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BEHAVIORAL ECOLOGY OF THE GRAPE BERRY MOTH, *ENDOPIZA VITEANA* CLEMENS, IN MICHIGAN AGROECOSYSTEMS

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BEHAVIORAL ECOLOGY OF THE GRAPE BERRY MOTH, *ENDOPIZA VITEANA* CLEMENS, IN MICHIGAN AGROECOSYSTEMS

By

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ABSTRACT

BEHAVIORAL ECOLOGY OF THE GRAPE BERRY MOTH, *ENDOPIZA VITEANA* CLEMENS, IN MICHIGAN AGROECOSYSTEMS

By

Natalia Botero-Garcés

Vitis spp. are the native hosts of the grape berry moth, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae), a primary pest of cultivated grapes throughout Eastern North America. Distribution within and between habitats in the grape agroecosystem was determined with pheromone traps placed at different heights in woods and vineyards. Moth relative abundance increased dramatically with height in woods, whereas 90.0% of moths caught in vineyards were at the canopy level. Relatively few moths (< 4%) were trapped in the interface between these habitats, where grapevines are not present. Overall, results indicate that earlier suggestions of greater numbers of adult moths in vineyards at the end of the season were based on insufficient understanding of the vertical distribution of *E. viteana.* The distribution of this specialist insect seems to be associated with the distribution of its wild and cultivated host throughout the agroecosystem. The level of larval infestation of grape clusters and the abundance of adult male grape berry moth were compared in commercial vineyards bordered by four types of uncultivated habitat: deciduous woods, coniferous woods, a single row of trees, and grasses. Wild grapevines were surveyed at each uncultivated habitat site for their presence or absence, fruiting, and abundance. Infestation was greatest in vineyard borders near deciduous woods, and lowest near grasses. Moth abundance inside vineyards was similar irrespective of bordering habitat, but fewer moths were captured in grass borders than in borders with trees. Wild grapevines were likely to be present in any habitat, but their fruiting was most common in deciduous woods. Larval infestation in vineyards and abundance of wild grapevines and wild clusters in neighboring habitats were correlated, indicating that the presence of wild grapevines adjacent to vineyards poses a risk of increased damage by grape berry moth in vineyards. To determine whether *E. viteana* are moving from these wild hosts into vineyards, a mark-release-recapture study was undertaken. A total of 3,505 marked moths was released at the center of a vineyard and 850 were released inside a neighboring woodlot. From the vineyard releases, 222 moths were recaptured in the vineyard using pheromone traps and passive interception traps. Of the moths released in the woods, 24 were recaptured, 18 of them in the vineyard, indicating that inter-habitat movement occurs in this species. This is the first such study to demonstrate active flight of female and male grape berry moth, and the data suggest greater flight capacity by males. To assess the potential for passive dispersal of pupae, leaves of vines at the vineyard border and interior were painted after harvest and sampled in the succeeding spring. Recovery of leaves in adjacent woods indicated that they dispersed during the winter season. This wind-driven movement may well be the means of transportation for the overwintering population of *E. viteana* in this agroecosystem.

With all love and admiration,

to my parents Benjamín Botero Forero and Beatriz Garcés de Botero,

and my sister Silvia Botero K.

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CHAPTER 1:

THE GRAPE BERRY MOTH, *ENDOPIZA VITEANA*, IN GRAPE AGROECOSYSTEMS

INTRODUCTION

History

For more than 30 years, the North American species of grape berry moth, *Endopiza viteana* Clemens (or *Paralobesia viteana* (Clemens) (see Appendix 1)) was considered the same species as the European vineyard pest, *Lobesia botrana* (Denis and Schiffermüller). This was a consequence of misidentifications by early taxonomists and inaccurate reports that it fed on a wide range of host plants (Johnson and Hammar 1912). To further complicate the issue, *E. viteana* had historically been placed in several other genera, including *Polychrosis* and *Lobesia*, and was described under the synonym of *Penthina vitivorana* by Packard in 1869 (J. Smith, pers. comm.). There is consensus today, however, that these last three synonyms are old and out of use. Early in the 20th century, Slingerland (1904) demonstrated that the grape berry moth was an exclusively American species, pointing out differences in habits that permitted separation of the two. Unlike the European *L. botrana*, larvae of the grape berry moth are monophagous and feed only on native and cultivated grapes (*Vitis* spp., Vitaceae), while pupation and overwintering occur in a rolled or folded leaf in the leaf litter rather than on posts or grape canes as is the case for *L. botrana* (Slingerland 1904). Today, the name used by most authors is *Endopiza viteana* Clemens (but see Appendix 1 for taxonomic discussion).

