Damage to grape flowers and berries by *Lobesia botrana* larvae (Denis & Schiffernüller) (Lepidoptera: Tortricidae), and relation to larval age

L. DELBAC[1,2] and D. THIÉRY[1,2]

[1] Unité Mixte de Recherches 1065 Santé et Agroécologie du Vignoble, Institut National de la Recherche Agronomique, Institut des Sciences de la Vigne et du Vin, Villenave d'Ornon Cedex 33882, France; [2] Unité Mixte de Recherches 1065 Santé et Agroécologie du Vignoble, Bordeaux Sciences Agro, Université de Bordeaux, Villenave d'Ornon Cedex 33882, France

Corresponding author: Dr Denis Thiéry, email thiery@bordeaux.inra.fr

Abstract

Background and Aims: Evaluation of pest damage and the population age of the pest are key factors in integrated pest management. Gaining such knowledge, however, can be time consuming and difficult in larvae that have cryptic habits, such as the European grapevine moth (EGVM, *Lobesia botrana*). An alternative is to measure the damage caused by different larval instars. Damage caused by different EGVM larval instars was described over 3 consecutive years.

Methods and Results: The first two larval generations of wild EGVM were sampled in an experimental vineyard in the Bordeaux area, France; 1945 samples of larval damage to inflorescences were collected and instars determined. Significant correlations were described between both in each generation.

Conclusions: Quantification of plant damage monitoring has potential to assist with assessing the characteristics of EGVM populations.

Significance of the Study: Using crop injury or damage to determine larval stage should provide a rapid and convenient method for pest management.

Keywords: *damage, grape protection, larval instar,* Lobesia botrana

Introduction

Efficient insect pest management and specifically the development of integrated pest management require an evaluation of the potential damage to the crop. This can lead to informed management decisions when the age structure of the pest population is taken into account. *Lobesia botrana* (the European grapevine moth, EGVM) is a major pest in European and Middle East vineyards and has recently been reported as a new grape pest in the Americas: California, Chile and Argentina (Varela et al. 2010, Gilligan et al. 2011). Because of its status as a serious pest, there have been many studies on its biology, but surprisingly rather limited information is available on its population dynamics in vineyards and on the direct damage caused by each generation. Several recent studies have focused on the population dynamics in vineyards (Delbac et al. 2010, Moreau et al. 2010, Ainseba et al. 2011, Harari et al. 2011, Ioriatti et al. 2011, Thiéry 2011, Thiéry et al. 2014). Current control of EGVM is achieved mainly by mating disruption against adults or by application of insecticide, either biological such as *Bt* toxin (Thiéry 2011) or not. Natural control by parasitoids or predators can be effective (Xuéreb and Thiéry 2006, Moreau et al. 2010) but so far, except for Trichogramma releases, no technique using natural enemies has been developed in viticulture. Grapegrowers mainly survey male flight dynamics or females caught in food traps to forecast oviposition dynamics (Thiéry 2011). This is sometimes coupled with the previous generation population number to inform management decisions (Delbac et al. 2006).

Grape moth larvae can feed on flower buds or berries and cause significant direct losses in grape production (Thiéry et al. 2014). These losses are often exacerbated by fungal damage, such as that caused by grey mould (Fermaud and Le Menn 1989) or by *Aspergillus carbonarius* and *A. niger* (Cozzi et al. 2006), which have the potential to produce ochratoxins, a class of mycotoxins. In certain cases, primary damage to the berries can also lead to infestation by secondary pests such as *Drosophila* which can lead to a greater incidence of sour rot (Blancard et al. 2000, Barata et al. 2012). *Lobesia botrana* normally has two to four generations per year in European vineyards, depending on the location (Thiéry 2008). The first generation (G1) occurs in spring, and can cause significant direct losses, especially in premium vineyards with a yield lower than 15–20 hL/ha, for example, Sauternes or white wine in Burgundy. Less than 24 h after hatching, the first larval instar (L1) may bore the flower corolla and feed on the ovaries (Coscollà 1997). When the individual flower is destroyed, the larva moves to the nearest flower and feeds again. During their development, first-generation larvae aggregate several individual flowers with silk (called glomeruli) in order to protect themselves against natural enemies and adverse conditions (Thiéry 2008). This protection mechanism has recently been examined through the larval immunity which appears inversely correlated to the individual silk production (Vogelweith et al. 2014).

