JOURNAL OF APPLIED ENTOMOLOGY
J. Appl. Entomol.

ORIGINAL CONTRIBUTION

Seasonal pattern of oviposition by the North American grape berry moth (Lepidoptera: Tortricidae)

L. A. F. Teixeira, K. S. Mason, S. Van Timmeren & R. Isaacs

Department of Entomology, Michigan State University, East Lansing, MI 48824, USA

Keywords
Paralobesia viteana, control, IPM, phenology

Correspondence
Luis Teixeira (corresponding author), 202 CIPS, Michigan State University, East Lansing, MI 48824, USA. E-mail: teixei10@msu.edu

Received: March 24, 2010; accepted: November 30, 2010.

doi: 10.1111/j.1439-0418.2010.01602.x

Abstract

The seasonal patterns of oviposition by the North American grape berry moth, *Paralobesia viteana* (Clemens) (Lepidoptera: Tortricidae) were monitored in juice grape (*Vitis labrusca*) vineyards in southwest Michigan. Egg deposition was recorded throughout the growing season at two vineyards in 2006, and at four vineyards from 2007 to 2009. In each vineyard, a random sample of 100 grape clusters was visually inspected twice-weekly and the number of newly laid eggs was counted. We found that oviposition was continuous but variable throughout the season. Egg deposition started in early June coinciding with early grape bloom, continued at low level until mid- to late July, intensified in August close to veraison, and ended in September often before harvest. There were no consistent periods without oviposition that would indicate distinct generations. To determine the contribution of moth immigration into the vineyard to the pattern of oviposition, six grape plants located at the edge of a vineyard next to woods were covered with field cages and stocked with infested fruit. Oviposition and berry infestation were followed weekly on covered and exposed plants. Although higher numbers of eggs and infested berries were found on fruit of exposed vines than enclosed vines, egg deposition and berry infestation followed the same pattern in both treatments. This result indicates that the seasonal pattern of egg deposition is not dependent on immigration of grape berry moth of wild grape origin. The pattern of oviposition by grape berry moth described here contributes to the difficulty of controlling this pest using conventional insecticides with short residual activity.

Introduction

Grape berry moth, *Paralobesia viteana* (Clemens) (Lepidoptera: Tortricidae), is native to eastern North America where it infests several species in the genus *Vitis* L., such as *Vitis labrusca* L. and *Vitis riparia* Micheaux. In the Midwest and Northeast United States, and the Niagara peninsula of Ontario, Canada, grape berry moth is the primary insect pest of cultivated varieties of American grapes grown for juice, and of European grapes *Vitis vinifera* L. planted for wine production (Taschenberg et al. 1974; Dennehy et al. 1990; Trimble et al. 1991). Wild hosts of grape berry moth are often found growing in natural or disturbed areas in the vicinity of vineyards and moths can move between habitats (Botero-Garcés and Isaacs 2004a,b). The number of generations varies with geographical location, with two or three generations reported in southwest Michigan and the Lake Erie region (Ingerson 1920; Gentner 1925; Gleissner and Worthley 1941) and central New York State (Hoffman et al. 1992), and up to four generations in southern Missouri (Biever and Hostetter 1989). Grape berry moth overwinters as a pupa enclosed in a silken protective cocoon in the leaf litter. In Michigan, male moth emergence begins in early May, as determined with pheromone-baited traps, but eggs are first found in vineyards in mid-June (Teixeira et al. 2009). A degree of protandry has been reported in grape berry moth (Tobin et al. 2002) and may be one of the reasons for the wide difference in the timing of male capture and egglaying. Females of the overwintering generation lay eggs singly on flowers or developing grape berries. Early in the season, the larvae of this generation spin protective retreats while feeding on flowers or developing grapes. Later in the season, and in subsequent generations, first instar larvae burrow into berries and later instars web these together and feed on several berries in a cluster (Luciani 1987).

