

Original article

# Feast and famine: previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*

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## Abstract

This study analyses the consequences of previous defoliation on the survival of the larvae of the pine processionary moth *Thaumetopoea pityocampa* (Denis and Schiffmüller) feeding on relict Scots pine *Pinus sylvestris* (L.) ssp. *nevadensis* Christ in the Sierra Nevada mountains (SE Spain). Egg batches of the pine processionary moth were placed on four groups of Scots pines that underwent different periods of herbivory. The larval survival was related to the nitrogen content, fibre, phenolics and terpenes in the needles. Larval survival was higher in undefoliated pines, lower in pines defoliated two consecutive years, and intermediate in pines defoliated only one year, suggesting a direct relationship between previous defoliation and larval survival. In contrast, none of the characteristics of the needles showed a clear relationship with larval survival. The resulting reduction in larval number also affects the capacity of the larvae to develop during winter, because it hampered nest warming. Thus, previous defoliation limits, although it does not impede, the possibility of repeated defoliation on Scots pine. © 2004 Elsevier SAS. All rights reserved.

**Keywords:** Chemical defences; Food quality; Larval survival; Nitrogen content; Phenols; Plant–herbivore interaction; Tannins; Terpenes

## 1. Introduction

Herbivory is often a major problem confronting plants (e.g. [Crawley, 1999](#); [Zamora et al., 1999](#)), and in the worst case may result in complete defoliation. Normally, a defoliated tree produces new leaves and thereby restores resources ([Lambers et al., 1998](#)), but the new plant tissues may show changes that reflect prior to damage. From the insect's perspective, these changes may result in lower food quality that may reduce the defoliator population ([Leather et al., 1987](#); [Tallamy and Raupp, 1991](#); [Lyytikäinen, 1994](#); [Karban and Baldwin, 1997](#); [Cornell et al., 1998](#); [Smits and Larsson, 1999](#)). Lower food quality after herbivory is called induced resistance (e.g. [Agrawal and Karban, 1999](#)), and has been repeatedly proposed as the cause for the end of the eruptive phase in many outbreak insects ([Battisti, 1988](#); [Haukioja et al., 1988](#); [Haukioja, 1990](#); [Price et al., 1990](#); [Karban and Baldwin, 1997](#)).

The present study uses a natural experiment to analyse the effect of previous defoliation of Scots pine *Pinus sylvestris* ssp. *nevadensis* on the population dynamics of the pine processionary moth *Thaumetopoea pityocampa*, a common outbreak pest that may inflict serious losses in several Mediterranean species of *Pinus*. The subspecies *nevadensis* of the Scots pine is protected under Spanish law ([Blanca et al., 1998](#); [Hódar et al., 2003](#)) and the two extant populations are found in protected areas (National Park in Sierra Nevada, Natural Park in Sierra de Baza, both high-mountains in SE Spain), where some management practices, such as the use of insecticides, are severely restricted. Scots pine is an important tree both in economic and ecological terms ([Giertych and Mátyás, 1991](#); [Kuper, 1994](#); [Archibald, 1995](#)), and the subspecies *nevadensis* in particular is widely used in afforestation and restoration programs in Sierra Nevada (e.g. [Castro et al., 2002](#)). Defoliation by the pine processionary moth has a severe impact on the growth and reproductive capacity of the Scots pines living in the autochthonous, relict forests ([Hódar et al., 2003](#)); however, no information is available concerning the effects of defoliation on the population dynamics of the

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pest. The pine processionary moth attacks mainly large-sized juvenile and adult pines. The size of the trees prevents a completely manipulative experiment with artificial defoliation, and the use of smaller juvenile trees (e.g. potted trees on greenhouse) would create unrealistic experimental conditions; therefore, trees previously defoliated in nature were used. The goal was to provide better knowledge of the interaction so as to predict the effects of defoliation on these relict pine populations.