A first objective of this work was to characterise the direct damage caused by wild EGVM larvae populations within each of the first two annual generations. Previous research indicates

doi: 10.1111/ajgw.12204

Table 1. Number of larvae of different instars during the three sample years.

n	1996		1997		1998	
	1† INRA‡ 22 May–7 June§	2 Preignac 11 July–14 August	1 INRA 7 May–2 June	2 INRA 9–31 July	1 INRA 19 May–2 June	2 INRA 9–30 July
Larval instar						
1	14	0	6	3	52	227
2	80	0	24	1	56	308
3	111	10	21	3	61	231
4	162	54	32	7	47	185
5	25	107	4	19	9	86
Number of larvae	392	171	87	33	225	1037

†Generation. ‡Location. §Period. INRA, Institut National de la Recherche Agronomique.

that a single larva can destroy three to eight flowers (Marchal 1912, Valli 1975, Coscollà 1997), with the amount depending on inflorescence size and architecture, and on the grape cultivar. Estimates of damage impact at the end of larval development varied, with one study reporting 3–16 flower buds (Coscollà 1997) and another 5–10 flower buds (Galet 1982). At the beginning of summer, neonate larvae of the second generation (G2) immediately after hatching penetrate green berries; they feed on grape pulp, but only rarely eat the pips (Galet 1982), because consumption of grape pips has a negative impact on larval fitness (Moreau et al. 2006). Often, larvae leave their original gallery and damage neighbouring berries, gathering berries together with silk. At the end of larval development, the damage can include two to six berries, depending on the grape cultivar (Girolami 1981, Pavan and Girolami 1986, Delrio et al. 1987, Pavan et al. 1987, Coscollà 1997, Thiéry 2008).

A second objective was to relate the magnitude of this individual damage to the larval stage and thus to propose an easy field evaluation of the larval age. Normally accurate determination of larval instar and age is done by measurement of the width of the head capsule (HC) (Walker 1987, Delbac et al. 2010, Benitez et al. 2014). This technique is, however, time consuming and requires careful microscopic measurements. Using crop injury or damage to determine larval stage (Walker 1987) should represent a more convenient method for pest management purposes.

Materials and methods

Experimental vineyards

Data from our survey database (1996–1998) were used from our experimental vineyard (INRA Bordeaux Research Centre, Villenave d'Ornon, France). In addition, data were obtained from a commercial vineyard in Preignac, France (single year 1996) that was 40 km away from the experimental vineyard. The two vineyards were naturally infested with EGVM and surrounded by cultivated vineyards and under conventional management. The experimental vineyard (described in Delbac et al. 2010) was planted with *Vitis vinifera* cv. Merlot and the Preignac vineyard (Badenhauser et al. 1999) was planted with *V. vinifera* cv. Sauvignon Blanc. No insecticides were applied in these survey plots, but a classical fungicide program was used to protect bunches against downy mildew and powdery mildew (cymoxanil with dithiocarbamate, fosetyl with folpel, demethylation inhibitors, wettable sulfur) (Savary et al. 2009). Because evaluation of direct damage on ripening grapes is difficult and confounded by indirect damage due to fungi and rots, this study was conducted only on the first two generations in the season. The sampling period was completed at the end of July, so potential infestation by grey mould (*Botrytis cinerea*) was not relevant (Deytieux-Belleau et al. 2009).

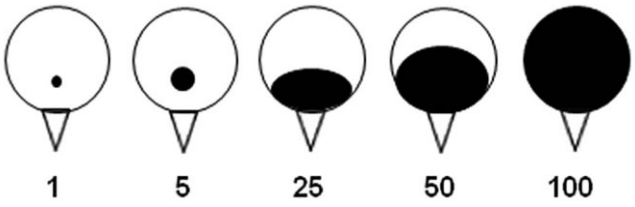

Figure 1. Key used to assess the severity of berry damage (%).

Larval sampling

Larval activity was monitored from hatching to pupation. Damaged single or grouped berries were collected during the first two generations in 1996–1998 (Table 1) and larval occurrence inside was checked a posteriori (see below). All samplings were collected in the INRA vineyard except the G2 sampling of 1996 (Preignac). Individual larva damage from G1 (during spring) was called glomerulus and the damage from a larva during G2 (early summer) was referred as foci which is the larva foraging on a group of berries. Given that the main objective of this study was to describe relationships between the extent of damage and larval age, only damage associated with internal larvae was considered. Empty foci were thus naturally discarded in such an analysis. The inflorescence parts with damage were collected during each generation, placed in Petri dishes, and placed immediately in a cold chamber (4°C) for less than 1 week to stop feeding and development before laboratory observations.

Laboratory measurements

The number of flowers (FB) per glomerulus and the number of flower buds destroyed (FBD) by G1 larvae, and the number of berries foraged (BA) by G2 larvae were determined under a binocular microscope (10×). The severity of the feeding gallery on each damaged berry was evaluated using a severity index (Walker 1987) (Figure 1). We noted the damage on each berry and calculated an average severity for the foci damage (ASBA). Only damage with at least one larva inside was considered. For instar determination, larvae were transferred into 70% ethanol and the width of their HCs was measured (Delbac et al. 2010). In practice, HC determination is highly accurate, even though variation due to food quality and quantity may generate overlaps in age categories (Delbac et al. 2010). Larvae were referenced L1–L5, respectively for larval instar 1–5.

