



Effect of periodic defoliations by *Thaumetopoea pityocampa* Schiff. on radial growth in cedar woodland in Chr  a, Algeria

Mohamed Sbabdji, Luc Lambs, Ahmed Haddad, Bachir Kadik

► To cite this version:

Mohamed Sbabdji, Luc Lambs, Ahmed Haddad, Bachir Kadik. Effect of periodic defoliations by *Thaumetopoea pityocampa* Schiff. on radial growth in cedar woodland in Chr  a, Algeria. *Revue d'  cologie (La Terre et La Vie)* , 2015, 70 (4), pp.371-386. <hal-03530777>

HAL Id: hal-03530777

<https://hal.science/hal-03530777v1>

Submitted on 17 Jan 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destin  e au d  p  t et    la diffusion de documents scientifiques de niveau recherche, publi  s ou non,   manant des   tablissements d'enseignement et de recherche fran  ais ou   trangers, des laboratoires publics ou priv  s.



HAL Authorization

EFFECT OF PERIODIC DEFOLIATIONS BY *THAUMETOPOEA PITYOCAMPA* SCHIFF. ON
RADIAL GROWTH IN CEDAR WOODLAND IN CHRÉA, ALGERIA

Mohamed SBABDJI^{1*}, Luc LAMBS², Ahmed HADDAD³ & Bachir KADIK⁴

¹ Corresponding author. Forestry departement, École national supérieure agronomique, El Harrach, 16010 Algeria. Tel.: 00 213 66 20 67 514; e-mail: sbabdji_mohamed@yahoo.fr

² CNRS-ECOLAB UMR5245, 118 route de Narbonne, 31062 Toulouse cedex, France

³ Agronomic Sciences Department, University Abdelhamid Ibn Badis, Mostaganem, 27000 Algeria

⁴ National Institute of Forestry Research (INRF), BP 73, Chéraga Alger, Algeria

RESUME.— *Effet des défoliations périodiques par Thaumetopoea pityocampa Schiff. sur la croissance radiale des cèdres du Chréa, Algérie.*— La forêt emblématique de cèdres (*Cedrus atlantica* Manetti) du parc national de Chréa, 40 km au sud-ouest d'Alger, est attaquée par la Processionnaire du pin (*Thaumetopoea pityocampa* Schiff.). Nous avons étudié l'impact des pullulations successives de cette processionnaire entre 1980 et 2009 sur la croissance des cèdres pour voir si un éventuel effet cumulatif pourrait affecter la vitalité de ces arbres. Nous avons corrélié la largeur des cernes de croissance (dendrochronologie) aux décomptes de nids de processionnaires afin de déterminer les pertes de croissance et les temps de récupération. La population du papillon culmine tous les 5 ou 6 ans, les arbres étant sévèrement défoliés durant les pics d'explosion de chenilles. Après 3 années d'attaque, la population de l'insecte disparaît pendant 2 ou 3 ans, durant lesquels la croissance des cèdres se rétablit. Il n'y a pas d'effet cumulatif sur la croissance des arbres. Les résultats suggèrent que ces derniers résistent aux défoliations. Toutefois, on ne sait pas clairement combien de temps peut perdurer cet équilibre. Les effets de l'homme et du changement climatique peuvent affecter la vitalité de la cédraie et en modifier la dynamique.

SUMMARY.— The emblematic cedar forest (*Cedrus atlantica* Manetti) of North Algeria in the Chréa National Park, 40 km south-west of Algiers, is being attacked by the pine processionary moth (*Thaumetopoea pityocampa* Schiff.). We studied the impact of successive outbreaks of the processionary moth on the growth of cedar trees from 1980 to 2009 to assess if there is a cumulative effect that can affect their vitality. We correlated tree-ring width (dendrochronology) with nest counting to determine growth loss and time of recovery. The population culminates every 5 or 6 years, the trees are severely defoliated during the outbreak peaks. After 3 years of attack, the insect population disappears for 2 or 3 years, during which time cedar growth recovers. There is no cumulative effect on tree growth. The results suggest the trees are resistant to defoliations. However, it is unclear how long this equilibrium can be maintained. The anthropogenic effect and climate change can affect the vitality of the cedar trees and thus alter the balance.

The Atlas Cedar (*Cedrus atlantica* Manetti) is a coniferous species endemic to North Africa, where it covers the tops of high mountains in Morocco (130 000 ha) and Algeria (27 000 ha) (Benabid, 1994; Terrab *et al.*, 2008). It is one of the most important coniferous species in the Mediterranean area and attracts interest because of its numerous features: rusticity, wood quality (El Azzouzi & Keller, 1998, Messaoudène *et al.*, 2004) low sensitivity to fire and remarkable aesthetic value (Toth, 1978; M'hirith, 1982). In spite of this importance, the Atlas Cedar continues to be exposed to several constraints that limit its extension and can even affect its existence. Indeed, several native cedar woodlands are currently declining as a result of drought and climate change (Bentouati & Bariteau, 2006; Demarteau *et al.*, 2007; Linares *et al.*, 2011). Some authors also suggest that additional factors, such as defoliation by insects, decrease the initial vigour of trees and render these trees more vulnerable to other severe stresses such as drought (Hartmann & Messier, 2008; Allen *et al.*, 2010).

The outbreaks can enhance the sensitivity of trees to climate change and can increase their predisposition to mortality (Lovett *et al.*, 2002).

In the Mediterranean region, the processionary moth (*Thaumetopoea pityocampa* Schiff.) is considered to be one of the most important pests of coniferous forest (OEPP/EPPO, 2004). It is widespread in pine forests, and is also common on Atlas Cedar. Cedar trees are also attacked by a specific processionary (*Thaumetopoea bonjeani* Powel), which differs from *T. pityocampa* by its larval development in the spring and the beginning of summer, and by the absence of winter nests (Démolin, 1989; Gachi, 1994; Mouna, 2013). But *T. pityocampa* is more widespread, even on cedar trees (Démolin, 1989; Sbabdji, 2009). This defoliator can generate 90 % of growth losses (Jacquet *et al.*, 2013) and can prevent more than 35 % of total wood production (Durkaya *et al.*, 2009). The life cycle of *T. pityocampa* is normally annual, but it may extend to two years or more at high altitude or in northern latitudes for part or the whole of the population (Huchon & Démolin, 1970). Adults emerge in the summer and live for a few days, during which time they reproduce. A small percentage of their pupae exhibit extended diapauses (Démolin, 1974; Carus, 2010). Females lay between 70 and 300 eggs (Huchon & Démolin, 1970) grouped in a single cylindrical batch on the base of one or two needles (pines) or on the bark of 1–2 cm diameter cedar branches (Sbabdji & Kadik, 2011). Larvae are gregarious throughout their development, which occurs during autumn and winter in five stages. During the third stage, the larvae can release urticating setae (Petrucco Toffolo *et al.*, 2014) and build silk nests in which they are protected from climatic risks (Petrucco Toffolo, 2008) and enemies (Barbaro & Battisti 2011). At the end of larval development, corresponding to the end of the fifth stage, the larvae leave the nest in a procession and search for a suitable underground pupation site.

In Algeria, the cedar forest of Chrea national Park is one of the numerous cedar forests severely defoliated by this insect (Sbabdji *et al.*, 2009). Although the trees grow new foliage after each defoliation (Sbabdji & Kadik, 2011), their health is not assured because their vigour can be decreased by repeated outbreak (Hartmann & Messier, 2008). The different control practices have not significantly reduced the defoliations, mainly due to the difficulty to access to the tree crowns. Aerial control is also very expensive and probably disturbs protected ecological systems (Anonyme, 1988; Sbabdji, 2012). In this situation, the defoliator has an high capacity to continue its attacks and even extend it as the trees can also be weakened by the climate change. In addition, the diapause extensions of 2 years or more allows the population to cope with unpredictable unfavourable years (Hanski, 1988) and can ensure his resumption after decline (Aimi *et al.*, 2006).

For this reason, assessment of tree vigour is necessary to optimize forest management (Pleshanov *et al.*, 1991). Although this evaluation remains difficult to measure, tree radial growth can be used as an indicator (Dobbertin, 2005). A greater understanding of the attacks' effect can be attained by comparing tree-ring growth between defoliated and non-defoliated trees. This approach is frequently used in the assessment of defoliation history (Swetnam & Lynch, 1989; Tailleux & Cloutier, 1993; Zhang & Alfaro, 2002; Carus, 2004; Avci & Carus, 2005; Carus & Avci, 2005; Esper *et al.*, 2007; Touchan *et al.*, 2008) and for estimating the consequent loss of growth (Carus, 2009, 2010; Durkaya *et al.*, 2009; Jacquet *et al.*, 2012).

