

Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming

José A. Hódar^{a,*}, Jorge Castro^{a,b}, Regino Zamora^a

^aGrupo de Ecología Terrestre, Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

^bBotanical Institute, University of Copenhagen, Øster Farimagsgade 2D, DK-1353, Copenhagen K, Denmark

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Abstract

The wide distribution of Scots pine (*Pinus sylvestris* L.) in Europe includes two relict populations in southern Spain (Sierra Nevada and Sierra de Baza), belonging to the subspecies *nevadensis*. These populations are isolated in high mountains, which tends to protect them from the attack of a severe defoliating Mediterranean pest, the pine processionary moth *Thaumetopoea pityocampa*. However, as a consequence of climate change, the pine processionary caterpillar has increasingly attacked populations of this pine in recent years. This work describes the detrimental effects of defoliation by the pine processionary caterpillar in *P. sylvestris* subsp. *nevadensis* in Sierra Nevada. Defoliation strongly reduced pine growth as well as all the reproductive parameters measured (female and male cone production, mature cone size, seed production and seed weight), in addition to some deaths. If winter temperatures continue to increase, the pine processionary caterpillar will have a dangerous impact in these relict pine populations, by further reducing the pine's weak regeneration capacity. We suggest some mitigation actions based on managing habitat structure, in order to reduce or avoid such negative impacts.

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1. Introduction

Scots pine (*Pinus sylvestris* L.) has a wide distribution in Europe and Asia (Gausen et al., 1964; Ceballos and Ruíz de la Torre, 1971), being a particularly important tree both in economic and ecological terms (Giertych and Mátyás, 1991; Kuper, 1994; Archibold, 1995). Its presence in Europe is known from the Tertiary (Molotkov and Patlaj, 1991), and its distribution area has undergone continual latitudinal and altitudinal changes during glacial–interglacial cycles of the Pleistocene (Bennet et al., 1991; Bennet, 1997; Willis et al., 1998). Today, its main range is in central and northern parts of the continent, while towards the south it is restricted to the high mountains, which act as microclimatic islands providing suitable conditions for its persistence (Ceballos

and Ruíz de la Torre, 1971; Franco, 1986; Ferreras and Arozena, 1987). These southern populations would have occupied a wider distribution during the last maximum glaciation (e.g. Peñalba, 1994), and are of great historical and biological interest. Firstly, they acted as refuges of the species during the maximum ice age, providing dissemination points for species to spread northwards during interglacial cycles (Bennet, 1997; Taberlet et al., 1998; Sinclair et al., 1999). Secondly, these populations have remained in continuous isolation owing to the repeated changes during glacial–interglacial cycles. This has fostered populations having particular morphological and ecological traits (Molotkov and Patlaj, 1991; Sinclair et al., 1999; Ceballos and Ruíz de la Torre, 1971), engendering infraspecific taxa that are exclusive to these mountain areas.

The Mediterranean mountains of Sierra Nevada and Sierra de Baza (southern Spain) mark the southernmost distribution area of Scots pine (Boratynski, 1991),

* Corresponding author. Fax: +34-958-243238.
E-mail address: jhodar@ugr.es (J.A. Hódar).

where populations are ascribed to the variety or subspecies *nevadensis* Christ, a taxon restricted exclusively to these mountains (Gausen et al., 1964; Molotkov and Patlaj, 1991; Blanca et al., 1998). Populations occupy a small area, each roughly 5–10 km² (Catalán, 1991), making them particularly vulnerable to the risk of extinction (Rivas-Martínez et al., 1991; Blanca et al., 1998). These forests are today strictly protected by National or Natural parks for their ecological importance, first recognized by the Swiss naturalist Charles Edmond Boissier in the 19th century (Boissier, 1839–1845). However, human impact has threatened the persistence of these forests throughout history; for example, Willkomm (1882), and later Voigt (1889), noted the reduction of the forests as a result of logging for fuel, while building and mining have considerably reduced forest populations during the 20th century (Sánchez-Quirante, 1998). Today, although under rigorous protection, these Scots pine forests are still threatened by several factors that hamper regeneration, such as very high rates of seed predation (Castro et al., 1999; Castro, 2000), extremely high rates of seedling mortality due, basically, to summer drought (Hódar et al., 1998; Castro, 2000; Castro et al., 2002), and high pressure from ungulate herbivory (Hódar et al., 1996, 1998; Gómez et al., 2001a; Zamora et al., 2001).