Statistical analysis

The variables of different instars within and between years for each instar were compared with ANOVA. Descriptors of damage are known to have skewed distributions. For example, the numerical scores obtained by rating scales (Figure 1) for G2 severity on berries are discontinuous (Walker 1987). Thus, as described by Southwood (1978), we applied a square-root transformation on count data [number of flower buds in the glomeruli and the number of flower buds destroyed in the glomeruli (G1); and the number of berries attacked (G2)] and a logarithmic transformation on percentage evaluation [damage severity of berries (G2)]. Data were analysed only if more than five individuals were available per instar and generation. The ANOVA model employed pairwise comparisons of means.

To define the relationship between the extent of damage and larval instar, we calculated Spearman rank correlation coefficient and critical values associated (Sprent 1989). We also used a 95% confidence interval (CI) as in Delbac et al. (2010) to delimitate the boundaries between instar distributions. This computation was done when more than 30 individuals were available. In such cases, the random variable converges towards Gaussian distribution, and the calculation of CI can be made (Scherrer 1984).

Systat 11 software (Systat Software, San Jose, CA, USA) was employed for all statistical tests, which were performed with a type-I error rate of 0.05.

Results

First generation

The timing of EGVM development was slightly different among the 3 years, so G1 damage was assessed on several dates between mid-May and early June of each year in order to obtain a sufficiently large sample size. From 1996 to 1998, 704 G1 damages with larva inside were collected (Table 1).

In 1996, most of the collected larval instars were L2–L4 (Table 1). The number of FB per glomeruli ranged from 1 to 69, and the number of FBD ranged from 1 to 12. For FB (Table 2), an average of 2.4 (L1) to 19.8 (L5) aggregated flowers was observed; these values were significantly different ($P < 0.001$) with the exception of only L1/L2, which was not significantly different. The FBD average was 1.3 (L1) to 3.7 (L5); only L5 was not significantly different from L3 and L4.

In 1997, the population was significantly smaller (four larvae per 100 inflorescences) than that in 1996 (~9 larvae per 100 inflorescences), and only 87 damaged glomeruli were collected (Table 1). Data from only L1–L4 were considered, as there were just four individuals in L5. The number of FB damage was 2–50 and the number of FBD was 1–13. For FB (Table 2), an average of 3.7 (L1) to 17.8 (L4) aggregated flowers was observed; there was a significant difference ($P < 0.001$) between L3, L4 and L1–L2, the latter were not different. The FBD average was 1.2 (L1) to 4.7 (L4). Two groups were significantly different: L1–L2 versus L3–L4.

In 1998, the sampling size was between that of 1996 and 1997, with 225 damaged glomeruli collected (Table 1). Data from all five instars were considered, even though there were only nine individuals in L5. For FB (Table 2), we observed an average of 2.5 (L1) to 24.8 (L5) individual flowers per glomerulus; these numbers were all significantly different ($P < 0.001$). The FBD average was 1.3 (L1) to 10.7 (L5). The damage caused by the larval instars was significantly different ($P < 0.001$).

Second generation

Second-generation (G2) damage was assessed from early July to mid-August and 1241 larval damaged foci were collected in the 3 years (Table 1).

In 1996, even though we collected samples for more than 1 month, we could collect only instars L3–L5 in a total of 171 larvae (Table 1). The BA per larva was 1–9 with the average 1.4 (L3) to 2.7 (L5) (Table 2). The level for L3 was significantly different from that of the others ($P = 0.005$). The difference in ASBA was also significant ($P < 0.001$), with severity for L5 higher than L3–L4.

In 1997, as with G1, there was a lower rate of infection by G2, with only 33 larvae collected (Table 1). Data from only L4 and L5 were analysed because the others had a sample size less than five. The BA per larva was 1–5 with an average of 2.4 (L4) and 2.6 (L5). This difference was not significant ($P = 0.698$) (Table 2). The range of ASBA was 5% and the difference in ASBA was significantly different (L4 = 26.3, L5 = 53.8, $P = 0.003$).

Table 2. Mean value and one-way ANOVA of the characteristics of plant damage by generation, descriptor and year.

