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Abstract: The gypsy moth, *Lymantria dispar*, is known as an important agent of hardwood forest defoliation in the northern hemisphere. Field observations in Corsica showed that caterpillars did not attack three hardwood species: *Olea europaea* (olive), *Fraxinus ornus* (flowering ash) and *Ficus carica* (common fig). Bioassays were conducted in the laboratory to test the toxic and/or repellent effect of these tree species on gypsy moth caterpillars. Control species were oaks (*Quercus ilex*, *pubescens* and *robur*). Three larval instar groups were tested (L1-L2, L3-L4, and L5-L6). The first group was tested in boxes on fresh cut leaves, the others directly on young trees, the caterpillars being maintained in insect-proof system. Larval nutrition and development were recorded every two days. The results confirm the observations made in Corsica: larvae on anti-feedant species did not molt to the next larval stage and died of starvation (leaves were not consumed). This confirms that the anti-feedant tree species had a negative impact on gypsy moth caterpillars. Incidentally, it was also observed that larval development could be negatively affected when host plants are water stressed. Additional chemical studies should be conducted in order to identify and isolate the molecules responsible for this anti-feedant, repulsive and/or toxic effect.

Key words: *Lymantria dispar*, defoliation, plant chemical defense, *Quercus* sp, herbivore feeding preferences

Introduction

In host plant-pest relationships one of the most notable features is the host-plant selection by pest (herbivores and pathogens) (see Schoonhoven *et al.*, 2005 for a review). Among other criteria, host-plant selection is linked to insects' preferences which determine a range of acceptable plants species with a given degree of acceptance. In the case of herbivorous insect-plant interactions, insect food preferences are mainly based on physical and chemical defenses developed by plants. Dethier *et al.* (1960) suggested a terminology to define the impact of various chemical compounds on insects' preferences. Plant organs could contain attractant, repellent, arrestant, deterrent or feeding stimulant compounds. Improve, promote and stimulate natural chemical defenses of plants could be an alternative to chemical treatments to forest pests.

Gypsy moth (*Lymantria dispar* L., Lepidoptera, Erebidae) is a defoliator native to the deciduous and mixed forests of Eurasia (Giese & Schneider, 1979). It undergoes periodic outbreaks (Campbell & Sloan, 1978) which can result in extensive damage: e.g., in 2009, caterpillars defoliated more than 3000 hectares of cork oak forest (*Quercus suber*) in the Var region (South of France; UEFM field observations). Gypsy moth is highly polyphagous with some preferences for the genus *Quercus* (see Barbosa *et al.*, 1987 for European species and Shields *et al.*, 2003 for American species), but it also attacks conifers and fruit trees. However, during recent outbreaks of this insect in Corsica, it was observed that olive trees

(*Olea europaea*), fig trees (*Ficus carica*) and flowering ash (*Fraxinus ornus*) were not defoliated. These field observations fitted well with Barbosa's *et al.* (1987) inventory of plant species according to the feeding preferences of Gypsy moth in which gypsy moth prefers *Quercus* species but not species from the Moraceae and Oleaceae families.

In order to determine a repellent/deterrent/toxic effect of olive tree, flowering ash and fig tree on gypsy moth larvae, we conducted bioassays under laboratory conditions. Different larval stages were exposed to the foliage of these plant species while others were exposed to oak foliage as control. The objective was to answer three main questions: (1) Are caterpillars able to feed on potential repellent/deterrent/toxic species when they have no other available source of food? (2) Is a plant species more repulsive than another? (3) Are plant species repellent/deterrent/toxic for every larval instar?

Material and methods

Biological material

Gypsy moth larvae were collected *in situ* at the experimental site of Arbois (E5.276° N43.494°, South of France) while following the phenology of larval development. Experiments were carried out on three groups of larval stages: L1-L2 (first- and second-instars); L3-L4 (third- and fourth-instars); L5-L6 (last instars). Larval instars were determined according to the evolution of larval pigmentation and head size (Fraval *et al*., 1989). For each experiment, 70 larvae were collected in the field with a brush and placed in moisturized boxes to avoid overheating. Then they were placed in tubes under laboratory conditions 2-3 days before the beginning of the experiment.