How do the trees respond to these successive outbreaks? Two hypotheses can be set forth. In the first case, the outbreak generates a growth loss and a new outbreak appears before the trees recover their complete vitality. This overlapping of the outbreaks will affect more and more the cedar trees by its cumulative effects. In the second case, the trees can recover their normal growth after each defoliation cycle, before they undergo the next attack. However, the growth loss generated by each outbreak remains limited and the tree can recover its vitality.

To check these two hypotheses, we have studied over a 30-year period the effects of defoliations engendered by repeated outbreaks of *T. pityocampa* on cedar trees in the Chr  a National Park, North Algeria, at an altitude of 1400 m. The trees vigour was evaluated from their radial growth (Dobbertin, 2005; Hartmann & Messier, 2008) and the outbreak periods were estimated by caterpillar nest counting.

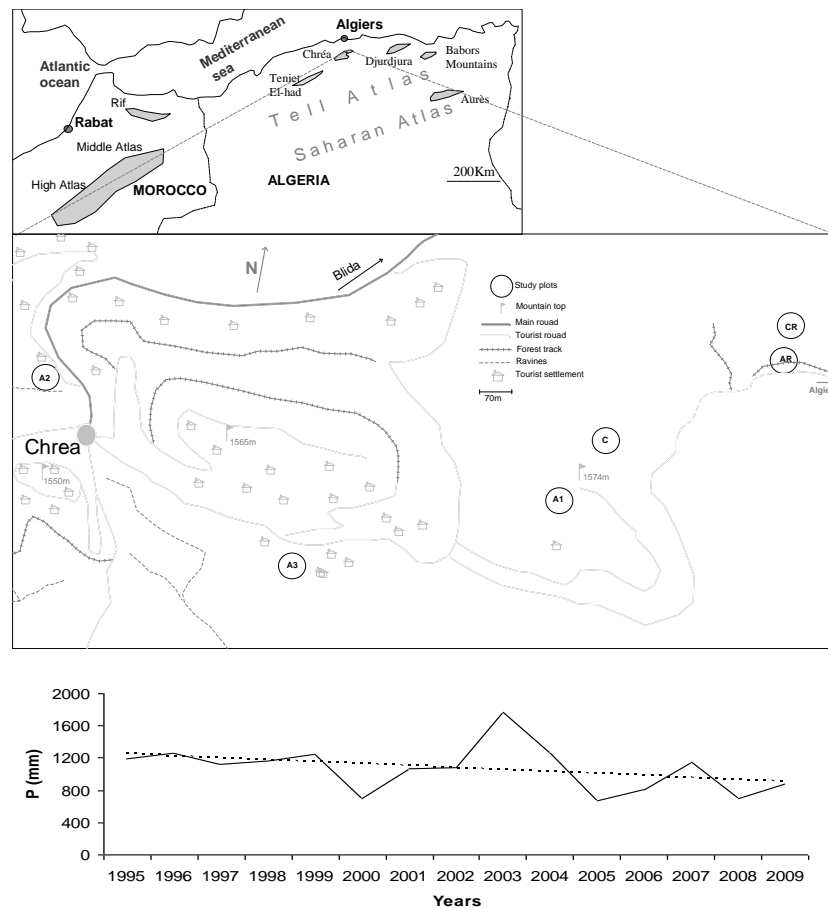


Figure 1.— a (above): Atlas Cedar distribution throughout North Africa and location of studied area in Chr  a with Localization of the controls plots (C, C_R), and the attacked plots (A₁, A₂, A₃, A_R); R stands for regeneration plots.
b (below): Annual rainfall pattern in Chr  a (1995–2009); the dotted line represents the global trend, data from the meteorological station of M  de  a.

MATERIAL AND METHODS

STUDY SITES

The study was performed in Chr  a National Park located in central area of Algeria (36  19' – 36  30'N and 2  38' – 3  02'E), about 40 km south-west of Algiers (Fig. 1a) just south of Blida town. It covers around 27 000 ha of higher mountains (900 -

1550 m) in the Mitidja area and is characterized by strongly sloped topography and a schistose soil. The climate is fresh and humid, with a mean annual rainfall of 950 - 1200 mm (Fig. 1b), monthly mean of temperatures between 3 - 7°C in winter and 18 - 23°C in summer; snow is relatively frequent (50 - 100 cm annually) (Sbabdji, 2012). The cedar woodland of Chr  a is composed of 1200 ha of native woodland and 30 ha of artificial woodland planted in 1968 - 1970; both occupy the higher elevations in the central part of the park between 1300 and 1550 m. The structure of the native woodland is homogeneous and of generally high density (distance between trees ~3 - 5 m). The trees are 80 - 120 years old, 15 - 25 m in height and 40 - 65 cm in diameter at breast height. However, on extreme south slopes and on the stripped high crest, the tree density is lower (about 70-100 trees/ha), leaving natural clearings with high levels of sunshine and frequent attacks by the pine processionary moth (Sbabdji *et al.*, 2009; Sbabdji, 2012). Because of the altitude, the undergrowth is mainly grass; however, some shrubs species such as *Taxus baccata* L., *Ilex aquifolium* L., *Acer obtusatum* Willd., *Juniperus oxycedrus* L. and others shrubs exist individually or in clusters (Meddour, 2002). In the artificial woodland, tree size is lower, 12 - 16 m in height and 35 - 50 cm in diameter at breast height; tree density is generally high (distance between trees about 3m) outside the clearings. The topography of the artificial woodland is less broken than that of native woodland.

TABLE I
Characteristics of sampling plots of wood cores

Batch plots	Plots	Geographical coordinates	Altitude (m)	Exposure	Structure	Age (y)	Tree numbers
Native woodland	Control (C)	36.431849°Lat - 2.885057°Long	1514	North	clearing	70-80	30
	Attacked 1 (A ₁)	36.430255°Lat - 2.884763° Long	1506	South-west	clearing	100	25
	Attacked 2 (A ₂)	36.427208°Lat - 2.875020° Long	1475	South-west	clearing	100	30
	Attacked 3 (A ₃)	36.427666° Lat - 2.878289° Long	1535	South-west	clearing	120	30
Artificial woodland	Control (C _R)	36.455890°Lat - 2.920463° Long	1468	mountain top « flat field »	closed woodland « relatively dense »	42	30
	Attacked (A _R)	36.455167°Lat - 2.919763° Long	1470	mountain top « flat field »	clearing	42	30

Two groups of plots were defined on a crest road at over 1400 m. The first group consisted of four plots in the native cedar woodland near the village of Chr  a, three attacked plots (A₁, A₂ and A₃) and one control plot (C). Tree ages ranged from 80 to 120 years. The second group of two plots, one attacked (A_R) and one control plot (C_R), was located ca 5 km north-east of the first group, in the artificial cedar woodland. Contrary to the plots of the native woodland located on broken topography, these two plots are on flat ground. Nearly all the trees from the south and south-west exposure (Tab. I), were infested by PPM. These areas are characterized by lower density (distance between trees around 10-12m) and higher sunlight, which favour highly the defoliator's installation (D  molin, 1969; Jacquet, 2012). On the contrary the control plots are chosen in northern exposure, to avoid the presence of the defoliator, due to the coolest conditions. According to Bouchon & Toth, (1971), the comparison between attacked and control plots with different exposure, remains possible, if the distance between the plots is small. For this reason, we chose attacked plots only 300 m away from the control plots.

ESTIMATE OF DEFOLIATION RATE AND DEFOLIATOR POPULATION LEVEL

From 1991 to 2009, the number of nests per tree was determined from 30 - 40 trees per plot at the end of larval development each year (February to March) (Dusaussay & Geri, 1969; G  ri & Millier, 1985). Because of the variations in canopy size and the number of moths per nest, the defoliation intensity for each sample tree was estimated visually to the nearest 5 % (5, 10, 15 ... 100 %). The defoliation rate by plot corresponds to the average value. For the period before 1991, data on attacks were not available; however some information could be obtained from the ranger's reports, who mention each year the health condition of woodlands (Anonyme, 1988).

GROWTH LOSSES AND CORE SAMPLING

Estimation of tree growth loss after defoliation by insects is based on a comparison between trees from infested vs control plots. Growth measurements were taken from the annual rings in extracted wood cores. This method has been adopted by researchers working on a variety of tree – defoliator relationships (Hoogesteger & Karlsson, 1992; Kanat *et al.*, 2005; Mayfield *et al.*, 2005).

During winter 2010, between 25 and 30 increment cores were sampled from each plot, attacked and non-attacked (one per tree) from the uphill face of the trunk at breast height (1.30 m). The wood cores were glued onto wooden mounts. After drying, fine sandpaper was used to better expose their rings. After preliminary dating, ring widths were measured with the help of a calibrated microscope under x10 magnification. Dating and measurement errors were corrected by verifying the synchronicity between the cores from a given plot and by using standard dendrochronology corrections (Lebourgeois, 2010).