Generation and descriptor†	Year	Mean value ± standard error of the mean					F	*P*
		1‡	2	3	4	5		
Generation 1								
FB	1996	2.4 ± 0.6 d	4.7 ± 0.4 d	8.9 ± 0.4 c	14.9 ± 0.6 b	19.8 ± 2.2 a	80.2	<0.001
	1997	3.7 ± 0.6 c	5.0 ± 0.4 c	10.4 ± 1.0 b	17.8 ± 1.6 a	–	30.3	<0.001
	1998	2.5 ± 0.2 e	4.8 ± 0.3 d	7.8 ± 0.4 c	16.5 ± 1.1 b	24.8 ± 2.1 a	117.8	<0.001
FBD	1996	1.3 ± 0.1 d	2.5 ± 0.1 c	3.2 ± 0.2 b	4.1 ± 0.2 a	3.7 ± 0.5 ab	17.6	<0.001
	1997	1.2 ± 0.2 b	1.5 ± 0.1 b	3.3 ± 0.3 a	4.7 ± 0.7 a	–	22.4	<0.001
	1998	1.3 ± 0.1 e	2.2 ± 0.1 d	3.8 ± 0.2 c	6.3 ± 0.5 b	10.7 ± 3.7 a	63.7	<0.001
Generation 2								
BA	1996	–	–	1.4 ± 0.2 b	2.4 ± 0.2 a	2.7 ± 0.1 a	5.4	0.005
	1997	–	–	–	2.4 ± 0.4	2.6 ± 0.2	0.2	0.698
	1998	1.1 ± 0.0 d	1.3 ± 0.0 d	1.5 ± 0.6 c	1.9 ± 0.1 b	2.3 ± 0.2 a	52.5	<0.001
ASBA	1996	–	–	18.1 ± 3.1 b	24.9 ± 2.1 b	42.5 ± 2.3 a	25.7	<0.001
	1997	–	–	–	26.3 ± 8.4 b	53.8 ± 5.5 a	10.8	0.003
	1998	4.6 ± 0.3 e	8.3 ± 0.6 d	15.5 ± 1.1 c	25.5 ± 1.6 b	38.7 ± 2.9 a	151.9	<0.001

Different letters within a row indicate significant difference ($P \leq 0.05$) as determined by Fisher's pairwise comparison test. †ASBA, average severity of all berries attacked per foci. ‡Instar number. BA, number of berries attacked; FB, number of flower buds; FBD, number of flower buds destroyed.

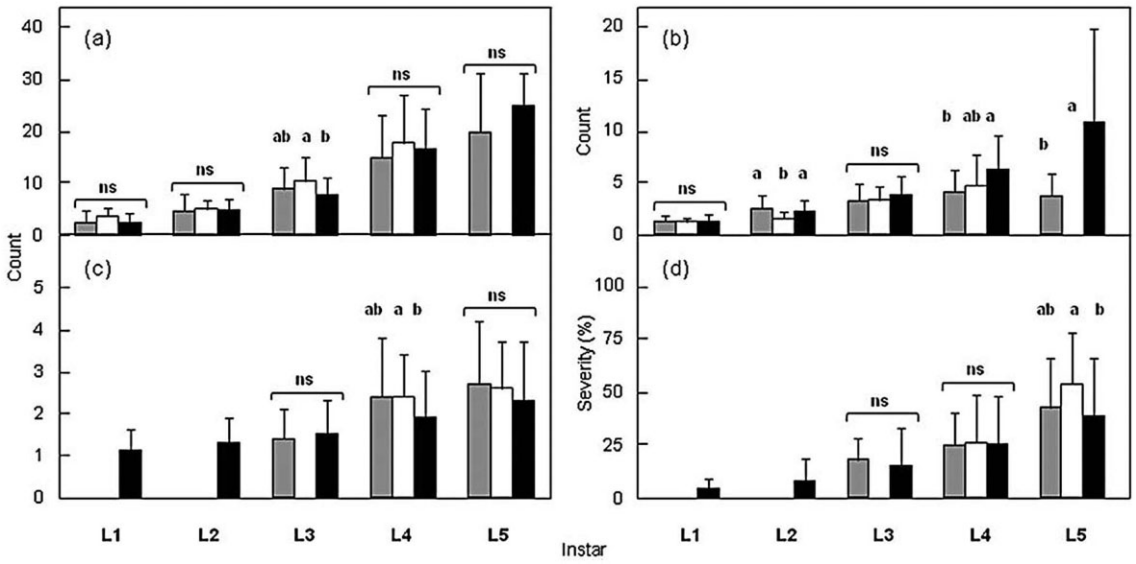

Figure 2. (a) Mean (+standard error of the mean) flower buds per nest with single larva (glomerulus) and (b) flower buds destroyed in first generation, and (c) number of berries attacked and (d) average severity of berries attacked in second generation per damage by different larval instars in 1996 (▒), 1997 (□) and 1998 (■). Different letters indicate a significant difference between years for each instar and variable ($P \leq 0.05$) as determined by Fisher's test and pairwise comparison; ns, no significant difference observed.

The 1998 sampling yielded the highest total number of larvae (1037) (Table 1). There were 86–308 larvae in each of the five instars. There was variation in BA among the different instars (range: 1–9), with an average of 1.1 (L1) to 2.3 (L5). These values, however, were significantly different by instar ($P < 0.001$), but not for L1 and L2 (Table 2). The range of ASBA was 1–100 and the mean ranged from 4.6 (L1) to 38.7 (L5). Again, the difference in ASBA for all larval instars was significant ($P < 0.001$).

