Impact of Defoliation by the Pine Processionary Moth (*Thaumetopoea pityocampa*) on Radial, Height and Volume Growth of Calabrian Pine (*Pinus brutia*) Trees in Turkey

Serdar Carus[1]

An outbreak of the pine processionary moth (PPM), *Thaumetopoea pityocampa* Schiff. (Lepidoptera: Thaumetopoeidae), began in spring 1998 and lasted 5 years in a *Pinus brutia* Ten. (Calabrian pine) stand. Tree volume and volume elements increments were examined throughout a PPM outbreak cycle from 1981 to 2003, for an even aged, pure, undisturbed, young Calabrian pine stand. Tree ring chronologies of 'control' Calabrian pine, which was not defoliated by PPM during the period of 1998–2003, were used to estimate potential growth characteristics in the 'host' Calabrian pine (moderate and high defoliation groups) for current and past outbreaks. Increment cores were collected from 70 host and 78 control dominant or co-dominant trees and annual radial growth indices from 1981–2003 were calculated for each defoliation group in a 41 point sampling. Growth functions were defined as the cumulative sum of radial, height, and volume increment, and graphically compared between host Calabrian pine (3 moderate and one high), four control Calabrian pine and one host Crimean pine (*Pinus nigra* Arnold) sample trees. At least three severe outbreak periods were identified (from 1981–86; 1992–97; and 1998–2003), much of the study area being severely affected by PPM. Tree ring evidence suggests that large scale (in 1981, 1992, 1998) and partial (in 1988) outbreaks occurred in the study area. Negative inflections of host radial growth curves relative to control height and volume indicated PPM activity. The periodic average diameter growth reductions (in %) in 1981, 1988, 1992 and 1998, respectively, were 0, 13, 5 and 0 for control, 12, 8, 7 and 2 for moderate, and 18, 5, 0 and 7 for high defoliation groups. Outbreaks appear to be associated with dry winter and spring weather prior to the autumn and winter in which feeding occurs.
KEY WORDS: Calabrian pine; *Thaumetopoea pityocampa* Schiff.; growth loss; tree ring analysis; dendrochronology.

INTRODUCTION

The natural distribution of Calabrian pine (*Pinus brutia* Ten.), one of the most important forest trees of Turkey, covers a total area of approx. 3,096,064 ha (7). Calabrian pine is negatively affected by various abiotic and biotic factors during its lifetime. Insect damage is undoubtedly the most important biotic factor. The pine processionary moth (PPM), *Thaumetopoea pityocampa* Schiff. (Lepidoptera: Thaumetopoeidae), feeds on the Calabrian pine needles and damages assimilation organs. PPM has a significant influence on stand dynamics by reducing tree growth. The population of PPM increased and excessive damage (100% needle loss) occurred during 1995–98 in Calabrian pine forests

Received Jan. 14, 2004; accepted May 23, 2004; http://www.phytoparasitica.org posting Sept. 28, 2004.
[1]Forest Management Department, Faculty of Forestry, Süleyman Demirel University, Isparta, Turkey [Fax: +90-246-237-1810; e-mail: scarus@orman.sdu.edu.tr].

in the eastern Mediterranean region of Turkey. Following the damage by PPM, a 38% diameter increment loss was measured (6).

The characteristics and the extent to which the outbreaks occurred synchronously over different areas are not well understood. PPM caused significant damage on *Pinus brutia*. On the other hand, its damage on some species such as *P. nigra, P. sylvestris, P. halepensis* and *Cedrus libani* is lower than on *P. brutia* in Turkey.

The insect damage on various main tree species in Turkey for wood lost averaged 221,909 m^3 (mostly by PPM) from 1997 to 2000, 3% of the annual wood harvest. The estimated reduction in growth between 2002 and 2003 was valued at $6.9 million. PPM outbreaks can affect forests over 1.5 million hectares in Turkey (7).

In the present study, we investigated the effects of defoliation on the development of radial, height and volume growth of young Calabrian pine trees attacked by PPM. When insects defoliate a tree, they remove not only a portion of the photosynthetic material but also the sites where chemicals such as growth hormones are produced, and this affects many vital functions.

