Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species

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Abstract. 1. The work reported here analysed host utilisation by the pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Thaumetopoeidae), the relationship between moth oviposition patterns and larval performance, the chemical characteristics of the plant in relation to the performance of different larval instars, and the role of these factors in the outbreak capacity of the species. In order to do this, a combination of field and laboratory techniques was used to study three pine species differing in nutritional characteristics.

2. Moths oviposited in the three pine species analysed, although cluster pine received a lower number of batches. Late-instar larvae were able to feed on all three pine species, however first-instar larvae developed on Scots and black pine but died on cluster pine. Consequently, oviposition in cluster pine can be considered an oviposition mistake, and indicates that moths are rather unselective when ovipositing on different pine species.

3. Chemical analysis of needles suggested that the quantity of nitrogen was the main factor responsible for the difference in survival of larvae.

4. The oviposition pattern of the moth and the larval susceptibility to food quality in *Thaumetopoea pityocampa* agree with the theory that unselective oviposition of the moth is a precondition for eruptive dynamics in phytophagous insects.

5. The success of the larvae depends mainly on the probability of the moth finding a suitable host. This probability is determined strongly by the changes of structure and coverage in Mediterranean pine woodlands, due to human management.

Key words. Chemical defences, larval performance, Lepidoptera, nitrogen content, outbreaks, oviposition selectivity, plant–herbivore interaction.

Introduction

Food quality, more than quantity, determines the distribution and abundance of many phytophagous insects (White, 1993). Vegetal tissues constitute low-quality food because they usually contain low levels of nitrogen and

combine this nutritional poverty with poisons, digestion inhibitors, or indigestible materials (Mattson, 1980; White, 1993; Zamora *et al.*, 1999). Thus, adults, larvae, or both, must recognise the best foods available and choose them for oviposition or feeding (Bernays & Chapman, 1994).

A high consistency between host-plant oviposition preference and offspring performance implies that females are able to recognise the properties of plants that influence larval development (Jaenike, 1978; Leather, 1985, 1994; Leather *et al.*, 1987; Nylin *et al.*, 1996). Sometimes, however, weak or negative correlations are found between host-plant selection by the mother and offspring

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performance (Thompson, 1988; Courtney & Kibota, 1990; see also Larsson & Ekbom, 1995; and references therein). Predation risk, abundance and apparency of the optimal host plant, and the surrounding habitat matrix have been invoked as explanations for these *oviposition mistakes* (Wiklund, 1974; Feeny, 1976; Denno *et al.*, 1990; Larsson & Strong, 1992; Ohsaki & Sato, 1994; Björkman *et al.*, 1997). The mismatch between the mother's choice and offspring performance produces conflicts between the different stages of the life cycle (Nylin & Janz, 1996; Nylin *et al.*, 1996). A better understanding of these correlations therefore requires consideration of different stages of the life cycle (see, for example, Rausher, 1980; Roininen & Tahvanainen, 1989; Nylin & Janz, 1999).

In this sense, special attention should be given to life-cycle phases that, *a priori*, are more dependent on food quality, such as first-instar larvae. In many insects, mortality is concentrated in the earlier instars, due to their lack of reserves and limited ability to cope with low-protein foods (e.g. Ezueh, 1981; Montgomery, 1982). Mortality of first-instar moth larvae is usually approximately 50% (Montgomery & Wallner, 1988; Tammaru *et al.*, 1995). Consequently, a change in the survival rate of these instars is key in determining the size of the population. Increased larval survival may trigger an eruptive episode, while decreased survival could force a crash in the population (see White, 1993, and references therein).

The pine processionary caterpillar *Thaumetopoea pityocampa* (Lepidoptera: Thaumetopoeidae) is a good case in point. Outbreaks of this species inflict serious economic losses in Mediterranean countries. For instance, in Andalusia (southern Spain) during the last decade, more than €12 million have been spent on the biological control of several forest pests, *T. pityocampa* being the main one (Mora-Figueroa, 2000). Work on the biology of this species usually concerns pine plantations (Battisti, 1988; Fernández de Córdova & Cabezuelo, 1995; Pérez-Contreras & Tierno de Figueroa, 1997), characterised by stands of uniform age, high density, regular spacing, low variability among individuals, and sometimes exotic species. In contrast, no study has analysed processes of the plant–insect interaction, such as host use by the moth and caterpillars in autochthonous pine woodlands.

The work reported here examined the host utilisation and growth capacity of *T. pityocampa* in three pine species, at a locality where these species grow together naturally. Because unselective oviposition has been considered a precondition for eruptive dynamics in phytophagous insects (Price *et al.*, 1990), it was hypothesised that the pine processionary moth, characterised by outbreak dynamics, should not select the plants for oviposition by reason of their nutritional quality for larvae. Consequently, the questions addressed were: Is there a correlation between moth oviposition preferences and larval performance? Is there a correlation between the larval performance and the nutritional characteristics of the plant? What is the potential role of moth oviposition preferences and larval survival in the outbreak capacity of *T. pityocampa*?