Grape agroecosystems in Eastern North America

The grape berry moth is a native tortricid, found only in Eastern North America. Its territory extends from Southern Canada and New England in the north to Florida in the south, and to Texas in the west, coinciding with the range of its ancestral host, wild grapevines (*Vitis* spp., Vitaceae) (Johnson and Hammar 1912, Isely 1917). Johnson and Hammar (1912) provided a list of states most affected by the grape berry moth (in order of importance): Ohio, New York, Pennsylvania, Indiana, Illinois, Michigan, Missouri, New Jersey, Virginia, Maryland, West Virginia, Iowa, Delaware, Arkansas, and less affected due to limited grape culture, Massachusetts, Connecticut, Kentucky, Kansas, Texas, Nebraska, and Wisconsin. More than 50 species of wild grape occur in N. America (Fergusson-Kolmes and Dennehy 1993) and these are commonly found in stands of young woods, perturbed habitats, and on the borders of mature forests (Morano and Walker 1995). Galet (1979) lists 10 principal American species, among which the most common are *V. aestivalis*, the common blue grape or winter grape, *V. labrusca*, known as the Fox grape, or Northern Muscadine, and *V. riparia*, called Bermuda vine, Riverbank grape and other names. Voss lists these, and one more rare species, *V. vulpina* present but scarce in southern Michigan (Voss 1985).

In Michigan agroecosystems, woods frequently border vineyards, and they typically contain wild grape. When clusters from these wild grapevines were sampled during August 1999, infestation by *E. viteana* was on average 84.9% in woods adjacent to vineyards (range 64.5-96.3) (N. Botero-Garcés, unpublished), similar to results from New York where 50-80% of wild berries have been reported to be infested (Dennehy et al.

1990a). The presence of woods is positively correlated with larval infestation in adjacent vineyards (Hoffman and Dennehy 1989, Hoffman et al. 1992), particularly at the borders where high levels of infestation are found. However, infestation by this pest can also be clumped in the vineyard interiors. Regional variation in vineyard risk to grape berry moth has been noted between Ontario (Canada) and New York, and this has been attributed to differences in absolute temperatures in winter (Dennehy et al. 1990a). Grape berry moth pupae exposed to low temperatures die after a single exposure to –24 °C, and this was found to be less common in vineyards with higher infestation than in less infested ones (Dennehy et al. 1990a). High levels of snow accumulation in winter in grape growing regions near the Great Lakes favor pupal survival (Dennehy et al. 1990a, Martinson et al. 1991).

Biology of the grape berry moth

Life cycle and description. This species overwinters as diapausing pupae. Emergence in spring usually spans six weeks and is determined largely by genetic factors and temperature (Tobin et al. 2002). Some overwintering individuals can emerge as early as April, while others may delay emergence until July or August, making generations difficult to distinguish (Tobin et al. 2002). In Michigan, adult moths start appearing at the end of April or beginning of May, having emerged from the leaf layer on the ground. This species is protandrous; the first males begin flight activity before females are present (Tobin et al. 2002). The adult moth varies in length between 4-6 mm, and is brown with slate-gray paintings on its dorsal wing surface, shaped like a saddle. The female can be distinguished from the male because she has a wider, rounder, and more blunt abdomen (see Appendix 2). The male has a slim abdomen that ends in a scaly tip, where two feathery claspers can be observed.

Grape berry moth females of the first flight emerge from pupation during grapevine bloom, and thus do not have access to grape clusters, but rather flowers and minute forming berries. Thus, first-generation eggs are laid on the rachis and stems of the clusters of flowers or tiny developing berries, where they are difficult to see. They are circular, flattened, but slightly convex, 0.8 mm in diameter (Tobin et al. 2002), and a pearly, translucent white. The dark head capsule can be observed through the chorion from the 3rd day of egg development.