Dendroecological methods (16) enable 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. Annual ring width is substantially reduced, to the point that radial increment data can be used to identify and 'index' the severity of past outbreaks (1,15,13). Several recent North American studies have used dendroecological analysis to investigate the effects of defoliating insects on radial growth (2,3,8-12,14,19). Our first objective was to analyze the impact of PPM on the radial, height and volume growth of the host Calabrian pine that survived the most recent outbreak. Our second objective was to detect periodicity of the PPM outbreaks.

MATERIALS AND METHODS

Biological properties of PPM The PPM has one generation a year. Moths are hatched early in the afternoon during the summer, the males usually preceding the females. After having mated, females become more active and search for the most suitable place to lay their eggs, usually at the top of trees. Larvae feed on the pine needles on warm winter days and in summer and autumn of alternate years. The heaviest defoliation occurs during February and March. The moths spin cottony webs when they are active, and the damaged parts of the tree with dead agglutinated needles remain long after the feeding period. The population then increases rapidly during late summer to peak in early to mid-autumn (6).

Study area The study area was located in Isparta, in the western Mediterranean part of Turkey. The 650-ha study area is situated at 37°34'N, 30°40'E, average slope 15°, predominantly north-facing aspect, $\sim$1240 m alt. Calabrian pine grows at up to 1300 m in Turkey. It is the climax tree of the Mediterranean region. The study area is found on calcareous formations. The soil is generally shallow or medium-deep, and stony, with a predominantly sandy-clay texture.

Climate data Mean monthly and annual temperature and rainfall data for the period 1940–2003 were obtained from the Isparta meteorological station. In the study area, the mean annual precipitation is 685 mm and falls mainly from October through May, with great deviations in the distribution and amount of precipitation during the study period. The region is in a transitional zone between the Mediterranean climate and the continental climate with its colder winters and hotter summers. Mean annual temperature is 10.8°C. In accordance with De Martonne's dryness coefficient (I=19.99), the study area is identified as semi-humid.

Experiment data This study investigated the relationship between defoliation and loss in productivity of trees in the Isparta region in the western Mediterranean of Turkey from 1981 to 2003. The investigation was based on a 27-year-old plantation of Calabrian pine where growth and foliage had been monitored since 1998. A pole-sized Calabrian pine stand at Isparta, approx. 4 ha in area, was selected to follow the impact of PPM on radial, height and volume growth of trees.

In 2003, the average tree density was 1075 trees per ha, mean diameter at breast height (dbh,1.3 m) 17.36 cm, mean height 7.72 m and basal area 17.10 m^2 ha^{-1}, and the stand was expected to achieve a yield class of 3.6 (*i.e.*, periodic mean increment of 3.6 m^3 ha^{-1} year $^{-1}$ and poor site quality).

The color changes of sample trees (from green to brownish red) were detected during the spring seasons of 1998–2003. Considering the PPM feeding habits, the sample trees were divided into control (0–15%), moderate (15–25%), and high (25–40%) classes according to the ratio of defoliation length in crown /total crown length. In 1998, 41 sampling points were selected in the study area. Each sampling point had selected trees with defoliation class and point sampling number marked at breast height. In 2003, mean defoliation classification of each sample tree was determined in order to analyze the data into control, moderate and high defoliation classes. It was realized that defoliation intensity (defoliation classes) of sample trees was not changed (remaining ~60%) by PPM during the years 1998–2003.

The sample trees were selected from each of three defoliation classes: control (n=78), moderate (n=36), high (n=34) and from dominant or co-dominant trees in the spring of 2003. Defoliation intensity for each sample tree was estimated visually to the nearest 5% by three persons, and the final assessment was the average of these three estimates.

In the autumn of 2003, increment cores were extracted at breast height from opposite sides of each sample tree parallel to the topographic contour. Cores were inserted in labeled plastic straws that were heat-sealed to prevent moisture loss and kept frozen until measured.

The total height and the diameter at breast height of each tree were measured. From these data, stem volume was calculated for each tree using the volume tables of Usta (17). In addition, crown length and diameter of sample trees were recorded.