Three oak species were used as control (*Quercus ilex*, *Q. pubescens* and *Q. robur*, respectively named QI, QP and QR thereafter). These species are known to be commonly consumed by gypsy moth (Barbosa *et al*., 1987). The three other species (*Fraxinus ornus*, *Ficus carica*, *Olea europaea*, respectively named FO, FC and OE thereafter) were considered as "test species". All the plants were produced in a nursery ("Pépinière des Milles", South of France), then stored in greenhouses at INRA-Avignon until the beginning of the experiment to synchronize plants bud break and larval hatching. Ultimately, plants were placed under laboratory conditions 2 or 3 days before each experiment. All trees were about the same size (≈ 40 cm high) and 1-3 years of age (except for *Q. robur* from which leaves were sampled directly on an adult tree, located at the INRA-Avignon site). Young trees were placed in perforated pots containing absorbent foam and arranged in water cup, to ensure a constant humidity.

Experimental set up

Three experiments were set up according to larval development. The first experiment was carried on early instars (L1 and L2): 5 larvae were placed in transparent boxes (352 cm^3) with or without leaves. Five replicates were done per plant species. Negative control (called "reference" hereafter) included boxes containing larvae but no leaves. Positive control referred to boxes containing larvae and QI or QR leaves. QP material was not available for the first experiment. Then, we replace by another deciduous oak, QR. Test boxes contained larvae with leaves from FO, FC or OE. Leaves were collected on young potted-plants (but old tree for QR) and placed in the boxes every two days to ensure that larvae had fresh and edible material.

The 2^{nd} and 3^{rd} experiments were carried out on the later instars (respectively L3-L4 and L5-L6) placed directly on young potted-plants with a system of insect-proof net and a plastic

plate for feces harvesting. 5 larvae were placed in each device for the 2nd experiment and only 3 larvae per device for the 3rd one. Five replicates were done per plant species. Bioassays and larva conditioning were made under natural light (no artificial light). Room temperature was controlled at 21 ± 5 °C.

Experimental protocol

Monitoring of mortality and larval molting was conducted every two days from the start of each experiment and during 8 days. The mortality rate was calculated from the number of live *versus* dead larva and given in percentage. The larval molting was determined by the ratio of the number of larvae which molted versus the number of total larvae, given in percentage.

Nutrition was assessed by measuring leaf consumption and feces weight according to the larval stage. Both parameters were measured at the end of the experiment (after 8 days). In order to quantify leaf consumption, we counted the difference between intact and damaged leaves at the end of the experiment. For L3-L4 and L5-L6 instars, the feces were collected in plastic plates and weighed. Feces weight was not measured for the first experiment because samples were too small.

Data analysis

Because of technical constraints, experimental conditions were not identical for the three sets of experiments (at leaf scale for the first experiment *vs* entire young plant for the others as well as the use of different control oak species). Consequently, the three experiments, conducted according to larval stages, were not statistically intercompared.

Data collected over time, such as mortality and larval molting were analyzed using a MANOVA. Considered factors were time and plant species (test or control). If significant differences were observed, we used a Bonferroni post-test to highlight the significant differences between species according to time variability. For data collected at the end of the experiment (feces weight and leaf consumption) a Kruskal-Wallis test was applied. In the case of significant differences, a post-test Dunn (multiple comparisons) was set in order to highlight these significant differences between species.

Results

Mortality and larval molting rates

Mortality and larval molting rates were significantly different over time for each experiment (MANOVA, Tables 1, 2). For the first two instars (L1-L2, Table 1a), mortality started the second day, reached over 60% on day 4 and 100% on day 6, whatever the plant species, except on QR for which no mortality was found. In parallel, we noticed that 100% of larva consuming QR developed to the next larval stage on day 8 (Table 1b).

