

# Defoliation by processionary moth significantly reduces tree growth: a quantitative review

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## Abstract

- **Context** Forests are important carbon sinks, but increasing temperatures may favour increases in insect populations, resulting in greater damage to trees. This, in turn, would lead to lower levels of carbon sequestration, intensifying global warming.
- **Aim** It is therefore important to predict the impact of insect defoliation on tree growth accurately. The main insect defoliators of conifers in Southern Europe and North Africa are pine and cedar processionary moths (Lepidoptera, Thaumetopoeidae).
- **Method** We conducted a meta-analysis based on 45 study cases, to estimate the effect of processionary moth defoliation on tree growth.
- **Result** Overall, processionary moth defoliation had a significant impact on tree growth, regardless of the tree and moth species considered. Mean relative tree growth loss increased with the rate of defoliation levelling out at ca. 50 %; it was significantly larger for young than for old trees.
- **Conclusion** These results suggest that estimates of processionary moth defoliation could easily be incorporated into tree growth models, to predict the effect of processionary moth outbreaks on carbon sequestration in Mediterranean forests.

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Jean-Sébastien Jacquet: collected the data.  
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## 1 Introduction

Forest ecosystems are major terrestrial carbon sinks (Hyvönen et al. 2007). In Europe, carbon sequestration in forests has increased in recent decades, mostly due to sustained increases in woody biomass (Luyssaert et al. 2010). However, some of this biomass is lost through natural disturbances, such as forest fires, windfalls and insect damage (Nabuurs et al. 2008). In the context of climate change, the predicted increase in net primary production (Nemani et al. 2003) due to higher temperatures and CO<sub>2</sub> concentrations may therefore be offset by changes in the frequency and intensity of biotic disturbances (Logan et al. 2003; Netherer and Schopf 2010). Early signs of global warming recently triggered a large-scale outbreak of mountain pine beetle in British Columbia (Bentz et al. 2010) resulting in the death of millions of trees and converting the pine forest from a carbon sink to a source of atmospheric carbon (Kurz et al. 2008). Insect defoliators are likely to have the same impact on forest ecosystems (Dymond 2010). In the shorter term, insect defoliation may also result in lost timber production (Alfaro 1991; Twery 1990). There is therefore a need to improve our knowledge of the consequences of insect defoliation for tree growth and carbon sequestration (Pinkard et al. 2011).

Due to their faster growth, conifers sequester carbon more effectively than broad-leaved species (Hyvönen et al. 2007). However, the defoliation of conifers by insect herbivores may have more severe effects on tree growth (Parsons et al. 2003), particularly because, unlike broad-leaved trees (and larch), they display no reflush growth after foliage consumption (Wainhouse 2005). Heavy defoliation of pine,

spruce or larch can result in a decrease in stem growth of more than 50 % (Kulman 1971) and the amount of this reduced growth is thought to be linearly proportional to defoliation intensity (Kulman 1971). However, this relationship may be affected by additional factors, such as site conditions, stand age and density, recurrence and time of defoliation (Wainhouse 2005).

The main insect defoliators of conifers in Southern Europe and North Africa are the pine or cedar processionary moths (Lepidoptera, Thaumetopoeidae): *Thaumetopoea pityocampa* (Dennis and Schiff.), *Thaumetopoea wilkinsoni* (Tams), *Thaumetopoea bonjeani* (Powel) and *Traumatocampa ispartaensis* (Doganlar and Avci). *T. pityocampa* is oligophagous on pines and cedars in Mediterranean countries (Devkota and Schmidt 1990; Masutti and Battisti 1990). *T. wilkinsoni* occurs in the eastern part of the Mediterranean Basin (in Turkey, for example) and its main hosts are *Pinus brutia*, *Pinus halepensis* and *Pinus nigra* (Halperin 1990). *T. bonjeani* is present in North Africa, where it feeds principally on *Cedrus* sp. (Gachi et al. 2005). The cedar processionary moth, previously known as *Thaumetopoea solitaria* (Freyer), has been observed in Turkey since 1975 and was identified as a new species named *T. ispartaensis* in 2001. *T. ispartaensis* is one of the most dangerous pests of *Cedrus libani* in the Middle East (Avci 2003).