Previous experiments (Hódar et al., 2002) suggest that survival of early larval instars of the pine processionary moth is affected by food quality. Several characteristics of pine needles, such as nitrogen and fibre content (Battisti, 1988; Devkota and Schmidt 1990), silica and phenolics (Schopf and Avtzis, 1987), and terpenes (Tiberi et al., 1999; Petrakis et al., 2001), have been related to differences in selection for oviposition by moth females and the performance of the hatching larvae. Therefore, the present study seeks to: (1) quantify, under field conditions, the effect of previous defoliation on survival of the pine processionary moth larvae; (2) determine the chemical characteristics of Scots pine needles (N content, fibre, phenolics and terpenes) in plants undergoing different levels of defoliation, and relate these characteristics to larval survival; and (3) explore the effects of previous defoliation on the pine processionary moth population dynamics.

## 2. Study area, material and methods

### 2.1. Study site

The study was conducted in the Collado de Ruquino (National Park of Sierra Nevada, Granada, SE Spain, 37°05' N, 3°28' W, 1750 m a.s.l.). The climate in the zone is continental Mediterranean with hot summers, cold winters and usually severe summer drought (July–August). The high altitude produces low temperatures in winter, frequently including snow. The mean minimum temperature in the coldest month (January) is  $-1.2^{\circ}\text{C}$ , and the mean maximum of the hottest month (July) is  $28.5^{\circ}\text{C}$ . Rainfall is concentrated mainly in autumn and spring, with an annual rainfall of 860 mm (the average for 1990–2002 at the Jardín Botánico de La Cortijuela, 1.5 km from Collado de Ruquino).

### 2.2. Study organisms

The life cycle of the pine processionary moth is univoltine. Adult flight and oviposition takes place at the end of summer, and larvae develop during autumn and winter. Larval development requires five instars, and takes place with larvae aggregated in a collective silk nest that protects from the winter cold (Breuer and Devkota 1990; Halperin 1990). At the end of winter, larvae crawl to the soil, bury themselves and pupate. Oviposition consists of a single egg batch per female that is attached to the current-year needles (see Hódar

et al., 2002 for a more detailed description of the outbreak biology). The moth attacks species of the genus *Pinus*, but larval developmental rates vary widely, depending on the host species and environmental conditions (Devkota and Schmidt, 1990; Masutti and Battisti, 1990). The main host for the pine processionary moth in the study area (and most of their distribution in south-western Europe) is the Black pine *Pinus nigra*, which usually lives at lower altitudes than does the Scots pine. The high altitude where Scots pine grows prevents the attack by the pine processionary moth, since the larval development depends heavily on minimum winter temperatures (Demolin 1969; 1970; Devkota and Schmidt, 1990; Masutti and Battisti, 1990; Hódar et al., 2002; 2003). However, the study area, and the pine plantations in Sierra Nevada and nearby mountains underwent outbreaks of pine processionary moth during the years of 1998–2000 (Hódar et al., 2001; 2003, Hódar and Zamora, 2004).

### 2.3. Experimental design

During 1997, a total of 80 juvenile Scots pines (from saplings to newly reproductive individuals, average height  $2.6 \pm 0.1$  m, range 1.5–4.0 m), were individually tagged, and the annual defoliation by *T. pityocampa* was monitored. All selected trees were intermingled in a woodland zone of ca. 5 ha, homogeneous in soil and exposure. The amount of defoliation (percentage of needles consumed during winter) was estimated by eye in 5% intervals at the end of the caterpillar activity period (March). In August 1999, four groups of 10 individuals each were selected from this pool of juveniles, according to the following defoliation categories: *Undefoliated* = pines not defoliated; *Defoliated D-1* = pines completely defoliated during the winter 1998–1999; *Defoliated D-2* = pines completely defoliated during the winter 1997–1998; *Defoliated two years* = pines completely defoliated during 1997–1998 and 1998–1999. No trees defoliated before the winter 1997–1998 were included in this study. A pine was considered completely defoliated when the degree of defoliation was  $\geq 95\%$ , and undefoliated when  $< 5\%$ .