Dendrochronological analysis In the laboratory, the ring widths were measured to the nearest 0.01 mm using a stereomicroscope. All the measured ring-width sequences were plotted and the patterns of wide and narrow rings were cross-dated among trees of the same area to identify possible false rings, missing rings, or measurement mistakes. The quality of cross dating was examined using the program COFECHA (5), which provides clues to the best match in ring patterns by calculating correlation coefficients among tree ring sequences.

The radial growth pattern in control Calabrian pine trees was used to adjust the outbreak signals in host Calabrian pine tree ring widths. To do so, we developed ring-width chronologies of control Calabrian pine. The host and control Calabrian pine chronologies were developed using the software ARSTAN (4), in which the measured tree ring sequences were standardized by dividing the ring width for each year by a fitted curve value for that year. The fitted curve, which represents the age-related biological growth trend, was selected as a negative exponential curve, or a regression line of negative slope. The subsequent standardized series were then averaged together by year among different samples. The resulting yearly values, called tree ring indices, formed chronologies for host and control Calabrian pine. The host pine chronologies were evaluated as moderate and high.

Tree growth Nine sample trees were cut in the study area. The number of trees according to defoliation group was determined as follows: host Calabrian pine (moderate, n=3 and high, n=1); control Calabrian pine (n=4); and host Crimean pine (n=1). Cross-sectional discs were then cut from the stem at stump height, 1.3 m, and at 1-m intervals upward for a total of seven to ten discs per tree. The discs were air-dried and polished, and the width of the growth rings was measured to an accuracy of ±0.01 mm along the maximum and minimum radii. 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 PPM. Height increment is determined by counting annual rings from discs; volumes are obtained by diameter and height. A complete radial, volume and height increment data-set was established for each sample tree.

Statistical analysis Differences in height, diameter and volume between the defoliation classes for all the years 1981 to 2003 were tested using ANOVA. Differences between main effects were assumed to be significant at $P<0.025$. Two types of statistical tests were used for the identification of any relation between the measurements. Average values were examined to assess damage differences among various variables of the trees, and ANOVA was conducted, to see if these differences were significant in 2003.

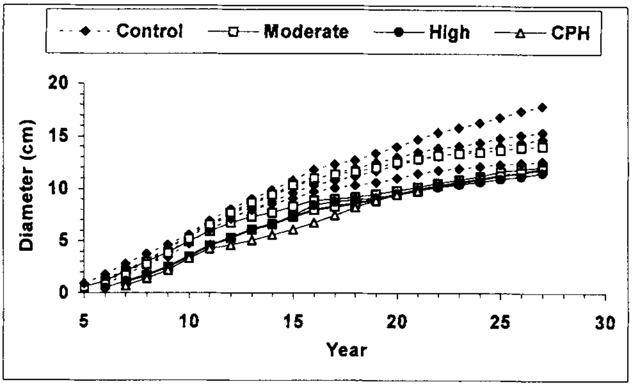
RESULTS

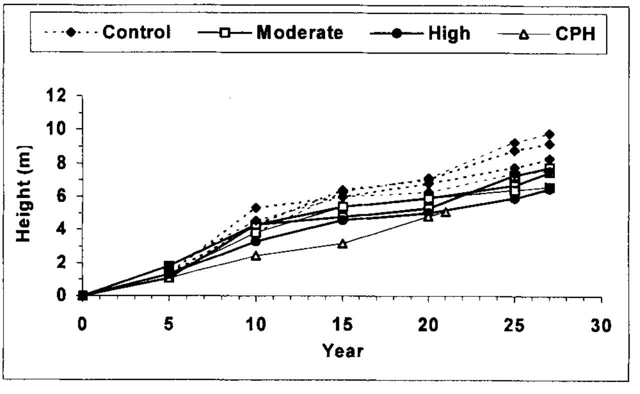
Increment cores were taken from 70 dominant and co-dominant host Calabrian pine trees and from 78 dominant and co-dominant control Calabrian pine trees. Table 1 presents some growth statistics of sample trees in three defoliation groups.

