Distribution of Grape Berry Moth, *Endopiza viteana* (Lepidoptera: Tortricidae), in Natural and Cultivated Habitats

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ABSTRACT The relative abundance of male grape berry moths, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae), was studied within Michigan grape agroecosystems during 1999–2001. Distribution within and between habitats was determined using pheromone traps placed at different heights between the interior of deciduous woods and interior of adjacent vineyards. Comparisons of relative moth abundance across habitats using traps at the standard 1.5 m sampling height confirmed that moths are more abundant in the woods in spring and in the vineyard later in the season. Traps placed at 1.5, 3.0, 6.0, and 9.0 m above ground level in woods and vineyards revealed that moth relative abundance increases with height in woods, whereas 90.0% of moths caught in vineyards were at 1.5 m above ground level. Sampling inside the woods up to 15.2 m revealed that 76.1% of moths were found at or above 9.0 m. Relatively few moths were trapped in the interface between these habitats, where grapevines are not present. The results of vertical sampling suggests that moths are not moving from woods to vineyards, but instead are most abundant high in the woods canopy. These results show that the relative abundance of grape berry moth varies within and between habitats, and suggest that distribution of this specialist insect is associated with the distribution of its wild and cultivated host.

RÉSUMÉ L'abondance relative des mâles de la tordeuse de la vigne, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae), a été étudiée dans l'écosystème agronomique des vignobles du Michigan aux États Unis, durant 1999–2001. La distribution relative intra- et inter-habitats (les bois adjacents et les vignobles) a été déterminée par l'utilization de pièges à phéromone placés à différentes hauteurs entre l'intérieur des bois et l'intérieur des vignobles contigus. Les comparaisons sur l'abondance relative de mâles en utilisant des pièges placés à la hauteur standard de 1.5 m, ont confirmé que les mâles sont plus abondants dans les bois au printemps et dans les vignobles plus tard dans la saison. Des pièges placés à des hauteurs de 1.5, 3.0, 6.0, et 9.0 m dans les bois et les vignobles adjacents ont montré que dans les bois, l'abondance relative augmente à mesure que la hauteur du piège augmente, pendant que dans les vignobles, le 90.0% des mâles capturés se trouvent à la hauteur de 1.5 m par-dessus le sol. En ayant des pièges placés jusqu'à une hauteur de 15.2 m dedans les bois, nous avons trouvé que le 76.1% des mâles se trouvaient à ou par-dessus le niveau de neuf mètres. Relativement peu de mâles furent capturés à l'interface entre ces deux habitats où les vignes sont absentes. Les résultats d'un échantillonnage vertical suggèrent que les mâles ne se déplacent pas des bois vers les vignobles, sinon qu'ils continuent tout le temps à être plus nombreux dans le haut des bois, les coupes des arbres. L'abondance relative de la tordeuse de la vigne varie non seulement intra- mais aussi inter-habitats, ce qui suggère que la distribution de cet insecte spécialiste soit associée avec la distribution de son hôte sauvage et cultivé.

KEY WORDS *Endopiza viteana*, *Vitis*, grape berry moth, ecology, distribution

THE GRAPE BERRY MOTH, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae), is a specialist herbivore, found in vineyards and woods throughout the Eastern United States and Southeastern Canada (Johnson and Hammar 1912). Females lay eggs individually on grape berries and the larvae hatch and enter the berries to feed and develop. When larvae are ready to pupate, they leave the berry for a nearby leaf in which they cut a crescent-shaped section and wrap it around while spinning a cocoon (Slingerland 1904, Johnson and Hammar 1912). First emergence of grape berry moth adults in spring generally occurs during bloom and can vary from early May (Dozier et al. 1932) to early June (Johnson and Hammar 1912, Ingerson 1920, Pettit 1932). Depending on weather conditions, there may be two or more generations per year with widely varying phenologies (Hoffman et al. 1992, Tobin et al. 2002), the last of which overwinters as pupae on

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leaves. When these leaves drop to the ground, the pupae may be blown by the wind to the edges of the vineyard and into woods (Johnson and Hammar 1912). The native ancestral host plant of *E. viteana* is the wild grape (*Vitis* spp., Vitaceae) commonly found in stands of young woods, perturbed habitats, and on the borders of mature forests (Morano and Walker 1995), which provides alternative habitats for *E. viteana* outside vineyards. A sex pheromone-baited trap (Taschenberg et al. 1974, Taschenberg and Roelofs 1977) is typically hung from the vineyard trellis at 1.5 m to monitor activity of *E. viteana,* and is used by viticulturists to determine phenology of grape berry moth and to time control measures (Dennehy et al. 1990).