CALCULATION OF THE DAMAGE PERIOD AND RADIAL GROWTH LOSSES

Damage period identification

By comparing the relative mean growth profile of the control plots with those from the attacked plots, it is possible to determine the damage period. These mean growth values are obtained by dividing the annual radial growth by the mean radial growth of the given plot. From that and with regard of population level, the damage periods can be known. The years where the control plots and the attacked plots present the same growth rates is considered to be the period without outbreak.

Radial growth loss calculation

The calculation method of growth loss was based on determination of potential ring of attacked plot by comparison between growths of attacked and control plots during the periods without attacks (Bouchon & Toth, 1971; Lemoine, 1977; Avci & Carus, 2005). After synchronisation in growth profiles of trees at attacked and control plots had been determined during the period without infestation (non-infestation period), the potential growth ring corresponding to infestation years could be determined (Avci & Carus, 2005; Çatal, 2011) as follows:

$$A'P \text{ (potential tree-ring relative to } A') = A - A(C - C') / C \quad (\text{Lemoine 1977})$$

where A' is the effective growth of the attacked plot during the year of infestation, A is reference tree-ring of attacked plot, it corresponds to mean growth of the attacked plot during the period without damage, C' is the growth of the control plot during the year of infestation, C is the reference tree-ring of control plot, it corresponds to mean growth of the control plot during the period without damage. The growth losses (Gl) because of defoliations can then be obtained by:

$$(\text{potential ring width} - \text{real ring width}) / \text{potential ring width} \times 100; \text{ therefore } Gl = [1 - (A'C / AC')] \times 100.$$

The growth recovery period corresponds to years between the year of highest losses and the year when growth returned to its normal level.

Comparison of growth profiles was made by graphic superposition with the Excel 2010 program (Microsoft Corporation, Washington, USA) and the level of significance was calculated using Pearson's r . The calculation method was based on radial growth and uses the increase in growth of the mean of several years during the known non-infestation period.

STATISTICAL ANALYSIS

Data were analysed with XLSTAT Pro 7.1 (Microsoft Corporation, Washington, USA). Analyses of variance (ANOVA) and non-parametric Kruskal-Wallis tests were used to analyse defoliator population behaviour. The correlation test was used to evaluate the synchronization between growths at the different plots.

RESULTS

DEFOLIATOR POPULATION FLUCTUATION

Analysis of the defoliator population in the native plantation indicates four outbreaks between 1991 and 2009 (Tab. II). Each one lasted 3 years. It begins at a relatively low level, between two and six nests per tree, and generates a slight defoliation. During the following year, it increases significantly ($f = 182.49$, d.f. = 1, $p < 0.0001$; ANOVA test for $p = 0.05$) to reach its peak, which sometimes exceeds 15 nests per tree. However the trees are severely or totally defoliated. During the

last year, the population collapses dramatically ($f = 741.48$, d.f. = 1, $p < 0.0001$; ANOVA test for $p = 0.05$) and disappears over the next 2 or 3 years.

TABLE II

Mean number with standard deviation of caterpillar nests and estimation of tree defoliation in sampled plots. (For the years that are not mentioned, the population level is zero.)

Plots	Parameter	1991-92	1992-93	1995-96	1996-97	1997-98	1998-99	2001-02	2002-03	2003-04	2006-07	2007-08	2008-09
C	Nest/tree	0.33 (± 0.57)	0.00 (± 0.00)	0.00 (± 0.00)	0.45 (± 0.68)	0.68 (± 0.92)	0.38 (± 0.67)	0.38 (± 0.72)	0.82 (± 0.88)	0.44 (± 0.76)	0.00 -	0.00 -	0.17 (± 0.47)
	Defoliation %	< 5											
A ₁	Nest/tree	15.45 (± 4.22)	2.30 (± 2.61)	0.00 -	3.70 (± 2.76)	5.50 (± 2.34)	1.80 (± 1.67)	2.30 (± 2.47)	6.20 (± 4.02)	2.40 (± 1.57)	0.00 -	0.00 -	2.00 (± 2.29)
	Defoliation %	100 -	10 (± 10.36)	0.00 -	20 (± 17.76)	30 (± 15.57)	5 (± 6.64)	10 (± 15.38)	25 (± 20.87)	5 (± 5)	0.00 -	0.00 -	5 (± 10.18)
A ₂	Nest/tree	18.55 (± 4.26)	0.75 (± 0.81)	0.00	6.53 (± 3.37)	14.02 (± 4.16)	1.98 (± 1.97)	3.33 (± 3.29)	13.22 (± 3.05)	2.02 (± 1.67)	2.19 (± 1.90)	7.58 (± 2.32)	10.25 (± 2.16)
	Defoliation %	100 -	5 (± 4.3)	0.00	40 (± 6.5)	75 (± 13.8)	5 (± 4.4)	10 (± 5.7)	90 (± 17.3)	5 (± 5.2)	5 (± 6.8)	10 (± 11.4)	25 (± 9.4)
A ₃	Nest/tree	16.20 (± 4.40)	2.62 (± 1.71)	1.08 (± 1.30)	8.22 (± 2.64)	3.73 (± 3.01)	0.84 (± 1.04)	6.30 (± 2.73)	9.33 (± 2.63)	2.03 (± 1.44)	2.19 (± 2.16)	7.59 (± 2.05)	4.30 (± 2.09)
	Defoliation %	100 -	10 (± 6.32)	4.34 (± 5.09)	60 (± 15.70)	13.16 (± 13.97)	2.82 (± 2.99)	60 (± 20.22)	60 (± 9.28)	5 (± 3.95)	10 (± 8.97)	40 (± 11.10)	15.12 (± 9.71)
C _R	Nest/tree	1.13 (± 1.16)	0.93 (± 0.95)	0.00 -	0.00 -	0.00 -	0.00 -	0.00 -	0.25 (± 0.63)	0.00 -	0.00 --	0.00 -	0.00 -
	Defoliation %	< 5											
A _R	Nest/tree	7.88 (± 2.34)	1.28 (± 1.43)	0.00 -	1.42 (± 1.50)	3.61 (± 2.09)	0.58 (± 1.00)	1.77 (± 1.60)	4.21 (± 4.07)	2.18 (± 2.35)	0.00 -	0.43 (± 0.63)	1.32 (± 1.25)
	Defoliation %	100 -	4.45 4.21	0.00 -	12 14.30	20 14.39	5 6.22	10 12.32	30 24.88	10 9.98	0.00 -	5 4.58	10 4.16

The population fluctuation was highly correlated between plots ($r > 0.8$). The population level corresponding to peak is significantly different between outbreaks ($f = 104.72$, d.f. = 3, $p < 0.0001$; ANOVA test for $p = 0.05$) and plots ($f = 414.14$, d.f. = 3, $p < 0.0001$; ANOVA test for $p = 0.05$). For the attacked plot of artificial woodland, variation of the defoliator population was similar, increasing between the two first years of outbreak ($f = 30.80$, d.f. = 1, $p < 0.0001$; ANOVA test for $p = 0.05$) and decreasing one year later ($f = 107.99$, d.f. = 1, $p < 0.0001$; ANOVA test for $p = 0.05$). The difference was significant between outbreaks ($H_{\text{obs}} = 68.07 > H_{\text{theo}} = 7.81$, d.f. = 3, $p < 0.0001$; Kruskal–Wallis test for $p = 0.05$) and the rate of defoliation was also highly correlated with the population level ($r = 0.98$). Obviously, the most important defoliations were observed during the peak of outbreak. However, the outbreaks remain less intense than those of native woodland, excluding the first one (that of 1991-1993), the population level during the peaks was lower than five nests per tree.