The processionary moth larvae prefer to feed on mature needles but may also feed on young needles, potentially resulting in defoliation of up to 100 % of crown volume. Defoliation decreases the activity of needles and their availability for photosynthesis, resulting in significant impact on tree growth (Hodar et al. 2003). Severe, repeated defoliation may even lead to the death of the tree, particularly if the tree is young or soil conditions are poor, because trees weakened by defoliation are more susceptible to secondary pests, such as bark beetles. In the last decade, it has been shown that *T. pityocampa* is spreading towards higher latitudes and altitudes, probably due to the global warming (Battisti et al. 2005; Robinet et al. 2007). For both peri-Mediterranean forests and more northern pine forests that are potentially susceptible to invasion, it is therefore important to better predict the impact of processionary moth damage on ecosystem functioning.

Several studies have evaluated the loss of tree growth due to processionary moth defoliation (Table 1). However, as for many other insect defoliators (Wainhouse 2005), many different methods have been used to quantify these losses. These methods have included the measurement of annual rings (i.e. dendrochronology), comparing tree circumference, height or volume between defoliated and unaffected trees or comparing growth in the same tree before and after attacks. This diversity of methodological approaches prevents generalisations regarding the patterns of tree growth in response to processionary moth defoliation. Moreover, the

lack of consistency in estimates of defoliation rate and the use of different tree species of different ages in these studies makes it difficult to draw firm conclusions about the relationship between growth loss and defoliation severity. We circumvented these problems, by carrying out a meta-analysis of existing studies to address the question of the impacts of processionary moth defoliation on pine or cedar growth. Meta-analysis is based on the use of a set of statistical tools to combine the outcomes of independent studies for evaluations of the overall effect of a particular factor and for assessing the influence of covariates on this effect (Gurevitch and Hedges 1999). Our main objectives were: (1) to determine whether processionary moth defoliation significantly effects tree growth, (2) to determine whether this effect increased significantly with the intensity of defoliation and (3) to investigate whether growth responses to processionary moth defoliation differed between young and mature trees.

## 2 Materials and methods

### 2.1 Data collection

We searched for studies investigating the effect of pine processionary moth defoliation on tree growth in online bibliographic databases (ISI Web of Knowledge and Google Scholar). Keyword searches were conducted with various combinations of relevant terms, such as: *Pinus* or *Cedrus* or pine or cedar, processionary or *Thaumetopoea*, defoliation or damage and radial or diameter or circumference or height or volume or growth. We also searched the references cited in relevant publications. Studies were included in the meta-analysis if they met the following four criteria:

1. Tree growth, estimated with circumference, height or volume variables, was compared between naturally defoliated and unaffected (control) trees. We excluded studies dealing with artificial defoliation because artificial defoliation might not correctly mimic the natural process of processionary moth defoliation in terms of timing and needle choice (Quentin et al. 2010).
2. Defoliation rate was estimated as percent defoliation, stratified into classes.
3. The mean of the growth response variable, a measure of its variance and the sample size for both defoliated and control trees were reported in the text or could be determined by the digitisation of graphs.
4. The reported paired comparison of growth, between defoliated and control trees, was made with the same experimental or observational protocol, on the same date and in the same region.