Hoffman and Dennehy (1989) found that infestation by *E. viteana* was unpredictable from year to year, from vineyard to vineyard, and within vineyards, and Biever and Hostetter (1989) suggested this was because of variation in winter survival and/or the presence of wild grapes in surrounding woods, from which moths could immigrate into the vineyard. The presence of woods near the vineyard is a significant factor in vineyard risk assessment because they harbor wild grape and are associated with greater vineyard infestations than at sites where no woods are found (Dennehy et al. 1990). However, woods containing *Vitis* spp. may also provide shelter and food sources for parasitoids of *E. viteana* (Seaman et al. 1990, Dennehy et al. 1990).

By placing traps at the edge of the woods and in adjacent vineyards, Johnson et al. (1988) found that *E. viteana* emergence in woods is about a week earlier than at the edge of the vineyard. In addition to the differential timing of emergence, authors have implied that more *E. viteana* are at the edge of vineyards than inside vineyards because of damage assessments (Dennehy et al. 1990, Trimble 1993). This pattern suggests greater abundance of *E. viteana* in natural habitats than managed habitats (Hoffman and Dennehy 1989), as occurs with the redbanded leafroller, *Argyrotaenia velutinana,* in grapes (Biever and Hostetter 1989). Johnson et al. (1988) described early season abundance at the woods and vineyard edge, with a subsequent shift toward the center of the vineyard as the season progressed. This pattern was supported by Hoffman and Dennehy (1989), who trapped grape berry moths at 15 different positions along a transect from a vineyard, into woods, an alfalfa field, another woods, and another vineyard. They showed that a higher percentage of moths were caught in the woods at the beginning of the season but near the time of harvest, more moths were caught inside the vineyard than anywhere else (Hoffman and Dennehy 1989). Similar patterns have been observed by Biever and Hostetter (1989) and Trimble et al. (1991).

Height is an important consideration for understanding insect distribution and abundance, particularly when there is considerable difference in canopy height between habitats in which the insect is distributed (Derrick et al. 1992, Humphrey et al. 1999, Boiteau et al. 2000a). The woods and vineyard habitats of grape berry moth vary markedly in their structure and complexity. In vineyards, grapes are on trellises typically $<$2 m high, whereas in woods, they extend up to 25 m high, with wild grape plants climbing on mostly deciduous trees. Thus, a response to habitat structure will be an important component of this insect's ecology in these two adjacent habitats.

The relationship between vertical distribution of Lepidoptera and host distribution has been reported for a few species. Derrick et al. (1992) placed traps at two heights for monitoring European corn borer, *Ostrinia nubilalis,* in potatoes and corn, and found that traps placed in the crop canopy caught the highest number of moths. In apple orchards, captures of the oriental fruit moth, *Cydia molesta,* increased with trap height (Peterson 1926), and the greatest captures were obtained whenever traps were placed in the fruit zone, irrespective of height (Rothschild and Minks 1977). Riedl et al. (1979) and Howell et al. (1990) examined vertical variation in captures of codling moth *Cydia pomonella,* though these studies differ in their conclusions. Howell et al. (1990) did not find a significant variation in moth captures with height, but concluded the tree canopy had the greatest effect because captures depended on whether traps were hung inside the canopy or on its periphery. Riedl et al. (1979), however, found that maximum captures of *C. pomonella* were found at greater heights in the canopy. Studies of the effects of trap design and height on captures of the European vine moth (or European grape berry moth) *Lobesia botrana,* and the vine moth, *Eupoecilia ambiguella* led Gabel and Renczés (1985) to emphasize the importance of adapting sampling to "the ethological and physiological characteristics of the particular pest."

