 would, however, result in increased nutrients, thus enhancing growth of hosts and explaining the positive relation between plot-level defoliation more than radial growth nonhost in plots 2 and 4 over a few years of outbreak (Table 3 and Fig. 1). Growth reduction in 1955, 1985 and 1998 for height was -23%, -76% and -49%, respectively, and that for volume was -12%, -31% and -22%, respectively (Fig. 1).

In each plot the average diameter and height increment of a host cedar tree was +2% (with CSM-caused tree mortality due to a thinning effect) and -8%, respectively, with a decrease in volume increment of ~3% (Table 3).

Growth losses and indexing CSM activity through radial increment analysis *Comparing host and nonhost chronologies:* The study area for development of diameter, height and volume growth and its growth curves indicated that growth of sample trees had been reduced in the past, presumably by the CSM. Defoliation of cedar generally resulted in a

TABLE 3. Stand characteristics of the host and nonhost sample plots

Sample plot no.	Individual tree (mean basal area)			Stand					
	d (mm)	h (m)	v (m ³)	G (Ig) (m ² ha ⁻¹)	V (Iv) (m ³ ha ⁻¹)	N (stem ha ⁻¹)	H _{dom} (m)	T (yrs)	SQ ^z (m)
1	186.78	9.76	0.16	27.67 (0.643) ^y	160.90 (4.787)	1010	13.00	59	16.88
2	194.48	10.81	0.18	32.67 (0.822)	197.43 (6.600)	1100	13.89	52	19.43
3	224.77	11.52	0.24	34.22 (0.964)	205.70 (7.176)	850	13.56	53	18.76
4	209.12	12.39	0.23	34.33 (1.569)	233.54 (9.463)	1000	15.75	55	21.29
<i>Means of host and nonhost sample plot groups</i>									
Host (1 and 3)	205.77	10.64	0.20	30.95 (0.822)	183.30 (5.982)	930	13.28	56	17.82
Nonhost (2 and 4)	201.80	11.60	0.21	33.50 (1.196)	215.49 (8.032)	1050	14.82	54	20.36
Host percentage ^x	+2	-8	-3	-8 (-31)	-15 (-26)	-11	-10	-12	

d, diameter; h, height; v, volume; G, basal area ha⁻¹; V, volume ha⁻¹; N, number of trees ha⁻¹; H_{dom}, top height of stand; T, age of stand; SQ= site quality.

^zSite quality (top height of stand for 100-year age), Site class I: 30-34 m; II: 25-29 m; III: 20-24 m; IV: 15-19 m; and V: 10-14 m.

^yIn parentheses, periodic mean increment (from 1998 to 2001) of stand.

^xHost Percentage = $\frac{(H-NH)}{NH} * 100$, where H is host and NH is nonhost. H and NH are for individual trees and stand of the volume and volume elements: d, h, v, G, Ig, V, Iv, N, H_{dom} and SQ.

TABLE 4. Summary statistics and a one-way analysis of variance comparing standard chronologies in the host and nonhost sample plots

Groups	Sample size	Sum	Average	Variance			
Sample plot 1 (Host)	48	49.517	1.032	0.080			
Sample plot 2 (Nonhost)	48	47.108	0.981	0.033			
Sample plot 3 (Host)	48	49.062	1.022	0.065			
Sample plot 4 (Nonhost)	48	45.414	0.946	0.068			
ANOVA							
Source of Variation	Sum of squares	df	Mean squares	F	P-value	F crit	
Among groups	0.223	3	0.074	1.210	0.307	2.653	
Within groups	11.556	188	0.061				
Total	11.779	191					

decline in radial increment. This relationship is illustrated by the increment chronology for cedar in Isparta (Table 4 and Fig. 2). A decline in increment associated with CSM defoliation occurred during the period 1985–1990. In Figure 2, the hatched areas indicate where the outbreaks were most evident. Tree ring records suggested that the outbreaks recur periodically every 15–30 years on average, during which rings generally exhibited a pattern of alternating wide and narrow increments. A peak reduction in cedar growth

occurred at intervals of ~16 years, in 1961, 1987, and 2001.

Analysis of variance was used to examine the differences between standard chronologies within host and nonhost cedar sample plot groups (7). Tables 4 and 5 show the results of ANOVA, which indicate that for each sample plot and for each host–nonhost group, there were no statistically significant differences among the standard chronologies.