During August 1999, egg batches from Scots pines in the area surrounding the plot were collected, pooled, and afterwards 8–10 batches were randomly assigned to each juvenile tree in the test. The egg batches were fixed at the end of a twig 1.5–2.5 m above ground (Hódar et al., 2002). Within the same tree, batches were spaced 0.5 m from each other, to minimize within-tree differences of the needles. Some egg batches depredated by birds and grasshoppers during the first 2 weeks were replaced; subsequent losses were not replaced. Egg batches were checked weekly and, as soon as larvae moulted to the second instar, both the nest with the larvae and the egg batch were collected. One control tree lost all egg batches and hence was excluded from the experiment. In the laboratory, egg batches were cleaned, and the number of hatched, unhatched, and parasitized eggs were counted under a binocular microscope. Nests were dissected, and the larvae

that had moulted to the second instar were counted. The study focused on first-instar larvae because they stay together and do not mix with larvae from other batches (as frequently happens with later instar larvae) and because the survival of first-instar larvae is more dependent on food quality (e.g. Cornell et al., 1998; Zalucki et al., 2002; see also Hódar et al., 2002). Larval survival was estimated on a per-pine basis—that is, larval survival within the tree was averaged across batches (see Appendix for details). The response variables analysed were:

1. Proportion of within-tree batches with larvae reaching the second instar.
2. Proportion of hatched larvae within-tree reaching the second instar.

#### 2.4. Chemical analysis of needles

The chemical composition of needles sampled from each pine was collected in September 1999, at the start of larval hatching. For each tree, five or six twigs scattered around the tree canopy were collected and mixed to provide an average sample. Only current-year needles were collected, since the moth consistently oviposited on current-year needles, which become the food for the first-stage larvae. Furthermore, this was the only age of needle available in trees defoliated the preceding year. Some of the needles were frozen at  $-20^{\circ}\text{C}$  within 2 h of the collection for terpene analysis, while the rest were dried in the dark at  $30\text{--}35^{\circ}\text{C}$ , and then milled to pass through a 1 mm sieve.

The variables used to characterize pine needles on each tree were:

1. *Nitrogen content.* N content was quantified by acid (sulphuric) digestion of 0.5 g dry needle powder, distillation in a semi-automatic Kjeldahl distiller (Büchi B-324, Switzerland) and subsequent titration. N content is expressed as the percentage of dry weight.
2. *Fibre content.* Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were analysed by the sequential procedure of Goering and Van Soest (1970) using the ANKOM200/220 fibre analyser (ANKOM Corporation® Technology Fairport, NY). Hemicellulose and cellulose were estimated as NDF (ash free)–ADF (ash free) and ADF (ash free)–lignin (ash free), respectively, and recalculated on the basis of dry matter, and the ash was estimated by burning the residual lignin at  $500^{\circ}\text{C}$ .
3. *Phenolic compounds.* Total phenolics were analysed by the Folin–Ciocalteu method, and condensed tannins were analysed by the proanthocyanidin assay (Waterman and Mole, 1994; also Hódar et al., 2002, for a detailed description of the procedures). For comparisons between treatments, direct values of absorbance were used, without transformation to standard equivalents (see Waterman and Mole, 1994).
4. *Terpenoids.* Mono- and sesquiterpenes were analysed following the procedure described by Kainulainen et al.

(1992), with some modifications. The extraction was made for 500 mg of freshly thawed leaves, cut in small pieces ( $\leq 1$  mm) with scissors, and placed overnight in 4 ml of *n*-hexane at room temperature. The internal standard was 1-chlorooctane (0.1 ml/l). The extract was analysed in a high-resolution gas chromatograph CARLO ERBA Series 8000 model 8060 (Thermo Instruments, UK). Terpenes were identified by comparison with known samples and the NIST/NBS and Wiley (6th ed.) library. Terpene amounts are expressed as  $\text{mg g}^{-1}$  of fresh needle weight. Only the terpenes that represented more than 1% of the total terpenes in any of the experimental groups are shown.

#### 2.5. Statistical analysis

Since all the data obtained were expressed as proportions, before the statistical analysis they were arcsin-transformed when they departed from normality (Zar, 1996), and then analysed using a one-way ANOVA. Means are shown  $\pm$  S.E. The analyses were performed with JMP 4.0.1 software (SAS Institute, 2000).

### 3. Results

The larval survival rates differed sharply between treatments, with undefoliated trees being highest and trees defoliated two consecutive years the lowest (Fig. 1). Significant differences among treatments also appeared in the chemical composition. The N content in needles was higher in defoliated trees, while most of the other allelochemicals analysed showed the opposite trend (Table 1). Significant differences in phenols and tannins were found between undefoliated trees and the pines defoliated the previous year. By contrast, the highest values for terpenoids were also found in undefoliated trees, with the minimum values found in trees defoliated two years before (also significantly different, Table 1). With respect to the results in fibre and ash, only hemicellulose showed significant differences between treatments (Table 1).