**Table 1** Published studies reporting on the effect of processionary moth on tree growth from 1897 to 2010

| Authors                          | Publication year | <i>Thaumetopoea</i> species | Tree species <sup>a</sup>              | Range of defoliation (%) | Type of comparison between defoliated and control trees <sup>b</sup> | Type of tree growth measurement <sup>c</sup> | Method of measurement <sup>d</sup> | Growth reduction (%) <sup>f</sup> | Number of case studies used in the meta-analysis |
|----------------------------------|------------------|-----------------------------|--|--------------------------|--|--|------------------------------------|-----------------------------------|--|
| Calas                            | (1897)           | <i>pityocampa</i>           | <i>P. nigra</i> , <i>P. sylvestris</i> | 100                      | Natural defoliation  | C  | Dendrochronology                   | 17                                |  |
| Cadahia et al.                   | (1970)           | <i>pityocampa</i>           | <i>P. radiata</i>                      | 5–75                     | Forced defoliation   | V  | Dendrology                         | 10–30                             |  |
| Bouchon et al.                   | (1971)           | <i>pityocampa</i>           | <i>P. nigra</i>                        | 50                       | Natural defoliation  | C  | Dendrology                         | 20–50                             |  |
| Joly                             | (1976)           | <i>pityocampa</i>           | <i>P. pinaster</i>                     | 100                      | Artificial defoliation   | C  | Dendrology                         |                                   |  |
| Lemoine                          | (1977)           | <i>pityocampa</i>           | <i>P. pinaster</i>                     | 100                      | Natural defoliation  | C  | Dendrology                         | 30                                | 18   |
| Laurent-Hervouët                 | (1986)           | <i>pityocampa</i>           | <i>P. nigra</i>                        | 75–100                   | Natural defoliation  | C  | Dendrochronology                   | 10–30                             |  |
| Battisti                         | (1988)           | <i>pityocampa</i>           | <i>P. nigra</i>                        | 100                      | Natural defoliation  | H  | Dendrology                         | 50                                | 2  |
| Graf et al.                      | (1994)           | <i>pityocampa</i>           | <i>C. atlantica</i>                    | 30–100                   | Removal in control   | V  | Dendrology                         | 20–40                             | 2  |
| Chatziphilippidis and            | (1994)           | <i>pityocampa</i>           | <i>P. brutia</i>                       | 100                      | Forced defoliation and removal in control                            | C/H  | Dendrology                         | 60                                |  |
| Markalas                         | (1998)           | <i>pityocampa</i>           | <i>P. pinaster</i>                     | 40–100                   | Natural defoliation  | H  | Dendrology                         | 40–60                             | 2  |
| Hodar et al.                     | (2003)           | <i>pityocampa</i>           | <i>P. sylvestris</i>                   | 1–100                    | Natural defoliation  | H  | Dendrology                         | 40–60                             | 4  |
| Carus <sup>e</sup>               | (2004)           | <i>pityocampa</i>           | <i>P. brutia</i>                       | 10–40                    | Natural defoliation  | C/H/V  | Dendrochronology                   | 20–30                             |  |
| Avci et al.                      | (2005)           | <i>ispartaensis</i>         | <i>P. libani</i>                       | 75–100                   | Natural defoliation  | C  | Dendrochronology                   | 10–40                             |  |
| Gachi et al.                     | (2005)           | <i>bonjeani</i>             | <i>C. atlantica</i>                    | 100                      | Natural defoliation  | C  | Dendrochronology                   | 30                                | 1  |
| Kanat et al.                     | (2005)           | <i>pityocampa</i>           | <i>P. brutia</i>                       | 70                       | Removal in control   | C  | Dendrochronology                   | 20                                | 1  |
| Barrento et al.                  | (2008)           | <i>pityocampa</i>           | <i>P. pinaster</i>                     | 5–100                    | Natural defoliation  | C  | Dendrology                         | 0–80                              | 6  |
| Hernandez et al.                 | (2008)           | <i>pityocampa</i>           | <i>P. radiata</i>                      | 75–100                   | Forced defoliation   | C  | Dendrology                         | 20                                |  |
| Carus <sup>e</sup>               | (2009)           | <i>wilkinsoni</i>           | <i>P. brutia</i>                       | 10–40                    | Natural defoliation  | C/H/V  | Dendrochronology                   | 20–30                             | 2  |
| Durkaya et al. <sup>e</sup>      | (2009)           | <i>pityocampa</i>           | <i>P. nigra</i>                        |                          | Natural defoliation  | C/H  | Dendrochronology                   | 20                                |  |
| Shabji et al.                    | (2009)           | <i>pityocampa</i>           | <i>C. atlantica</i>                    | 5–100                    | Natural defoliation  | C  | Dendrochronology                   | 20–50                             | 2  |
| Arnaldo et al.                   | (2010)           | <i>pityocampa</i>           | <i>P. pinaster</i>                     | 25–50                    | Natural defoliation  | C/H/V  | Dendrology                         | 50–70                             | 4  |
| Carus <sup>e</sup>               | (2010)           | <i>wilkinsoni</i>           | <i>P. nigra</i>                        | > 70                     | Natural defoliation  | C/H/V  | Dendrochronology                   | 20                                |  |
| Pestaña and Santolamazza-Carbone | 2010             | <i>pityocampa</i>           | <i>P. pinaster</i>                     | 20–80                    | Artificial defoliation   | C/H  | Dendrology                         | 10–30                             |  |
| Erkan                            | (2010)           | <i>wilkinsoni</i>           | <i>P. brutia</i>                       | 30–100                   | Natural defoliation  | C/H/V  | Dendrochronology                   | 35–55                             | 1  |