After four days under normal temperature and light conditions (25°C, 16L:8D), a single 1 mm long larva hatches, crawling out from a slit of the chorion near the edge of the egg. First instars of this first generation crawl on stems and produce webbing in the forming cluster. After feeding externally for 14-16 days, during which the larvae are relatively unprotected against biotic and abiotic factors, mature larvae (4th instars) find leaves in which to pupate. They do this by pulling a corner of the leaf over themselves, or cutting a crescent-shaped section on the middle of the leaf body, and wrapping themselves into it to spin their cocoon. The pupa is blue green soon after the molt, but turns to a dark brown until the adult emerges some six to nine days later.

Insects in the second flight, or first generation, behave in the same manner as the previous (overwintering) generation, except that females lay eggs on top of the small berries, sometimes several per berry under high infestation cases. Upon hatching, 1st instars direct themselves toward the stem to enter the berry. Other preferred entrance points include contact spots where two berries touch, and skin folds where molds have developed. Once inside, the larva feeds under the berry skin, causing discoloration and premature ripening of the area. Full-grown larvae emerge from the berry in the 4th stage and move to nearby leaves to pupate. After pupating, second generation adult moths (called the 3rd flight) will fly, mate, and lay eggs again on the ripe grapes, but usually this last generation will not fully develop as adults until the next year. Instead, the pupae will enter diapause and spend the winter on fallen leaves.

Early studies in New York claimed there was only one full and one incomplete brood of larvae per year (Johnson and Hammar 1912), but further data collection has determined that, depending on weather conditions, the number of generations ranges from two to three per year (Hoffman et al. 1992) and up to four (Tobin et al. 2002). Phenological studies undertaken by several authors (Clark and Dennehy 1988, Biever and Hostetter 1989, Hoffman and Dennehy 1989, Alm et al. 1989) have attributed variation to differences in soil types (Pfeiffer et al. 1990), in degree-day accumulation (Hoffman et al. 1992, Tobin et al. 2001), and in possible moth races, as proposed by Tobin et al. (2002). It is not known whether 1st and 2nd generation adults show the same protandry exhibited by the overwintering population, but preliminary data suggest that males develop faster than females (Tobin et al. 2002). Observations in the laboratory with a colony of this species under constant temperature conditions (N. Botero-Garcés, unpublished) indicate that males emerge at least a day earlier than females of the same age.

Reproductive biology. There is little data on reproductive biology of this species. Comparisons are usually made with the European grape berry moth, *L. botrana*, but it must be remembered that *L. botrana* is a generalist herbivore whose survival therefore depends less on critical choices made by adult moths. Data on phenology of female *E.*

viteana are not available, primarily due to the lack of trapping studies and an effective female attractant. The presence of a sex pheromone and identification of its main component as (Z)-9-dodecenyl acetate (Z9-12Ac), was reported by Roelofs et al. (1971). The pheromone was later used by Taschenberg and others to develop mating disruption strategies (Taschenberg et al. 1974, Taschenberg and Roelofs 1977). In recent studies, Witzgall et al. (2000) extracted pheromone glands from female grape berry moths and found that each contained approximately 1.2 ng of pheromone on the 2-3rd day of life. Apart from the main component, eight other compounds were identified for this moth; (Z) and (E)-11 tetradecenyl acetate; dodecyl acetate, dodecanol, (Z)-9-dodecenol, tetradecyl acetate, tetradecanol and hexadecanol, some serving as synergists and others as precursors of the main sex pheromone (Witzgall et al. 2000).

Though no studies have been carried out to determine onset of pheromone release in grape berry moth, one-day-old females are believed to attain maximum pheromone release on the second and third days of calling (Witzgall et al. 2000). Mating occurs within the first three days of adult life for both sexes and most egglaying occurs on the 4-7th day of adult life (G. English-Loeb, pers. comm.).

In the laboratory, one female may lay from a few to several tens of eggs in one night (N. Botero-Garcés, pers. obs.); most egg laying occurs one-hour either before or after scotophase (Clark and Dennehy 1988). Studies on the European grape berry moth, *L. botrana,* showed an oviposition capacity of approximately 30 eggs per female per day (Feldhege et al. 1995); 90% of eggs were laid during the first ten days of the female's life (Savopoulou-Soultani et al. 1998). The adult lifespan of *E. viteana* ranges from 4 to 23 days (Johnson and Hammar 1912, N. Botero-Garcés, pers. obs.), depending mainly on water availability. It is not known whether *E. viteana* mates once or multiple times, but monandry has been demonstrated in *L. botrana* and two other important tortricid pests, the oriental fruit moth, *Cydia molesta,* and the codling moth, *C. pomonella* (Torres-Vila et al. 1997). Clark and Dennehy (1988) showed that, *E. viteana* oviposit exclusively on grape berries in the field. There was a positive correlation between the number of berries available and the number of eggs laid. In the laboratory, some eggs were found on petioles and grape leaves, particularly when females were given the limited alternate choice of an artificial grape substrate, but again most oviposition was on the clusters (Clark and Dennehy 1988).