Comparison of the 3 years sampled

Comparisons were made over the 3 years (Figure 2); for G1, there was no difference in FB between years for instars 1, 2 and 5 ($P = 0.118$–0.451). The only difference was observed for instar 3 among years 1997 and 1998 ($P = 0.037$). There was no significant difference in FBD between years for instars 1 and 3 ($P = 0.878$ and 0.052, respectively). For the others, a difference occurred in a single year for instars 2 and 4 ($P = 0.010$ and <0.001, respectively). For the last larval instar (5), a significant difference was found between years ($P = 0.005$); the year 1998 exhibiting twice as much damage as 1996.

For G2, only comparisons on L3 for 2 years (1996 and 1998) and L4 and L5 for all 3 years could be made. For L3, no significant difference of the descriptors was noticed between 1996 and 1998 ($P_{BA} = 0.605$ and $P_{ASBA} = 0.224$) (Figure 2). For L4, BA was significantly different between years, 1998 having the lowest value ($P = 0.006$) but ASBA was not (ANOVA, $P = 0.317$). For L5, ASBA was significantly different between the years ($P = 0.006$) but BA was not ($P = 0.155$).

Relationship between the magnitude of larval damage and larval instars

As there were so few significant differences between the years in the FB and ASBA variables, the data over the 3 years were pooled to estimate the mean value aggregated for each larval instar (Table 3). Analysis was undertaken on 700 larvae for FB variable, with a range of 34–241 individuals per larval instars. Confidence intervals did not show any overlapping between larval instars, thus instars were considered as separated classes for FB and ASBA. The damage increased positively with the larval instar as shown by the significant Spearman coefficient ($\rho = 0.758$, $P < 0.01$). The same occurred for Spearman coefficient ($\rho = 0.682$, $P < 0.01$) in ASBA (1234 larvae ranging from 212 to 308 individuals per larval instars).

Table 3. Plant damage retained per generation for each larval instar.

Generation and descriptor	Instar	Mean (± SEM)	CI 95% lower	CI 95% upper
Generation 1				
FB	1	2.6 ± 0.2	2.2	3.0
	2	4.7 ± 0.2	4.4	5.2
	3	8.7 ± 0.3	8.2	9.3
	4	15.6 ± 0.5	14.5	16.6
	5	21.2 ± 1.8	17.5	24.8
Generation 2				
ASBA	1	4.6 ± 0.3	4.0	5.2
	2	8.4 ± 0.6	7.2	9.5
	3	15.7 ± 1.1	13.5	17.8
	4	26.0 ± 1.3	22.8	28.0
	5	42.0 ± 1.7	38.5	45.3

ASBA, average berry damage per foci (%); CI, confidence interval; FB, number of damaged flower buds per glomerulus; SEM, standard error of the mean.

Discussion

As it has been observed in other pests (Smith et al. 1986, Luttrell and Mink 1999, Toews et al. 2007), the results presented here allow a correlation of the extent of the damage at the larval stage, which may be attributed to increased feeding activity (Devereau et al. 2003).

Larval feeding behaviour varies according to the generation in the year and the grape phenology. First-generation larvae of EGVM displace much within a single bunch, and affect a large proportion of the inflorescence, while second-generation larvae feed on a limited number of berries. During G1, larvae attack a few flower buds in the glomeruli, and tie together with silk other flowers within the inflorescence. The vine is a plant in which flowers will not form berries all the time (Creasy and

Creasy 2009). Compared to other cultivars, Merlot and Cabernet Sauvignon have a low rate of fruitset (Dry et al. 2010), Merlot having, for example, 33–57% of flowers leading to fruit according to the rootstock and year (Kidman et al. 2013). This is, however, compensated by a high initial number of flowers on the inflorescence (Dry et al. 2010). Various studies have shown an ability of grapevines to compensate for spring damage in inflorescences (Roehrich and Boller 1991). In Cabernet Sauvignon, little or no loss of mass or number of berries was observed despite the removal of 30 flowers per bunch (Roehrich and Schmid 1979). In another study on Savvatiano, a cultivar with large inflorescences, the removal of up to 400 flowers per inflorescence (or 39% of the inflorescence) did not lead to loss at harvest (Moschos 2005). The author pointed out that the plant was offset by increased proportion of fruitset as the number of berries and mass of these berries are identical to that of the control. This recovery capacity is, however, less for cultivars with a low number of flowers per inflorescence such as Pinot Noir (Roehrich and Boller 1991). This explains why the spring generation of larvae generally does not cause serious damage (Bovey 1966), except in low-yield vineyards (e.g. Sauternes), and at this time, the risk of developing *Botrytis* or grape bunch rots is low (Deytieux-Belleau et al. 2009, Pavan et al. 2014).

It is difficult, however, to estimate the number of flower buds destroyed, and this number is often under-evaluated since they generally abscise as soon as they are damaged. Thus, the count of flower buds attacked is not relevant and the number of flower buds in a glomerulus provides a better estimate of the larval instar stage.