<sup>a</sup> Tree genera: *P.* = *Pinus*, *C.* = *Cedrus*<sup>b</sup> Type of comparison: natural defoliation, natural defoliation/natural control; artificial defoliation, artificial defoliation/natural control; forced defoliation, processionary moth winter nest inoculation/natural control; removal in control, natural defoliation/artificial control through processionary moth winter nest removal<sup>c</sup> Tree growth measurement: C circumference, H height, V volume<sup>d</sup> Method of measurement: dendrology, direct measurement of tree circumference or height; dendrochronology, tree ring analysis<sup>e</sup> Both dendrology and dendrochronology were used in those study cases<sup>f</sup> We reported the circumference growth reduction interval when it was available as it was the most common type of measurement among studies

Our literature search identified 24 published studies describing the effect of processionary moth on tree growth. Six of these studies had insufficient statistical data, four lacked information about defoliation rate and two were based on artificial defoliation (Table 1). We rediscovered the archived data for Lemoine's (1977) study, making it possible to distinguish between two independent sampled stands. This meta-analysis was therefore based on 45 pairwise comparisons derived from 12 publications or reports published between 1977 and 2010.

## 2.2 Calculating effect sizes and defining explanatory variables

The effect of processionary moth defoliation on tree growth was estimated by using the log response ratio  $\ln R$  (Eq. 1) as standardised effect size for each pairwise comparison (Hedges et al. 1999). The use of  $\ln R$  (rather than Hedges'  $d$  or another measurement of effect size) has recently become more common in biological studies because it assumes that effects can be multiplicative and is less sensitive to error than other methods (Morris et al. 2007). The variance of  $\ln R$  ( $v_{\ln R}$ ) was calculated as in Eq. (2) and the inverse of this variance was used as the weighting in calculations of weighted means (Hedges et al. 1999). A negative value of  $\ln R$  indicates a growth loss in defoliated trees (less growth in defoliated trees than in control, unaffected trees).

$$\ln R = \ln \left( \frac{\bar{X}_{\text{DEF}}}{\bar{X}_{\text{CTL}}} \right) \quad (1)$$

where  $\bar{X}_{\text{DEF}}$  is the mean growth measurement for defoliated trees and  $\bar{X}_{\text{CTL}}$  is the mean growth measurement for unaffected, control trees.

$$v_{\ln R} = \frac{(\sigma_{\text{CTL}})^2}{N_{\text{CTL}}(\bar{X}_{\text{CTL}})^2} + \frac{(\sigma_{\text{DEF}})^2}{N_{\text{DEF}}(\bar{X}_{\text{DEF}})^2} \quad (2)$$

where  $N$  is the sample size and  $\sigma$  is the standard deviation.

Because the effect size is a ratio, it has no unit. It is thus theoretically possible to combine studies reporting different types of growth measurements. However, radial and height growth may respond differently to processionary moth defoliation. We therefore assessed the effect of the type of growth measurement used on  $\ln R$ . Both circumference and height growth data were available for the same trees in six papers accounting for 11 mean values per defoliation class (Chatziphilippidis and Avtzis 1994; Carus 2004, 2009, 2010, Durkaya et al. 2009; Pestaña and Santolamazza-Carbone 2010). A simple linear regression analysis was used to compare mean  $\ln R$  values per class of defoliation for circumference and height. It showed that there was a highly significant correlation between the two values of  $\ln R$  ( $n=11$ ,  $F=212.2$ ,  $R^2=0.91$ ,  $P<0.0001$ ) which were almost

equal to each other ( $\ln R_{\text{cir}}=1.1 \ln R_{\text{height}}$ ). We therefore pooled studies reporting either circumference or height losses in the same dataset.

For studies reporting tree growth estimates for several years, we used only the data for the first year. Two independent experiments (different stands or sites) reported in the same paper were considered as two separate comparisons.