Current trends in climate change may bring new threats for the persistence of these Scots pine forests. In particular, rising temperatures are encouraging the uphill spread of the pine processionary caterpillar (*Thaumetopoea pityocampa* Dennis and Schiff., Lepidoptera: Thaumetopoeidae; hereafter PPC) (Hódar et al., 2001a,b). This pest feeds on several Mediterranean *Pinus* species, such as *P. nigra*, *P. brutia* and *P. halepensis*, inflicting serious economic and ecological losses (Hódar et al., 2002). The Scots pine is not among the usual hosts of PPC in nature, because the altitude at which the pine grows naturally has temperatures too low for PPC larval development (Torrent, 1958; Demolin, 1969a; Huchon and Demolin, 1971). However, field observations corroborate that PPC inflicts serious defoliation of Scots pine when it occurs within the distribution range of the pest (Torrent, 1958; Demolin, 1969b; Huchon and Demolin, 1971). Furthermore, laboratory tests demonstrate that the caterpillar develops quite well when fed on Scots pine needles (Devkota and Schmidt, 1990; Hódar et al., 2002).

In the present study, we investigate the impact of PPC on natural populations of Scots pine in southern Spain, currently exposed to the first intrusions of PPC into higher altitudes. For this, we specifically investigate: (1) the impact of PPC defoliation on the survival and growth of juvenile trees; and (2) the implications of PPC defoliation on the survival and reproductive parameters of adult trees, considering (i) male and female flower

production, (ii) cone development, (iii) seed production, and (iv) seed quality. Our objective is to evaluate the consequences for forest regeneration and thereby prescribe appropriate guidelines to prevent the potential devastation of the pest.

2. Methods

2.1. Study system

The study was conducted between 1997 and 2000 in the Trevenque area (37°05'N, 3°28'W), National Park of Sierra Nevada, where native *Pinus sylvestris nevadensis* populations grow on calcareous soils at an altitude of 1600–2200 m, forming the treeline. The climate in the area is continental Mediterranean, with rainfall (837 mm per year on average) heaviest in autumn and spring, alternating with hot, dry summers, and cold winters. The study site was located in the lower parts of the forest, where heavy defoliations by PPC occurred during 1998 and 1999 (Junta de Andalucía, 2001). These forests are composed almost exclusively of Scots pine, with scattered individuals of other tree species, such as *Acer granatense*, *Quercus ilex*, *Taxus baccata* or *Pinus nigra*. The tree cover is around 30% in a typical stand (see Castro et al., 1999, for more details on community structure and composition). In these mountains, flowering and pollination of Scots pine occurs around April (year 0). Female strobili remain small for one year, and then are fertilized (year 1). Cones develop from May of year 1 to January of the year 2, when dispersion takes place. Thus, 22 months elapse from pollination to seed dispersion (see also Koski, 1991).

The pine processionary caterpillar is univoltine. Adult flight and egg laying occurs in mid-summer (Devkota and Schmidt, 1990)—July–August in the study area. Eggs are laid in the canopy of the trees and hatch in about 45 days, usually in early September. Throughout the autumn and winter, the larvae develop in a collective silk nest, protected from the cold, and usually placed in the most insulated part of the canopy, in order to be warmed by sunlight. Larvae abandon the nest during the night to feed, except when temperature is too low. Below –7 °C isolated larvae cannot survive, and below –15 °C even caterpillars in nests die (Demolin, 1969a). Most defoliation occurs between January and March, when larvae are in the fourth and fifth instar. Since Scots pine in SE Spain flush new leaves around April, all defoliation takes place on old foliage. When larvae are fully developed, they abandon their nests and form processions to reach the ground, where they burrow and pupate, usually near the host tree (see Hódar et al., 2002, for a detailed description of the plague biology). Hereafter winter refers to November of one year to February of the following year, and year refers to the

period from October of one year to September of the following year (e.g., winter 1999 means November 1998–February 1999, and year 1999 means October 1998–September 1999). This chronology corresponds to the PPC life cycle.

2.2. Sampling on juvenile Scots pine

In September 1997 we randomly marked 63 juvenile pines (1–3 m height). From 1998 to 2000, during each April we recorded survival and visually estimated ($\pm 5\%$) the percentage of defoliation suffered during the period of plague activity. At the end of the summer, we measured both the total height and the growth of the leader shoot of each pine. To estimate the annual growth rate, we divided the season's growth of the pine by its initial height at the beginning of the season.

2.3. Sampling on adult Scots pine

In April 1997 we randomly marked 57 adult pines. From 1998 to 2000 we recorded survival and estimated the percentage of defoliation in the same way as for juveniles (see above). The consequences of PPC defoliation on reproductive parameters were studied by analysing the effects on flower, cone and seed production on these marked pines.