TABLE 1. Summary of sample trees used in the chronologies

Defoliation class	Number of cores used	Average diameter (cm)	Average height (m)	Average volume (dm^3)	Crown diameter (m)	Crown length (m)	Series correlation
Control	78	17.38	7.73	86.13	2.99	4.29	0.54
Moderate	36	16.86	7.46	80.62	2.96	4.40	0.43
High	34	16.44	7.75	81.70	2.92	4.53	0.47

The F values of ANOVA for diameter, height, volume, crown diameter and crown height were found to be 1.961, 0.464, 0.546, 0.343 and 0.503, respectively. The cumulative effect of PPM on final tree size was small in relation to some of the reductions in annual increment, but rose because annual growth was reduced only partially, and in only 11–12 years out of the total 27-year life of the stand. Viewed in this context, the effect on final tree size could not be much greater. The final size of the trees at felling was reduced significantly by PPM outbreaks; final diameter was reduced 3% and 5%, and height by 6% and zero, for the moderate and high defoliation rating, respectively (Table 1).





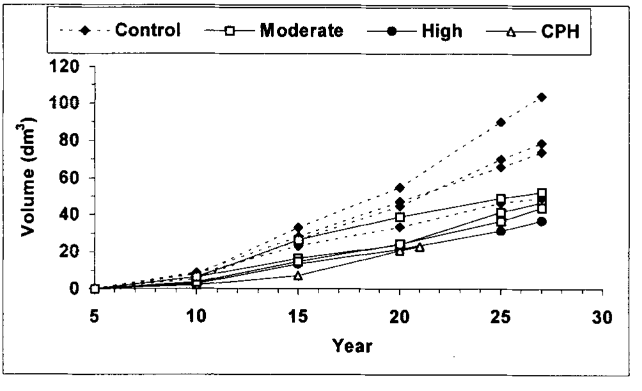


Fig. 1. Development trend of diameter, height, and volume as a function of age of control, moderate and high Calabrian pine defoliation groups, and host Crimean pine (CPH) sample trees.

The tree ring samples used to build chronologies showed significant inter-serial correlation in the study area. Mean inter-serial correlation, which describes the amount of common signal among tree ring series of different samples, ranged from 0.43 to 0.56 for the defoliation groups (Table 1). This indicated that the increment growth of individual samples

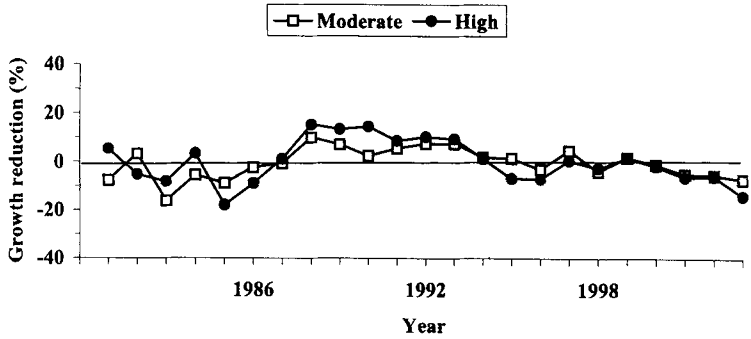


Fig. 2. Radial growth reductions (%) in the moderate and high Calabrian pine defoliation groups.

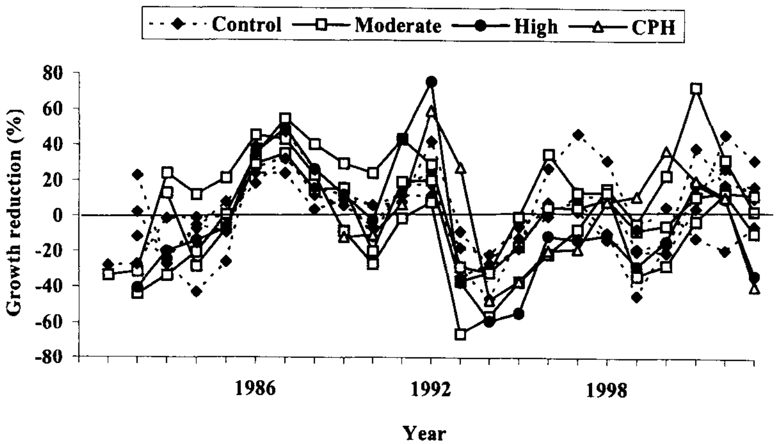


Fig. 3. Growth reduction (%) of radial increment in the control, moderate and high Calabrian pine defoliation groups.

responded simultaneously to environmental influence (including defoliation) within each defoliation group.