We split the dataset into classes for tree age and percentage of defoliation. Trees were considered 'young' if they were less than 15 years old and 'old' if they were greater than 15 years old. We defined four classes of processionary moth defoliation rate: class 1, 5–24 %; class 2, 25–49 %; class 3, 50–74 %; and class 4, 75–100 %. In many cases, groups of trees with different rates of defoliation were compared with the same control group (unaffected trees) within a given study. These comparisons are not truly independent. To account for this problem of multiple comparisons, we used the method proposed by Borenstein et al. (2009). We collapsed the data from all groups of defoliated trees to generate a combined sample size, mean and standard deviation. We then calculated a new effect size for a comparison of the control group with the new merged group. This reduced the entire dataset to 15 fully independent comparisons, for which a new meta-analysis was carried out. The weighted mean of growth loss obtained with the complete dataset (–43 %) was very similar to the grand mean effect size calculated with the reduced set of independent studies (–0.38 %) and was within the confidence interval for the reduced set of independent studies (–26 to –48 %). We therefore decided to use the complete dataset with 45 pairwise comparisons, to ensure that a maximum of information was retained and to maximise statistical power in tests for the effect of covariates, such as the rate of defoliation.

We combined effect sizes across all comparisons, using the random effect model (Gurevitch and Hedges 1993) to calculate a weighted mean of growth loss (i.e. the grand mean effect size,  $E_{++}$ ). Because individual studies did not have similar sample sizes, and because the variance of effect size is a function of sample size, it was necessary to calculate a weighted average of effect sizes to estimate cumulative effect size for our sample of studies (Eq. 3)

$$E_{++} = \frac{\sum_{i=1}^n w_i \ln R_i}{\sum_{i=1}^n w_i} \quad (3)$$

with  $w_i = \frac{1}{v_{\ln R_i}}$ .

The mean effect size was considered statistically significant if its bias-corrected bootstrap confidence interval (CI), estimated with 9,999 iterations, did not include zero.

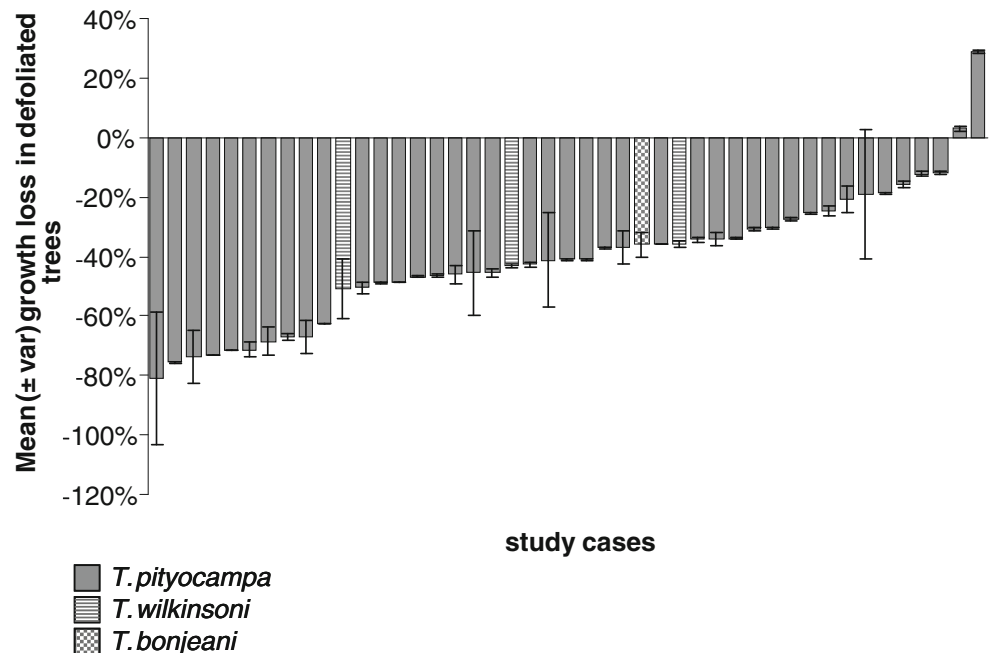
We used a mixed-effect model to assess between-class heterogeneity (for each covariate) and to evaluate the significance of the class effect (Gurevitch and Hedges 1999), assuming a fixed effect across classes and a random effect within classes (Borenstein et al. 2009). The weighted mean effect size  $E_j$  (Eq. 4) and a bias-corrected bootstrap confidence interval were then calculated for each class of covariate (tree age and defoliation rate).