In G2, fewer numbers of berries were attacked as compared to the number of flower buds in G1. Larvae at hatching first drill a hole in one berry. Based on biotic and abiotic conditions, it can move to neighbouring berries in the same bunch. At this green berry stage, visual evaluation of damage is easy because the larval gallery entry has a purple colour (Viala and Marsais 1927). The severity of berry damage increased over time as a function of larval age, but the number of berries damaged alone did not allow determination of larval instars. Thus, to assess which larval instar caused the damage, the most suitable technique was shown to be the estimation of the average severity of berry attack.

The development of sampling planes, for the first and second generations, is an important tool to estimate accurately the pest population. For that, spatial and frequency distribution of grape berry moths larvae should be considered (Pavan et al. 1998). The frequency distribution of *L. botrana* larvae often reveals aggregation at the vinestock scale (Badenhauser et al. 1999, Ifoulis and Savopoulou-Soultani 2007), and thus the individual vine is a suitable sampling unit. Classically 100 inflorescences per plot are often sampled to estimate population level, and practical examples (from 50 to 150 inflorescences per plot) are given by Ifoulis and Savopoulou-Soultani (2006a,b) which correspond to the sampling range.

The present study shows that assessment of plant damage can be used as an adequate and simple tool for estimating the population dynamics of the different larval instars of EGVM in a vineyard. Damage is a function of larval age; hence observation of damage provides information that can inform pest management. As a first step, the distribution of ages or instars within a population could be determined by extension service experts and this would be helpful in order to forecast the population dynamics of the subsequent adult generation and the consequent egg-laying periods which are needed for scheduling optimal control strategies especially with mating disruption or short persistent treatments such as *Bt*.

Further studies should consider such evaluation under different levels of pest population, different grape moth species, such as for example *Eupoecilia ambiguella*, and different grape cultivars. The effect of climatic conditions on the magnitude of damage should also be studied, especially since larval feeding could be enhanced and thus the extent of damage by global warming.

Acknowledgements

Authors are indebted to Dr Lucia Varella, United States Department of Agriculture, University of California, Davis, CA, USA, for valuable comments on the draft and English editing. We are grateful to Mr Jean-Marie Brustis from our laboratory for his valuable technical assistance during the trap monitoring and to Mr Patrice Lecharpentier (INRA) for his contribution to study design and assistance with data collection. This work is part of the Labex COTE scientific programme.

References

Ainseba, B., Picart, D. and Thiéry, D. (2011) An innovative multistage, physiologically structured, population model to understand the European grapevine moth dynamics. Journal of Mathematical Analysis and Applications **382**, 34–46.

Badenhauser, I., Lecharpentier, P., Delbac, L. and Pracros, P. (1999) Contributions of Monte-Carlo test procedures for the study of the spatial distribution of the European Vine Moth *Lobesia botrana* Den. and Schiff. (Lepidoptera: Tortricidae) in European vineyards. European Journal of Entomology **96**, 375–380.

Barata, A., Correia Santos, S., Malfeito-Ferreira, M. and Loureiro, V. (2012) New insights into the ecological interaction between grape berry microorganisms and drosophila flies during the development of sour rot. Microbial Ecology **64**, 416–430.

Benitez, H.A., Püschel, T., Lemic, D., Cacija, M., Kozina, A. and Bazok, R. (2014) Ecomorphological variation of the wireworm cephalic capsule: studying the interaction of environment and geometric shape. PLoS ONE **9**, e102059.

Blancard, D., Gravot, E., Jailloux, F. and Fermaud, M. (2000) Etologie de la pourriture acide de la vigne dans le sud-ouest de la France. IOBC/WPRS, Bulletin OILB/SROP **23**, 51–54.

Bovey, P. (1966) Super famille des Tortricidae. Balachowsky, A.S., ed. Entomologie appliquée à l'agriculture, Tome 2. Premier volume (Masson et Cie: Paris, France) pp. 456–893.

Coscollà, R. (1997) La polilla del racimo de la vid (*Lobesia botrana* Den. y Schiff.), Serie technica (Generalitat Valenciana, Conselleria de Agricultura, Pesca y Alimentación: Valencia, Spain).

Cozzi, G., Pascale, M., Perrone, G., Visconti, A. and Logrieco, A. (2006) Effect of *Lobesia botrana* damages on black *aspergilli*'s rot and ochratoxin A content in grapes. International Journal of Food Microbiology **111**, 88–92.

Creasy, G.L. and Creasy, L.L. (2009) Grapes. Crop production science in horticulture (The Centre for Agriculture and Bioscience: Wallingford, England).

Delbac, L., Brustis, J.M., Delière, L., Cartolaro, P., van Helden, M., Thiéry, D. and Clerjeau, M. (2006) Development of decision rules for pest vineyard management. IOBC/WPRS Bulletin, Bulletin OILB/SROP **29** (11), 41–42.

Delbac, L., Lecharpentier, P. and Thiéry, D. (2010) Larval instars determination for the European Grapevine Moth (Lepidoptera: Tortricidae) based on the frequency distribution of head capsule widths. Crop Protection (Guildford, Surrey) **29**, 623–630.