For instars L3 and L4 (Table 2a) mortality appeared from day 4 on any plant species, including control; it reached 100% on day 6 on FO and OE, and 100% on day 8 on all plant species. More than 40% of larvae reached the next instar on day 8 on QI and only 20% on day 8 on QP (Table 2b). For instars L5 and L6 (Table 2a), mortality appeared from day 4, varied between 20 and 40% on day 6 and reached 100% on day 8 for the three plant test species when only a few deaths were observed on control species (4 ± 6.4% for QI and et 8 ± 9.6% for QP). Larvae started to molt at day 2 on OE, FO and QP (less than 20% have molted). At day 8 between 10 and 30% of larvae molted to next instar when fed with test species, and between 46.7 ± 24% and 53.3 ± 24% with control species (Table 2b)

Table 1. Time variation of the mortality rate (% Avg ± SE) and larval molting rate (% of larvae which molted *vs* the total larvae Avg ± SE) of L1-L2 gypsy moth larvae fed on various plants species (QI: *Quercus ilex*; QR: *Q robur*; FC: *Ficus carica*: FO: *Fraxinus ornus;* OE: *Olea europaea*; R: negative control = no plant species). MANOVA p-values were calculated according to factors time and plant species. On a given line "a", "b", "c", "d" mean significant differences according to plant species.

a) Mortality rate

		Plant Species						**MANOVA Test** P-value		
		QI	QR	FC	FO	OE	R	Time	Species	Time x Species
Time (days)	0	0±0	0±0	0±0	0±0	0±0	0±0	< 0.0001	< 0.0001	< 0.0001
	2	68^{d}±25.6	0^{a}±0	20^{ab}±19.2	28^{bc}±33.6	44^{c}±20.8	60^{cd}±8			
	4	100^{b}±0	0^{a}±0	64^{c}±22.4	92^{b}±9.6	96^{b}±6.4	100^{b}±0			
	6	100^{b}±0	0^{a}±0	100^{b}±0	100^{b}±0	100^{b}±0	100^{b}±0			
	8	100^{b}±0	0^{a}±0	100^{b}±0	100^{b}±0	100^{b}±0	100^{b}±0			

b) Larval molting rate

		Plant Species						**MANOVA Test** P-value		
		QI	QR	FC	FO	OE	R	Time	Species	Time x Species
Time (days)	0-4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	< 0.0001	< 0.0001	< 0.0001
	6	0^{b} ± 0	16^{a} ± 12.8	0^{b} ± 0	0^{b} ± 0	0^{b} ± 0	0^{b} ± 0			
	8	0^{b} ± 0	100^{a} ± 0	0^{b} ± 0	0^{b} ± 0	0^{b} ± 0	0^{b} ± 0			

Larval nutrition assessment

The first two instars (L1-L2) only consumed leaves from control species (Table 3). The rate of leaves showing herbivore attack reached 34.7 ± 12.8% and 91.8 ± 4.2%, respectively for QI and QR. Faeces weight was not recorded for these instars because they were too small for weighting.

For instars L3-L4, the leaf consumption rate was smaller (Table 3). It reached 25.5 ± 12.3% for QP; 26.1 ± 15.3% for QI; 5% for FC and 0% for FO and OE. Feces weight results were consistent with leaf consumption rates with 0.27 ± 0.1, 0.25 ± 0.1, and 0.02 ± 0.03 mg of faeces produced by larvae fed on QP, QI, and FC, respectively).

L5-L6 larvae consumed 59.1 ± 16.4% on QP and 76.2 ± 17.7% of leaves on QI while test species were not consumed (except for a slight rate of 0.4 ± 0.06 mg on FO which means 1.6% leaf area consumed on one of the 63 leaves available). Weight feces results were consistent with leaf consumption rates: 0.96 ± 0.3 mg, 1.16 ± 0.4 mg and 0.4 ± 0.06 mg on QP, QI and FO, respectively.

Table 2. Time variation of the mortality rate (% Avg ± SE) and larval molting rate (% of larvae which molted out of the total larvae Avg ± SE) of L3-L4 and L5-L6 gypsy moth larvae fed on various plants species (QI: *Quercus ilex*; QP: *Q. pubescens*; FC: *Ficus carica*: FO: *Fraxinus ornus*, OE: *Olea europaea*;). MANOVA p-values were calculated according to factors time and plant species. On a given line "a", "b", "c" mean significant differences according to plant species.