TABLE III

Maximum; Minimum and mean value of radial growth (mm) and interdatation coefficients

Batch plots	Plots	Max tree-ring width (year)	Min tree-ring width (year)	Mean tree-ring width (mm)	Crossdating
Native woodland.	Control (C)	2.38(1988)	1.05 (1999)	1.69 (± 0.34)	0.85
	Attacked (A ₁)	1.81 (1988)	0.64 (1999)	1.19 (± 0.29)	0.80
	Attacked (A ₂)	1.11 (1989)	0.35 (2003)	0.73 (± 0.21)	0.61
	Attacked (A ₃)	1.70 (1984)	0.58 (2002)	1.23 (± 0.29)	0.65
Artificial woodland.	Pilot (C _R)	8.96 (1985)	3.4 (2009)	5.36 (± 1.49)	0.68
	Attacked (A _R)	6.67 (1988)	2.98 (1992)	4.99 (± 1.02)	0.65

The coefficient of crossdating assesses the level of synchronization between trees

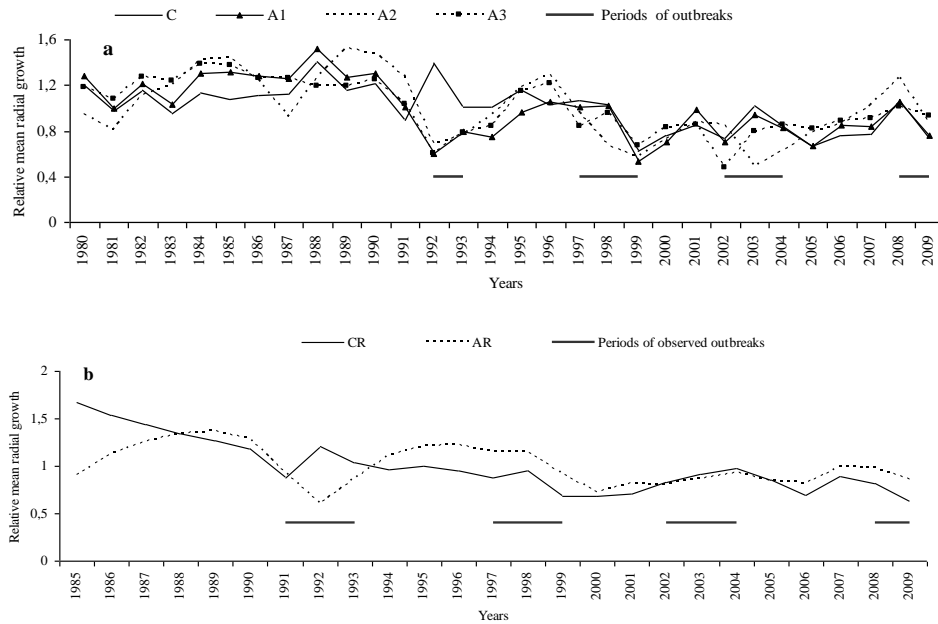


Figure 2.— Relative growth means variation for the native woodland (a) and the artificial woodland (b). The infestation period (observed defoliation) is given at the bottom of the figure.

SYNCHRONIZATION BETWEEN PLOTS GROWTH AND REFERENCE TREE-RINGS

In the case of native cedar woodland, the highest radial growth was recorded at the control plot, whereas the lowest was at the second attacked plot (Tab. III). The mean of annual radial growth of control plot is positively correlated with those of the attacked plots ($r = 0.67, 0.45$ and 0.51 for A₁, A₂ and A₃, respectively). The annual variation in mean relative radial growth allowed better identification of periods without damage (Fig. 2a). The growth of attacked plots drops during the infestation periods. The effect is strongest during the first attack period (1992–1994) for the three plots. For the other

attack periods, the growth losses are relatively low and different between plots. The first attacked plot (A_1) is highly synchronized with the control plot except for 1992–1995 ($r = 0.95$). Therefore, the reference period was based on those years (i.e., 1980–1991 and 1996–2009). The reference tree-ring width was 1.65 ± 0.33 mm for C and 1.23 ± 0.29 mm for A_1 .

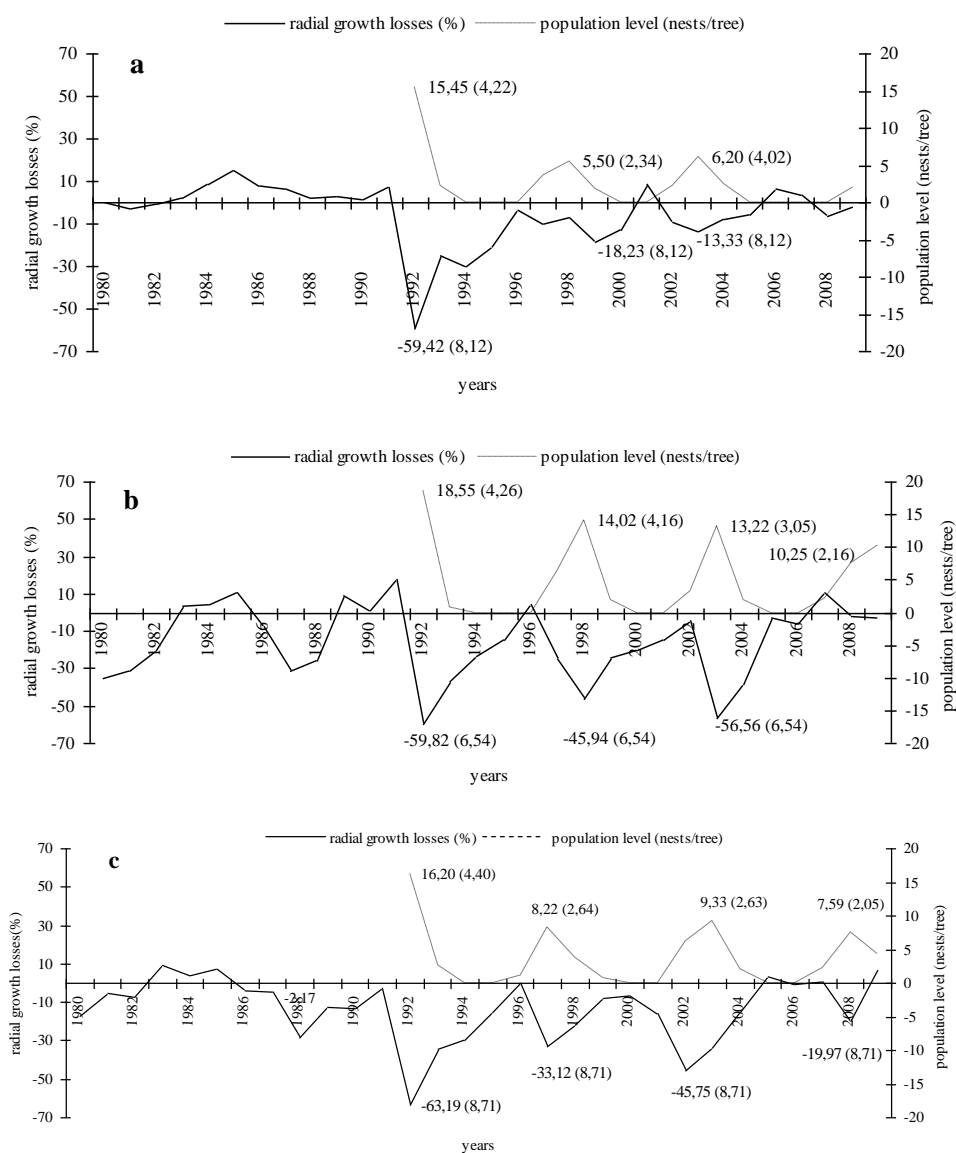


Figure 3.— a, b, c Variation in radial growth losses follows the population level at the plots of native cedar woodland (A_1 in a, A_2 in b and A_3 in c) in Chr a, with mean value and standard deviations.

The other two attacked plots in native woodland (A_2 and A_3) appear only weakly synchronized with the control. Consequently, their reference periods were reduced compared with that of the first plot: 2005–2009 for A_2 ($r = 0.95$) and 1980–1987 for A_3 ($r = 0.63$). There was no notable defoliation at the second plot in 2008 and 2009 because of a high proportion of reduced nests (weak colonies). The reference tree-ring width for plot A_2 was 1.35 ± 0.26 mm for C and 0.70 ± 0.13 mm for A_2 ; for plot A_3 , it was 1.82 ± 0.14 mm for C and 1.56 ± 0.12 mm for A_3 .

The two plots (attacked and control) of artificial woodland display similar but relatively lower correlation ($r = 0.44$). However, they show good synchronization after the first gradation (1991–1993) (Fig 2b). Indeed, the more recent gradations have not induced substantial defoliation in this woodland. However, the small divergence in 2002, 2003 and 2004 suggests a weak effect from this outbreak. Therefore, the reference periods are 1994–2001 and 2006–2009 ($r = 0.92$) with the reference ring width being 4.4 ± 0.72 mm for C_R and 4.95 ± 0.85 mm for A_R .

GROWTH LOSS FLUCTUATIONS FOLLOW POPULATION LEVEL

For all plots, the maximal growth loss, around 60 %, was found to have occurred in 1992 (Fig. 3a–c). This corresponds to the peak of highest outbreak of 1991–1993, which totally defoliated all trees in all plots without exception. The corresponding population levels exceeded 15 nests per tree in the native woodland, and seven nests per tree in the artificial woodland. On the other hand, the extent of the other outbreaks remained less important. Their peak was low, at five nests per tree in artificial woodland and at 10 nests per tree in native woodland; except in the second plot, which recorded between 10 and 14 nests per tree. For the case of highest attack of 1991–92, the growth losses persisted four years for the native woodland, but only 2 years in the artificial woodland (Fig. 4).