TABLE 5. Summary statistics and a one-way analysis of variance comparing standard chronologies in the host and nonhost cedar groups

<i>Groups</i>	<i>Sample size</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>		
Host (Sample plot 1+3)	48	49.289	1.027	0.058		
Nonhost (Sample plot 2+4)	48	46.261	0.964	0.036		
ANOVA						
<i>Source of Variation</i>	<i>Sum of squares</i>	<i>df</i>	<i>Mean squares</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Among groups	0.096	1	0.096	2.053	0.155	3.942
Within groups	4.374	94	0.047			
Total	4.470	95				

After measuring and matching individual chronologies, a master chronology of cedar was constructed for each group (Fig. 2). The nonhost cedar trees might have been damaged by CSM during past outbreaks. Based on Figure 3, we can reach the conclusion that a large-scale outbreak might have occurred in 1955 and affected the whole study area until 1966. The present nonhost groups have more likely preserved their ring-width characteristics during the period 1966–1985.

The host tree ring-width chronologies showed lower mean sensitivity than the nonhost trees. Mean sensitivity of the nonhost cedar chronology was found to be 0.103, indicating a low response to climatic factors. This finding indicates that cedar trees produced regular annual ring widths, and low mean sensitivity revealed relatively low variation in the chronology, since climatic conditions have a minimal effect on ring widths when trees have ample moisture. Low growth in the preceding year ($t-1$) was a limiting factor for tree ring widths (Table 2).

Outbreaks were evident as low growth indices in the host series that were not apparent in the nonhost series (Fig. 2). The graphical comparison of the host and nonhost chronologies should provide some evidence that CSMs have caused radial growth reduction in the host trees. Host trees, however, may also have been responding to other environmental factors, such as drought, which may have caused growth reduction. Equation 1 corrects a host tree chronology by first scaling residuals from the control site chronology to the same variance as the host-tree chronology to be corrected. These scaled residuals are called the ‘predicted residual indices’ (PRI). The PRIs are then simply subtracted from the host-tree indices to produce the ‘corrected indices’ (CI). The purpose of the CI is to remove the host-tree ring chronologies’ environmental effects common to both host and nonhost chronologies, so that more precise estimates of growth reduction can be derived from the corrected host series. The corrected series (Eqs. 1 and 2 and Fig. 2) were used to identify the timing of outbreaks, the duration of CSM-induced low growth periods, and the maximum annual and periodic radial growth losses (22). Subtracting the corrected indices during outbreaks from the potential growth value (1.0) and multiplying by 100 derived the

latter two values. Thus, the radial growth reduction values are expressed in relative terms as a percentage of expected growth.

$$PRI = \frac{SDEV(H)}{SDEV(NH)}(INDEX(NH) - MEAN(NH)); \text{ and} \quad (1)$$

$$CI = INDEX(H) - PRI \quad (2)$$

SDEV (H) and SDEV (NH) are the standard deviations for the host and nonhost series, INDEX (H) and INDEX (NH) are each index value of the host and nonhost series, respectively, and MEAN (NH) is the mean of the nonhost series (~ 1.0).

For all sample plots, the collected increment cores were successfully cross-dated and consequently were included in the tree ring analysis. Mean correlation of all cores with their master chronology was >0.5. The number of cores included in sample plot chronologies was between 8 and 9, and starting dates ranged from 1944 to 2001 (Table 1). Sample size increased steeply in 1954.

Measures of growth reduction: The corrected host-tree indices (Eq. 2) can be used in many ways to quantify CSM-induced growth reduction. Measuring the radial, height and volume of growth reduction during an outbreak was done in order to determine the maximum growth reduction for one year and to calculate the radial, height and volume periodic mean growth reduction. Each of the growth reduction measurements was converted to percent reduction from expected growth by multiplying the computed values by 100.

Trees with a high CSM population during the period 1998–2001 lost 100% of the leader needles as well as the needles of the upper whorl branches. By the middle of the growing season, the length of new shoots produced at these positions was reduced significantly. Shoots in the lower canopy were less severely damaged and new shoots at these positions showed little or no growth reduction. Leader and height growth were reduced immediately because of bud feeding by the CSM; severe defoliation took place early in the year, before or during shoot extension.

Response to drought: Our climatic data show that growth of cedar trees in the study area was most strongly correlated with below-average temperatures and above-average precipitation in the preceding year (from October to December). A tendency towards negative correlation of growth with precipitation of the current spring at some of the higher elevation sites may reflect earlier snowmelt and, hence, a longer growing season.