Study area and methods

Study area

The study was carried out in the Collado de Ruquino (National Park of Sierra Nevada, Granada, SE Spain, 37°05′30″N, 3°28′15″W, 1750 m a.s.l.), with some additional data from the surroundings of the Jardín Botánico de La Cortijuela (1.5 km from Collado de Ruquino, 1650 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 induces low temperatures in winter, frequently with snow. The mean minimum temperature in the coldest month (January) is $-0.9\,°C$, the mean maximum in the hottest month (July) is $29.0\,°C$, and the annual average temperature is $11.5\,°C$. Rainfall is concentrated mainly in autumn and spring, with an annual rainfall of 825 mm (data from the climatic station at the Jardín Botánico de La Cortijuela, average for 1990–1998). The study area underwent a strong drought in 1995 (385 mm rainfall for the year October 1994 to September 1995) and two very wet years in 1996 and 1997 (1450 and 1318 mm respectively).

Organisms studied

Thaumetopoea pityocampa attacks plants of the genus *Pinus*, although it may eventually feed on other coniferous genera (see, for example, Devkota & Schmidt, 1990). Even within the genus *Pinus*, the ability of *T. pityocampa* to develop varies widely, depending on the pine species and its living conditions (Devkota & Schmidt, 1990; Masutti & Battisti, 1990). *Thaumetopoea pityocampa* is univoltine. Adult flight and egg laying occurs in mid-summer (Devkota & Schmidt, 1990); in the study area, this occurs about July–August. Eggs are laid in the canopy of the trees and need about 45 days to hatch, usually in early September. Larvae move by crawling, and lack ballooning capacity. Development requires five instars, and takes place during autumn and winter, with larvae aggregated in a collective silk nest, protected from the cold in winter. Larvae are strongly gregarious, and individuals from different batches frequently mix in the same nest, because a larger number of larvae per nest allows better and quicker development (Breuer & Devkota, 1990; Halperin, 1990; see also Ruf & Fiedler, 2000). From February to April, fifth-instar larvae abandon their nests and form processions to reach the ground, where they burrow and pupate, usually near the host tree. Pupae may remain in diapause for several years.

Three pine species inhabit the study zone: cluster pine *Pinus pinaster* occupies the most insolated and dry exposures, black pine *Pinus nigra salzmannii* is at its optimum in the area, and Scots pine *Pinus sylvestris nevadensis* occupies both the highest areas as well as the shadiest and coolest exposures. Autochthonous patches of the three species, similar in age and height, appear intermingled roughly at the same density in the Collado de Ruquino in a few

hectares. All field observations and most of the field experiments were made at this site because the proximity of the three pine species in a small area ensured that the abiotic conditions, and hence phenology, would be homogeneous both for the trees and caterpillars. Pines are dormant during most of the infestation period by *T. pityocampa*.

The three pine species are known *T. pityocampa* hosts, although with markedly different attack intensities (Avtzis, 1986; Breuer *et al.*, 1989; Devkota & Schmidt, 1990; Masutti & Battisti, 1990; Schmidt, 1990). To avoid the effects of previous defoliation on larval development (Leather *et al.*, 1987; Battisti, 1988; Smits & Larsson, 1999), only trees that had undergone no more than 5% defoliation from the previous year were used, and most had not been attacked at all. Most of these trees were, nevertheless, defoliated during the winter of 1998, in which the area of the outbreak of processionary caterpillar almost doubled (from 10 000 ha in winter 1997 in Granada province to 18 000 ha in 1998; Junta de Andalucía, 1999), indicating that the pines selected for the experiment were not resistant or immune to the attack of this caterpillar.

Time schedule

Field work was carried out in August–September 1998, and laboratory studies were carried out in the winters of 1997–1998 (cafeteria experiment with second- to third-instar larvae) and 1998–1999 (all the other laboratory experiments).

Field observations

Egg-batch distribution among tree species. Censuses of egg batches were carried out in the three hosts. In 30 randomly selected trees per pine species, a 1-min-duration census was performed, counting the number of egg batches before most batches had hatched. Eggs were counted on foot by scanning the outer canopy of the trees, and by hand searching the branches between 1.5 and 2.5 m from the ground. Egg batches are easily identifiable and stand out from the green back of the needles (Schmidt, 1990), and there were no apparent differences in the detectability of egg batches among the three pine species.