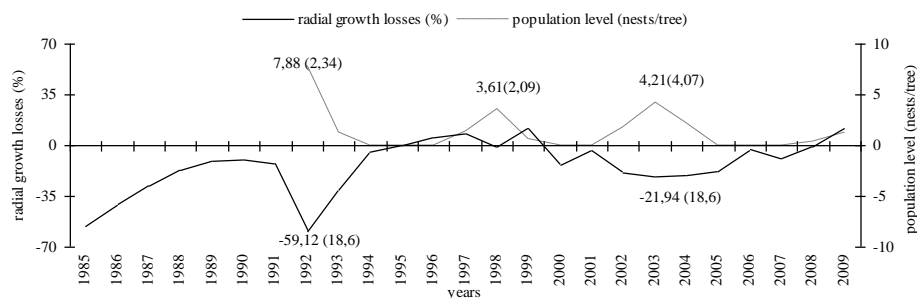


Figure 4.— Variation in radial growth losses follows the population level in the plots of artificial cedar woodland (A_R) in Chréa, with mean values and standard deviations.

Growth rate recovery occurred in 1996 in the native woodland and in 1994 in the artificial woodland. With regard to the other gradations, the recorded losses were relatively less important and differed between plots and gradations. They were low for the first native woodland plot and the artificial woodland plot (< 22 %), average in the third native woodland plot (20 – 46 %) and relatively high in the second native woodland plot (46 – 57 %). The difference of losses between plots and outbreaks are explained by relativity between losses and intensity of attacks. Indeed, the growth losses depend on the population level at the corresponding outbreak peak ($r = 0.93$) and on the total nests per outbreak ($r = 0.92$). In other words, they are related to defoliation intensity ($r = 0.95$) during the outbreak peak and to mean defoliation intensity during all outbreak years ($r = 0.94$). The duration of

recovery period is more related to defoliation intensity during the outbreak peak ($r = 0.69$) than to defoliations mean intensity produced during the years of outbreak ($r = 0.52$).

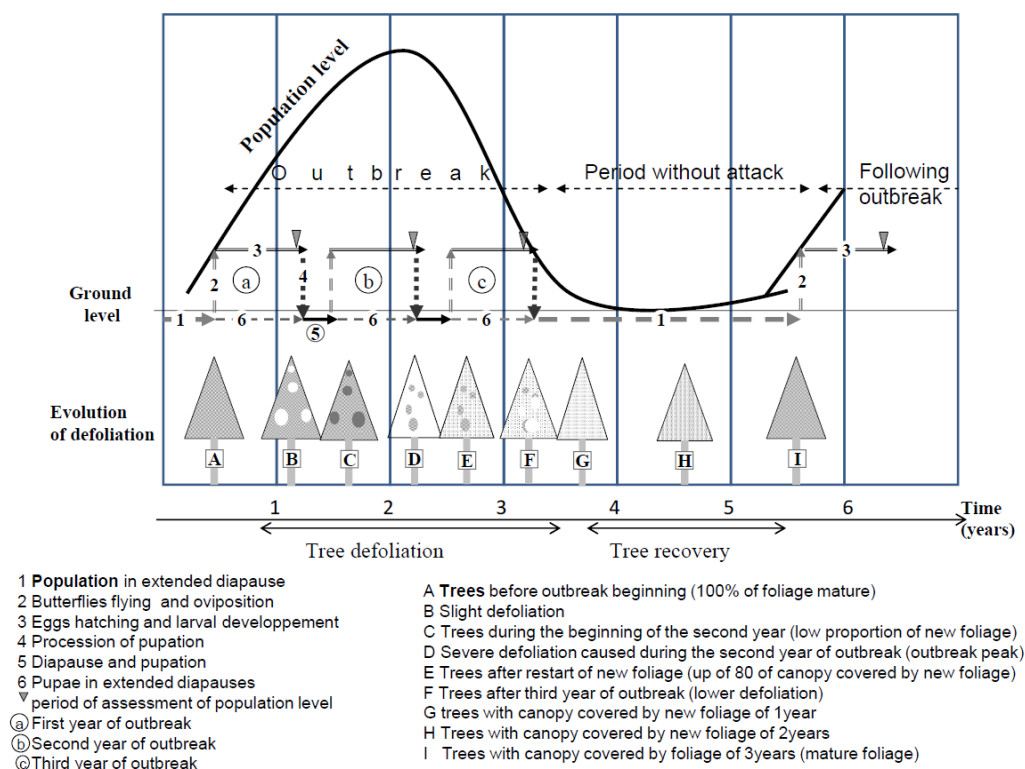


Figure 5.— Annual biological cycle of the pine processionary moth and pluri-annual outbreak cycle.

DISCUSSION

OUTBREAKS AND DEFOLIATIONS

Forest defoliation by insects is one of the most crucial problems of forest management. The difficulties are related to the persistence of insects against enemies, control actions and also to their high reproductive potential. The pine processionary moth is one among these species which inflict serious economic and ecological losses by their severe defoliations on several Mediterranean conifers (Hodar *et al.*, 2002). Since over a century, it continues to be a serious concern of management and focus for numerous studies. Several among recent works have mentioned that their outbreaks can be accentuated and extended by climate change (Battisti *et al.*, 2005; Buffo *et al.*, 2007; Petrucco Toffolo *et al.*, 2006). However, they can have other effects than growth losses. They can threaten tree vitality of their hosts in current or potential range (Hodar *et al.*, 2003; Allen *et al.*, 2010). They can broaden and intensify the effects of the accentuation of climate warming through the limitation of carbon

sequestration (Jacquet *et al.*, 2012 and 2013). For this reason, studies of tree resistance over years after intense and repeated outbreaks are primordial. Thus, the results of the present work sign up in this context and provide interesting information for forest management, mainly for protection of one among the major Mediterranean forest species, the Atlas Cedar highly threatened by climate change.

Thirty years of analyses indicate that cedars are able to resist successive defoliations. Since 1991, the recording of insect population level shows that this woodland was severely attacked about every 5 years (1992, 1998, 2003 and 2008). For the period between 1980 and 1990, radial growth losses and the rangers' reports (Anonymous 1988) suggest two other attacks, the first between 1980 and 1982, and the second between 1986 and 1988. A simulated sinusoid fits well with the gradations of 1981–1983, 1987–1988, 1991–1993, 1997–1999, 2002–2004, 2008–2009 and a period of 5.6 years (figure not shown). This overall period of 5 to 6 years is given in Fig. 5, and corresponds to 2–3 years of defoliator outbreak, followed by 2–3 years without attack. Similar indications of fluctuations are given by Graf & Mzibri (1994) on cedar woodlands in Morocco, Bouhot-Delduc & Lévy (1994) on the Landes maritime pine woodland, Battisti (1988) on Austrian pine in northern Italy and more recently by Jacquet *et al.* (2013) on maritime pine in Landes de Gascogne, south-western France. A similar periodicity of outbreaks is obtained on Crimean pine in Turkey by Carus (2004) and Kanat *et al.* (2005) through tree-ring analysis. However, the periodicity of outbreaks was more pronounced for cedar woodland in Chr  a where the population disappeared during 2 or 3 year after each outbreak. Currently no definite reason is found, but it involves probably complex interactions between defoliator density and microclimate with host. The increasing diapauses time period after a decline of foliage quality was also reported on the Oblique banded Leaf roller (*Choristoneura rosaceana*) (Hunter & McNeil, 1997) and on the Pine Sawfly (*Diprion pini*) (Geri *et al.*, 1988). During the third year of outbreak, larvae are constrained to feed on unfit new foliage which develops after severe defoliation (second year of outbreak). This young toxic foliage causes mortality among first stage larvae (Sbadjji & Kadik, 2011), but can also induce extended diapauses period. Indeed, high rate of extended diapauses ensures the permanent presence of a large stock of fungus in the soil (Battisti *et al.*, 1998), mainly in moist soil condition. Thus, the mortality of pupae can reach 96 % in worse case (Markalas, 1989). For the moist Chr  a area, in the more attacked sites, a preliminary examination shows that 57 % of the pupae population remains in extended diapauses before an outbreak period, and up to 85 % of the population die before the next flight period (Sbadjji, 2012).

RADIAL GROWTH LOSS AND RECOVERY

The radial growth fluctuations following successive outbreaks show that the most severe attack was between 1991 and 1993, with growth losses of about 60 % during the year of peak outbreak. The mean growth loss was about 33 % (33.8 %, 33.63 % and 35.46 % for A₁, A₂ and A₃, respectively) during these 4 years. Yearly values decline from year to year since the first attack as reported by other authors (Joly, 1970; Cadahia & Insua, 1970). Carus (2010) noted the same mean growth loss on Crimean pine in Turkey but prolonged on seven years. Gachi *et al.* (2005) have obtained similar mean of growth loss (33.77 %) during five years on the cedar woodland of B  lezma (eastern Algeria) defoliated by the cedar processionary moth (*Thaumetopoea bonjeani* P.). For the same period of persistence (four years), the value of growth losses noted by Kanat *et al.* (2005) on Calabrian pine (*Pinus brutia*) was relatively lower (21 %).