Flower production was monitored in spring 2000. We counted, with the aid of binoculars (Zeiss 10 \times 40), the number of female cones and estimated the production of male cones. The estimation of male cones was on a qualitative scale: 0=no production, 1=very scarce, 2=cones in 5–25% of the tree canopy, 3=cones in 26–75%, 4=cones in 76–95%, 5=cones in >95%; however, no tree scored 4 or 5.

Cone development and seed production were analysed using two complementary procedures. First, in January 1997 we selected 10 adult trees that had suffered heavy defoliation on some branches but no defoliation on others during the winter of 1996. This means that the collected cones were ripening from May 1996 to January 1997, i.e. just after the heavy defoliation in the case of defoliated branches. From each tree, we collected 15 ripe cones from each branch type and, in the laboratory, we measured length and diameter. Then, cones were held individually in paper envelopes and kept at 40 °C until all seeds were released. For each cone, we counted the number of healthy seeds and calculated their average weight. Seeds from one pine were lost during the handling of the samples. For the second procedure, in spring 2000, we selected 10 individuals almost completely defoliated during the two previous winters, and ten with low or no defoliation. We collected 20 ripe cones on each selected pine, and measured the maximum length of the cone.

2.4. Statistical analysis

We used Spearman rank correlation to analyse the effect of defoliation intensity on annual growth rate in juvenile pines. Nonparametric correlation was used because defoliation intensity severely departed from normality (Zar, 1996). To examine male cone production in defoliated versus undefoliated adults, we used a Chi-square analysis, while for female cones we used one-way ANOVA.

The comparison of cone length between defoliated and undefoliated adult trees was made with Student's *t* test, using as replicates the mean cone size per tree. The comparison of cone length, cone diameter, number of seeds per cone and average seed weight between defoliated and undefoliated branches within the same tree were analysed with a repeated-measures MANOVA. Multivariate analysis was used, instead of univariate rmANOVA, because the severe deviations from orthonormality and sphericity condition for the response design matrices (SAS Institute Inc., 2000).

All analyses were performed using procedures in the JMP 4.0 statistical package (SAS Institute Inc., 2000). Throughout the paper, means are showed ± 1 SE.

3. Results

3.1. Effect of defoliation on juvenile pines

No juvenile pines died during the study period, but rather defoliation notably reduced growth (Fig. 1). The defoliation in the winters of 1998 and 1999 significantly reduced the annual growth rate of the following growing season (Fig. 1). In 2000, with the end of the eruptive phase of the infestation, most of the pines underwent low or no defoliation, and no relationship was found between the growth rate of the trees and the degree of defoliation ($r_s = -0.126$, $P = 0.320$, $n = 63$).

3.2. Effect of defoliation on adults

Thirty-four adult pines suffered >50% of defoliation in one of the three years studied. From these, two died at the end of this period, representing 5.9% mortality.

Defoliation sharply reduced reproductive capacity, pines defoliated in the winter of 1999 registering lower production of both male ($\chi^2 = 23.71$, d.f. = 3, $P < 0.0001$, Fig. 2) and female cones (one-way ANOVA, $F = 21.33$, $df = 1,48$, $P < 0.0001$, Fig. 2) in the spring of 2000. Furthermore, mature cones collected in spring 2000 from PCC-infested pines, and consequently developed during two years of intense defoliation, showed a major size reduction (cone length 21.2 ± 1.0 mm) compared with cones from undefoliated trees (43.9 ± 1.0 mm; $t = 15.37$, $df = 18$, $P < 0.0001$).