Larval survival among tree species. As soon as larvae hatch, they usually start to feed on the closest foliage, and form a small silk nest in which the first moult takes place. The larvae of some of the egg batches move from this nest to another before the first moult, and sometimes starve before reaching the second instar. To evaluate the capacity of first-instar larvae to feed on the different hosts, newly hatched batches were located in the three pine species, the number of nests near the batch was counted, and survival and instar of the larvae were recorded. A total of 60 egg batches per pine species was checked.

Transposition experiments

Field experiment on larval survival. A transposition experiment under field conditions was performed to evaluate how the host species influences larval development. A total of 30 batches from each host (90 in total) was collected. From this pool, one egg batch from each host (hereafter *host species*) was fixed in each of 10 selected pines of each species (hereafter *food species*), totalling 30 pines with three batches each (see Fernández de Córdova & Cabezuelo, 1995, for details of the method). Egg batches were fixed at the end of a twig 1.5–2.5 m above ground, facing south-east. The batches were fixed to the same tree 0.5 m apart, to minimise within-tree differences in the canopy needles. Several egg batches preyed on by birds and Tettigoniidae in the first 2 weeks were replaced quickly. Egg batches were checked once a week and, as soon as larvae moulted to the second instar, the nest and the batch were collected. Two nests with mixtures of larvae from different egg batches were discarded from the analysis. In the laboratory, egg batches were cleaned, and the number of hatched, unhatched, and parasitised eggs was counted under a binocular microscope. Nests were dissected to record the number of larvae moulted to the second instar.

Laboratory experiment on larval survival. To corroborate the results of the field experiment, an equivalent experiment was performed in the laboratory. For this, groups of 20 first-instar larvae from the three host species were placed in three sets of 12 Petri dishes (108 dishes, 2160 larvae in total). Once a day, fresh, recently collected needles of each food species were added to each dish, and a piece of filter paper placed on the disc was watered to prevent drying. Once a week, dishes were cleaned and the number of surviving larvae was counted. The experiment was ended on day 24, when all larvae had either died or moulted to the second instar.

Cafeteria experiments

The food choice by larvae was studied by means of two cafeteria experiments. Needles from the three pine species were offered simultaneously to larvae collected from the three hosts. Needles came from 10 selected autochthonous trees per species. The experiment was made with second- to third-instar and fourth- to fifth-instar larvae. Each replicate consisted of three larvae placed in a Petri dish, maintained until the end of the experiment, and each treatment had 20 replicates. Three larvae per dish rather than one were used because single larvae spent most of their time crawling in search of other larvae and did not eat, while a group of three remained together and fed normally. Each experiment was repeated in three trials with the same larvae per Petri dish. Each trial lasted 24 h, with at least 24 h between trials. Larvae were not fed for 12 h before the beginning of a trial. All trials belonging to the same experiment were performed within a maximum of 10 days. During the experiments, larvae were kept at room temperature (19–22 °C), with diffuse light for 10–12 h per day.

Before the trial, the needles to be offered to the larvae were weighed (precision: 0.1 mg) and identified using permanent markers. A set of 10 dishes was placed with needles exactly as in the experimental units, and at the same time, as a control for needle desiccation. All needles were placed in excess, to ensure that the larvae were never forced to eat one needle type because the preferred type was depleted. Once the trial was finished, the remains of the needles in all treatments were cleaned and weighed. The difference between the original weight and the final weight of each sample, corrected for desiccation effect, indicated the consumption of each needle type presented to larvae.

Larvae in the field may have needles available on the same tree flushed in four to six different years, and this would be a strong source of bias in the experiments (see, for example, Smits & Larsson, 1999). To determine larval preferences for different cohorts of needles, a test with larvae from the three hosts and needles belonging to the last three cohorts of each host (i.e. needles flushed in 1996, 1997, and 1998) was performed. For the three hosts, larvae did not show a significant preference for any needle age (ANOVA, $F_{2,151} = 0.468$, $P = NS$), so only last-year needles were used in all cafeteria experiments, because female moths usually oviposit in last-year needles and this is the first food that first-instar larvae have available at hatching.

Quality of trees as food

An additional experiment was performed to determine the effect of food chemistry on larval performance, measured as food ingestion, digestibility, and larval growth. Thirty Petri dishes with three fifth-instar larvae each were maintained without food until the larvae produced no more frass, then dishes were separated into three groups of 10. Each group received fresh needles of a pine species, weighed previously, and the larvae were allowed to feed for 48 h. The food was then removed and the larvae were kept without food until they stopped depositing frass. Ingestion rate was calculated as dry food ingested per fresh weight of larvae, and apparent digestibility as the difference between food ingested and frass produced with respect to the food ingested (in both cases $mg\,mg^{-1}$ in 48 h, expressed as a percentage of weight). Larval growth was expressed as the percentage of fresh weight gain in 48 h. For calculations of dry weight, a parallel series of needles was dried to determine the amount of dry matter per pine species.