Cumulative growth function (CGF): No important differences were observed between CGF graphs of pine defoliation (Fig. 1). However, obvious negative departures of the control Calabrian pine curve relative to the host pine occurred in the PPM-infested stands. Host Calabrian pine is generally attacked again when the next generation of larvae hatches; this larval generation can then cause heavy damage to host trees. As Figure 1 indicates, the Crimean pine sample tree (abbreviated as CPH) is considered in the high defoliation group.

Growth losses and indexing PPM activity through radial increment analysis

Comparing host and control chronologies: After measuring and matching of individual chronologies, a master chronology of Calabrian pine was developed for each defoliation group (Fig. 2). The nondefoliated trees might have been defoliated during a previous outbreak in the past. Visual examination of the host chronologies showed that growth reductions occurred more or less synchronously four times (1981, 1988, 1992 and 1998) in

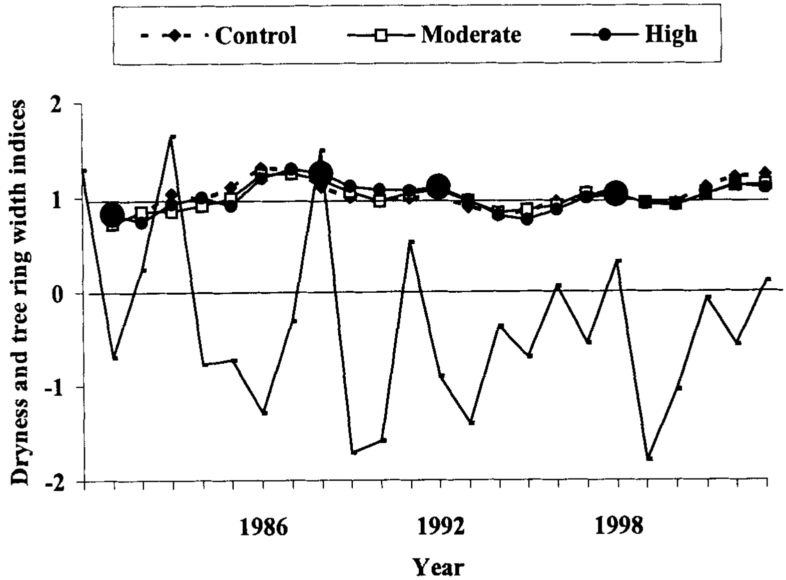


Fig. 4. Comparisons of De Martonne's dryness index (line) and tree width ring indices in the control, moderate and high Calabrian pine defoliation groups (black dots indicate outbreak years).

the past 23 years in the Isparta region. Since the signal of climatic influence on the growth of host trees had been minimized by the control chronology, the growth reductions were most likely caused by PPM outbreaks.

Defoliation of Calabrian pine generally resulted in a decline in radial increment. This relationship is illustrated by the increment chronology for Calabrian pine in Isparta. We developed a single host chronology for each defoliation group by averaging the chronologies from both host/control Calabrian pine and Crimean pine sample trees (Fig. 2).

Four outbreaks were identified in the past 27 years, although the initiation date and the intensity of these outbreaks varied from time to time. Although individual tree records of defoliation in this region were not available for the decline periods in 1981, 1988 and 1992, according to a forestry official (personal communication) an outbreak was present in this area.