In Eastern North America, the grape berry moth exists in habitats of different structure, environmental conditions, and host distribution. The study described herein aimed to determine the relative distribution of this highly specialist herbivore in natural and cultivated habitats. The specific objectives of this study were to determine: (1) the vertical distribution of grape berry moth, (2) the horizontal distribution of grape berry moth across the vineyard-woods landscape, (3) the simultaneous vertical and horizontal distribution of grape berry moth through the season.

Materials and Methods

This study was conducted in juice grape (*Vitis labrusca,* var. Concord and Niagara) vineyards in Van Buren County, MI. All sites had a history of grape berry moth and were bordered on at least one side by deciduous woods. Relative moth abundance was measured using pheromone traps (large plastic delta trap, Suterra LLC, Bend, OR) each baited with a lure containing 0.1 mg of synthetic sex pheromone of *E. viteana* (90:10 ratio of (Z)-9–12Ac and (Z)-11–14Ac). Trap inserts were replaced as needed and pheromone lures were changed monthly, using the same batch of lures for all traps at each change. All traps were checked

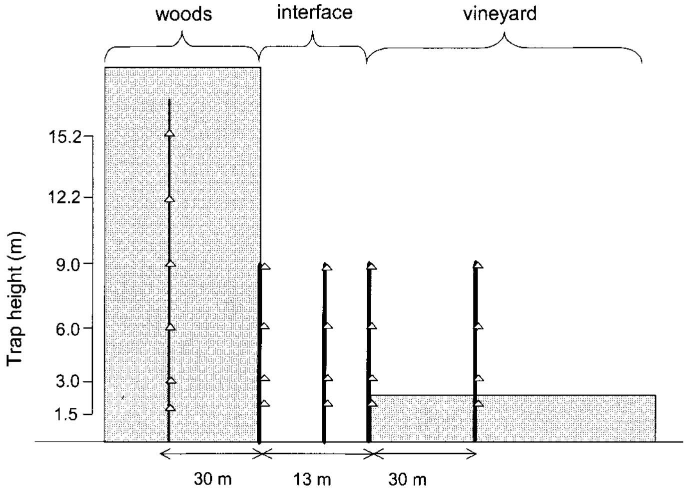

Fig. 1. Schematic representation (not to scale) of a study site in 2001. Pheromone traps (triangles) were hung at different heights on poles or ropes in five positions across the vineyard-woods habitats. Gray boxes represent the extent of the two habitats.

weekly and the number of grape berry moth males recorded.

Vertical Distribution. To determine variation in *E. viteana* abundance with trap height, two vertical transects of traps were placed 8.0–10.0 m apart on the edge of woods bordering four vineyards, in a complete block design. Traps were suspended by a loop of rope hung from a tree branch at least 10 m above the ground. Four pheromone traps were hung on each rope at 1.5, 3.0, 6.0, and 9.0 m above the ground. By using a rope at least 27 m long, the highest trap could be easily lowered, checked, and pulled back up. The number of male grape berry moths trapped was recorded weekly from 1 July to 21 October 1999.

In 2000, grape berry moth vertical distribution was sampled next to the woods, on the grassy 7–14 m wide interface surrounding each vineyard, used by growers to maneuver machinery. Two 10 m tall PVC poles were placed at least 3 m from the woods edge at each of four vineyard-woods interfaces, in a complete block design. Each pole was constructed from PVC pipe, using a 3.3 m × 10.4 cm i.d. piece connected to two 3.3 m × 9.1 cm i.d. pieces that were joined by an overlapping 70 cm piece of 10.4 cm i.d. PVC. All pole connections were secured with steel bolts. A horizontal 2 m piece of PVC was attached to the top of the pole using a T-shaped PVC connector with a 3.3 cm eye-bolt at one end. This was used to hold the rope carrying pheromone traps, as described above. The base of each pole was buried 10 cm into the ground, and stabilized with four guy ropes attached 3 m below the top and tied to 1.2 m reinforced steel bars inserted into the ground. Traps were checked weekly from 3 June until 3 October 2000.