A sample of needles from the trees used in the experiments was used for chemical analysis. Because phenols have been shown to play a significant role in the larval mortality of *T. pityocampa* (Schopf & Avtzis, 1987), total phenolic compounds and condensed tannins were quantified in needles. Both phenols and tannins are reputedly feeding deterrents and/or digestibility inhibitors (Waterman & Mole, 1994). Total phenols were extracted from 0.5 g needle dry powder with 10 ml of 50% (v/v) methanol in an ultrasonic bath for 15 min, and ultracentrifuged at 2500 r.p.m. for 15 min. Total phenols were analysed by the

Folin–Ciocalteau method (Waterman & Mole, 1994). An aliquot was diluted with water and assayed with Folin–Ciocalteau phenol reagent and 20% sodium carbonate, to reach a final concentration of $1\,mg\,ml^{-1}$, and absorbance was measured at 740 nm (see Hódar & Palo, 1997). Condensed tannins were analysed by the proanthocyanidin assay (Waterman & Mole, 1994). To compare species, direct values of absorbance were used, without transformation to standard equivalents (see Waterman & Mole, 1994, for a full explanation of this procedure). The nitrogen content was quantified in needles using a Fisons-Carlo Erba EA 1108CHNS-0 (Thermo Finnigan, San Jose, California) element analyser.

Statistical analysis

All observational data were analysed using non-parametric statistics, either Mann–Whitney or Kruskal–Wallis (Zar, 1996). When a Kruskal–Wallis test was significant, the differences between levels were established by a non-parametric multiple comparison for balanced data (Nemenyi test; Zar, 1996).

In the transposition experiments, hatching and parasitism were expressed as a percentage of the total number of eggs in the egg batch, and survival was expressed as a percentage of the number of eggs that had hatched in the egg batch. Data from the cafeteria experiments were expressed as a percentage of the total food consumed from any type of needle used in the experiment, i.e. for each Petri dish, the different types of food consumed by the larvae always added up to 100%.

The data from the field experiment were tested using one-way ANOVA, while laboratory experiments were analysed using a multivariate repeated-measures analysis of variance (MANOVA), in which time (for survival experiment) or trial (for cafeteria experiments) was the between-subject factor. Non-significant interactions among sources of variation in one-way ANOVA were pooled with the error term to improve the test (Zar, 1996). Prior to all these parametric analyses, the ratio variables were arcsin transformed when they departed from normality (Zar, 1996). Means are presented ± 1 SE.

Results

Field observations

The number of egg batches observed per census differed significantly among the three hosts considered (Kruskal–Wallis $H = 11.31$, d.f. = 2, $P < 0.01$), with higher values in the Scots and black pine (7.6 ± 0.9 and 7.2 ± 0.7 egg batches per census) than in the cluster pine (4.1 ± 0.4; Nemenyi test, $P < 0.025$ against Scots pine, $P < 0.01$ against black pine). With respect to the newly hatched larvae in the three hosts, there were no differences in the number of nests developed (Kruskal–Wallis $H = 5.50$, d.f. = 2, $P = NS$);
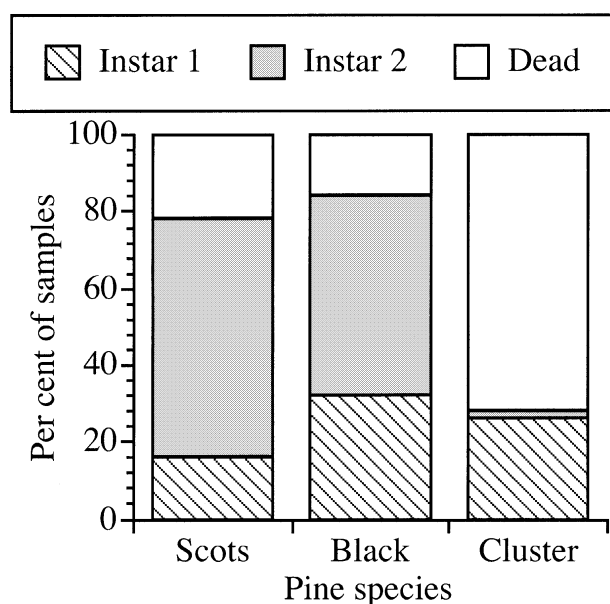
Fig. 1. Results of the survey of newly hatched egg batches of *Thaumetopoea pityocampa* in three pine species.

however >75% of nests in the Scots and black pine contained larvae, most of which moulted to the second instar, while in the cluster pine the percentage of nests with live larvae was <30%, mostly first instar (Fig. 1); these differences in larval development were significant ($\chi^2 = 55.16$, d.f. $= 4$, $P < 0.001$).