a) Mortality rate			**Plant Species**					**MANOVA Test** P-value		
			QI	QP	FC	FO	OE	Time	Species	Time x Species
L3-L4	**Time** (days)	0-2	0±0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	< 0.0001	< 0.0001	< 0.0001
		4	12^{a} ± 14.4	28^{ab} ± 17.6	36^{b} ± 24	72^{c} ± 25.6	48^{b} ± 20.8			
		6	38^{a} ± 14.4	76^{b} ± 17.6	40^{c} ± 0	100^{c} ± 0	100^{c} ± 0			
		8	100^{a} ± 24	100^{b} ± 12.8	100^{b} ± 0	100^{b} ± 0	100^{b} ± 0			
L5-L6	**Time** (days)	0-2	0 ± 0	0 ±0	0 ± 0	0 ± 0	0 ± 0	< 0.0001	< 0.0001	< 0.0001
		4	0^{a} ± 0	0^{a} ± 0	18.7^{b} ± 22.4	24^{ac} ± 19.2	0^{c} ± 0			
		6	0^{a} ± 0	0^{a} ± 0	37.3^{b} ± 13.9	26.7^{b} ± 27.7	32^{b} ± 9.6			
		8	4^{a} ± 6.4	8^{a} ± 9.6	100^{b} ± 0	100^{b} ± 0	100^{b} ± 0			

b) Larval molting rate			**Plant Species**					**MANOVA Test** P-value		
			QI	QP	FC	FO	OE	Time	Species	Time x Species
L3-L4	**Time** (days)	0-4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.0004	0.0001	0.0003
		6	30^{a} ± 20	0^{b} ± 0	0^{b} ± 0	0^{b} ± 0	0^{b}± 0			
		8	40^{c} ± 24	18.3^{a} ± 22	0^{b} ± 0	0^{b} ± 0	0^{b} ± 0			
L5-L6	**Time (days)**	0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	< 0.0001	0.2420	0.0140
		2	0 ± 0	20 ± 16	0 ± 0	0 ± 0	13.3 ± 16			
		4	0^{a} ± 0	20^{ab} ± 16	6.7^{ab} ± 10.7	0^{ab} ± 0	33.3^{b} ± 13.3			
		6	26.7 ± 32	26.7 ± 10.7	6.7 ± 10.7	0 ± 0	33.3 ± 13.3			
		8	46.7^{a} ± 24	53.3^{a} ± 24	6.7^{bc} ± 10.7	0^{ac} ± 0	33.3^{ac} ± 13.3			

Table 3. Leaf consumption (in %, Avg ± SE) and feces weight (in mg, Avg ± SE) according to larval instars (L1-L2; L3-L4; L5-L6) and plant species (QI: *Quercus ilex*; QR: *Q robur*; OE: *Olea europaea*; FC: *Ficus carica*: FO: *Fraxinus ornus*). On a given line "a", "b" means significant differences between plant species.

		Plant species					**Kruskal-Wallis Test**
		QI	QR/QP	FC	FO	OE	P-value
L1-L2 instar	**Leaf consumption** (% Avg ± SE)	34.7[a] ± 12.8	91.84[a] ± 4.2	0.0[b] ± 0.0	0.0[b] ± 0.0	0.0[b] ± 0.0	0.0003
L3-L4 instar	**Leaf consumption** (% Avg ± SE)	26.1[a] ± 15.3	25.5[a] ± 12.3	5.0[ab] ± 8.0	0.0[b] ± 0.0	0.0[b] ± 0.0	0.0009
	Faeces weight (mg Avg ± SE)	0.25[a] ± 0.1	0.27[a] ± 0.1	0.02[ab] ± 0.03	0.0[b] ± 0.0	0.0[b] ± 0.0	0.0003
L5-L6 instar	**Leaf consumption** (% Avg ± SE)	76.2[a] ± 17.7	59.1[a] ± 16.4	0.0[b] ± 0.0	0.32[b] ± 0.51	0.0[b] ± 0.0	0.0009
	Faeces weight (mg Avg ± SE)	1.16[a] ± 0.4	0.96[ab] ± 0.3	0.0[b] ± 0.0	0.04[b] ± 0.06	0.0[b] ± 0.0	0.0003

Discussion

In general, data on the nutritional ecology of gypsy moth demonstrate that tree species differ in their suitability (see Barbosa *et al*., 1987 for a review). Oak consumption by gypsy moth results in a rapid larval development as we observed in our study. Indeed, except for the second experiment whose results will be discussed later, larval mortality was lower on control oak species than on test species. No larvae died in the first experiment on oak species and all of them molted after 8 days (Table 1). In the third experiment (Table 2), a few old larvae died (< 10%) on *Quercus* spp and between 40 to 50% molted to the next instar. On the contrary, larvae did not even consume leaves from test plant species and died of starvation in our three experiments (except a marginal recording on FC for the L3-L4 instar; and on FO for the L5-L6 instar).