Horizontal Distribution. To determine the relative abundance of grape berry moth in different parts of the vineyard-woods ecosystem, pheromone traps were placed 1.5 m above the ground (spaced 8.0–10 m apart) at four positions between the woods interior and vineyard interior, at six commercial vineyards bordered by deciduous woods. At each vineyard, a transect of traps was established at four positions from the woods interior to the vineyard interior. Three traps were placed 30 m inside the woods, five traps along the edge of those woods, five traps directly across the interface on the first row of vines, and three traps 30 m inside the vineyard. Traps were checked weekly from 15 April to 21 October 2000. The average number of male *E. viteana* captured per trap was compared among the four positions for each of the three flights to determine the temporal change in relative distribution between woods and vineyards.

Vertical and Horizontal Distribution. During 2001, the vertical and horizontal distribution of *E. viteana* was simultaneously compared across the three flights. This was done in two vineyards at each of four farms, at sites where vineyards were bordered by deciduous woods on at least one side. At each vineyard, 9.2 m tall steel telescoping poles (Channel Master, Smithfield, NC) were placed in each of four positions: at the edge of the woods, on the interface, at the edge of the vineyard and 30 m inside the vineyard, each with four pheromone traps hung at 1.5, 3.0, 6.0, and 9.0 m above the ground (Fig. 1). Inside the woods, where the poles could not be erected, loops of rope were hung from tree branches, at 1.5, 3.0, 6.0, 9.0 m. Wherever tree height allowed it, traps were also hung further up, at 12.2, and 15.2 m above the ground. Loops of rope were passed over tall tree branches using a bow with an adapted arrow and a string attached. Traps were installed during the spring, when few obstacles hindered the arrow's path and total visibility of the canopy was possible. All traps were deployed by 19 April and checked weekly until 15 October 2001.

Data Analysis. Shapiro–Wilkinson and Kolmogorov–Smirnov tests revealed that raw data were nonnormal, and so all were transformed (log n+1) to meet the criteria of normality and homogenous variance

Table 1. Average number of *Endopiza viteana* caught at four different heights at the woods edge and the vineyard-woods interface in two different years

Trap height (m)	Mean ± SE moths caught per trap	
	Woods edge (1999)	Vineyard-woods interface (2000)
1.5	42.0 ± 13.6c	4.5 ± 7.3a
3.0	43.5 ± 14.9c	3.7 ± 3.3a
6.0	79.1 ± 26.0b	3.2 ± 4.3a
9.0	264.6 ± 93.8a	1.7 ± 7.0a

Means within a column followed by the same letter are not significantly different (Tukey $\alpha = 0.05$).

among treatments. Main factors tested included height, position, and flight. All analyses were performed with the SAS program (SAS Institute 1996). For all significant factors, Tukey's test was performed to determine differences between means at the 5% probability level. In vertical distribution experiments, data were analyzed with a one-way analysis of variance (ANOVA) using PROC GLM (SAS, version 8.0). In the horizontal distribution experiment, data were analyzed with a one-way ANOVA using PROC MIXED (SAS, Version 8.0), with flights as repeated measures. Data from the three-dimensional (vertical and horizontal and time) study were analyzed using an ANOVA with a two-way treatment structure (height and position) with repeated measures (flights) using PROC MIXED (SAS, version 8.0). To test the significance of differences among positions only, data from the four heights were pooled within positions and analyzed for each flight.

Results

Vertical Distribution. A total of 3,434 moths was trapped at the edge of the woods, and moth captures varied significantly with height ($F_{3,25} = 31.37$, $P < 0.0001$) (Table 1). Traps at 9.0 m caught significantly more moths than traps at lower heights ($P < 0.0001$), with >61% of all moths caught at 9.0 m. This compared with only 9.8% caught at the typical trap deployment height of 1.5 m. There was no significant difference in captures between traps at 1.5 and 3.0 m ($P = 0.74$). When traps were placed at the vineyard-woods interface moth captures were low (556 males) and did not vary significantly with height ($F_{3,25} = 1.93$, $P = 0.15$)

Table 2. Average number of *E. viteana* caught per flight in traps placed at a height of 1.5 m in four different positions within the habitats sampled during 2000

Flight	Mean ± SE moths caught per trap			
	Woods		Vineyard	
	Inside	Edge	Edge	Inside
1	211.9 ± 61.3a	184.4 ± 32.9ab	79.1 ± 19.3b	75.1 ± 25.2b
2	68.9 ± 22.4a	102.2 ± 29.7a	77.5 ± 18.9a	142.5 ± 27.8a
3	3.7 ± 1.0b	10.0 ± 2.3ab	13.3 ± 2.9ab	31.9 ± 9.8a

Means within a row followed by the same letter are not significantly different (Tukey $\alpha = 0.05$).