$$E_j = \frac{\sum_{i=1}^{k_j} w_{ij} \ln R_{ij}}{\sum_{i=1}^{k_j} w_{ij}} \quad (4)$$

We calculated the variation in effect size explained by the categorical model ( $Q_{\text{Between}}$  or  $Q_B$ ). This between-class heterogeneity was tested against a  $\chi^2$  distribution, to evaluate the significance of the class effect. We back-transformed effect size values with the exponential function to provide a direct estimate of relative growth loss as a percentage of mean growth in unaffected trees.

The publication bias problem was addressed by calculating a fail-safe sample size corresponding to an estimate of the number of studies with a null effect size that we would need to add to the analysis to render the result of the meta-analysis non-significant. The weighted method proposed by Rosenberg (2005) was used to calculate the fail-safe number for our dataset, and this number was then compared with Rosenthal’s conservative critical value of  $5n+10$ , where  $n$  is the total number of comparisons (Rosenberg et al. 2000). All meta-analyses were carried out with METAWIN 2.0 software (Rosenberg et al. 2000).

**Fig. 1** Mean growth loss (as a percentage of growth in control trees) in trees defoliated by three species of processionary moth



### 3 Results

The qualitative examination of all retrieved published papers on the effects of processionary moth defoliation indicated that, in all but one case, tree growth was reduced by defoliation (Table 1). However, the relative growth loss attributed to processionary moth defoliation greatly varied between studies, and even for complete defoliation (100 %), it ranged from 20 to 80 % (Table 1).

Our quantitative review (meta-analysis) gave less ambiguous results. It clearly revealed that defoliation by processionary moth caterpillars resulted in a significant decrease in tree growth. The grand mean effect size was  $-0.55$  (CI= $-0.67$  to  $-0.45$ ), indicating a mean growth loss of 43 % (CI=36 to 49 %) with respect to unaffected trees. The weighted fail-safe sample size was 55,265, about 235 times larger than the critical value of 235 ( $(5 \times 45) + 10$ ). Thus, these results are unlikely to be affected by publication bias. In all but 2 of the 45 cases, individual growth rates were negative (Fig. 1). The two cases of a positive effect size, indicating greater growth in defoliated than in unaffected trees, corresponded to the same study (Barrento et al. 2008) and concerned 10–25-year-old trees with 1–25 % of defoliation by *T. pityocampa*. The tree growth response to defoliation by *T. bonjeani* and *T. wilkinsoni* fell within the range of variation for the tree growth response to defoliation by the more common species *T. pityocampa*.

#### 3.1 Effects of percent defoliation

Percentage defoliation had a highly significant effect on growth loss in defoliated trees ( $df=3$ ,  $Q_B=11.7$  and  $P=0.01$ ).



The mean effect size was negative and significantly different from zero for all defoliation rate classes, and its magnitude increased with the rate of defoliation. However, the effect of defoliation on growth loss seemed to level out from defoliation rates of 50 % on (Fig. 2). Low rates of defoliation (5–24 %) resulted in a growth loss of about 20 %, whereas severe defoliation (>50 %) induced growth losses of almost 50 %.

### 3.2 Effect of tree age

We tested the effect of tree age hierarchically within each class of processionary moth defoliation rate. We found a significant effect of tree age on tree growth response to processionary moth defoliation within the 5–24 % class ( $df=1$ ,  $Q_B=6.4$ ,  $P=0.03$ ) and the 75–100 % class ( $df=1$ ,  $Q_B=5.4$ ,  $P=0.05$ ) but not within the 50–74 % class ( $df=1$ ,  $Q_B=0.38$ ,  $P=0.48$ ). By grouping these three classes of defoliation, we observed an overall significant effect of tree age on growth response to processionary moth defoliation ( $df=1$ ,  $Q_B=6.0$ ,  $P=0.02$ ) with young trees exhibiting larger growth losses than old trees (Fig. 3). Too few replicates were available to allow testing this effect in the 25–49 % class.