The control tree ring width chronologies had a lower first-order autocorrelation than the host trees; the moderate, high and control values first-order autocorrelation were calculated as r= 0.706, r=0.729 and r=0.694, respectively, very likely reflecting the effects of PPM. The graphical comparison of the host and control chronologies should provide some evidence that PPMs have caused radial growth reduction in the host trees. However, host trees may also have been responding to other environmental factors, such as drought, that may have caused growth reductions. The purpose of corrected indices (CI) is to remove the host-tree-ring chronologies' environmental effects common to both host and control chronologies, so that more precise estimates of growth reduction can be derived from the corrected host series.

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 CIs.

The corrected series (Eq. 1 and Fig. 2) were used to identify the timing of outbreaks, the duration of PPM-induced low-growth periods, and the maximum annual and periodic radial growth losses (15). Subtracting the CIs during outbreaks from the potential growth value (1.0) and multiplying by 100 gave the latter two measures. Thus, the radial growth reduction measures are expressed in relative terms as a percentage of expected growth.

$$\mathrm{PRI} = \frac{\mathrm{SDEV(H)}}{\mathrm{SDEV(NH)}}[\mathrm{INDEX(NH)} - \mathrm{MEAN(NH)}];$$

and

$$\mathrm{CI} = \mathrm{INDEX(H)} - \mathrm{PRI} \tag{1}$$

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

To confirm this visual comparison of chronologies, a two-way analysis of variance was performed to detect any statistical significance. The analysis was conducted using years and ratings as defoliation groups and standard chronology as the response variable. These results [years, $F_{22;44} = 20.191$*** ($P<0.001$); chronologies, $F_{2;44} = 1.066$ ($P=0.35$)] indicated that there were no significant differences among the standard chronologies due to differences in defoliation classification of the trees in the stand.

Growth in relation to defoliation There was a considerable difference in variability of the defoliation data in stands rated high, moderate, and control, as was expected from the original classification scheme. Growth loss was calculated using Eq. 1, as the proportional reduction in observed growth relative to expected growth. There was also a clear pattern in average defoliation (Figs. 2, 3), with trees rated high having the highest average defoliation, followed by trees rated moderate and low. The magnitude of the damage varied from tree to tree in the stand (Fig. 3).

The corrected chronology of host Calabrian pine was compared with that of control Calabrian pine. The correlation coefficients were found to be 0.89 and 0.81 for moderate and high defoliation groups, respectively.

Effect of defoliation on growth

Radial growth: Sample trees exhibited an abrupt growth reduction starting at 5 (1981), 12 (1988), 16 (1992) and 22 (1998) years of age and lasting between 6, 4, 6 and 6 years, respectively (Fig. 1). Average annual ring widths of Calabrian pine were smaller during an outbreak than before and after an outbreak, indicating a temporary decline in growth due to feeding by PPM (Fig. 1). The periodic average diameter growth reductions (in %) in 1981, 1988, 1992 and 1998, respectively, were 0, 13, 5 and 0 for control, 12, 8, 7 and 2 for moderate, and 18, 5, 0 and 7 for high defoliation groups.

Height and volume growth The lack of response or increment in control (Fig. 1) during periods of increment decline in hosts may be used as another indicator of a PPM outbreak. However, defoliation of hosts in defoliation groups would result in increased nutrients, thus enhancing growth of hosts and explaining the positive relationship between stand defoliation more than the control defoliation group over a few years of outbreak. Average height growth reductions in the PPM outbreaks (1981, 1988, 1992 and 1998) were 16% (moderate) and 26% (high); average growth reductions for volume were 38% (moderate) and 52% (high) (Fig. 1).

Response to drought: Trees in control and host defoliation groups responded to a drought, which occurred during the period 1998–2003, with a substantial decrease in annual radial increment (Fig. 4). In 1997, De Martonne's dryness coefficient and total monthly precipitation was 15.05 (semi-humid) and 614 mm, respectively. The observed decrease in growth began in 1999 and reached a minimum in 2001. However, this pattern was not observed in the control trees for the same interval (Fig. 4). The coefficients of correlation (r) between De Martonne's dryness coefficient and ring width index for control and host Calabrian pine defoliation groups (moderate and high) were found to be 0.15, 0.04 and 0.03, respectively. The very low r calculated for the PPM outbreak stands suggests that PPM altered pine radial growth. In the absence of PPM, the near unity slopes and higher r show that host and control Calabrian pine of similar dominance and size are also similar in radial growth pattern.