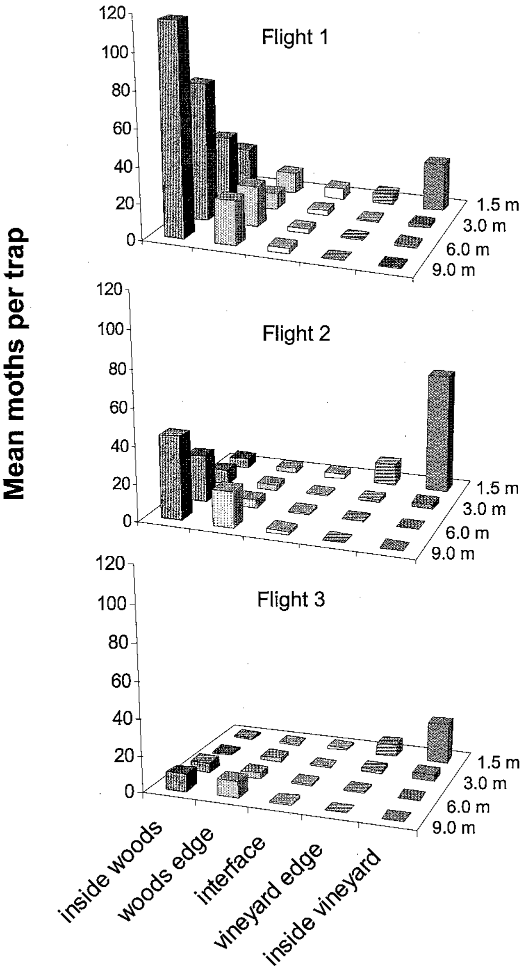

Fig. 2. Average number of male *E. viteana* caught per trap during each flight in 2001, trapped at four heights across five positions in the vineyard-woods agroecosystem.

(Table 1). The variability in these data reflects differences in populations among the four farms.

Horizontal Distribution. The number of male moths captured varied according to the position of the traps in the vineyard-woods system and time of season. Almost three times as many moths (23,275) were caught in the woods habitat than in the vineyard habitat (8,453). During Flight 1, 84% of moths were caught in the woods, whereas 52% and 49% were trapped in the woods in flights two and three, respectively, indicating variation in distribution between habitats over time. There were 12,058 moths (38% of the moths trapped all season) caught in Farm 2, and contrary to the trend observed in the other five farms, consistently fewer moths were trapped inside the vineyard during all three flights at this farm. Analysis that included Farm 2 showed similar trends in abundance among positions to analysis excluding it, but because of the numerical difference between Farm 2 and the other five farms, the normality assumption

Table 3. Average number of *E. viteana* caught in traps per position (1.5–9.0 m heights pooled), during three flights sampled during 2001

Flight	Mean ± SE moths caught per trap				
	Woods		Interface	Vineyard	
	Inside	Edge		Edge	Inside
1	254.5 ± 44.2a	68.3 ± 31.0b	14.0 ± 4.4b	7.6 ± 2.1b	30.1 ± 7.1b
2	81.5 ± 13.1a	28.9 ± 4.2b	6.5 ± 1.3b	13.0 ± 3.4b	65.3 ± 11.0a
3	17.8 ± 6.1ab	16.4 ± 3.4ab	4.1 ± 1.8b	10.0 ± 2.2b	27.1 ± 4.4a

Means within a row followed by the same letter are not significantly different (Tukey $\alpha = 0.05$).

could not be met. Therefore, Farm 2 was excluded from further analysis.

In the five remaining farms, total moth captures were significantly different among the three flights of 2000 ($F_{2,109} = 132.16$, $P < 0.0001$) and there was a significant interaction between positions and flights ($F_{6,105} = 8.76$, $P < 0.0001$) (Table 2). During Flight 1, 71.5% of moths were caught in the woods habitat, a proportion that decreased to 46.8% during Flight 2, and to 27.4% in Flight 3. Although the difference in relative abundance of grape berry moth was not significant among vineyard positions, more moths were captured inside the vineyard than at the vineyard edge for Flights 2 and 3 (Table 2).