After 1993, the outbreaks were less intense (~5–6, 10–14, 8–9 and 3–4 nests/tree for A₁, A₂, A₃ and A_R, respectively) and generated relatively low growth losses (Jacquet *et al.* 2013). Exceptions were in 1998 (45.95 %) and 2003 (56.56 %) for A₂ and in 2003 (45.75 %) for A₃, where the population peaks were also high (14.02, 13.22 and 9.33 nests per tree, respectively), because the adults were

attracted by the urban lighting (Pouvreau, 1998). Questienne & Mieroment (1979) and Dajoz (1980) have affirmed that in sites near urbanistic areas, trees undergo more attacks than elsewhere. In contrast, at the other two attacked plots (A_1 and A_R), which are far from urban disturbance, the population level remained very low after the decline in 1994. However, for all plots, the growth losses recorded during the peak of higher outbreak of 1991-1993 are very similar, about 60 % (59-63 %), and concur with Jacquet *et al.* (2012) who mention that defoliation rates of 76-100 % generate 50 % of loss. For the others outbreaks, growth losses differ depending on defoliation rate (Jacquet *et al.*, 2013).

In spite of this exceptionally strong attack in 1991, the trees of the native woodland progressively recovered their normal growth rate over the next 4 years (1992–1995). During the fifth year after the peak of outbreak (1996), that is one year before the beginning of the following outbreak, the trees reached their usual mean growth. This ability of growth recovery after each defoliation, for the three plots, confirms that these century-old cedars do not accumulate side-effects after several gradations. In the artificial woodland (A_R), the younger cedar trees recover their growth more quickly than the older native trees.

This result suggests that cedar trees resist to periodic attack by pine processionary and explains why those attacks do not affect their vitality. It seems that tree resistance is ensured by double alternation between the active periods of both species. At the yearly scale, the greatest needs of the defoliator for foliage coincide in winter with the vegetative latency of trees. As soon as the insect completes its larval development and returns to the diapauses phase, the trees grow new foliage to synthesize resources (a phenological yearly relationship). At the pluri-annual scale of the outbreak cycle, the insect population increases during the first two years but affects tree growth. During the next two to three years, when the trees recover their growth, insect numbers collapse dramatically. So in the first years, defoliator population increases and tree growth decreases, in the latter years, defoliator population decreases and trees recover their original growth rate.

This alternation enables cedar trees to better resist defoliator effects. This dual relationship suggests a rational use of foliage resources by insect. The period without attacks is ensured by the prolonged diapauses of the defoliator population and by the bad food quality of the young foliage that occurs after defoliation (Battisti, 1988; Hodar *et al.*, 2004; Sbabdji & Kadik, 2011) (Fig. 5).

Following this observation, in this case there is no problem on trees vitality by repeated defoliation every 5 or 6 years, but the risks remain depending on tree growth recovery. Thus, the young trees of artificial woodlands appear less threatened. Indeed, they recover more quickly their growth, two year before the next outbreak. But for the older trees of native woodland four or five years are needed for growth recovery, this means only one year before the beginning of a new outbreak. They are then more likely to suffer from the cumulative effects of successive outbreaks. This probably indicates that vulnerability to defoliation can increase with tree age (Joly, 1952; Jacquet, 2012). However the quick recovery of young trees can be equally related to site characteristics, mainly when located on flat ground. In this type of area, soil is stable and deep, trees grow better and their resistance to difficult circumstances such as drought is improved (Lecompte & Lepoutre, 1975; Linares, 2011).

This suggests that tree growth fluctuations, responding to defoliations, can be changed by the environmental factors. However, the growth recovery by the older native trees, only one year before the beginning of the following outbreak, represents a short quiet period. The accentuation of drought, remarkable in northern Africa since the 1980s, may affect their vitality (Allen *et al.*, 2010; Bentouati, 2008; Lambs & Labiod, 2009; Linares *et al.*, 2011), and decrease their capacity to recover growth after defoliations. Figure 1b shows the rainfall variations in Chr  a and the downward trend. The annual mean rainfall was ~1385 mm for the period 1913–1960 (Halimi, 1980). The values of 1995-2009 are definitely weaker (1072 mm of mean) and tend towards the regression (Fig. 1b). Near Chr  a, the

measurements at two rainfall stations, Médéa and Hakou-Ferraoune, at a similar altitude (~940m) and located on opposite slopes, reveal that the south location could receive up to 30 % less rainfall. This means that during a dry year, and especially for trees located on a south slope, the hydric conditions are poor (≤ 600 mm rainfall). As such, the cedars are more vulnerable to infestation. This statement seems very worrying, because the climate change and drought can also increase the pressure of pests (Démolin *et al.*, 1996; Battisti *et al.*, 2005; Jacquet, 2012) and the repetition of outbreaks linked to or happening after a drought event can lead to tree mortality (Allen *et al.*, 2010).

CONCLUSIONS

The Atlas Cedar (*C. atlantica* Manetti) is an endemic species of the North African mountains from Morocco to Algeria. Although having a relatively large tolerance to climate and soil type variations, it is threatened by climatic change, particularly since the early 1980s (Bentouati & Bariteau, 2006). These severe droughts and temperature increases particularly affect the southern cedar woodland, which receives the Sahara wind. Northern cedar woodlands seem behaving better but undergo a high pest attacks and anthropogenic pressure that may also affect their health. Results of the present work suggest that in Chréa area cedars have overcome much severe defoliation by the pine processionary. Defoliated each 5 or 6 years, they recover their growth during the periods between outbreaks which allows them not to undergo the cumulated effect of outbreaks. This result adds to those showing that, after defoliation, trees develop a foliage unfit for defoliators (Sbaddji & Kadik, 2011), suggesting that trees can probably avoid continuous defoliations. Until now, neither tree mortality nor tree dieback is observed on Chréa's cedars. How will these trees support the defoliations stress plus the climate change? This question looks very worrying, because climate change can also increase pests pressure (Démolin *et al.*, 1996; Battisti *et al.*, 2005; Jacquet, 2012) and the repetition of outbreaks linked to or happening after drought events can lead to tree mortality (Allen *et al.*, 2010). More work is required to obtain longer tree growth records and climate data to understand these interactions, needed to better protect the endemic cedar forests.

ACKNOWLEDGEMENTS

We would thanks the numerous reviewers for their valuables remarks, corrections and suggestions

REFERENCES

- AIMI, A., ZOCCA, A., MINERBI, S., HELLRIGL, K., GATTO, P. & BATTISTI, A. (2006).— The outbreak of the pine processionary moth in Venosta/Vinschgau: ecological and economic aspects. *Forest Observer*, 2/3: 69-80.
- ALLEN, C.D., MACALADY, A.K., CHENCHOUNI, H., BACHELET, D., MCGOWELL, N., VENNETIER, M., KITZBERGER, T., RIGLING, A., BRESHEARS, D., HOGG, E.H., GONZALEZ, P., FENSHAM, R., ZHANG, Z., CASTRO, J., DEMIDOVA, N., LIM, J.-H., ALLARD, G., RUNNING, S.W., SEMERCI, A. & COBB, N. (2010).— A global overview of drought and heat- induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol. Manag.*, 259: 660-684.
- ANONYME (1988).— Rapport sur le traitement aérien contre la chenille processionnaire du pin (*Thaumetopoea pityocampa* Schiff.) au niveau de la cédraie de Chréa. *Conservation des forêts de la wilaya de Blida*. Algérie.
- AVCI, M. & CARUS, S. (2005).— The impact of cedar processionary moth [*Traumatocampa ispartaensis* (Doğanlar & Avci) (Lepidoptera: Notodontidae)] outbreaks on radial growth of Lebanon cedar (*Cedrus libani* A. Rich.) trees in Turkey. *J. Pest Sci.*, 78: 91-98.
- BARBARO, L. & BATTISTI, A. (2011).— Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). *Biol. Contr.*, 56: 107-114.