Transposition experiments

The egg batches used in the transposition experiment in the field did not differ among hosts in number of initial eggs, although the percentage of hatching was higher in egg batches from the cluster pine, and the percentage of eggs parasitised was higher in the black pine (Table 1, Fig. 2). The percentage of larvae that reached the second instar was not related to their host species but rather to the food species (Table 1), survival being slightly higher for larvae feeding on Scots pine than black pine, and almost null for larvae feeding on cluster pine (Fig. 3).

The MANOVA on the transposition experiment in the laboratory showed all factors and interactions to be significant, although food was the factor with higher

Table 1. Results of experiments in which *Thaumetopoea pityocampa* larvae were fed on different pine species to examine their effect on larval development. In the field experiment, the characteristics of egg batches as well as the percentage of larval survival were analysed.

	d.f.	SS	F	P
Field experiment				
Number of eggs per batch, $R^2 = 0.000$				
Host	2	4661.9	1.116	0.3325
Food	2	1022.6	0.245	0.7836
Error	82	171249.4		
Percentage of eggs hatched, $R^2 = 0.100$				
Host	2	1.293	6.377	0.0027
Food	2	0.077	0.378	0.6864
Error	82	8.314		
Percentage of eggs parasitised, $R^2 = 0.053$				
Host	2	0.020	3.668	0.0298
Food	2	0.004	0.735	0.4826
Error	82	0.221		
Percentage of surviving larvae, $R^2 = 0.425$				
Host	2	0.213	0.784	0.4601
Food	2	8.722	32.090	0.0001
Error	79	10.736		

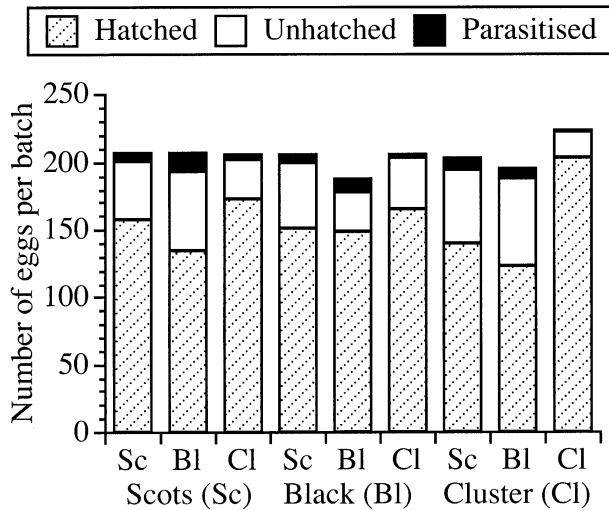|	d.f.	Wilks' λ	F	P
Laboratory experiment				
Host	2,99	0.800	12.380	0.0001
Food	2,99	0.163	253.329	0.0001
Host × food	4,99	0.753	8.101	0.0001
Time	2,98	0.613	30.996	0.0001
Time × host	4,196	0.864	3.721	0.0061
Time × food	4,196	0.578	15.453	0.0001
Time × host × food	8,196	0.750	3.782	0.0004

Fig. 2. Characteristics of the egg batches used in the experiment of transposition in the field. The upper row in the *x*-axis represents the plant to which egg batches were fixed; the lower row represents the host plant from which egg batches were collected.

F value (Table 1). Scots pine was the only food that allowed larvae to develop to the second instar, while in the black pine some larvae survived for a week but then died. In the cluster pine, almost all larvae died in the first 2 or 3 days of the experiment (Fig. 3).

Cafeteria experiments

Food selection was related to the age of the larvae. The second- and third-instar larvae preferred their host species, except in the case of larvae from the black pine, for which host species proved to be the least preferred (Fig. 4). By contrast, in fourth- and fifth-instar larvae, the preferred food was consistently the cluster pine, followed by black pine then Scots pine (Fig. 4). The statistical analysis showed food to be the main factor, although the older larvae showed a much more clear-cut selection (Table 2).

Quality of trees as food

The chemical analysis of secondary compounds in the three tree species showed scant differences among species (Table 3); however, there was large contrast in the nitrogen content and amount of dry matter in needles, pointing to nutritional dissimilarities among species, with Scots pine having the highest nitrogen content and cluster pine the lowest. This was corroborated by the apparent inequalities in digestibility but not in ingestion rates; nevertheless, these variations did not result in significant differences in larval growth (Table 3).