Ecology of the grape berry moth

Insects are rarely distributed evenly in space and time (Schowalter 2000). For phytophagous insects, the distribution of host plants is often a major determinant of the insect's distribution. *E. viteana* is a specialist, and would be expected to be closely linked to the host plants on which it lays eggs and feeds as larvae. Most grape agroecosystems in Eastern North America consist of vineyards bordered by woodlots of several ages and stages of succession, riparian areas unsuited for agriculture, windbreaks made of an individual or two rows of trees, fallow and cultivated fields, or grasses. Grape berry moths have been trapped mainly in vineyards (Biever and Hostetter 1989, Dennehy et al. 1990a, Trimble 1993), but surveys of wild grapevines invariably found eggs or larvae present in grape clusters (Nagarkatti et al. 2002a).

Pheromone traps are a useful tool for identifying the start and peak of moth flight activity, as was observed by Johnson et al. (1988). Traps placed at the edge of woods adjacent to a vineyard captured moths six days earlier than traps placed at the edge of the vineyard. It has been observed early in the season that more *E. viteana* are caught in traps placed at or near the edge of vineyards than in traps placed inside vineyards (Biever and Hostetter 1989, Hoffman and Dennehy 1989, Trimble et al. 1991). Johnson et al. (1988) described how moth abundance at the woods and vineyard edge shifted towards the center of the vineyard as the season progressed. Hoffman and Dennehy (1989) 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 greater proportion of moths were caught in the woods at the beginning of the season, but that this changed near harvest when more moths were caught inside the vineyard than anywhere else (Hoffman and Dennehy 1989). These previous studies, however, used data from three traps removed from the woods edge position and relocated to the vineyard as the season progressed (Johnson et al. 1988) or on only one transect of 15 traps in a single vineyard/adjacent habitats setting was used (Hoffman and Dennehy 1989). A more robust sampling system is needed to determine the patterns of male relative abundance within and among habitats in Michigan vineyard ecosystems, in which vineyards are smaller in area (0.4-2 ha) and most often bordered by woods on at least one side.

The importance of trap placement in relation to crop height, particularly in fruit crops, has been demonstrated for many economically important pests (Peterson 1926, Rothschild and Minks 1977, Riedl et al. 1979, Gabel and Renczés 1985, Howell et al. 1990). The vertical distribution of insects has been studied with Lepidoptera in woods (Boiteau et al. 2000a) and the rainforest (DeVries et al. 1999), with parasitoid communities in forest stands (Nyrop and Simmons 1986), and with Carabidae and

Elateridae beetles for flying profiles in deciduous woods (Boiteau et al. 2000b). These studies usually found that different species of insects maintained a particular height of flight that often dependended on the structure of the habitat they were in.

Pheromone traps for *E. viteana* are commonly hung from the trellis at 1.5 m above the ground. This recommendation stems from two considerations: first, it is the average height of the grape canopy, and second, this is convenient when checking the traps. However, this species inhabits a grape agroecosystem with considerable differences in canopy heights. The vineyard and woods habitats of grape berry moth vary markedly in their structure and complexity. In the former, grapes are tied on to trellises typically less than 2 m high, whereas in the latter, grape vines extend vertically up to 25 m or more, by climbing on trees. A response to habitat structure may be an important component of the ecology of this insect in this agroecosystem, however, no study of optimal trap height has been conducted for the grape berry moth.