Among the terpenoid compounds, monoterpene  $\alpha$ -pinene and sesquiterpene germacrene D were the most abundant compounds, together averaging 75–83% of the total terpenoids found in the needles (Table 2). In trees defoliated the previous year, the levels of these terpenoids were lower than in undefoliated pines, while the levels of  $\beta$ -pinene and  $\gamma$ -cadinene were higher. The other two defoliation treatments show levels similar to or lower than control for all terpenes analysed.

### 4. Discussion

The larvae feeding on defoliated pines registered higher mortality. In undefoliated pines, 90% of egg batches pro-

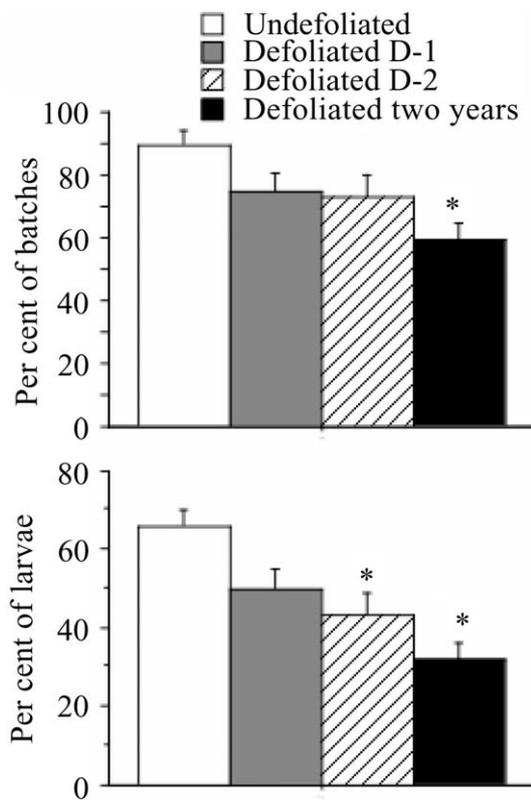


Fig. 1. Survival of larvae of pine processionary caterpillar growing on Scots pines that had undergone different defoliation patterns. Upper figure shows the percentage of batches with any larvae reaching the second instar ( $F_{3,35} = 5.22$ ,  $P = 0.0044$ ), lower figure shows the percentage of hatched larvae reaching the second instar ( $F_{3,35} = 8.28$ ,  $P = 0.0003$ ). Bars are expressed  $\pm 1$  S.E.,  $n = 10$  in all, except in undeveloped = 9. \* are significantly different from undeveloped with a posteriori Bonferroni–Dunn test.

duced larvae and more than 65% of larvae reached the second instar. This finding agrees with previous results in the same zone (Hódar et al., 2002). In pines defoliated two consecutive winters, the values fell to 59% and 32%, respectively. Defoliation during either winter resulted in intermediate survival.

Table 1

Results of the analysis of N (Kjedahl, percentage of dry weight), fibre analysis (Goering and van Soest, percentage of dry weight), phenols (Folin–Ciocalteu, absorbance at 740 nm), condensed tannins (proanthocyanidin, absorbance at 550 nm) and terpenes (GC, mg by g of fresh needle) on current-year needles of Scots pines that had undergone different defoliation patterns