Delrio, G., Luciano, P. and Prota, R. (1987) Researches on grape-vine moths in Sardinia. Proceedings of the Meeting of the EC Experts Group; 26–28 September 1985; Portoferraio, Italy (Balkema, A.A.: Rotterdam, The Netherlands) pp. 57–67.

Devereau, A.D., Gudrups, I., Appleby, J.H. and Credland, P.F. (2003) Automatic, rapid screening of seed resistance in cowpea, *Vigna unguiculata* (L.) Walpers, to the seed beetle *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) using acoustic monitoring. Journal of Stored Products Research **39**, 117–129.

Deytieux-Belleau, C., Geny, L., Roudet, J., Mayet, V., Donèche, B. and Fermaud, M. (2009) Grape berry skin features related to ontogenic

resistance to *Botrytis cinerea*. European Journal of Plant Pathology / European Foundation for Plant Pathology **125**, 551–563.
Dry, P.R., Longbottom, M.L., McLoughlin, S., Johnson, T.E. and Collins, C. (2010) Classification of reproductive performance of ten winegrape varieties. Australian Journal of Grape and Wine Research **16**, 47–55.
Fermaud, M. and Le Menn, R. (1989) Association of *Botrytis cinerea* with grape berry moth larvae. Phytopathology **79**, 651–656.
Galet, P. (1982) Les maladies et les parasites de la vigne – Tome 2: les parasites animaux (Paysans du Midi: Montpellier, France).
Gilligan, T.M., Epstein, M.E., Passoa, S.C., Powell, J.A., Sage, O.C. and Brown, J.W. (2011) Discovery of *Lobesia botrana* ([Denis & Schiffermüller]) in California: an invasive species new to North America (Lepidoptera: Tortricidae). Proceedings of the Entomological Society of Washington **113**, 14–30.
Girolami, V. (1981) Evaluation des dégâts dus aux vers de la grappe. Lutte intégrée en viticulture. Bollettino di Zoologia Agraria e di Bachicoltura ser. II **16**, 6–18.
Harari, A.R., Zahavi, T. and Thiéry, D. (2011) Fitness cost of pheromone production in signaling female moths. Evolution **65**, 1572–1582.
Ifoulis, A.A. and Savopoulou-Soultani, M. (2006a) Use of geostatistical analysis to characterize the spatial distribution of *Lobesia botrana* (Lepidoptera: Tortricidae) larvae in Northern Greece. Environmental Entomology **35**, 497–506.
Ifoulis, A.A. and Savopoulou-Soultani, M. (2006b) Developing optimum sample size and multistage sampling plans for *Lobesia botrana* (Lepidoptera: Tortricidae) larval infestation and injury in Northern Greece. Journal of Economic Entomology **99**, 1890–1898.
Ifoulis, A.A. and Savopoulou-Soultani, M. (2007) Probability distribution, sampling unit, data transformations and sequential sampling of European vine moth, *Lobesia botrana* (Lepidoptera: Tortricidae) larval counts from Northern Greece vineyards. European Journal of Entomology **104**, 753–761.
Ioriatti, C., Anfora, G., Tasin, M., De Cristofaro, A., Witzgall, P. and Lucchi, A. (2011) Chemical ecology and management of *Lobesia botrana* (Lepidoptera: Tortricidae). Journal of Economic Entomology **104**, 1125–1137.
Kidman, C.M., Dry, P.R., McCarthy, M.G. and Collins, C. (2013) Reproductive performance of Cabernet Sauvignon and Merlot (*Vitis vinifera* L.) is affected when grafted to rootstocks. Australian Journal of Grape and Wine Research **19**, 409–421.
Luttrell, R.G. and Mink, J.S. (1999) Damage to cotton fruiting structures by the Fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Journal of Cotton Science **3**, 35–44.
Marchal, P. (1912) Rapport sur les travaux accomplis par la mission d'études de la Cochylis et de l'Eudémis (Librairie Polytechnique Paris et Liège: Paris, France).
Moreau, J., Arruego, X., Benrey, B. and Thiéry, D. (2006) Differences in nutritional quality of parts of *Vitis vinifera* berries affect fitness of the European grapevine moth. Entomologia Experimentalis et Applicata **119**, 93–99.
Moreau, J., Villemant, C., Benrey, B. and Thiéry, D. (2010) Species diversity of larval parasitoids of the European grapevine moth (*Lobesia botrana*, Lepidoptera: Tortricidae): the influence of region and cultivar. Biological Control **54**, 300–306.
Moschos, T. (2005) Yield loss quantification and assessment of economic injury level for the anthophagous generation of the European grapevine moth *Lobesia botrana* Den. et Schiff. (Lepidoptera: Tortricidae). International Journal of Pest Management **51**, 81–89.
Pavan, F. and Girolami, V. (1986) Lotta guidata alle tignole della vite su uve da vino nell'Italia nord-orientale. L'Informatore Agrario **42**, 35–41.