Role of surrounding habitats in pest insect abundance

Habitat heterogeneity is a common feature of many grape-growing regions of the Eastern United States. This heterogeneity is high in Michigan because vineyards are smaller and agricultural diversity is high, second after California. This diversity in crops and uncultivated habitats is not only important in insect conservation, but can be an asset to agriculture by aiding in maintaining low insect pest populations (Altieri 1983, Welch 1990, Macdonald and Smith 1990, Ekbom 2000), while at the same time increasing the effectiveness of natural enemies (Wratten and Thomas 1990). The other side of the issue is that uncultivated habitats may be so good at conserving some insects, that they facilitate pest survival and disease transmission from wild or alternate hosts, as well as acting as reservoirs of certain pest populations (Barrett 2000, Jeanneret 2000).

In general, studies on the impact that adjacent uncultivated habitats have on crops have focused on negative effects such as pest immigration, or positive effects such as conservation of natural enemies (Seaman et al. 1990, Dorn et al. 1999). Few studies have concentrated on native hosts within these wild habitats and their relationship with the crop pest. Dennehy et al. (1990b) showed that woods were a risk factor for infestation by *E. viteana*, but the importance of wild grape near vineyards for vineyard infestation by *E. viteana* has not been investigated. It is unclear to what extent wild host abundance varies with habitat type and how this is related to the levels of vineyard infestation.

Local dispersal of tortricid moths

It is generally accepted that insect populations within the agricultural landscape are dynamic and able to flow from one habitat to the next in space and time (Kareiva 1983, Landis 1994, Ekbom 2000). Traditional trapping data (at 1.5 m) and comparisons on relative abundance at different positions in the vineyard suggest that grape berry moth populations may be moving from wild habitats into vineyards during the growing season (Hoffman and Dennehy 1989). Researchers have implied that discrepancy in trap data and cluster infestation levels may be due to female immigration from woods to lay their eggs in vineyard grapes (Taschenberg et al. 1974, Hoffman and Dennehy 1989, Trimble et al. 1991, Trimble 1993). Such movement between wooded habitats and vineyards has not yet been demonstrated categorically for *E. viteana*, but rather the reports assume movement has occurred from the changing distribution of adults and larval damage.

The flight capacity of another tortricid fruit pest, *C. pomonella*, has been examined according to the insect's physiological state and sex (Schumacher et al. 1997). Mated or virgin adults of both sexes can have equal flight capacity, with maximum dispersal measurements of 11 km. Flight ability was greatest during the 2nd to 7th day of life, and females were not likely to engage in long (between-habitat) flights before having oviposited, in disagreement with the oogenesis-flight syndrome described by Johnson (1969). In contrast, the oriental fruit moth, *C. molesta*, has much lower flight capacity (approximately 1 km) and tends to be more sedentary; a small proportion of moths ventured into long flights and gravid females were more likely to be the colonizers (Hughes and Dorn 2002). One of Davis' (1980) explanations for the preponderance of short-fliers in dispersal studies, is that, rather than a strategy, this is a limitation of flight-range experiments. Nonetheless, this type of study yields important knowledge that may help improve the efficiency of pest management, i.e., chemical controls, pheromone disruption, and cultural controls aiming for removal of abandoned crop lands (orchards) and wild hosts (Dorn et al. 1999). For example, mating disruption can fail when gravid females immigrate from areas where they have mated into crop areas to lay eggs. Wild host removal also becomes ineffective if insect mobility exceeds the distance between the original and new habitat. Finally, insecticide resistance may develop more slowly if gene flow is high between insect populations (Dorn et al. 1999).

In the case of *E.viteana*, there is no information on how far individual moths can fly and whether differences between sexes and mating status exist. Understanding the dispersal potential of adult moths is an important component of unraveling the behavior and ecology of a key pest, such as the insect's ability to adapt to changing and/or deteriorating environments and colonizing new habitats, all of which may undermine the effectiveness of management strategies (Keil et al. 2001, Hughes and Dorn 2002).

Economic impact of grape berry moth

Historical importance in agriculture. There has historically been such a profusion of wild grapes in North America, that in 1000 the Norse Viking "Leif the Lucky", upon exploring New England, called it "Vineland" (Hendrickson 1913). The grape berry moth evolved in this ecosystem exploiting the grapes and supporting its suite of natural enemies (Slingerland 1904, Seaman et al. 1990). With the advent of commercial grapes, first European and then improved American varieties, the grape berry moth had the opportunity to exploit this new food source with its particular conditions of light, humidity, and inter- and intra- specific competition. In 1852, the Concord grape was introduced in Massachusetts, marking the beginning of successful large-scale grape growing in Eastern North America. By the early 1860s, more than 2,428 ha (6,000 acres) of grapes were grown east of the Mississippi, and 40 years later, the area had increased to 97,128 ha (240,000 acres) (Hendrickson 1913). Coincident with the increase in grape hectareage, problems with grape berry moth infestation became more significant and the object of study by entomologists (and concern by growers).