## 4 Discussion

The impact of insect defoliation on the growth of evergreen tree species has been extensively studied and most of these studies have concluded that even low levels of defoliation can reduce radial or height growth. In a seminal literature review, Kulman (1971) discussed many cases of damage caused by moth and sawfly conifer defoliators and found that light defoliation induced a significant loss of 10 to 30 % of radial growth. The results of our meta-analysis are consistent with these findings, as we estimated that 5 to 24 % defoliation by processionary moth would reduce pine

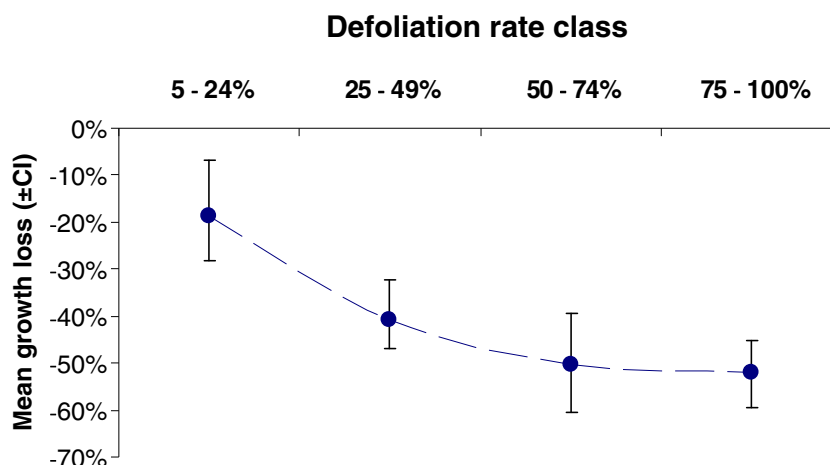
growth by about 20 %. At the other end of the gradient, heavy defoliation had a much greater impact, with 30 to 95 % growth loss (Kulman 1971). Similarly, severe defoliation by the sawflies *Diprion pini* (L.) on Scots pine (Langstrom et al. 2001; Lyytikäinen-Saarenmaa and Tomppo 2002), *Cephalcia lariciphila* (Wachtl) on larch (Vejpustková and Jaroslav 2006) and *Neodiprion abietis* (Harr.) on spruce (Parsons et al. 2003) reduced radial growth by 40 to 70 %. Radial increment in Scots pine was reduced by about 30 % at the peak of pine looper moth *Bupalus piniaria* (L.) outbreaks (Straw 1996) and by about 90 % in jack pines following heavy defoliation by *Choristoneura pinus* (Freeman) (Kulman 1963). Similarly, we found that 76 to 100 % defoliation by processionary moth caused ca. 50 % growth loss in conifers.

Only one study reported a positive effect of processionary moth on pine growth (Barrento et al. 2008), but this may be a false causal effect. Processionary moth females are known to select taller trees for oviposition (Démolin 1969). Young tall trees are likely to exhibit faster growth rates than smaller trees of the same age. If young and tall trees are only very lightly infested by processionary moth, this may not have any detrimental effect on their growth. Thus, growth rates may remain greater for taller defoliated trees than for smaller trees that have not been infested at all (which were considered as control).

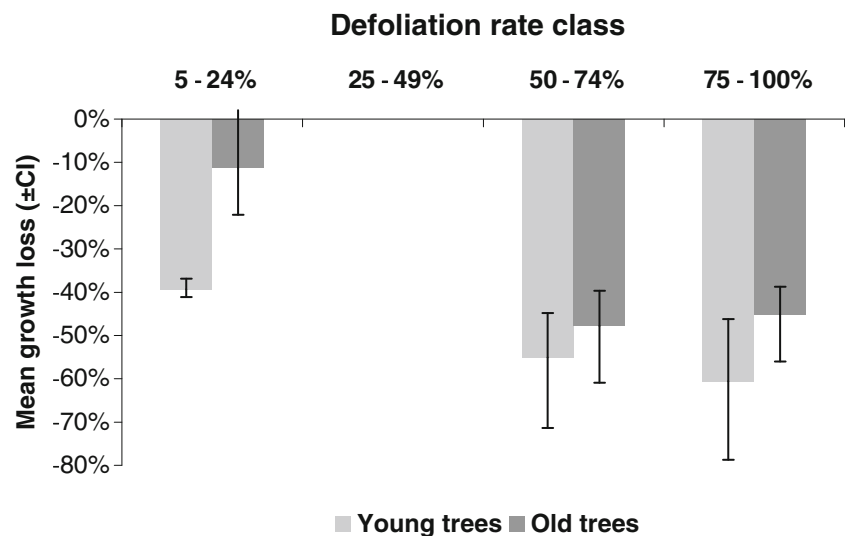
There is a broad consensus that the magnitude of growth loss is proportional to the amount of foliage removed by insect herbivores (Kulman 1971; Piene and Little 1990; Gross 1992; Reich et al. 1993). However our meta-analysis revealed an asymptotic relationship, since the effect of processionary moth damage on tree growth levelled out from 50 % of defoliation on (Fig. 2).