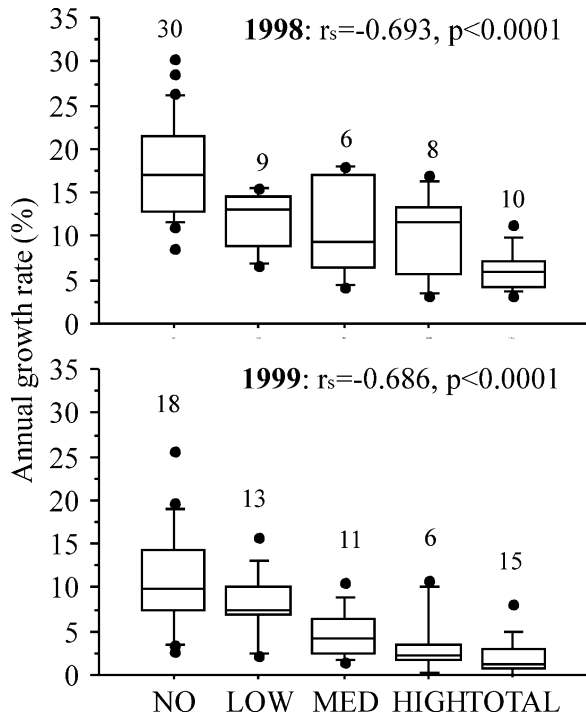


Fig. 1. Effect of winter defoliation in the annual growth rate of juvenile pines. Pines were grouped in categories to simplify the graphics (No = 0% defoliation, Low = 1–25%, Med = 26–75%, High = 76–95%, Total = >95%), and percentage of annual growth rate is shown as mean \pm 1 SE, with the number of pines (n) in the upper part. The n total for the Spearman rank correlation is 63 in both cases.

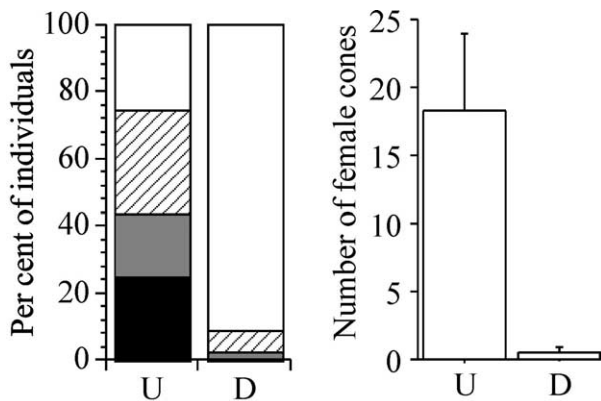


Fig. 2. Cone production in the year 2000 by adult pines that had undergone defoliation (D) or not (U) by the pine processionary caterpillar during winter 1999. On the left side, male cone production, expressed as the percentage of individuals bearing male cones (white = no production, grey = scattered cones in the canopy, striped = cones in 5–25% of the canopy, black = cones in 26–75% of the canopy). On right side, mean (\pm 1 SE) number of female cones borne by tree.

Similar results for the impact of defoliation appeared when branches were compared within a tree. Defoliated branches produced shorter and thinner cones (cone length: 49.5 ± 2.2 mm versus 33.9 ± 1.7 mm in undefoliated and defoliated branches, respectively; cone width: 24.8 ± 0.7 mm versus 18.9 ± 0.7 mm), with fewer and

Table 1

Effect of individual variation (Tree, between-subject factor) and defoliation due to the pine processionary caterpillar (Defoliated vs. undefoliated branch, within-subject factor) in four response variables related with the reproductive success of Scots pine; df represents the degrees of freedom (Num, numerator and Den, denominator); λ is the Wilks' lambda and F is the F -ratio value of each effect

Factor	df Num	df Den	λ	Exact F	P
<i>Cone length</i>					
Tree	9	139	2.87	44.25	0.0001
Defoliation	1	139	5.53	768.60	0.0001
Defoliation \times Tree	9	139	0.38	5.88	0.0001
<i>Cone diameter</i>					
Tree	9	139	1.81	27.95	0.0001
Defoliation	1	139	5.44	756.73	0.0001
Defoliation \times Tree	9	139	0.35	5.40	0.0001
<i>Seeds per cone</i>					
Tree	8	125	1.58	24.64	0.0001
Defoliation	1	125	0.55	69.37	0.0001
Defoliation \times Tree	8	125	0.45	7.06	0.0001
<i>Seed weight</i>					
Tree	8	125	4.51	44.58	0.0004
Defoliation	1	125	4.44	350.95	0.0001
Defoliation \times Tree	8	125	0.42	4.15	0.0004

lighter healthy seeds (number of seeds per cone: 19.2 ± 3.3 versus 12.6 ± 3.0 ; seed weight: 12.4 ± 0.8 mg versus 7.2 ± 0.5 mg). Although individuals varied markedly, the most important factor determining a reduction for all the measured reproductive estimates proved to be defoliation (Table 1).

4. Discussion

The results show that PPC defoliation drastically reduces the growth and the reproductive capacity of *P. sylvestris nevadensis*. Defoliated juvenile trees grow, on average, less than half the amount that undefoliated ones grow, whereas defoliated adult trees produced 50% fewer seeds and had seeds almost 40% lighter than in undefoliated trees. Defoliation therefore alters the pattern of growth and reproduction of trees and can hamper tree survival, due either directly to the lack of photosynthetic tissues or indirectly to greater susceptibility to other negative factors such as drought or pathogen attack (Crawley, 1997; Zamora et al., 1999).