Larvae of grape berry moth cause economic damage to the grape crop from feeding on grapes and from increasing the incidence of fungal diseases, thereby reducing yield. In addition, contamination with larvae can lead to rejection of grape loads at juice processing plants, or force growers not to harvest vineyard blocks with significant economical costs. Growers manage grape berry moth mostly by using broad-spectrum insecticides, such as carbamates, organophosphates and pyrethroids. Novel insect growth regulator (IGR) insecticides and products for mating disruption are also available but are less widely used (Jenkins and Isaacs 2007a; Trimble 2007). In Michigan vineyard IPM programmes, pheromone-baited traps have been of limited value in providing phenological information on grape berry moth beyond the earlier part of the season. Captures of male moths begin in early May, peak during June and continue at much lower levels throughout the rest of the season, whereas damage to grape clusters starts at a low level in June and peaks late in the season (Botero-Garcés and Isaacs 2003; Teixeira et al. 2009). This pattern of moth capture has precluded the use of pheromone-baited traps for determining the beginning of a new generation, or for identifying optimal timing of insecticide sprays to protect clusters from larval entry in the later part of the season.

Effective control of grape berry moth requires phenological information for accurate timing of sprays to protect clusters from this pest. With this study, our objective was to determine the oviposition phenology of grape berry moth as a tool to support vineyard pest management decisions. During four growing seasons, we visually examined grape clusters and counted grape berry moth eggs twice weekly at several farms in southwest Michigan. In addition, we conducted an experiment comparing egg deposition and berry infestation over time on exposed vs. caged grape plants to determine the importance of moth immigration into vineyards for the pattern of oviposition.

Materials and Methods

Monitoring egglaying in vineyards

We determined egglaying by grape berry moth at two vineyards in 2006 and four vineyards from 2007 to 2009. The vineyards were planted with *Vitis labrusca* cv. Concord and were located in Berrien and Van Buren Counties, Michigan, USA. Monitoring took place in managed vineyards because few grape clusters remain intact to the end of the season in abandoned or unmanaged vineyards, due to insect feeding and diseases. The edge of the vineyard was chosen for monitoring because grape berry moth population density tends to be low in the interior of managed vineyards. The vineyards were managed using grower standard practices that included fungicide sprays and one spray with a broad-spectrum insecticide targeting grape berry moth ~10 days after grape bloom, in mid-June, and 1–2 sprays with similar insecticides at variable timings later in the season. Egglaying on grape berries was monitored twice-weekly, starting in late May and ending in late September to October. In each vineyard, we visually inspected a sample of 100 clusters consisting of five randomly selected clusters from each of 20 vines spread along the outer edge of the vineyard. A hand lens was used to observe the appearance of the eggs and only newly laid eggs were counted. Newly laid grape berry moth eggs initially look opaque and later show signs of embryonic development, while hatched eggs appear clear or have a visible opening.

Egglaying on caged and exposed grapevines

To determine the role of grape berry moth immigration on the pattern of oviposition in vineyards, $2 \times 2 \times 2$ m field cages made of fine plastic screen (Bioquip, Rancho Dominguez, CA) were deployed over grape plants cv. Niagara in a research vineyard at the Trevor Nichols Research Complex in Allegan County, Michigan. In early July 2009, 12 grapevines were chosen from the vineyard edge facing a wooded area containing wild *Vitis* spp., and were randomly assigned to be covered or left exposed. Cluster infestation was determined by examining all grape clusters in each vine and counting the number of infested berries. Then, infestation was increased and equalized among caged grape plants by collecting infested clusters in other locations of the same vineyard and placing them over the clusters in the caged grape plant. Our objective with this procedure was to increase the probability that the population inside the cages would persist until the end of the season. Each caged grape plant was left with 17 infested berries, which was the highest number of infested berries initially found on the grapevines. An unknown number of adult moths was probably also enclosed with the caged plants. Weekly, grape berry moth oviposition on caged and exposed plants was monitored by examining 10 clusters in each plant for recently laid eggs. The number of infested berries was also determined because eggs were difficult to see when grapevines were covered with the screen cage and we expected that few eggs would be found. Monitoring ended in September. No insecticide sprays were applied to the edge area where the cages were located.