Vertical and Horizontal Distribution. Captures of grape berry moth varied significantly across habitats (positions) ($F_{4,97} = 63.94$, $P < 0.0001$) and during each individual flight ($F_{2,206} = 56.82$, $P < 0.0001$) (Fig. 2), with a significant position by flight interaction ($F_{38,206} = 4.04$, $P < 0.0001$). Combining captures of *E. viteana* between 1.5 and 9.0 m, a 1.9-fold decrease in moth capture from Flight 1 (total of 2,994 moths) to Flight 2 (1,561) and a subsequent 2.6-fold decrease to Flight 3 (603) were observed (Table 3). During Flight 1, 86% of the moths were caught in the woods habitat (both inside and edge) compared with only 10% caught in the vineyard habitat (both edge and inside). However, during Flight 2, the proportion of moths trapped in the woods habitat decreased to 57% and increased in the vineyard habitat to 40%. Captures were similar in both habitats during Flight 3, with 45% of captures in the woods and 49% in the vineyards. Simultaneous sampling of *E. viteana* adults across horizontal and vertical gradients confirmed the pattern observed in separate studies of horizontal and vertical distribution in 2000. Captures in the interface were low throughout the season (Fig. 2), and more moths were trapped inside the vineyard that at the edges. This difference was significant in Flights 2 and 3 (Table 3).

When relative abundance was compared across heights, some clear patterns were seen (Fig. 2). Moth captures varied significantly according to height ($F_{3,97} = 25.12$, $P < 0.0001$), and this variation was significantly influenced by flight and position ($F_{38,206} = 4.04$, $P < 0.0001$). The capture of moths at different heights depended on where (position and habitat) the trap was placed (at 1.5 m $F_{4,97} = 19.89$, at 3.0 m $F_{4,97} = 7.96$, at 6.0 m $F_{4,97} = 40.35$, at 9.0 m $F_{4,97} = 75.79$; $P < 0.0001$). At all positions except the interface ($F_{3,97} = 1.63$, $P = 0.19$), there was a significant variation in moth relative abundance among heights (inside woods $F_{3,97} = 14.64$, at the woods edge $F_{3,97} = 10.20$, at the vineyard edge $F_{3,97} = 31.40$, and inside the vineyard $F_{3,97} = 73.96$; $P < 0.0001$), with the greatest number of moths caught in the higher traps in the woods habitat and in the lowest traps in the vineyard habitat (Fig. 2).

When captures at 1.5 m were considered separately because of their relevance to monitoring for this insect, more moths were always captured inside the vineyard than inside the woods (Fig. 2), though this

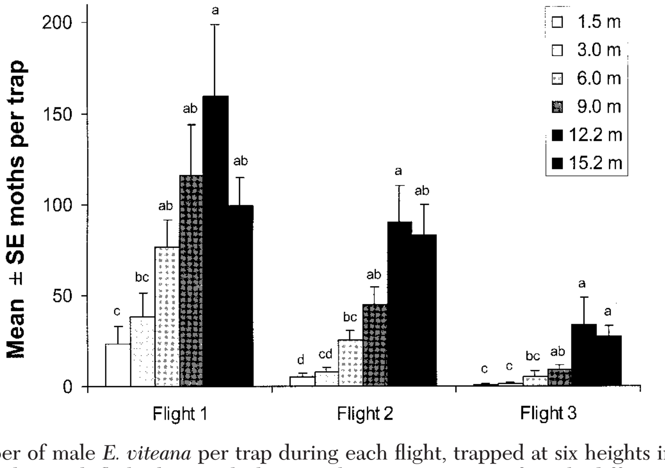

Fig. 3. Average number of male *E. viteana* per trap during each flight, trapped at six heights inside woods adjacent to vineyards during 2001. Within each flight, bars with the same letters are not significantly different (Tukey $\alpha = 0.05$).