The negative effect of PPC defoliation is greater when considered in combination with several traits of these relict Scots pine forests. Growth rate of Scots pine in southern Spain is much lower than in northern countries (Zamora et al., 2001, and references therein). An unbrowsed sapling takes 21 years to reach 150 cm in height, while a sapling browsed by ungulates takes around 30 years (Zamora et al., 2001). If pines have

now to suffer a reduction in growth rate due to defoliation by PPC, they will require more time (as much as 50%) for the leading shoot to outgrow the reach of ungulate herbivores. As a result, the time needed to reach the reproductive stage will again increase, with consequent negative effect on forest regeneration.

Reduction in the reproductive capacity also has negative consequences for seedling recruitment. The Mediterranean populations of Scots pine have a low tree density (see Section 2), and as a consequence have a considerably lower seed shed in comparison with other pine woodlands in Europe (Koski, 1991; see Castro et al., 1999). This scant seed production is further severely reduced by high losses of seeds to pre- and post-dispersal seed predation (Castro et al., 1999; Castro, 2000). Finally, seedling mortality is extremely high during the summer due to the summer drought typical in Mediterranean environments (Castro, 2000). Therefore, high seed production is critical for forest regeneration; however, seed production is currently low and the damage by PPC suggests that it will be even lower in future, since defoliation strongly reduces the seed set of pines. Furthermore, the reduction in seed mass caused by PPC defoliation threatens to lower seedling success, since seed mass is positively correlated with seedling performance in Scots pine (Reich et al., 1994; Castro, 1999). Thus, high PPC incidence has the potential to constrain the regeneration of these forests, either by its direct effect upon tree performance, or in combination with other factors currently limiting Scots pine regeneration.

The great adult longevity in Scots pine provides these southernmost populations with a buffer that partially offsets losses to unfavourable environmental conditions, and may give a false impression of stable population dynamics (Eriksson, 1996; García et al., 1999). However, the intrusion of PPC, causing retarded growth, losses in reproduction, and even adult tree mortality, might completely change this status quo. Models for climatic change predict rising temperatures for the Mediterranean basin (Osborne et al., 2000; Rodó and Comín, 2001), and in fact the Iberian Peninsula has shown a steady rise in temperature during the past century, both in annual (Esteban-Parra et al., 1995; Piñol et al., 1998) and seasonal series (Esteban-Parra et al., 1995), mainly due to the increase of minimum temperatures. In particular, winter temperatures are currently warming, reducing the number of days with frost. This is a key factor determining the outbreak capacity of PPC, as low winter temperature strongly determines the larval survival of this insect (e.g. Breuer et al., 1989; Halperin, 1990). Warmer temperatures can trigger an uphill displacement of pests limited by low temperature (Ayres, 1993; Possingham, 1993; Harrington et al., 2001; Bale et al., 2002), as corroborated in our study system (Hódar et al., 2001a,b). Thus, the current protection of Scots pine against PPC defoliation provided by high

altitudes will end with future warming, enabling PPC to become a new, serious threat for the survival of these isolated, relict populations.

5. Conclusions and guidelines

This study shows that the effect of global warming via the uphill invasion of PPC may have a profoundly negative effect on the regeneration of the last populations of Scots pine in southern Spain. Consequently, the conservation of these relict forests needs appropriate management to confront the negative effects of PPC. Biological control (pheromones, parasitoids, etc.), though an option, has proven to have limited effectiveness upon PPC during the outbreak phase (Hódar et al., 2001b, 2002). In addition, this approach must be used for every new outbreak, constituting a logistic and economic problem.

Methods based on self-perpetuating characteristics of the system that hamper the outbreak capacity of PPC are preferable, both from ecological and economic standpoints. Over the short term, the increased tree diversity and community complexity in adjacent reforested pine stands could greatly reduce the spread of PPC towards natural populations of Scots pine (Hódar et al., 2001b, see also Watt, 1992; Schönenberger, 2001). Over the long-term, reforestation programmes helping both the spread towards adjacent areas as well as the migration of Scots pine in altitude will be valuable for preventing attack by PPC. This task may be achieved with techniques already developed *in situ* using shrubs as nurse plants to increase seedling survival (Castro et al., 2002; Gómez et al., 2001b), thereby minimizing the ecological impact of reforestation on these protected high-mountain ecosystems.

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