	Undeveloped	Defoliated D-1	Defoliated D-2	Defoliated two years	$F_{3,35}$	$P$
<i>Nitrogen content</i>						
% N	1.01 $\pm$ 0.03	1.14 $\pm$ 0.03 <sup>a</sup>	1.07 $\pm$ 0.03	1.10 $\pm$ 0.03	3.14	0.0376
<i>Fibre analysis</i>						
Hemicellulose	54.4 $\pm$ 0.4	54.9 $\pm$ 0.6	52.2 $\pm$ 0.8	53.4 $\pm$ 0.3	3.91	0.0165
Cellulose	37.5 $\pm$ 0.4	37.5 $\pm$ 0.7	36.1 $\pm$ 0.5	36.3 $\pm$ 0.4	2.00	ns
Lignin	14.6 $\pm$ 0.3	14.8 $\pm$ 0.2	14.3 $\pm$ 0.3	13.8 $\pm$ 0.3	2.50	ns
Ashes	0.28 $\pm$ 0.03	0.26 $\pm$ 0.04	0.34 $\pm$ 0.03	0.38 $\pm$ 0.04	2.73	ns
<i>Secondary compounds</i>						
Phenols	0.96 $\pm$ 0.06	0.76 $\pm$ 0.05 <sup>a</sup>	0.82 $\pm$ 0.04	0.83 $\pm$ 0.03	2.94	0.0466
Tannins	0.28 $\pm$ 0.06	0.13 $\pm$ 0.02 <sup>a</sup>	0.13 $\pm$ 0.02 <sup>a</sup>	0.15 $\pm$ 0.03	3.13	0.0223
Monoterpenes <sup>b</sup>	5.03 $\pm$ 0.45	4.76 $\pm$ 0.29	2.97 $\pm$ 0.29 <sup>a</sup>	3.80 $\pm$ 0.49	3.98	0.0156
Total terpenes <sup>b</sup>	5.82 $\pm$ 0.45	5.54 $\pm$ 0.66	3.40 $\pm$ 0.31 <sup>a</sup>	4.61 $\pm$ 0.57	4.32	0.0111
$N$	9	10	10	10		

<sup>a</sup> Means followed by are significantly different from undeveloped with a posteriori Bonferroni–Dunn test.

<sup>b</sup> In the  $n$  value is 8 for control trees and dF in  $F$  are 3.34.

This suggests a direct link between larval survival and previous defoliation. However, despite this clear response, the correspondence between larval survival and the broad array of parameters analysed in needles is weak. Our work analyses all the substances that have been associated with the survival of the pine processionary caterpillar (Schopf and Avtzis, 1987; Battisti, 1988; Devkota and Schmidt 1990; Tiberi et al., 1999; Petrakis et al., 2001; Hódar et al., 2002), without a conclusive result. Another possibility is that the original degree of defoliation in pines could be due to an active selection by moths regarding the optimal place for larval development, following some physical or chemical cue of the pines which we failed to detect. This possibility seems improbable because, despite the fact that undeveloped trees are better for larval survival, they are not chosen for oviposition, while previously defoliated trees were chosen for oviposition. This suggests that these moths are rather unselective when ovipositing (Demolin, 1969; Schmidt, 1990; Petrakis et al., 2001; Hódar et al., 2002; see also Tammaru et al. (1995) for a detailed analysis in *Epirrita autumnata*).

The use of a natural experiment, instead of a completely manipulative one in which the degree of defoliation undergone by trees was randomly assigned, might limit our ability to find the reasons for which trees have higher levels of defoliation, and/or others have lower levels of larval survival after defoliation. Certainly, a completely manipulative experiment would help in this sense. However, this natural experiment has the advantage of its reliability; that is, our experimental situation is completely realistic since is a natural setting and not a laboratory simulation. Therefore, the conclusions are directly informative about the dynamics of the pine processionary moth in a natural situation.

The nitrogen levels are higher in defoliated pines (Smits and Larsson, 1999; Nykänen and Koricheva, 2004), suggesting that this foliage is of better quality for larval feeding. By contrast, fibre in needles is lower in defoliated pines, as are phenolics, which are known to be digestion inhibitors (Wa-

Table 2

Concentrations of individual terpenes (GC, mg by g of fresh needle) on current-year needles of Scots pines that had undergone different defoliation patterns

	Undefoliated	Defoliated D-1	Defoliated D-2	Defoliated two years	$F_{3,34}$	$P$
Tricyclene	0.07 ± 0.01	0.09 ± 0.01	0.05 ± 0.01	0.07 ± 0.01	2.995	0.0443
$\alpha$ -Pinene	4.11 ± 0.41	3.60 ± 0.44	2.40 ± 0.26 <sup>a</sup>	2.95 ± 0.42	3.570	0.0240
Camphene	0.43 ± 0.06	0.52 ± 0.09	0.25 ± 0.03	0.40 ± 0.06	3.337	0.0307
$\beta$ -Pinene	0.15 ± 0.02	0.26 ± 0.04	0.12 ± 0.02	0.16 ± 0.02	5.085	0.0051
$\beta$ -Myrcene	0.10 ± 0.01	0.12 ± 0.03	0.06 ± 0.01	0.08 ± 0.01	2.960	0.0460
$\beta$ -Caryophyllene	0.17 ± 0.04	0.17 ± 0.03	0.10 ± 0.02	0.15 ± 0.03	1.692	ns
Germacrene D	0.74 ± 0.14	0.59 ± 0.10	0.40 ± 0.06	0.75 ± 0.17	1.746	ns
$\gamma$ -Cadinene	0.06 ± 0.01	0.19 ± 0.05 <sup>a</sup>	0.03 ± 0.01	0.06 ± 0.01	6.954	0.0009
$n$	8	10	10	10		