Degree-day accumulation

Daily degree-day (DD) accumulations were obtained online from Michigan Automated Weather Network sites closest to the sampled vineyards. Weather stations were available within 3 km of all sites used for monitoring oviposition. Degree-days were calculated using numerical integration of hourly air temperature. Degree-day accumulation started on 1 March, using 8.41°C as the lower developmental threshold (Tobin et al. 2001) and no upper developmental threshold.

Data analyses

The pattern of grape berry moth oviposition in different years was compared using plots of yearly percentage of season-long oviposition vs. DD accumulation. We started by calculating a cumulative season-long distribution at 0, 1, 5, 10, …, 90, 95, 99, 100% oviposition in relation to degree-day accumulation for each vineyard, using PROC UNIVARIATE of SAS (SAS Institute 2001). Next, yearly distributions were calculated as the mean of the cumulative oviposition distributions for each vineyard. To compare moth flight among years on the same degree-day scale, we determined the per cent of season-long oviposition in relation to DD accumulation at 100 DD intervals, based on the yearly cumulative oviposition distributions. This procedure was necessary because the yearly distributions were not continuous with respect to DD accumulation. The oviposition distribution for the 4 years was calculated as the average of the distributions for each year in relation to DD accumulation. The same method using PROC UNIVARIATE was used to determine the per cent of season total oviposition in relation to calendar date. The number of eggs and infested berries in caged vs. exposed grapevines were compared by ANOVA using PROC MIXED of SAS (SAS Institute 2001) with grape exposure and assessment date as fixed effects and grapevine as a random effect.

Results

Monitoring egglaying in vineyards

Over the 4 years of the study (table 1), oviposition began (1%) at 523.5 ± 45.6 DD (mean ± SD) coinciding with early grape bloom, reached median (50%) at 1250.1 ± 154.0 DD close to veraison, and ended (99%) at 1589.5 ± 119.1 DD, often before harvest. In terms of calendar date (table 1), oviposition began on 16 June ± 9.8 days (mean ± SD), reached median at 11 August ± 10.7 days, and ended on 10 September ± 8.4 days. A seasonal average of 206.5 ± 30.5 (mean ± SE), 199.0 ± 77.0, 114.0 ± 37.9 and 171.8 ± 70.3 eggs per monitoring site were observed from 2006 to 2009, respectively. The beginning of oviposition was followed by a distinct peak in 2006 only (fig. 1). In other years, oviposition proceeded at relatively low level for 600 DD in 2009 to 1000 DD in 2007. The seasonal peak in oviposition occurred between 1200 DD in 2009 and 1600 DD in 2006. Although variable in its timing and relative size, the late-season peak occurred every year. With the exception of 2006 when no eggs were recorded at 1200 DD, the pattern of oviposition

Table 1 Accumulated degree-days from 1 March base 8.41°C (mean ± SD) and average date (mean ± SD) of percentile season-long oviposition in southwest Michigan from 2006 to 2009

Oviposition (%)	DD accumulation (mean ± SD)	Date (mean ± SD)
1	523.5 ± 45.6	16 June ± 9.8
5	596.0 ± 45.7	22 June ± 9.3
10	700.5 ± 68.3	30 June ± 0.9
25	967.2 ± 60.6	21 July ± 10.4
50	1250.1 ± 154.0	11 August ± 10.7
75	1408.6 ± 128.9	23 August ± 9.3
90	1458.6 ± 158.9	27 August ± 9.0
95	1508.2 ± 123.9	2 September ± 10.7
99	1589.5 ± 119.1	10 September ± 8.4