Discussion

Oviposition by moths and larval survival in the three pine species

Adult female *T. pityocampa* are normally flightless before egg laying, and reach their host tree by climbing (Schmidt, 1990; but see Demolin, 1969a). They usually deposit a single egg batch within 24 h of emergence. With such limitations, fine tuning of host selection would be difficult for this moth (see Tammaru *et al.*, 1995, for similar conclusions on *Epirrita autumnata*). This may explain oviposition in the cluster pine despite being the poorest host species for larval survival (see below). Moths appear to climb to the nearest pine available after emergence and mating; in the study area, this is sometimes a cluster pine. Due to the low survival rate of larvae in cluster pine, however, most batches on cluster pine must come from moths that developed on neighbouring Scots or black pine, on which larvae survive. As a consequence, egg batches in cluster pine were at lower density than in Scots or black pines. This would also account for the lower incidence of egg parasitism in cluster pine (Fig. 2). As sex-pheromone traces remaining on the egg mass have been suggested to attract parasitoids (Battisti, 1989), a lower number of batches would be less attractive. There are different opinions concerning the plant characteristics that the female moth follows for oviposition. Demolin (1969a) suggested that the female moth is able to select the tree for oviposition, but following visual rather than chemical (and hence nutritional) cues, while Tiberi *et al.* (1999) found a negative selection of female moths on *Pinus pinea* due to the amount of the terpene limonene in this pine species.

The high proportion of empty nests and the bad condition of newly hatched larvae (usually dead) in cluster pine hosts indicates that, in comparison with the Scots or black pine, the cluster pine is a poor resource for first-instar larval survival (Fig. 1). Field transposition experiments led to the same conclusion. Egg batches from the three hosts had potentially the same capacity to develop on a given host (Table 1, Fig. 3). While the Scots and black pine are equally adequate as food for the development of first-instar larvae of *T. pityocampa*, however, the cluster pine was inadequate, with the number of surviving larvae ≈60% in the two former species and only 5% in the last. Laboratory transposition experiments showed similar results for Scots and cluster pines, although mortality was also high in the black pine (Table 1, Fig. 3).

Correlation between food quality and larval survival

Food-quality indices, such as nitrogen content and apparent digestibility in pine needles, rank the pine species studied as Scots > black > cluster (Table 3). This ranking reflects the survival rate of first-instar larvae, suggesting that nitrogen and digestibility are crucial in determining larval survival, especially in the early stages of larval
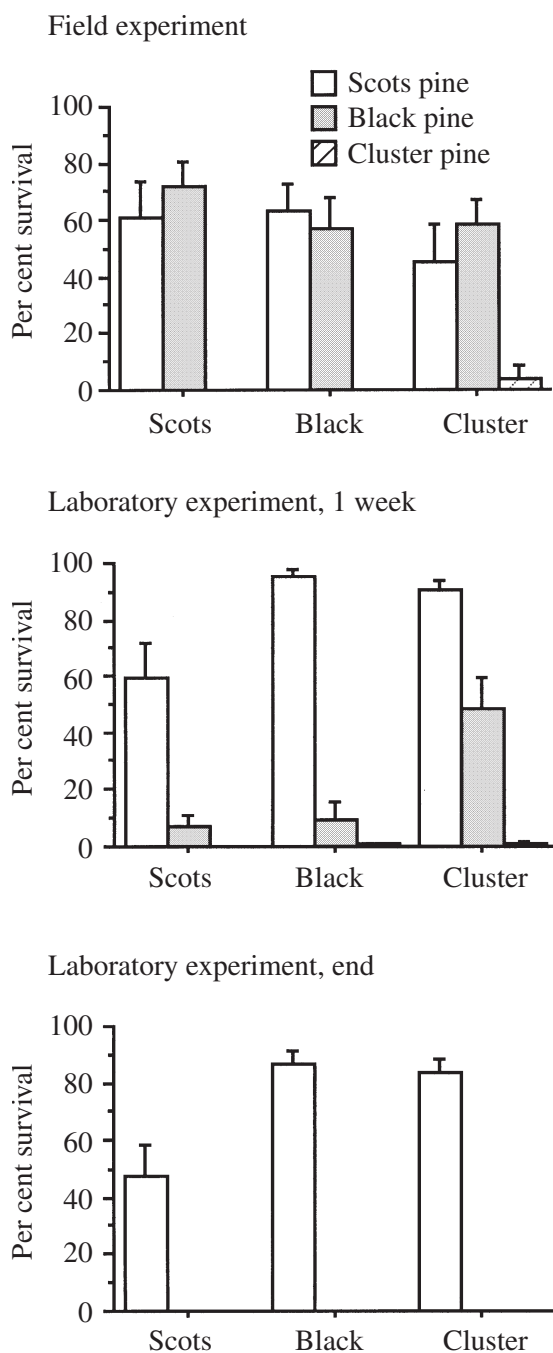
Field experiment

Laboratory experiment, 1 week

Laboratory experiment, end

Fig. 3. Results of the experiments of transposition, both in the field and laboratory. The host plant from which larvae were collected is indicated on the *x*-axis and bars represent the percentage of survival feeding on each pine species offered. Bars are presented + SE.