<sup>a</sup> Means followed by are significantly different from undefoliated with a posteriori Bonferroni–Dunn test.

terman and Mole, 1994). Comparing the different pine species at the same study site, Hódar et al. (2002) proposed a direct relationship between nitrogen in needles and larval survival, while phenols and tannins did not show significant differences. However, Schopf and Avtzis (1987), when comparing different species, found variations in larval survival related to the quantity of phenols and silica in needles. Finally, the most abundant terpenes had lower concentrations in defoliated pines, while two scant terpenes found in undefoliated trees,  $\beta$ -pinene and  $\gamma$ -cadinene, were significantly higher in pines defoliated one year before, but not in trees defoliated two years before or having two consecutive defoliations. This suggests that the terpenes in Scots pine are much more constitutive than inducible (Lewinsohn et al., 1991). Terpenes are usually considered non-inducible compounds because of their genetically controlled production (Muzika, 1993; Haukioja et al., 1998). Some authors consider terpenes as determinant in the feeding preference of the pine processionary caterpillar (Petrakis et al., 2001) or in determining oviposition preference by the moth (Tiberi et al., 1999), but conclusive evidence is lacking.

Some authors have considered the effect of a preferred food, such as pollen cones instead of foliage or a specific needle age, on larval survival of other outbreaking species (jack pine budworm *Choristoneura pinus* upon jack pine *Pinus banksiana*; Nealis and Lomic, 1994; pine looper *Bupalus piniarius* upon Scots pine; Smits and Larsson, 1999). This seems not to be the case, and most authors studying the pine processionary caterpillar suggest a single chemical characteristic to be responsible for larval survival. A lack of agreement between the chemical profile of a plant and the response of the insects feeding or ovipositing in that plant is common (e.g. Leather et al., 1987; Sadof and Grant, 1997; Kinney et al., 1997; McKinnon et al., 1999; Smits and Larsson, 1999; Rocchini et al., 2000), even when, as in this study, a varied set of possible response variables is analysed. The identification of the substance (or substances) causing resistance and hence detrimental effects in a herbivore, is difficult because the effect on the herbivore is “the sum of the plant’s responses plus the herbivore’s response to the plant’s responses” (Karban and Baldwin, 1997). In any case, the easiest and most direct way to determine whether plant responses provide induced resistance is to challenge damaged plants

with living herbivores (Karban and Baldwin, 1997), and in this sense the response of the pine processionary caterpillar feeding on defoliated Scots pine is reasonably clear cut: the more defoliation, the lower larval survival.

In this way, the *T. pityocampa* population could be driven to lower levels due to increased mortality among the newly hatched larvae feeding on trees previously defoliated (Cornell et al., 1998; Zalucki et al., 2002). However, a different question is whether this reduction in larval survival is enough to produce a population crash after the eruptive phase. The fact that some pines suffered complete defoliation two consecutive winters and partial defoliation the third (Hódar et al., 2003), suggests that the mechanism is not completely effective. In *T. pityocampa*, the reduction in the number of caterpillars during early instars is critical because larval survival during winter depends strongly on their number (Breuer et al., 1989; Breuer and Devkota, 1990; Halperin, 1990; Pérez-Contreras et al., 2003). A group of 200–250 larvae keeps the nest temperature 6 °C above that of a group with only 30–60, which means that larvae in the larger group grow a 9% larger and develop in a time around 11 days shorter than the smaller one (Halperin, 1990). This author also estimated that a group of 90 larvae have a chance of 50% to overwinter, around 30 larvae have just a 25%, and below 20 larvae the group is not able to construct an effective nest. Thus, larvae in small silk nests produced on pines defoliated during previous winters have a higher risk of dying during the current winter.