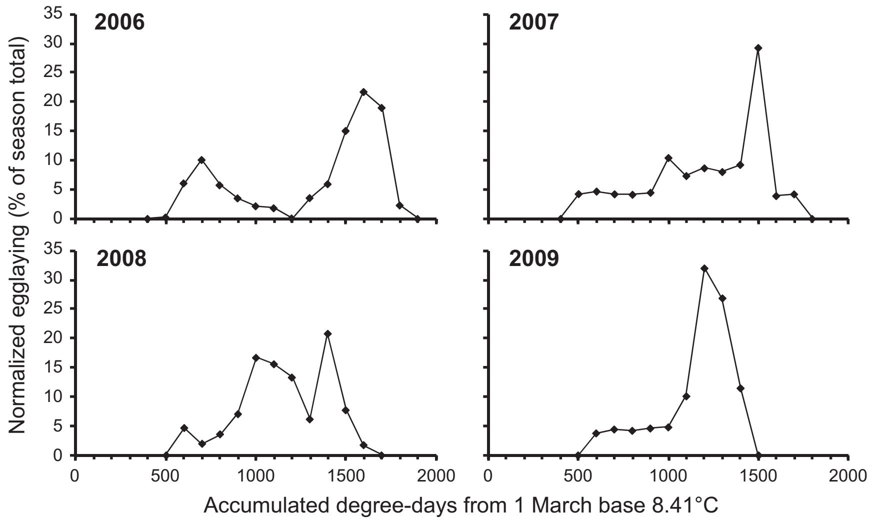

Fig. 1 Normalized percentage of season total egglaying by grape berry moth in relation to degree-day accumulation, in vineyards located in southwest Michigan, from 2006 to 2009.

showed no breaks that could indicate intervals between oviposition by distinct generations.

Egglaying on caged and exposed grape plants

Freshly laid eggs were found from July to September at 700 to 1500 DD on both caged and exposed grape clusters (fig. 2a). The average number of eggs per vine was relatively low but eggs were found throughout the whole period. Oviposition on exposed grape clusters peaked at ~1400 DD. On caged vines, the late-season peak in oviposition was less marked but occurred at the same DD accumulation. Overall, more eggs were found on exposed clusters than in clusters on caged plants ($F = 8.84$, d.f. = 1,115; $P = 0.004$). The number of infested berries followed a pattern similar to that of egg deposition, with a more marked increase starting at ~1400 DD (fig. 2b). More infested berries were found on exposed clusters than in clusters on caged plants ($F = 28.69$, d.f. = 1,115; $P < 0.001$), but the pattern of seasonal variation was similar. Infested berries were found on all caged vines indicating that the population of grape berry moth persisted inside all of the six cages. Eggs were observed on three of the six covered vines, and on all exposed vines. Adult moths or late-stage pupae must have been enclosed with the grape plants because eggs were recorded at the first monitoring date, 5 days after the cages were closed.

Discussion

This study shows that oviposition by grape berry moth in Michigan vineyards is continuous through-

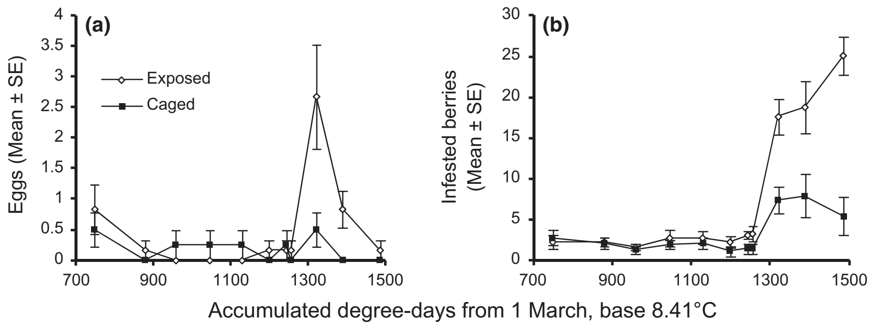

Fig. 2 Number of eggs (a) and number of infested berries (b) found on caged and exposed *Vitis labrusca* cv. Niagara grape vines. Vines were located at the edge of a vineyard facing a wooded area containing wild grape, in southwest Michigan, 2009.

out the season, with no predictable gaps between generations. The pattern of oviposition is further characterized by an increase in the number of eggs laid towards the end of the season. This peak of oviposition activity is consistent in its occurrence from year to year, but variable in its annual timing and size. Our findings are similar to those of Hoffman et al. (1992) who monitored oviposition on wild grape, *V. riparia*, over 2 years and found that oviposition was continuous throughout the season, with variable egg deposition timing and intensity. The continuous pattern of egg deposition is likely one of the reasons why grape berry moth is difficult to manage with conventional insecticides. Another reason may be that most egglaying occurs towards the end of the season, when growers are less concerned with insect management and already preparing for harvest.