In conifers, initial shoot elongation makes use of stored photosynthates from the previous growing season, whereas summer wood growth and needle elongation are mostly dependent on current-year photosynthates (Kulman 1971).

**Fig. 2** Effect of the rate of defoliation by processionary moth on growth loss in defoliated trees



**Fig. 3** Effect of tree age on percent growth loss in defoliated trees, for two rates of defoliation by processionary moth. Note that the 25–49 % defoliation class is missing due to lack of data



According to the carbon/nutrient balance hypothesis (Krause and Raffa 1996), evergreen trees that store a large proportion of their biomass in needles may lose a large proportion of their carbohydrate reserves during defoliation. It has been also suggested that the elimination of old leaves during defoliation induces a shift in carbon allocation to higher priority sinks and, in particular, to the production of new foliage. This would result in carbohydrate shortage for stem diameter growth (Mayfield et al. 2005). For these reasons, conifers would be expected to suffer substantial growth loss in response to insect defoliation, with this impact evident in the same growing season, as observed with processionary moth.

Processionary moth caterpillars feed on pine and cedar needles in autumn and winter. They avoid feeding on young needles unless the mature ones are missing (A. Battisti personal communication). Old foliage contributes a significant part of the tree crown, for example 55 % of tree crown area in maritime pine (*Pinus pinaster* Ait.) (Porté et al. 2000). The consumption of old foliage is therefore likely to have a significant effect on tree growth (Parsons et al. 2003). However, new foliage produced in spring is known to have higher photosynthetic activity (Porté and Loustau 1997). A small fraction of new foliage regenerated by trees heavily defoliated in the previous winter could then be sufficient to resume growth, which could explain why complete processionary moth defoliation (76–100 %) decreased growth by only about 50 % (Fig. 2).

We found no difference in the effect of processionary moth defoliation on relative growth loss when estimated from circumference and height data. Similarly, Kulman (1971) and Wainhouse (2005) cited several studies in which the impact of insect defoliation on height growth was as severe as that on radial growth. However, we did observe a significant effect of tree age on growth responses to

processionary moth defoliation. Kulman (1971) and Wainhouse (2005) argued that young trees are more likely than old trees to die following severe defoliation, but that the growth-reducing effect of defoliation seems to be independent of tree age. Yet, young and older trees differ in term of canopy structure and nutrient storage capacity, and these differences are likely to influence their response to defoliation (Kelly et al. 1995; Straw et al. 2002, 2011). The proportion of older foliage is higher in old than young pine trees (Porté et al. 2000). Because processionary moth caterpillars start feeding on older foliage, for the same percentage defoliation, they will begin feeding on young foliage earlier in younger trees. Since young foliage contributes more to tree growth, the effect of processionary moth defoliation on younger trees is expected to be greater. Larger trees are also expected to mitigate some of the effects of defoliation by using stored nutrient reserves (Niinemets 2010). Although, we compared young and old trees through a meta-analysis of a number of different studies, it would be preferable to test the effect of processionary moth defoliation on the growth of trees of different age classes within the same experimental study, with the same site conditions and processionary moth population levels.

Overall, our meta-analysis, based on all available published papers on the topic, confirms that processionary moth defoliation has a significant impact on pine and cedar growth, even when only a small proportion of the foliage is consumed. Our findings also indicate that growth loss is more pronounced for younger than for older trees and would level out at ca. 50±10 % for heavily defoliated trees. These results suggest that estimates of processionary moth defoliation could easily be incorporated into tree growth models, to predict the effect of processionary moth outbreaks on carbon sequestration in Mediterranean forests.

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