development, the segment of the life cycle most sensitive to food quality (White, 1993, and references therein). By contrast, the quantity of secondary compounds (phenols and condensed tannins) in leaves did not differ among hosts (Table 3).
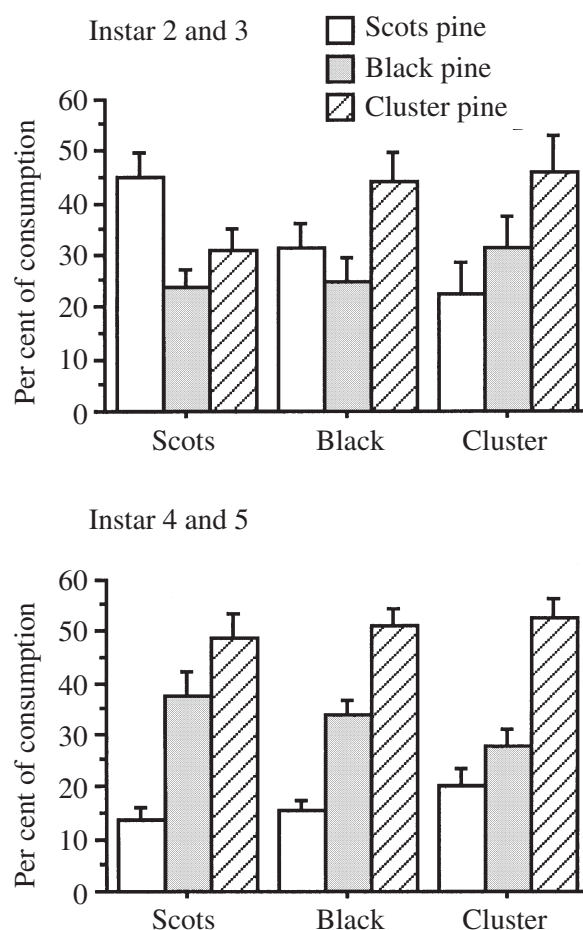
Instar 2 and 3

Instar 4 and 5

Fig. 4. Relative consumption of the three pine species in the cafeteria experiment. The host plant from which larvae were collected is indicated on the *x*-axis and bars represent the percentage of consumption of each pine species offered. Bars are presented + SE.

Some authors (e.g. Devkota & Schmidt, 1990) have also considered needle toughness to be a possible cause of early larval death, and certainly cluster pine is characterised by large, tough needles (Franco, 1986). First-instar larvae, however, are able to fed on cluster pine needles (J. A. Hódar and J. Castro, pers. obs.), and *T. pityocampa* grow in cluster pine (Avtzis, 1986; Breuer *et al.*, 1989; Buxton, 1990; Devkota & Schmidt, 1990; Masutti & Battisti, 1990; Schmidt, 1990; Pérez-Contreras & Tierno de Figueroa, 1997), although infestation rates are much lower than in the Scots and black pine. Furthermore, the apparent growth rate of older larvae feeding on the three species did not differ significantly (Table 3), and cluster pine needles may even be a preferred food, as shown by the cafeteria experiments, although this is an artificial situation; in nature, larvae never have needles of three different hosts available at the same time.

Table 2. Results of the cafeteria experiments in which *Thaumetopoea pityocampa* larvae were fed on different pine species to examine food selection.

	d.f.	Wilks' λ	F	P
Food selection (second- and third-instar larvae)				
Host	2,171	0.987	1.108	0.3326
Food	2,171	0.962	3.419	0.0350
Host × food	4,171	0.921	3.660	0.0069
Trial	2,170	0.985	1.287	0.2788
Trial × host	4,340	0.933	3.020	0.0181
Trial × food	4,340	0.937	2.813	0.0254
Trial × host × food	8,340	0.908	2.098	0.0354
Food selection (fourth- and fifth-instar larvae)				
Host	2,171	0.998	0.181	0.8346
Food	2,171	0.674	41.376	0.0001
Host × food	4,171	0.980	0.879	0.4778
Trial	2,170	0.996	0.301	0.7403
Trial × host	4,340	0.997	0.129	0.9719
Trial × food	4,340	0.963	1.624	0.1677
Trial × host × food	8,340	0.934	1.476	0.1645

The strong effect of mortality of the cluster pine needles is restricted to the very young larvae, given that after the first instar the three pine species seem to be able to sustain the development of the larvae. This contradicts earlier results (Avtzis, 1986; Devkota & Schmidt, 1990) showing a direct influence of pine species through the larval development. In any case, the high mortality in the first instar reduces the number of larvae per batch greatly, and this is important because the capacity of larvae to construct good nests for overwintering is reduced greatly when the number of larvae is low (Breuer & Devkota, 1990; Halperin, 1990). That is, the initial effect on first-instar survival may reduce the probability of survival of the whole batch via the reduction in the number of larvae (Halperin, 1990), even if there is no effect of food quality on larval development for second- and third-instar larvae.