During the 4 years when oviposition was monitored, the first eggs were found starting in mid-June, ~45 days later than the date (early May) when male moths are first captured with pheromone-baited traps in Michigan (Botero-Garcés and Isaacs 2003; Jenkins and Isaacs 2007a; Teixeira et al. 2009). This difference may result from protandry (Tobin et al. 2002), or from environmental conditions that are not suitable for mating and/or oviposition during the early part of the season. It is also possible that monitoring male moths using pheromone-baited traps is more effective than visually examining a sample of grape clusters to detect eggs, which may create a bias in favour of earlier detection of male moths. After the first eggs were detected in mid-June, oviposition proceeded at low intensity for a period of time. An extended emergence period by the overwintering generation is likely the cause of the initial period of low-intensity egglaying. For example, field observations of overwintering grape berry moth emergence in the Lake Erie region recorded adults of the overwintering generation emerging as late as August (Johnson and Hammar 1912). In addition, a 6-week emergence period was recorded by Tobin et al. (2002) with laboratory-reared larvae. The oviposition pattern of grape berry moth complicates the characterization of individual generations and contrasts with that of the European grape berry moth, *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae). This moth presents a variable number of non-overlapping flights and generations per year in the Palearctic region (Del Tío et al. 2001; Milonas et al. 2001; Gallardo et al. 2009).

The late-season peak of egglaying was variable in its timing but occurred in all 4 years of the study. This variability is probably a function of the long sequence involving developmental processes and adult behaviour that shapes the timing of the peak. Among these factors is the wide oviposition period of the previous generation, egg and larval development, pupation, adult emergence and mating, events that are only partially controlled by temperature as measured by degree-day accumulation. Nevertheless, the consistent oviposition pattern recorded in this study suggests the occurrence of two generations of grape berry moth, one the overwintering generation, and another the first, summer generation. A second summer generation may have been responsible for the late conclusion of the oviposition period in some of the years. This generation consists of the fraction of the offspring of the first summer generation that did not enter diapause. Diapause is induced below a photoperiod threshold of ~15 h that in southwest Michigan is reached in mid- to late July (Nagarkatti et al. 2001; Tobin et al. 2008). Some individuals may not enter diapause, depending on the environmental conditions prior and during the period of diapause induction, and instead emerge and lay eggs towards the end of the season, resulting in an extended oviposition period.

Immigration of grape berry moth from wild hosts into vineyards is not necessary for the late-season peak to occur, as increases in egglaying and grape infestation were recorded at similar timing with caged grapevines. Wild hosts are the initial source of grape berry moth infestation in vineyards, and likely the reason why the edges of the vineyards tend to have higher infestation than the interior (Hoffman and Dennehy 1989). However, Jenkins and Isaacs (2007b) found that removing wild vines to a distance of 60 m from the edge of the vineyard over a 3-year period did not affect vineyard infestation by grape berry moth, suggesting that once a population is established the intensity of the infestation is not a function of moth immigration. Edge effects may also contribute to higher infestation at the edge of the vineyards (Hsu et al. 2009). Similar timing of late-season peaks of egglaying on exposed and covered clusters indicates that the occurrence of the peak requires only the presence of grape berry moth for up to 700 DD in the cages. The larger number of eggs and infested berries on exposed than covered clusters suggests the occurrence of oviposition by dispersing moths.