Mortality events on test species started from the 2nd day of the 1st experiment (young larval instars) and from the 4th day of the other experiments (L3-L6). Knowing that larvae were collected in the field 2-3 days before the beginning of the tests, the first results corroborate field observations showing that young caterpillars could disperse by wind during 3-5 days without eating (limits of food reserves according to Forbush & Fernald, 1896). Indeed, females of European gypsy moth are incapable of flight and host selection is affected by wind-dispersion of early instar larvae. Moreover, in the 3rdexperiment, larval molting occurred even on test species (Table 2b), but without leaf consumption and feces production (except marginal quantities on FO, cf. Table 3). The larvae collected *in situ* already accumulated enough reserves to survive several days and to molt without any supplementary food. Cambini & Magnoler (1997) observed extra molting due to starvation. Nevertheless, mortality rate reached 100% on test species on day 8 showing that larvae died of starvation between days 4 and 8 (Table 2b). Late instars are more resistant than young ones and in the

field they are able to migrate from tree to tree to avoid repellent plant species and find trees with suitable foliage.

On the other hand, no larvae molted on oak species and a low mortality rate (Table 2) was observed at the end of the 3rd experiment when leaf consumption reached 100% (Table 3). This slow larval development could be due to a lack of food, which may also explain some mortality events.

A high mortality rate however was observed for L1-L2 instars on holm oak (QI) from the second day of the 1st experiment while this tree species is considered as one of the "gypsy moth preferred food" (Barbosa *et al.*, 1987). At the beginning of this experiment, holm oak buds did not burst yet so that only 1-year old leaves were available for larval consumption. As 30% of leaves were consumed and mortality reached 100% at day 4, it confirms that 1-year old holm oak leaves are indigestible or toxic to early instars, as stated by Fraval *et al*. (1989). Cambini & Magnoler (1997) also noticed a negative impact of mature foliage from holm oak due to an excess of tannins in leaves which make the leaves indigestible for gypsy moth larvae. Moreover, Staudt & Louthellier (2007) observed an induction of sesquiterpene compounds inside holm oak leaves under gypsy moth attack. These compounds could be responsible for this toxic effect. From an ecological point of view, this result highlights the significance of synchronicity between bud break and egg hatching in an evergreen oak forest for gypsy moth (Fraval *et al*., 1989). If egg hatching occurs before bud breaks, young instars could apparently not feed on 1-year old leaves. Indeed, Foster *et al.* (2013) found that phenological asynchrony could explain 60% of the total explained variance of the spatial dynamic of gypsy moth attack. On the other hand, *Q. ilex* 1-year old leaves were consumed by the older larval instars which correlates earlier results (Barbosa et *al.*, 1987; Cambini & Magnoler, 1997) that gypsy moth tend to have more stringent host acceptance standards in early than in older larval instars.

During the 2nd experiment, we observed significant differences between control and test species on larval molting (0% for test species; up to 40% for oak species) and on feces weight and leaf consumption. *Ficus carica* was an exception with only one leaf in one replicate consumed and only 25% of the leaf area damaged. However, we also observed a non-expected and strong mortality of larva for all plant species, including control oak species An explanation for this result might be related to water stress. Indeed, some plant samples showed signs of fungus infection even before the start of the experiment. To control the infection, we decreased water input to decrease humidity, which probably affected plant water status. When the amount of water in foliage drops, its nutritional value decreases. The negative impact of insufficient leaf water content on insect growth rate has been shown in various experiments (see Schoonhoven et *al*., 2005 for a review). This negative impact is particularly true on tree leaves when they naturally have lower nitrogen and water contents compared with herbal foliage (Scriber, 1979). We can therefore suggest that in this experiment, leaves became less nutritious for caterpillars, altering their development.