Linking oviposition, food quality, larval survival, and population dynamics

The lack of oviposition selectivity has been proposed (Tammaru *et al.*, 1995) as a side effect of a strong progressive selection for large female (= abdomen) size in *E. autumnata*. The larger the egg load of the female, the poorer its flying ability and consequently its possibility for host selection. This theory seems to fit well with *T. pityocampa*, as there is a high correlation between female size and egg load (Pérez-Contreras & Tierno de Figueroa, 1997), and both the low ability of moths to fly and their short lifespans (Devkota & Schmidt, 1990; Schmidt, 1990) strongly limit their possibilities for host selection.

The unselective oviposition has been considered (Price *et al.*, 1990) a precondition for eruptive dynamics in phytophagous insects: when eggs are left indiscriminately, the survival success of the cohort is determined entirely by unpredictable factors, such as weather [rainfall in *Ochrogaster lunifer* (Floater, 1997), mild winter temperature in *E. autumnata* (Tenow, 1972; Tenow & Bylund, 1989) and *T. pityocampa* (Demolin, 1969b, 1970)]; however the outcome of this plant–herbivore relationship is mediated by the structure of the habitat where the interaction takes place (Masutti & Battisti, 1990). In a homogeneous, extensive stand of planted pines, a non-selective ovipositing moth has a high probability of finding a suitable host, while in a heterogeneous stand with scarce, scattered suitable hosts, the moth has a lower probability of finding suitable hosts. Several authors have shown stable caterpillar populations in diversified habitats with mixed plant species and outbreaks when the habitats are regular plantations or extensive woodlands (Tammaru *et al.*, 1995, for *E. autumnata*; Floater & Zalucki, 2000, for *O. lunifer*). While diverse habitats with mixed plant species promote population stability, open disturbed habitats or regular plantations allow a more even distribution of egg batches across high-quality hosts, resulting in more unstable populations, with site-wide outbreaks (Floater & Zalucki, 2000). In the Mediterranean area, natural pine woodlands are low-density forests, usually mixed with different tree species

Table 3. Characteristics of needles from the three pine species analysed. Phenols and tannins are expressed as absorbance values (read in spectrophotometer at 740 and 550 nm), ingestion rate is expressed as mg of dry needles ingested by mg of fresh larvae in 48 h, apparent digestibility as the difference between food ingested and frass excreted, and apparent growth as the percentage of weight increase of larvae in 48 h. Figures are mean ± SE.

	Scots pine	Black pine	Cluster pine	F	P
Phenols	1.51 ± 0.14	1.58 ± 0.16	1.64 ± 0.17	0.15	0.8577
Tannins	0.57 ± 0.08	0.51 ± 0.08	0.52 ± 0.09	0.19	0.8270
Per cent of nitrogen	1.67 ± 0.04	1.34 ± 0.05	1.09 ± 0.06	34.33	0.0001
Per cent of dry matter	40.69 ± 0.27	44.33 ± 0.28	40.90 ± 0.31	50.42	0.0001
Ingestion rate	0.75 ± 0.04	0.86 ± 0.05	0.74 ± 0.03	2.18	0.1328
Per cent apparent digestibility	14.32 ± 1.29	12.51 ± 1.23	7.79 ± 1.25	6.96	0.0036
Per cent apparent growth	19.53 ± 2.08	21.62 ± 1.65	17.04 ± 1.12	1.65	0.2112

(e.g. *Quercus* sp.; Mesón & Montoya, 1993), thus discouraging *T. pityocampa* from reaching outbreak proportions. A forest structure with suitable hosts in a density low enough and scattered among unsuitable hosts would dilute the effect of the population explosion, because unsuitable hosts, such as cluster pine, would receive egg batches that would not develop into adult *T. pityocampa* (Buxton, 1990). Where pine species with different suitabilities for *T. pityocampa* development grow intermingled, unsuitable hosts would act as sinks for moths coming from suitable hosts, those acting as sources; however, the massive pine plantations during the last century (Junta de Andalucía, 1990; see also Masutti & Battisti, 1990), characterised by monospecific, even-aged stands, high density, regular spacing, and low variability among individuals, created a habitat in which *T. pityocampa* moths easily find suitable hosts at high density. Under these conditions, an increase in larval survival translates immediately to eruptive dynamics and hence outbreaks. Therefore, an ecologically healthy and economical way to prevent *T. pityocampa* outbreaks is to reproduce the heterogeneous and diverse original structure of natural pine woodlands in Mediterranean ecosystems.

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