The beginning of the oviposition period was much more consistent from year to year compared to events later in the season. For grape pest management, this is an unfortunate situation because larvae hatching from late-season eggs are the most economically important, as they cause damage and contamination of grapes at harvest. A risk assessment programme (Hoffman et al. 1992) is available to determine the need for insecticide sprays based on grape sampling. However, this method was developed when insecticides that were highly effective against grape berry moth, such as methyl-parathion, were registered. The use of the risk management protocol with currently registered carbamate, organophosphate or pyrethroid insecticides does not result in satisfactory control of grape berry moth at harvest (R. Isaacs, unpublished data). A reliable method for determining the onset of late-season egglaying would greatly improve management of grape berry moth, but, based on our results, it does not appear that simple degree day accumulation will provide accurate prediction of the initiation of oviposition late in the season (see above). Nevertheless, data in this study indicate that controlling the late-season oviposition peak may be the key to low berry infestation at harvest. For this reason, we are currently evaluating and refining a degree-day model that includes wild grape phenology as a biofix. As an alternative chemical approach, the use of IGR insecticides with long residual efficacy, such as tebufenozide and methoxyfenozide (Jenkins and Isaacs 2007a; Teixeira et al. 2009), or mating disruption products (Trimble 2007; Jenkins and Isaacs 2008) may help address the problem of the variable timing of late-season oviposition.

Acknowledgements

The authors thank Lindsey Bock, Geordan Hudson, Jillian Kallenbach, Mike Playford, John Pote, Bob Rector, Courtney Rockenbach, Steve Saylor, Meghan Sheridan, Jonathon Wyma, and Adam Young from Michigan State University for technical assistance. We thank the grape growers who provided access to their vineyards for this research. This work was funded in part by grants from Project GREEEN, the USDA Crops at Risk Program and National Grape Cooperative.

References

Biever KD, Hostetter DL, 1989. Phenology and pheromone trap monitoring of the grape berry moth, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae) in Missouri. J. Entomol. Sci. 24, 472–481.

Botero-Garcés N, Isaacs R, 2003. Distribution of grape berry moth, *Endopiza viteana* (Lepidoptera: Tortricidae), in natural and cultivated habitats. Environ. Entomol. 32, 1187–1195.

Botero-Garcés N, Isaacs R, 2004a. Infuence of uncultivated habitats and native host plants on cluster infestation by grape berry moth, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae), in Michigan vineyards. Environ. Entomol. 33, 310–319.

Botero-Garcés N, Isaacs R, 2004b. Movement of the grape berry moth, *Endopiza viteana*: displacement distance and direction. Phys. Entomol. 29, 443–452.

Del Tío R, Martínez JL, Ocete R, Ocete ME, 2001. Study of the relationship between sex pheromone trap catches of *Lobesia botrana* (Den. & Schiff.) (Lep., Tortricidae) and the accumulations of degree-days in Sherry vineyards (SW of Spain). J. Appl. Ent. 125, 9–14.

Dennehy TJ, Hoffman CJ, Nyrop JP, Saunders MC, 1990. Development of low-spray, biological, and pheromone approaches for control of grape berry moth, *Endopiza viteana* Clemens, in the eastern United States. In: Monitoring and integrated management of arthropod pests of small fruit crops. Ed. by Bostanian NJ, Wilson LT, Dennehy TJ, Intercept Ltd., Andover, NH, 261–282.

Gallardo A, Ocete R, López MA, Maistrello L, Ortega F, Semedo A, Soria FJ, 2009. Forecasting the flight activity of *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera, Tortricidae) in Southwestern Spain. J. Appl. Ent. 133, 626–632.

Gentner LG, 1925. Some important grape insects. Michigan State Agric. Exp. Sta. Bull. 148, 3–10.

Gleissner BD, Worthley HN, 1941. Evidence for a third brood of the grape berry moth, *Polychrosis viteana* Clemens, in the Great Lakes region. J. Econ. Entomol. 34, 426–431.

Hoffman CJ, Dennehy TJ, 1989. Phenology, movement, and within-field distribution of the grape berry moth, *Endopiza viteana* (Clemens) (Lepidoptera: Tortricidae), in New York vineyards. Can. Entomol. 121, 325–335.