difference was not significant during the first flight. At the edge and interior of the vineyard, significantly more moths were trapped at 1.5 m than at any other height (Tukey $P = 0.0068$ between 1.5 and 6.0 m, $P = 0.0013$ between 1.5 and 9.0 m at the vineyard edge, and $P < 0.0001$ for the same comparisons inside the vineyard), with very few moths found in traps placed above the canopy (Fig. 2). When the full height of the tree canopy in wild habitats was taken into consideration, the greatest captures of moths were made in traps at 12.2 and 15. 2 m height. Indeed, moth captures increased significantly with height of trap inside the woods ($F_{5,29} = 21.76$, $P < 0.0001$), so that 76.1% of moths captured in the vertical transects within the woods were caught at or above 9.0 m (Fig. 3). This change in relative abundance with height in the woods was consistent across flights (Fig. 3), and the change among flights was consistent with results during 2000 (Table 2).

Discussion

Our results indicate there is differential spatial and temporal distribution of grape berry moth across vineyard-woods landscapes. Relative abundance of grape berry moth was found to vary significantly with the type of habitat in which this insect was sampled, and with the height at which samples were taken. The greatest captures of *E. viteana* males were made during Flight 1, with decreasing captures for successive flights. There are several possible explanations for this pattern. Hamstead et al. (1972) found a similar pattern in *A. velutinana,* and suggested that early in the season lower temperatures favored traps over sexually mature females, whose release of pheromone was reduced. Another explanation could be that diapause frequency in *E. viteana* increases after 25 June (Flight two and three) as daylength shortens (Nagarkatti et al. 2001). Tobin et al. (2002) suggested that *E. viteana* is protandrous, which would explain abundant captures of males early in the season when only the lures inside traps are releasing pheromone. The decreasing captures of males in successive flights have been explained by increasing abundance of virgin female moths, which increasingly compete with the pheromone traps as the population grows through the season (Howell 1974, Hoffman and Dennehy 1989, Dennehy et al. 1990, Aslam et al. 1990).

Sampling across vineyard-woods habitats throughout the season showed that captures of *E. viteana* vary significantly with sampling position and trap height, a trend that could be because of the response of this species to the structure and composition of its habitat. Although results obtained from traps at 1.5 m agree with previous findings (Hoffman and Dennehy 1989, Lewis and Johnson 1999), by placing traps between 1.5 and 9.0 m above the ground in these different habitats, we have shown that a majority (90.2% in 1999) of *E. viteana* males in woods are consistently distributed above the typical height for trap placement (Table 1; Figs. 2 and 3). Hoffman and Dennehy (1989) found that pheromone traps placed at wood edges captured few moths even though high numbers of eggs were deposited in the same area on wild grapes, suggesting that male *E. viteana* emigrate from areas of oviposition activity. The number of times female *E. viteana* mate is not known, but if they usually mate only once as found for *L. botrana* (Torres-Vila et al. 1997), emigration from areas of oviposition would improve a male moth's chance of locating virgin females. However, in view of our results, previous studies using traps within easy reach have probably missed moths flying high in the woods. Traps placed at different heights in the woods canopy showed that more moths were captured high in the woods than in traps placed at 1.5 m in the vineyard. This suggests that, rather than a shift in abundance of this species from the woods to the vineyard as the season progresses, there is a distribution of moths in which their abundance is greatest in the higher canopy. Relative abundance is highest in the woods throughout the season, but because of the typical 1.5 m monitoring position used, this has remained unnoticed.

Low captures of *E. viteana* in traps placed in the vineyard-woods interface in 2000 and 2001, coupled with the similar captures at different heights (Table 1; Fig. 2.) indicate that the lack of host plant in this position provided no host substrate to which the moths could respond. In vineyards, the greatest moth captures were consistently within the canopy, with few moths captured above 1.5 m. Taken together with the results in woods described above, these results agree strongly with those of Hoffman and Dennehy (1989), suggesting that *E. viteana* distribution is tightly coupled to the structure of the habitat where its host is present.