These results suggest that alone, even complete defoliation for two consecutive winters is not enough to prevent repeated defoliation in Scots pine, defoliation that eventually causes death (Hódar et al., 2003). Only when the effects of previous defoliation are reinforced by winter larval mortality could prevent repeated massive defoliations. Supporting this is the observation that the strong outbreak of pine processionary moth in Sierra Nevada and nearby mountains during the years 1998–2000 collapsed during the colder winters in 1999 and 2000 (Hódar and Zamora 2004). However, in Spain (Esteban-Parra et al., 1995; Piñol et al., 1998) and throughout the Mediterranean (Osborne et al., 2000; Rodó and Comín, 2001), winter temperatures are rising due to the global climate warming. Hence, as warm winters become increasingly more frequent, winter mortality will be less effective in preventing repeated defoliation.

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## Appendix

Means ( $\pm$  S.E.) per tree of: number of eggs per batch, proportion of unhatched eggs, proportion of parasitized eggs, proportion of eggs that hatch and develop into larvae, and number of larvae that survived into second instar. The number of batches per tree is also indicated

Treatment	No. tree	No. batches	No. eggs/batch	% Eggs unhatched	% Eggs parasitized	% Eggs hatched	No. larvae to second
<i>Undeveloped</i>	1	7	207 $\pm$ 15	31.0 $\pm$ 9.5	3.5 $\pm$ 1.0	65.5 $\pm$ 9.4	78 $\pm$ 20
	2	8	190 $\pm$ 17	42.2 $\pm$ 7.9	10.7 $\pm$ 3.0	47.1 $\pm$ 8.3	46 $\pm$ 19
	3	8	182 $\pm$ 11	28.3 $\pm$ 5.0	5.1 $\pm$ 1.6	66.6 $\pm$ 4.8	90 $\pm$ 10
	4	6	202 $\pm$ 22	11.5 $\pm$ 1.7	3.2 $\pm$ 0.9	85.3 $\pm$ 2.4	98 $\pm$ 18
	5	10	194 $\pm$ 8	24.3 $\pm$ 8.5	2.7 $\pm$ 0.8	73.0 $\pm$ 8.9	92 $\pm$ 21
	6	9	201 $\pm$ 20	33.7 $\pm$ 8.5	4.3 $\pm$ 1.9	62.0 $\pm$ 9.1	91 $\pm$ 19
	7	6	184 $\pm$ 15	24.4 $\pm$ 5.0	7.0 $\pm$ 4.0	68.5 $\pm$ 8.1	108 $\pm$ 15
	8	8	179 $\pm$ 14	23.7 $\pm$ 4.8	7.4 $\pm$ 1.5	68.9 $\pm$ 6.1	103 $\pm$ 19
	9	8	175 $\pm$ 2	45.1 $\pm$ 7.3	9.7 $\pm$ 1.8	45.2 $\pm$ 7.7	54 $\pm$ 21
<i>Defoliated D-1</i>	1	7	199 $\pm$ 21	33.0 $\pm$ 8.4	8.2 $\pm$ 2.4	58.8 $\pm$ 9.9	46 $\pm$ 27
	2	8	169 $\pm$ 16	29.6 $\pm$ 6.1	6.0 $\pm$ 2.1	64.4 $\pm$ 6.5	44 $\pm$ 16