Hoffman CJ, Dennehy TJ, Nyrop JP, 1992. Phenology, monitoring, and control decision components of the grape berry moth (Lepidoptera: Torticidae) risk assessment program in New York. J. Econ. Entomol. 85, 2218–2227.

Hsu CL, Agnello AM, Reissig WH, 2009. Edge effects in the directionally biased distribution of *Choristoneura rosaceana* (Lepidoptera: Tortricidae) in apple orchards. Environ. Entomol. 38, 433–441.

Ingerson HG, 1920. Life history of the grape berry moth in northern Ohio. U.S. Agr. Dep. Bull. 911, 1–38.

Jenkins PE, Isaacs R, 2007a. Reduced-risk insecticides for control of grape berry moth (Lepidoptera: Tortricidae) and conservation of natural enemies. J. Econ. Entomol. 100, 855–865.

Jenkins PE, Isaacs R, 2007b. Cutting wild grapevines as a cultural control strategy for grape berry moth (Lepidoptera: Tortricidae). Environ. Entomol. 36, 187–194.

Jenkins PE, Isaacs R, 2008. Mating disruption of *Paralobesia viteana* in vineyards using pheromone deployed in

SPLAT-GBM™ wax droplets. J. Chem. Ecol. 34, 1089–1095.

Johnson FA, Hammar G, 1912. The grape berry moth. U.S. Dept. Agric. Bur. Ent. Bull. 116, Part II, 15–71.

Luciani MA, 1987. The biology of the grape berry moth, *Endopiza viteana* (Clemens) (Lepidoptera: Tortricidae) in southern Ontario. M.S. Thesis, University of Guelph, Guelph, ON, Canada.

Milonas PG, Savopoulo-Soultani M, Satavridis DG, 2001. Day-degree models for predicting the generation time and flight activity of local populations of *Lobesia botrana* (Den. and Schiff.) (Lepidoptera, Tortricidae) in Greece. J. Appl. Ent. 125, 515–518.

Nagarkatti S, Tobin PC, Saunders MC, 2001. Diapause induction in the grape berry moth, *Endopiza viteana* (Clemens) (Lepidoptera: Tortricidae). Environ. Entomol. 30, 540–544.

SAS Institute, 2001. SAS/STAT User's Manual, Version 8.2. SAS Institute, Cary, NC.

Taschenberg EF, Carde RT, Hill A, Tette JP, Roelofs WL, 1974. Sex pheromone trapping of the grape berry moth. Environ. Entomol. 3, 192–194.

Teixeira LAF, Mason K, Isaacs R, 2009. Control of grape berry moth *Paralobesia viteana* (Clemens) (Lepidoptera: Tortricidae) in relation to oviposition phenology. J. Econ. Entomol. 102, 692–698.

Tobin PC, Nagarkatti S, Saunders MC, 2001. Modeling development in grape berry moth (Lepidoptera, Tortricidae). Environ. Entomol. 30, 692–699.

Tobin PC, Nagarkatti S, Saunders MC, 2002. Diapause maintenance and termination in grape berry moth (Lepidoptera, Tortricidae). Environ. Entomol. 31, 708–713.

Tobin PC, Nagarkatti S, Loeb G, Saunders MC, 2008. Historical and projected interactions between climate change and insect voltinism in a multivoltine species. Glob. Change Biol. 14, 951–957.

Trimble RM, 2007. Comparison of efficacy of pheromone dispensing technologies for controlling the grape berry moth (Lepidoptera: Tortricidae) by mating disruption. J. Econ. Entomol. 100, 1815–1820.

Trimble RM, Pree DJ, Vickers PM, Ker KW, 1991. Potential of mating disruption using sex pheromone for controlling the grape berry moth, *Endopiza viteana* (Clemens) (Lepidoptera: Tortricidae) in Niagara Peninsula, Ontario vineyards. Can. Entomol. 123, 451–460.