Trees on host and nonhost sample plots responded to a severe drought, which occurred over the period 1998–2001, with a substantial decrease in annual radial increment (Fig. 4). Not only was total annual precipitation well below average for these years, but also the total number of days in the growing season was low as well. The observed decrease in growth began in 1999 and reached a minimum in 2001. In 1986, when a similar precipitation deficit occurred, the corresponding decrease in radial increment was as great as in 1987 (Fig. 4).

The 2000 ring was half the size of a normal ring and had very thin latewood; the latewood was thinner than normal throughout the entire period of growth reduction. A gradual return to the pre-outbreak growth rate occurred during the years 1985–1990 (Fig. 4). This pattern was repeated with each outbreak.

The height increment growth pattern for cedar approximated a sigmoid curve (Fig. 1), whereas radial increment growth patterns showed sharp declines in growth in 1985 and

1990, suggesting that height increment was less sensitive than radial increment to year-to-year variations in precipitation. There was a decline in height increment the first year of the drought and then a recovery in the peak drought year of 1986. Furthermore, the relative magnitude of the decline in height increment was proportionately more than that for radial increment (-60% and -41%, respectively).

In 1986, more than 59% of the host trees had 42% reduced radial growth relative to the growth in the previous year, whereas only 8% of the nonhost trees had such growth reduction. In 1986, a larger number of both host and nonhost trees showed a growth reduction. It is possible that the adverse weather in 1986 also played a role in reducing insect activity. Extensive defoliation was observed in 1998. The ring width of cedar decreased dramatically in the year following the defoliation. In 1999, 4% of cedar trees had 6.5% reduced radial growth relative to the growth in the previous year. Radial growth in defoliated trees was minimal for 2000. However, this pattern was not observed in the nonhost trees for the same time intervals. The magnitude of the damage varied from tree to tree (Fig. 3).

Cumulative growth function (CGF): Non-significant differences were observed between CGF graphs of cedar from the CSM-free stands (Fig. 1). However, obvious negative departures of the host cedar curve relative to nonhost cedar occurred in the stands. Inflections of the host curve correspond closely to the known occurrences of CSM outbreaks in the stand, and presumably represent the growth-retarding influence of CSM at the time.

In the spring, larvae of the CSM feed on buds and foliage of cedar trees. Severe outbreaks by the CSM have been reported to kill the terminal buds of cedar trees and cause their stems to fork (3). All studies which lasted for more than one year showed that leader lengths were also reduced in the second season after defoliation, when CSMs were scarce, and that in general height increments of cedar trees were likely to be reduced for 2–3 years after an attack (Fig. 1).

Stem analysis of two host cedar (plots 1 and 3) and one nonhost cedar (plot 2) trees indicated a growth decrease beginning in the upper section of the stem, corresponding to the first year of a severe insect defoliation. Furthermore, after defoliation, the reaction at the crown level was more intense than at the stem base (Fig. 4f). Radial growth reduction occurred one year after the defoliation, suggesting that the stored photosynthates from the previous year play a key role in the cambial activity in a given year (1).

The maximum growth reduction for one year and periodic average diameter growth reductions around 1955, 1985 and 1998 were 20% and 40%, 76% and 46%, and 21% and 7% of potential growth, respectively.

In summary, the response of tree ring growth to observed defoliation suggested that CSM outbreaks caused growth reduction in 1955, 1985 and 1998, and an alternating pattern of narrow tree rings for a few years is characteristic of the CSM (Fig. 4).

DISCUSSION

Defoliation estimates were comparable between the host cedar (plots 1 and 3) and nonhost cedar (plots 2 and 4) trees and reflected CSM populations in outbreak years, with a steep decline in populations within a few years following extensive defoliation. There was a sharp decline in the growth increment of host cedar during and directly after a CSM outbreak (in 1955, 1985 and 1998 year) (Figs. 1 and 2). In contrast, growth of

nonhost cedar declined only slightly during the outbreak and increased significantly in post-outbreak years. A recovery period for ring widths to pre-outbreak levels should last 6 to 12 years.

In this study we have shown that CSM defoliation negatively influences radial, height and volume increment in hosts, irrespective of the quality of that host. Increment reduction occurred during the year of defoliation, and decreased growth is noted in the year following defoliation. Our analysis indicates that both current and the previous year's defoliation affected growth (Fig. 4).