Wild grapes comprise four species of *Vitis* in the Eastern United States and are common throughout wild and perturbed habitats (Morano and Walker 1995). At the edge of woods, vines grow on border trees, sometimes covering them from the ground to the canopy top. Inside the woods, they grow on trees, developing fully into the canopy where light intensity is greatest. The majority of fruiting occurs at this height, typically 16–18 m high in the deciduous woods surrounding Michigan vineyards (N.B.-G., unpublished data). The variation in captures of male moths with height may be a response to canopy height, fruit distribution, or virgin female distribution. Correlations between fruit moth abundance and canopy height have been described before for the two grape pests *E. ambiguella* and *L. botrana* (Gabel and Renczés 1985), for *C. pomonella* (Riedl et al. 1979, Howell et al. 1990) and for *C. molesta* (Rothschild and Minks 1977). Vertical distribution of foraging insects can be tightly linked to resource vertical distribution (Muirhead-Thompson 1991, Cisneros and Rosenheim 1998) and there can be species-specific (Nyrop and Simmons 1986) and family-specific (Taylor 1974, Humphrey et al. 1999, Boiteau et al. 2000a, Boiteau et al. 2000b) vertical distribution patterns driven by dispersal, foraging, mating and oviposition behaviors.

There is an adaptive benefit to behaviors that maximize abundance of male *E. viteana* in regions where grape clusters are numerous, because female oviposition is strictly on this resource (Clark and Dennehy 1988). Vertical distribution of eggs within the vineyard canopy is closely correlated with fruit density (Clark and Dennehy 1988) and so mated female *E. viteana* are assumed to be most abundant near their oviposition substrate, as predicted for specialized herbivores (Miller and Strickler 1984, Hamilton and Zalucki 1993). It is not known whether virgin female *E. viteana* release pheromone only when on grape clusters but the likelihood of males finding females is assumed to be greatest if they are in proximity to this oviposition site. Male *C. pomonella* are trapped in much greater numbers in pheromone traps placed in the host canopy compared with those placed outside the canopy (Howell et al. 1990), and Riedl et al. (1979) argued that more *C. pomonella* males were caught in traps placed in the higher tree canopy because of the preference for mating near the canopy top. In another polyphagous insect, the tortricid *Archips podana*, morphological and temporal heterogeneity of populations is tightly related to larval food preference (Safonkin 1988). Evidence for larval habitat directly influencing mating behavior of adult moths has recently been described by Takacs et al. (2002) with webbing clothes moths. In this case, males seek larval habitats and produce pheromone and sonic signals to enhance recruitment of females to a patchy and temporary resource.

Our vertical sampling results complement the study by Hoffman and Dennehy (1989) by showing that moths remain abundant high in the woods canopy throughout the season. These findings can help answer questions posed by these and other researchers (Dennehy et al. 1990, Trimble 1993, Lewis and Johnson 1999) of why few male *E. viteana* are trapped in woods adjacent to vineyards with high levels of cluster infestation and why pheromone disruption is less effective at vineyard borders (Taschenberg et al. 1974, Trimble et al. 1991, Karg and Sauer 1995). Explanations of high larval infestations where few male moths have been caught have centered on mated females flying into the vineyard to lay eggs, both in *E. viteana* (Taschenberg et al. 1974, Biever and Hostetter 1989, Trimble et al. 1991) and in *L. botrana* (Karg and Sauer 1995). Our findings show that a large proportion of the adult population of *E. viteana* is in areas outside those targeted by management programs, reinforcing the need to consider the whole landscape when studying the ecology of native insects (Burel et al. 2000) and tortricids in particular (Barrett 2000). This approach will also be of value when considering enhancement of biological control (Wratten and Thomas 1990, Marino and Landis 2000), or cultural practices such as removal of wild hosts to reduce the impact of grape berry moth on grape production.

Movement of insects between wild and cultivated habitats has been reviewed by Macdonald and Smith (1990), Woiwod and Stewart (1990), and Ekbom (2000). Schumacher et al. (1997)) stated that both mated and virgin female *C. pomonella* are capable of movement between orchards, with important implications for pest management strategies such as pheromone disruption and resistance management (Dorn et al. 1999). Trimble (1993) concluded that high levels of larval infestation by *E. viteana* at vineyard borders could be a result of mated females entering the vineyard from woods to lay eggs, but direct movement of *E. viteana* has as yet to be conclusively demonstrated. Discovery of a female attractant, as recently described for *C. pomonella* (Light et al. 2001), would greatly assist in determining the significance of immigration by mated female moths from wild grape into adjacent vineyards.

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