- BATTISTI, A. (1988).— Host-plant relationships and population dynamics of the pine processionary caterpillar *Thaumetopoea pityocampa* (Denis & Schiffermuller). *J. Appl. Entomol.*, 105: 393-402.
- BATTISTI, A., LONGO, S., TIBERI, R. & TRIGGIANI, O. (1998).— Results and perspectives in the use of *Bacillus thuringiensis* Berl. var. *kurstaki* and other pathogens against *Thaumetopoea pityocampa* (Den. & Schiff.) in Italy (Lep., Thaumetopoeidae). *Anz. Schädlingsskde. Pflanzensch. Umweltsch.*, 71: 72-76.
- BATTISTI, A., STASTNY, M., NETHERER, S., ROBINET, C., SCHOPF, A., ROQUES, A. & LARSSON, S. (2005).— Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Applic.*, 15: 2084-2096.
- BENABID, A. (1994).— Biogéographie phytosociologie des cédraies de l'Atlas à *Cedrus atlantica* Manetti. *Ann. Rech. For. Maroc*, 27: 62-76.
- BENTOUATI, A. (2008).— La situation du cèdre de l'Atlas dans les Aurès (Algérie). *Forêt méditerranéenne*, 29: 203-208.
- BENTOUATI, A. & BARITEAU, M. (2006).— Réflexions sur le dépérissement du Cèdre de l'Atlas des Aurès (Algérie). *Forêt méditerranéenne*, 27: 317-322.
- BOUCHON, J. & TOTH, J. (1971).— Étude préliminaire sur les pertes de production des pinèdes soumises aux attaques de la processionnaire du pin *Thaumetopoea pityocampa* Schiff. *Ann. Sc. For.*, 23: 323-340.
- BOUHOT-DELDUC, L. & LEVY, A. (1994).— Rôle de la chenille processionnaire du pin dans les dépérissements du pin maritime Landais en 1990 et 1991. *Rev. For. Fr.*, 5: 431-435.
- BUFFO, E., BATTISTI, A., STASTNY, M. & LARSSON, S. (2007).— Temperature as a predictor of survival of the pine processionary moth in the Italian Alps. *Agric. For. Entomol.*, 9: 65-72.
- CADAHIA, D. & INSUA, A. (1970).— Estimación de los danos producidos por *Thaumetopoea pityocampa* Schiff. en repoblaciones de *Pinus radiata* D. DON. *Bol. Serv. Plagas Forestales*, 13: 159-171.
- CARUS, S. (2004).— Impact of defoliation by the pine processionary moth (*Thaumetopoea pityocampa*) on radial, height and volume growth of Calabrian pine (*Pinus brutia*) trees in Turkey. *Phytoparasitica*, 32: 459-469.
- CARUS, S. (2009).— Effects of defoliation caused by the processionary moth on growth of Crimean pines in western Turkey. *Phytoparasitica*, 37: 105-114.
- CARUS, S. (2010).— Effect of defoliation by the pine processionary moth (PPM) on radial, height and volume growth of Crimean pine (*Pinus nigra*) trees in Turkey. *J. Environ. Biol.*, 31: 453-460.
- CARUS, S. & AVCI, M. (2005).— Growth loss of Lebanon Cedar (*Cedrus libani*) stands as related to periodic outbreaks of the Cedar Shoot Moth (*Dichelia cedricola*). *Phytoparasitica*, 33: 33-48.
- ÇATAL, Y. (2011).— The effects of pine processionary moth (PPM) defoliation degree on radial growth of brutian pine (*Pinus brutia*). *Afr. J. Agric. Res.*, 6 (21): 4931-4936.
- DAJOZ, R. (1980).— *Écologie des insectes forestiers*. Bordas, Paris
- DEMARTEAU, M., FRANCOIS, L., CHEDDADI, R. & ROCHE, E. (2007).— Responses of *Cedrus atlantica* when faced with past and future climatic changes. *Geo. Eco. Trop.*, 31: 105-146.
- DEMOLIN, G. (1969).— Comportement des adultes de *Thaumetopoea pityocampa* Schiff. Dispersion spatiale, importance économique. *Ann. Sci. Forest.*, 26: 81-102.
- DEMOLIN, G. (1974).— Incidence du climat sur les gradations de population de la processionnaire du pin *Thaumetopoea pityocampa* Schiff. Recherches d'éléments ou d'incidences sur les potentialités négatives des populations. *Prognose C.R. fin de contrat D.G.R.S.T. n° 70 0 2174*: 1-17.
- DEMOLIN, G. (1989).— *La processionnaire du cèdre*: *Thaumetopoea bonjeani* Powel. *Rapport scientifique et rapport iconographique*. Projet : DP-FO-ALG/83/013.
- DÉMOLIN, G., ABGRALL, J.F. & BOUHOT-DELDUC, L. (1996).— Évolution de l'aire de la processionnaire du pin en France. *Cahiers du DSF*, 1: 26-28.
- DOBBERTIN, M. (2005).— Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur. J. For. Res.*, 124: 319-333.
- DURKAYA, A., DURKAYA, B. & DAL, S. (2009).— The effects of the pine processionary moth on the increment of Crimean pine trees in Bartin, Turkey. *Afr. J. Biotechnol.*, 8: 2356-2361.
- DUSAUSSOY, G. & GERI, C. (1969).— Étude des fluctuations du niveau de population de la Processionnaire du pin dans la vallée du Niolo en Corse (*Thaumetopoea pityocampa* Schiff.). Dispositif d'étude et premiers résultats. *Ann. Sci. For.*, 26: 103-125.
- EL AZZOUI, K. & KELLER, R. (1989).— Propriétés technologiques du bois de cèdre de l'Atlas (*Cedrus atlantica* Manetti). *Forêt méditerranéenne*, 19 : 11-33.

- ESPER, J., FRANK, D., BÜNTGEN, U., VERSTEGE, A. & LUTERBACHER, J. (2007).— Long-term drought severity variations in Morocco. *Geophys. Res. Lett.*, 34: 1-5.
- GACHI, M. (1994).— Note sur la présence en Algérie de la processionnaire du cèdre : *Thaumetopoea bonjeani* Powell (Lepidoptera ; Thaumetopoeidae). In : Le cèdre de l'Atlas. Actes du séminaire international sur le cèdre de l'Atlas. Ifrane (Maroc), 7 – 11 Juin 1993. *Ann. Rech. Forest. Maroc*, 27, spécial: 528-537.
- GACHI, M., DEMOLIN, G., ZAMOUM, M., & KHEMICI, M. (2005).— An evaluation of the radial growth losses of Atlas cedar following defoliation by *Thaumetopoea bonjeani* in the Belezma massif (Aurès, Algeria). *Entomological research in Mediterranean forest ecosystems. Inra editions*: 117-122
- GERI, C., GOUSSARD, F., ALLAIS, J.P. & BURATTI, L. (1988).— Incidence de l'alimentation sur le développement et la diapause de *Diprion pini* L. (Hym., Diprionidae). *J. Appl. Entomol.*, 106: 451-464.
- GÉRI, C. & MILLIER, C. (1985).— Mesure des populations de Processionnaire du Pin (*Thaumetopoea pityocampa* Schiff., Lépidoptère Thaumetopoeidae) au Mont-Ventoux. *Ann. Sci. Forest.*, 42: 143-184.
- GRAF, P. & MZIBRI, M. (1994).— L'infestation du cèdre de l'Atlas (*Cedrus atlantica* Manetti) par la chenille processionnaire (*Thaumetopoea pityocampa* Schiff.) au Maroc et son impact sur la productivité. *Ann. Rech. Forest. Maroc*, 27: 613-624.
- HALIMI, A. (1980).— *L'Atlas blidéen – climat et étages végétaux*. Office des Publications Universitaires, Hydra, Alger.
- HANSKI, I. (1988).— Four kinds of extra long diapause in insects: a review of theory and observations. *Ann. Zool. Fenn.*, 25: 37-53.
- HARTMANN, H. & MESSIER, C. (2008).— The role of forest tent caterpillar defoliations and partial harvest in the decline and death of Sugar Maple. *Ann. Bot.*, 102: 377-387.
- HODAR, J.A., CASTRO, J. & ZAMORA, R. (2003).— Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biol. Conserv.*, 110: 23-129.
- HODAR, J.A., ZAMORA, R., CASTRO, J. & BARAZA, E. (2002).— The effect of an outbreak of pine processionary caterpillar in the autochthonous woodlands of Sierra Nevada (SE Spain): suggestions for the plague control. Pp 327-332 in: K. Radoglou (ed.), *Forest Research: A Challenge for an Integrated European Approach*, vol. I. NAGREF, Forest Research Institute, Thessaloniki, Greece.
- HODAR J.A., ZAMORA R., CASTRO J. & BARAZA E. (2004).— Feast and famine: previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*. *Acta Oecol.*, 26: 203-210.
- HOOGESTEGE, J. & KARLSSON, P.S. (1992).— Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). *Funct. Ecol.*, 6: 317-323.
- HUCHON, H. & DÉMOLIN G. (1970).— La bioécologie de la processionnaire du pin: dispersion potentielle et dispersion actuelle. *Rev. Forest. Fr.*, XXII, N° spécial (*La lutte biologique en forêt*): 220-234.
- HUNTER M.D. & MCNEIL, J.N. (1997).— Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology*, 78: 977-986.
- JACQUET, J.S. (2012).— *Impacts des défoliations de la processionnaire du pin (Thaumetopoea pityocampa) sur la croissance du pin maritime (Pinus pinaster)*. Thèse de doctorat, université de Bordeaux 1.
- JACQUET, J.S., BOSC, A., ANTHONY, O.P. & JACTEL, H. (2013).— Pine growth response to processionary moth defoliation across a 40-year chronosequence. *Forest Ecol. Manag.*, 293: 29-38.
- JACQUET, J.S., ORAZIO, C. & JACTEL, H. (2012).— Defoliation by processionary moth significantly reduces tree growth: a quantitative review. *Ann. For. Sci.*, 69: 857-866.
- JOLY, R. (1952).— Influence des défoliateurs forestiers sur l'accroissement. *Ann. Inst. Feder. Rech. Forest.*, XXVIII: 233-237.
- JOLY, R. (1970).— Action des déprédations dues aux insectes défoliateurs sur le pin maritime. *Rev. Forest. Fr.*, XXII, N° spécial (*La lutte biologique en forêt*): 205-210.
- KANAT, M., ALMA, M.H. & SIVRIKAYA, F. (2005).— Effect of defoliation by *Thaumetopoea pityocampa* (Den. and Schiff.) (Lepidoptera : Thaumetopoeidae) on annual diameter increment of *Pinus brutia* Ten. in Turkey. *Ann. For. Sci.*, 62: 91-94.
- LAMBS, L. & LABIOD, M. (2009).— Climate change and water availability in north-west Algeria: investigation by stable water isotopes and dendrochronology. *Water Int.*, 34: 280-286.
- LEBOURGEOIS, F. (2010).— *Principes et méthodes de la dendrochronologie*. Agro Paris Tech, Laboratoire d'Étude des Ressources Forêt-Bois (LERFOB), Équipe Écologie Forestière ENGREF, Nancy.
- LECOMTE, M. & LEPOUTRE, B. (1975).— Bilan de l'eau et conditions d'existence de la cédraie dans le moyen Atlas basalitique (Maroc). Utilisation d'une analyse d'information mutuelle entre les espèces et les variables du milieu. *Ann. Rech. Forest. Maroc*, 15: 1-269.