Immediate effect on height growth The immediate (short-term effect) reduction in leader length on the defoliated trees in 2001 is indicative of damage or disruption of growth before or at the time of shoot extension. The growth loss is most likely related to a direct effect of bud feeding by CSM.

Delayed effects on diameter and volume increment A reduction in diameter and volume increment in the year after defoliation may occur in response to defoliation early in the season of the previous year. In this case larger growth losses are also seen in the year of damage, or in response to defoliation late in the previous season after growth for that year has terminated. In the latter scenario, there is no effect on increment in the year of damage. In both situations, height and diameter increments tend to be reduced by equal amounts. The delayed response in diameter and volume increments, without an effect in 1998, and the analogous reduction and recovery in height increment in the second and third years, suggest that these later increment reductions are related to the loss of needles in late summer and autumn after the epidemic.

We estimated that several years would pass before severely defoliated trees regained their normal growth rate (Figs. 1–3). Nevertheless, if the alternate growth rhythm shows up in quite a few host trees but not in nonhost trees, it is most likely that such growth rhythm is caused by defoliation by the CSM. The ongoing drought has resulted in low stand growth rates in the study area for some time and defoliation by the CSM has reduced growth even further.

The effect of the defoliation on current annual radial increment ranged from an estimated reduction of 40% in 1955 to 76% in 1985 and 7% in 1998, with an average of 11% over the outbreak period of 50 years.

Following defoliation, dendrochronological analyses revealed the percent growth reduction in the ring width at different stem heights. The time lag between the initial defoliation and the first growth loss observed as reduced radial increment has been found to range from zero to 5 years. The reduction starts in the crown and continues with a delay of a few years at the stem base of trees (13). A similar one-year lag effect was described for cedar defoliated by CSM (Fig. 4f).

Radial growth and drought When nonhost cedar trees are sampled in nearby sites and their ring series examined in comparison with the host cedar trees, effects of climatic variation can be distinguished from the host-specific defoliation effects. Independently derived tree ring reconstruction of De Martonne's dryness index from nonhost cedar trees shows that, over the past 50 years, CSM outbreaks generally coincided with dry periods, whereas low CSM population levels corresponded to wet periods (Fig. 5). Defoliation by the CSM and drought in 1955, 1985 and 1998 led to reduced growth. From 1955 to 1985, host and nonhost cedar show very similar growth patterns (Fig. 5). After 1985,

the two groups showed a similar pattern, although after 1986 growth in the nonhost group was higher than in the host group. Beginning in 1998, however, a different pattern emerged. From that point on, the host cedar group chronology declines steeply, resulting in 3 years of very low radial growth, in 1999, 2000 and 2001. These years coincide with CSM outbreak and severe drought in this region. We conclude that the ecological role of the CSM is an important disruptive effect in the western Mediterranean cedar forests.

The coefficients of correlation (r) between De Martonne's dryness coefficient and ring width index for host and nonhost cedar sample plot groups were found to be +0.01 and -0.18, respectively. The very low r (absolute) calculated for the CSM outbreak stands suggests that the CSM altered cedar radial growth. In the absence of the CSM, the near unity of slopes and higher r show that host and nonhost cedar of similar dominance and size are also similar in radial growth pattern.

Extreme cold or drought episodes may have caused some of the observed growth changes. Past droughts have contributed to CSM outbreaks. However, cold winter temperatures can kill CSM larvae and cool spring temperatures can result in poor synchrony between larval populations and host plant development (4,15).

Water deficits modify both increment and earlywood-latewood production, and inasmuch as defoliation resembles water deficits by reducing leaf area, the effect would be similar. Earlywood production precedes defoliation by the CSM; thus, the effect of defoliation would be manifested in latewood production. Increases in the proportion of earlywood correspond with the defoliation periods and the loss in total increment. We concluded that a narrow latewood band is a significant indicator of defoliation by the CSM. Speer *et al.* (21) also demonstrated that defoliation reduced latewood formation. In addition to the parameters based on total ring width variations, we visually confirmed the timing of identified outbreaks by scrutinizing the dated tree ring specimens. The total ring width was typically reduced during the first year (and continued for a few years) of heavy defoliation and the latewood was very thin or lighter in color than latewood formed during years without defoliation (Fig. 4).

Developing accurately dated long-term host and nonhost tree ring chronologies also could identify trends in frequency, extent, duration and severity of outbreaks. This information might prove useful in refining simulations and models, as well as providing data for ecological studies of the relations between CSM outbreaks, stand density, species diversity, site history (fire control and logging) and climatic events.

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