	3	8	213 $\pm$ 10	20.8 $\pm$ 4.4	2.5 $\pm$ 0.8	76.7 $\pm$ 4.8	112 $\pm$ 22
	4	8	169 $\pm$ 17	35.4 $\pm$ 5.4	5.9 $\pm$ 1.8	58.7 $\pm$ 6.9	55 $\pm$ 23
	5	7	205 $\pm$ 15	42.0 $\pm$ 8.9	6.6 $\pm$ 2.6	51.4 $\pm$ 9.6	36 $\pm$ 13
	6	8	194 $\pm$ 9	26.8 $\pm$ 6.5	3.2 $\pm$ 1.2	70.0 $\pm$ 6.2	54 $\pm$ 22
	7	9	204 $\pm$ 10	25.3 $\pm$ 3.5	3.4 $\pm$ 1.0	71.3 $\pm$ 4.2	91 $\pm$ 15
	8	8	178 $\pm$ 13	29.9 $\pm$ 4.7	13.3 $\pm$ 4.5	56.8 $\pm$ 8.4	36 $\pm$ 16
	9	8	188 $\pm$ 14	36.1 $\pm$ 6.2	10.5 $\pm$ 3.6	53.4 $\pm$ 8.0	86 $\pm$ 20
	10	8	181 $\pm$ 14	44.1 $\pm$ 9.9	8.8 $\pm$ 2.6	47.1 $\pm$ 11.5	44 $\pm$ 17
<i>Defoliated D-2</i>	1	7	196 $\pm$ 17	16.9 $\pm$ 6.7	2.5 $\pm$ 1.1	80.6 $\pm$ 7.6	72 $\pm$ 21
	2	8	206 $\pm$ 11	23.7 $\pm$ 6.0	5.1 $\pm$ 2.9	71.2 $\pm$ 7.8	65 $\pm$ 15
	3	8	176 $\pm$ 16	30.8 $\pm$ 6.8	6.4 $\pm$ 3.1	62.8 $\pm$ 7.4	43 $\pm$ 25
	4	9	200 $\pm$ 13	21.1 $\pm$ 4.8	4.0 $\pm$ 1.2	74.9 $\pm$ 5.5	54 $\pm$ 16
	5	8	184 $\pm$ 9	26.4 $\pm$ 4.6	5.3 $\pm$ 1.0	68.3 $\pm$ 5.4	20 $\pm$ 13
	6	6	210 $\pm$ 20	18.2 $\pm$ 6.0	3.0 $\pm$ 0.8	78.8 $\pm$ 6.6	83 $\pm$ 34
	7	8	191 $\pm$ 17	39.0 $\pm$ 8.6	10.0 $\pm$ 4.1	51.0 $\pm$ 8.8	11 $\pm$ 8
	8	7	196 $\pm$ 8	31.2 $\pm$ 3.2	4.3 $\pm$ 1.1	64.5 $\pm$ 3.9	90 $\pm$ 20
	9	8	190 $\pm$ 11	44.7 $\pm$ 8.2	9.5 $\pm$ 2.9	45.8 $\pm$ 9.2	48 $\pm$ 11
	10	7	185 $\pm$ 23	33.9 $\pm$ 7.0	3.8 $\pm$ 1.0	62.3 $\pm$ 6.8	48 $\pm$ 18
<i>Defoliated two</i>	1	8	168 $\pm$ 18	27.4 $\pm$ 3.7	4.2 $\pm$ 1.5	68.3 $\pm$ 4.5	11 $\pm$ 6
	2	8	187 $\pm$ 15	21.5 $\pm$ 3.5	2.2 $\pm$ 1.0	76.3 $\pm$ 4.3	54 $\pm$ 15
	3	10	216 $\pm$ 10	16.1 $\pm$ 4.3	2.4 $\pm$ 1.2	81.4 $\pm$ 4.5	32 $\pm$ 15
	4	6	164 $\pm$ 14	42.3 $\pm$ 8.6	3.3 $\pm$ 2.5	54.4 $\pm$ 9.3	19 $\pm$ 11
	5	8	168 $\pm$ 14	35.4 $\pm$ 6.5	7.9 $\pm$ 2.9	56.7 $\pm$ 8.5	19 $\pm$ 12
	6	8	184 $\pm$ 14	42.5 $\pm$ 10.5	2.7 $\pm$ 1.2	54.8 $\pm$ 11.2	48 $\pm$ 23
	7	8	174 $\pm$ 16	27.9 $\pm$ 7.5	7.9 $\pm$ 3.0	64.2 $\pm$ 8.7	53 $\pm$ 17
	8	9	183 $\pm$ 13	26.2 $\pm$ 4.4	9.4 $\pm$ 5.1	64.5 $\pm$ 6.1	63 $\pm$ 20
	9	8	189 $\pm$ 20	21.0 $\pm$ 5.0	7.0 $\pm$ 1.7	72.0 $\pm$ 6.4	24 $\pm$ 12
	10	8	193 $\pm$ 16	35.2 $\pm$ 7.6	5.2 $\pm$ 1.7	59.6 $\pm$ 8.8	60 $\pm$ 23

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