DISCUSSION

PPM activity and growth losses Outbreaks of PPM seem to occur periodically. There was a sharp decline in increment of host pine during and directly after a PPM outbreak. In contrast, growth of control Calabrian pine declined only slightly during the outbreak but increased greatly directly after the outbreak. Control group radial growth decreased in growth in 1988, most likely due to severe defoliation by PPM. From that point on, control Calabrian pine defoliation groups declined steeply in 1988–1994 and eventually ended with 6 years of very low radial growth. These years coincide with PPM outbreak and severe drought in this region (Figs.1 and 2).

Water deficits modify both increment and earlywood–latewood production in trees, and inasmuch as defoliation resembles water deficits by reducing leaf area, the effect would be similar. Earlywood production precedes defoliation by PPM. Increases in the proportion of earlywood correspond to the defoliation periods and the loss in total increment. The 2003 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 1992–1997 (Figs. 1–3). We concluded that a narrow latewood band is a significant indicator of defoliation by PPM.

When control Calabrian pine trees are sampled at the same site, and their ring series examined in comparison with the host Calabrian pine trees, effects of climatic variation can be distinguished from the host-specific defoliation effects (18). Independently derived tree ring reconstruction of De Martonne's dryness index from control Calabrian pine shows that, over the past 23 years, PPM outbreaks generally coincided with dry periods (Fig. 4).

Defoliation by PPM and drought in the time around 1981, 1988, 1992 and 1998 led to reduced growth. The growth reduction phase was followed by a growth recovery phase lasting 4 to 6 years, in which ring width gradually returned to pre-outbreak levels. The effect of the defoliation on current annual radial increment ranged from an estimated reduction of 16% in 1981 to 15% in 1988, 10% in 1992, 4% in 1998 and 14% in 2003, averaging 12% over the outbreak period of 23 years.

Growth patterns *vs* defoliation In this study, the number of cores used in defoliation groups for control, moderate, and high was 78, 36 and 34, respectively (Table 1). There were generally no significant growth reductions (Fig. 1). Final diameter, height and volume of the trees at felling for the moderate defoliation groups, were reduced by an average of 16%, 16%, and 38%, respectively; the respective figures for the high defoliation group were 24%, 36% and 52%.

The average diameter in 1987 (age of stand = 10) was 53, 46 and 35 mm for control, moderate and high defoliation group sample trees, respectively (Fig. 1). PPM outbreaks caused differences between damage classes with respect to tree height, diameter and volume in 2003 (Fig.1). The total diameter increments during 1987–2003 were 91, 81 and 80 mm, respectively, for control, moderate and high defoliation group sample trees. Height increments of control, moderate and high defoliation group sample trees during 1987–2003 were 4.2, 3.2 and 3.2 m, respectively. The total volume increments were 69, 42 and 34 dm^3, respectively, for control, moderate and high defoliation group sample trees during 1987–2003.

Since the PPM outbreaks there have been decreases in height and radial increments of affected trees, compared to those of unaffected trees (Fig. 3). There was a steady, continuous decrease in height increment of affected trees during 1987–1997, compared to that of unaffected trees. Since 1987 the height increments of moderately and severely affected trees have been approx. 33% and 26%, respectively, of the increment of unaffected trees (Fig. 2).

The radial increment of affected trees decreased in 1988, 1992 and 1998, especially in lightly affected trees (Fig. 2). A similar development was not observed for moderately affected trees. The radial increment of this group has remained at ~75% of that of unaffected trees since 1992 (Figs. 2 and 3). These findings indicate that the same trees were generally being defoliated during outbreaks in each year. In addition, we assumed that several years would pass before severely defoliated trees would regain their normal growth rate (Figs.1–3).

Future prospects Developing accurately dated long-term host and control tree ring chronologies also could identify trends in frequency, extent, duration and severity of outbreaks. This information may prove useful in refining simulations and models, as well as providing data for ecological studies of the relationships among PPM outbreaks, stand density, species diversity, and climatic events. 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.