Pavan, F., Sacilotto, G. and Girolami, V. (1987) Damage evolution, larval sampling and treatment period for grape moths. Proceedings of the Meeting of the EC Experts Group; 26–28 September 1985; Portoferraio, Italy (Balkema, A.A.: Rotterdam, The Netherlands) pp. 39–49.
Pavan, F., Girolami, V. and Sacilotto, G. (1998) Second generation of grape berry moths, *Lobesia botrana* (Den. and Schiff.) (Lep., Tortricidae) and *Eupoecilia ambiguella* (Hb.) (Lep., Cochylidae): spatial and frequency distributions of larvae, weight loss and economic injury level. Journal of Applied Entomology **122**, 361–368.
Pavan, F., Bigot, G., Cargnus, E. and Zandigiacomo, P. (2014) Influence of the carpophagous generations of the European grapevine moth *Lobesia botrana* on grape bunch rots. Phytoparasitica; Israel Journal of Plant Protection Sciences **42**, 61–69.
Roehrich, R. and Boller, E. (1991) Tortricids in vineyards. van der Geest, L.P.S. and Evenhuis, H.H., eds. Tortricid pests, their biology, natural enemies and control (Elsevier Science Publishers: Amsterdam, The Netherlands) pp. 507–514.
Roehrich, R. and Schmid, A. (1979) Lutte intégrée en viticulture. Tordeuse de la grappe: evaluation du risque, détermination des périodes d'intervention et recherche de méthodes de lutte biologique. Proceedings of International Symposium of IOBC/WRPS on Integrated Control in Agriculture and Forestry; 8–12 October 1979; Wien, Austria (Organisation Internationale de Lutte Biologique: Kapaa, HI, USA) pp. 245–254.
Savary, S., Delbac, L., Rochas, A., Taisant, G. and Willocquet, L. (2009) Analysis of non linear relationships in dual epidemics, and its application to the management of grapevine downy and powdery mildews. Phytopathology **99**, 930–942.
Scherrer, B. (1984) Biostatistique (Gaëtan Morin: Chicoutoumi, QC, Canada).
Smith, J.D., Goyer, R.A. and Woodring, J.P. (1986) Instar determination and growth and feeding indices of the Forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae), reared on Tupelo gum, *Nyssa aquatica* L. Annals of the Entomological Society of America **79**, 304–307.
Southwood, T.R.E. (1978) Ecological methods: with particular reference to the study of insect populations, Second edn (Chapman & Hall: London, England).
Sprent, P. (1989) Applied nonparametric statistical methods (Chapman & Hall: London, England).
Thiéry, D. (2008) Les tordeuses nuisibles à la vigne. Kreiter, S., ed. Ravageurs de la vigne, Deuxième édition (Féret: Bordeaux, France) pp. 214–246.
Thiéry, D. (2011) Gaps in knowledge for modern integrated protection in viticulture: lessons from controlling grape berry moths. IOBC/WPRS Bulletin, Bulletin OILB/SROP **67**, 305–311.
Thiéry, D., Monceau, K. and Moreau, J. (2014) Different emergence phenology of European grapevine moth (*Lobesia botrana*, Lepidoptera: Tortricidae) on six varieties of grapes. Bulletin of Entomological Research **104**, 277–287.
Toews, M.D., Perez-Mendoza, J., Throne, J.E., Dowell, F.E., Maghirang, E., Arthur, F.H. and Campbell, J.F. (2007) Rapid assessment of insect fragments in flour milled from wheat infested with known densities of immature and adult *Sitophilus oryzae* (Coleoptera: Curculionidae). Journal of Economic Entomology **100**, 1714–1723.
Valli, G. (1975) Lotta integrate nei vigneti: ricerche evalutazioni preliminary sulle Tignole. Notiziaro sulle malattie delle piante **92–93**, 407–419.
Varela, L.G., Smith, R.J., Cooper, M.L. and Hoenisch, R.W. (2010) First report of European grapevine moth, *Lobesia botrana*, in Napa Valley vineyards. Practical Winery & Vineyard Journal **(March/April)**, 1–5.
Viala, P. and Marsais, P. (1927) Les traitements contre les vers de la grappe. Revue de Viticulture **66**, 229–268.
Vogelweith, F., Thiéry, D., Moret, Y., Colin, E., Motreuil, S. and Moreau, J. (2014) Defense strategies used by two sympatric vineyard moth pests. Journal of Insect Physiology **64**, 54–61.
Walker, P.T. (1987) Measurement of insect pest populations and injury. Teng, P.S., ed. Crop loss assessment and pest management (APS Press: St Paul, MN, USA) pp. 19–29.
Xuéreb, A. and Thiéry, D. (2006) Does natural larval parasitism of *Lobesia botrana* (Lepidoptera: Tortricidae) vary between years, generation, density of the host and vine cultivar? Bulletin of Entomological Research **96**, 105–110.

Manuscript received: 26 February 2015
Revised manuscript received: 22 May 2015
Accepted: 11 June 2015