- LEMOINE, B. (1977).— Contribution à la mesure des pertes de production causées par la chenille processionnaire (*Thaumetopoea pityocampa* Schiff.) au pin maritime dans les Landes de Gascogne. *Ann. Sci. Forest.*, 34: 205-214.
- LINARES, J.C., TAÏQUI, L. & CAMARERO, J.J. (2011).— Increasing drought sensitivity and decline of Atlas Cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas forests. *Forests*, 2: 777-796.
- LOVETT, G.M., CHRISTENSON, L.M., GROFFMAN, P.M., JONES, C.G., HART, J.E. & MITCHELL, M.J. (2002).— Insect defoliation and nitrogen cycling in forests. *BioScience* N°1.
- MARKALAS, S. (1989).— Influence of soil moisture on the mortality, fecundity and diapause of the pine processionary moth (*Thaumetopoea pityocampa* Schiff.). *J. Appl. Entomol.*, 107: 211-215.
- MAYFIELD, A.E., ALLEN D.C. & BRIGGS, R.D. (2005).— Radial growth impact of pine false webworm defoliation on eastern white pine. *Canad. J. For. Res.*, 35: 1071-1086.
- MEDDOUR, R. (2002).— Bioclimats, étages et séries de végétation de l'Atlas Blidéen (Algérie). *Phytocoenologia*, 32: 101-128.
- MESSAOUDENE, M., LOUKKAS, A., JANIN, G., TAHER, M., DILEM, A. & JOAQUIM GONCALEZ, J. (2004).— Propriétés physiques du bois d'éclaircie des cèdres (*Cedrus atlantica*), contenant du bois de compression, provenant de l'Atlas du Djurdjura (Algérie). *Ann. For. Sci.*, 61: 589-595.
- M'HIRITH, O. (1982).— Étude écologique et forestière des cédraies du Rif Marocain : Essai sur une approche multidimensionnelle de la phytoécologie et de la production du cèdre de l'atlas. *Ann. Rech. For. Maroc*, 2: 1-499.
- MOUNA, M. (2013).— Les insectes du cèdre (*Cedrus atlantica* Manetti) dans le Nord de l'Afrique. *Trav. Instit. Scient., Série Zoologie*, n°48: 1-81.
- OEPP/EPPO (2004).— Diagnostic protocols for regulated pests *Thaumetopoea pityocampa*. *Bull. OEPP/EPPO*, 34: 155-157.
- PLESHANOV, A.A., VARONIN, V.I., KHLIMANKOVA, E.S. & EPOVA, V.I. (1991).— Tolerance to insect defoliation: Biocenotic aspect. In: Y.N. Baranchikov, W.J. Mattson, F.P. Hain & T.L. Payne (eds), *Forest insect guilds: Patterns of interaction with host trees*. U.S. Dept. Agric. For. Sew. Gen. Tech. Rep. NE-153.
- PETRUCO TOFFOLO, E. (2008).— *Climate change and pine processionary moth. Role of the host plant*. Thèse de doctorat en sciences agronomiques et environnementale, université de Padova, Italie.
- PETRUCO TOFFOLO, E., BERNARDINELLI, I., STERGULC, F. & BATTISTI, A. (2006).— Climate change and expansion of the pine processionary moth, *Thaumetopoea pityocampa*, in northern Italy. Pp 331-340 in: *IUFRO Working Party 7.03.10 Proceedings of the Workshop 2006*. Gmunden, Austria
- PETRUCO TOFFOLO, E., ZIVI, D., PERIN, C., PAOLUCCI, P., ROQUES, A., BATTISTI, A. & HORVATH, H. (2014).— Size and dispersion of urticating setae in three species of processionary moths. *Integr. Zool.*, 9: 320-327.
- POUVEAU, A. (1998).— Les insectes venimeux urticants. *Insectes*, 114 (3): 9-12.
- QUESTIENNE, P. & MIERMONT, Y. (1979).— Contribution à la connaissance de *Thaumetopoea pityocampa* (Schiff.). Étude de la chenille processionnaire du pin et du cèdre au Maroc. *Ann. Rech. Forest. Maroc*, 19: 80-147.
- SBABDI, M. (2012).— *Étude des infestations de la cédraie de Chréa par la processionnaire du pin, Thaumetopoea pityocampa Schiff.: description spatiotemporelle et interaction arbre- défoliateur*. Thèse de doctorat, ENSA, El Harrach, Alger.
- SBABDI, M., EL HADI, O., HADDAD, A., KADIK, B. & LAMBS, L. (2009).— Cedar tree growth (*Cedrus atlantica* Manetti) in Chréa national park, Algeria, and the influence of defoliation by the pine processionary caterpillar (*Thaumetopoea pityocampa* Schiff.). *Rev. Ecol. (Terre et Vie)*, 64: 323- 332
- SBABDI, M. & KADIK, B. (2011).— Effets of Atlas cedar (*Cedrus atlantica*) defoliation on performance of the pine processionary moth (*Thaumetopoea pityocampa*). *J. Pest Sci.*, 84: 213-217.
- SWETNAM, T.W. & LYNCH, A.M. (1989).— A tree-ring reconstruction of Western Spruce Budworm history in the Southern Rocky Mountains. *For. Sci.*, 35: 962-986.
- TAILLEUX, I. & CLOUTIER, C. (1993).— Defoliation of tamarack by outbreak populations of larch sawfly in subarctic Quebec: Measuring the impact on tree growth. *Can. J. For. Res.*, 23:1444-1452.
- TERRAB, A., HAMPE, A., LEPAIS, O., TALAVERA, S., VELA, E. & STUESSY, T.F. (2008).— Phylogeography of North African Atlas cedar (*Cedrus atlantica*, Pinaceae): combined molecular and fossil data reveal a complex Quaternary history. *Am. J. Bot.*, 95: 1262-1269.
- TOTH, J. (1978).— *Contribution à l'étude de la fructification et de la régénération du Cèdre de l'Atlas (Cedrus atlantica M.) dans le Sud de la France*. Thèse Doc. Ing. Fac. St. Jérôme. Marseille, France.
- TOUCHAN, R., ANCHUKAITIS, K.J., DAVID, M., MEKO, D.M., SAID ATTALAH, S., BAISAN, C. & ALOUI, A., (2008).— Long term context for recent drought in northwestern Africa. *Geograph. Res. Lett.*, 35, L13705, 5p.
- ZHANG, Q.B. & 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.