As a conclusion, larvae did not feed on fig tree, olive tree and flowering ash, even if they had no other source of food. These results corroborate field observations that gypsy moth did not affect these plant species during a recent outbreak in Corsica. The repellent/toxic effect of these three species on gypsy moth could be linked to chemical defenses in leaves. During the "contact phase" (when herbivorous insects touches a plant), insects evaluate physical and chemical plants traits that could not be perceived from a distance. Indeed, many species base their initial behavioural decision to reject or not the plant organ just contacted, on physical and/or chemical surface characteristics (Schoonhoven *et al*., 2005; Martin & Shields, 2012). In our experiments, all the larvae reared on test species died of starvation, most of them before ingesting any significant plant material. This suggests that gypsy moth rejected the test

species. We know that insects have specific receptors to plant secondary metabolites, including deterrent compounds. Furthermore, volatiles or semi-volatiles compounds such as sesquiterpenes could interact with caterpillars as this walking insect often sway their heads when they move over the plant surface, facilitating orientation to odors. At last, Joseph *et al.* (1991) have shown that allelochemicals such as terpenes and phenols have negative effects, especially on the larval growth of gypsy moth.

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References

Barbosa, P., & Krischik, V. A. 1987: Influence of alkaloids on feeding preference of eastern deciduous forest trees by the gypsy moth *Lymantria dispar*. Am. Soc. Nat. 130(1): 53-69.

Cambini A., & Magnoler A. 1997: The influence of two evergreen oaks on development characteristics and fecundity of the gypsy moth. Redia 80: 33-43.

Campbell, R. W. & Sloan, R. J. 1978: Natural maintenance and decline of gypsy moth outbreaks. Environ. Entomol. 7(3): 389-395.

Dethier, V. G., Barton, B. L. & Smith, C. N. 1960: The designation of chemicals in terms of the responses they elicit from insects. J. Econ. Entomol. 53: 134-136.

Forbush, E. H. & Fernald, C. H. 1896: The Gypsy moth. Wright & Potter, Boston.

Foster, J. R., Townsend, P. A. & Mladenoff, D. J. 2013: Spatial dynamics of a gypsy moth defoliation outbreak and dependence on habitat characteristics. Landscape Ecol. 28: 1307-1320.

Fraval, A., Graf, P., Hamdaoui, M., Kadiri, Z., Ramzi, H., Villemant, C. 1989: *Lymantria dispar*. Actes Editions. Rabat: Documents scientifiques et techniques, 191 pp.

Giese, R. L. & Schneider, M. L. 1979: Cartographic comparisons of Eurasian gypsy moth distribution (*Lymantria dispar* L.; Lepidoptera: Lymantriidae). Entomol. News 90(1): 1-16.

Joseph, G., Miller, J. C., Berry, R. E., Wernz, J., Moldenke, A. F. & Kelsey, R. G. 1991: White alder and douglas-fir foliage quality and interegg-mass influences on larval development of gypsy moth, *Lymantria dispar*. J. Chem. Ecol. 17(9): 1783-1799.

Martin, T. L. & Shields, V. D. C**.** 2012: Detection of alkaloids and carbohydrates by taste receptor cells of gypsy moth larvae, *Lymantria dispar* (L.). Arthropod-Plant Interactions 6: 519-529.

Scriber, J. M. 1979: Effects of leaf-water supplementation upon post-ingestive nutritional indices of forb-, shrub-, vine- and tree-feeding Lepidoptera. Ent. Exp. & Appl. 25: 240-55.

Shields, V. D. C. & Broomell Salako, J. O. B. 2003: Host selection and acceptability of selected tree species by Gypsy moth larvae, *Lymantria dispar (L.)* Ann. Entomol. Soc. Am. 96: 920-926.

Schoonhoven, L. M., Van Loon, J. J. A. & Dicke, M. 2005: Insect-Plant biology. Second edition, Oxford University Press, Oxford.

Staudt, M. & Louthellier, L. 2007: Volatile organic compound emission from holm oak infested by Gypsy moth larvae: evidence for distinct responses in damaged and undamaged leaves. Tree Physiol. 27: 1433-1440.