REFERENCES

1. Carlson, C.E. and McCaughey, W.W. (1982) Indexing western spruce budworm activity through radial increment analysis. *U.S. Dep. Agric. For. Serv.* RP-INT-291.
2. Carolyn, A.C. and Marc, D.A. (2003) Dendroecology in young stands: case studies from jack pine in northern Lower Michigan. *For. Ecol. Manage.* 182:247-257.
3. Colbert, J.J. and Fekedulegn, D. (2001) Effects of gypsy moth defoliation on tree growth – preliminary models for effects of cumulative defoliation on individual host tree radial increment. *Proc. Integrated Management and Dynamics of Forest Defoliating Insects* (1999, Victoria, B.C., Canada), *U.S. For. Serv. Gen. Tech. Rep.* NE-277, pp. 16-30.
4. Cook, E.R. and Holmes, R.L. (1986) Guide for computer program ARSTAN. *in:* Tree Ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin. University of Arizona Press, Tucson, AZ, USA. pp. 50-65.
5. Holmes, R.L. (1983) Computer assisted quality control in tree ring dating and measurement. *Tree Ring Bull.* 43: 69-78.

6. Kanat, M. (2002) A research on the effects of pine processionary moth (*Thaumetopoea pityocampa* (Schiff.)) and tending activities on the diameter increment of Calabrian pine (*Pinus brutia* Ten.) trees in Kahramanmaraş. *Symp. Country Forests, Pine Processionary Moth Problem and Solution Proposals* (Kahramanmaraş, Turkey), pp. 44-51 (Turkish, with English summary).
7. Konukcuoglu, M. (1999) Turkish Forestry. Planning Organization of Government. Ankara, Turkey (Turkish, with English summary).
8. Krause, C. (1997) The use of dendrochronological material from buildings to get information about past spruce budworm outbreaks. *Can. J. For. Res.* 27:69-75.
9. Muzika, R.M. and Leibhold, A.M. (1999) Changes in radial increment of host and nonhost tree species with gypsy moth defoliation. *Can. J. For. Res.* 29:1365-1373.
10. Naidoo, R. and Lechowicz, M.J. (2001) Effects of gypsy moth on radial growth of deciduous trees. *For. Sci.* 47:338-348.
11. Piene, H. (1989) Spruce budworm defoliation and growth loss in young balsam fir. Recovery of growth in spaced stands. *Can. J. For. Res.* 19:1616-1624.
12. Piene, H. and Little, C.H.A. (1990) Spruce budworm defoliation and growth loss in young balsam fir: artificial defoliation of potted trees. *Can. J. For. Res.* 20:902-909.
13. Ryerson, D.E., Swetnam, T.W. and Lynch, A.M. (2003) A tree ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. *Can. J. For. Res.* 33:1010-1028.
14. Speer, J.H., Swetnam, T.W., Wickman, B.E. and Youngblood, A. (2001) Changes in Pandora moth outbreak dynamics during the past 622 years. *Ecology* 82:679-697.
15. Swetnam, T.W. and Lynch A.M. (1989) A tree ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *For. Sci.* 35:962-986.
16. Swetnam, T.W., Thomson, M.A. and Sutherland, E.K. (1988) Using Dendrochronology to Measure Radial Growth of Defoliated Trees. *U.S. For. Serv. Spruce Budworms Handb.* 639.
17. Usta, H.Z. (1991) A study on the yield of *Pinus brutia* Ten. plantations. *Tech. Bull. Turk. For. Res. Inst.* no. 219 (Turkish, with English summary).
18. Zhang, Q. and Alfaro, R.I. (2002) Periodicity of two year cycle spruce budworm outbreaks in central British Columbia: a dendro-ecological analysis. *For. Sci.* 48:722-731.
19. Zhang, Q., Alfaro, R.I. and Hebda, R.J. (1999) Dendroecological studies of tree growth, climate and spruce beetle outbreaks in central British Columbia, Canada. *For. Ecol. Manage.* 121:215-225.