Reports from the grape growing regions of Eastern United States and Southern Canada show this insect was present in vineyards without causing much damage until 1869. It was first reported as an injurious pest that year, because of yield losses estimated to be up to 50% in Cleveland and Hudson, Ohio, as well as Missouri, and Southern Illinois (Johnson and Hammar 1912). Isely (1917) states that the exact pest status of the grape berry moth was unclear since there were few economic estimates of grape loss, and the pest showed erratic patterns of infestation not only within vineyards but around grape growing regions, being particularly limiting in certain areas of Pennsylvania and New York, and very little in Michigan from where few complaints had arisen. After visiting Lawton and Paw Paw production regions in Michigan, Isely (1917) confirmed that although the pest was present everywhere, the small numbers probably had caused its damage to be confused with black rot in the past. R.H. Pettit first described the destructiveness of the grape berry moth in Michigan in 1922, though there is no quantified yield loss (Pettit 1932).

Current agricultural importance. As of 1990, the total area of vineyards in North-Eastern America, comprising New York, Pennsylvania and the province of Ontario, Canada, was 32,376 ha (80,000 acres) (Dennehy et al. 1990b). Michigan grape area is increasing and is currently 6,070 ha (15,000 acres), including grapes grown for wine in the Northwest of the Lower Peninsula. During recent years, damage from grape berry moth in some vineyards has exceeded 50% cluster infestation (reaching 99% at some sites in 2002), a level far above an economic threshold for juice grape production. Isaacs and others (unpublished) found that yield loss from grape berry moth larval infestation could amount to two tons per hectare in vineyards when no treatment was applied. In 2002, levels of infestation by grape berry moth were higher than usual in New York, Pennsylvania, Michigan and Ohio, and unprecedented load rejections occurred in the first three of these states due to direct grape berry moth damage or decay associated with it. In Michigan, this amounted to more than 1,000 tons of grapes worth $300,000 (T. Davenport, pers. comm.).

Management of grape berry moth. The grape berry moth causes extensive damage to grapes, not only by directly feeding on the berries, but because larval feeding infects berries with *Botrytis cinerea* as has been reported for the European berry moth *L. botrana* (Fermaud and Le Menn 1989, 1992), and predisposes them to other pathogens such as sour rots. Management of this species in the 1920s consisted of application of the few available products and cultural methods that followed the general wisdom brought about by behavioral and phenological studies of the pest. Pettit (1932, 1933) recommended applications of Bordeaux mixture and arsenical poison sprays, including the "Kedzie Mixture" invented by Dr. R.C. Kedzie, chemist of the Michigan Agricultural College (Anonymous 1911). Cultural control measures included mounding of earth around the vines and sanitation of vineyards by removal or destruction of trash and leaf litter to reduce pupal densities (Smythe 1913). Pettit (1933) pointed out that neither neglected vineyards nor wild grapes ought to be allowed near vineyards because it could make grape berry moth pest pressure very intense. This prompted the removal of abandoned vineyards undertaken by the Michigan Department of Agriculture through the signing of Act No. 72, Public Acts of 1945, with the help of growers (Ball and Lovitt 1968). This eradication program removed 2,966 ha (7,329 acres) of grapes in 12 years (Ball and Lovitt 1969), and 134.4 ha (332 acres) more between 1968, when the program was reinstated, and 1971 (Ball and Lovitt 1971).

The discovery of *E. viteana* sex pheromone components and the subsequent synthesis of these components for a lure to bait traps precipitated research aimed at mating disruption, using the delivery of high and constant quantities of pheromone into a vineyard (Taschenberg et al. 1974, Taschenberg and Roelofs 1977). The application of pheromone to crops, successful in many fruit systems such as European vineyards with *L. botrana* (Sauer and Karg 1998) and other tortricids and leafrollers in a number of countries (Deland et al. 1994), proved to be a safe alternative because the materials are innocuous to non-target organisms and the environment at large. Overall, varying results were obtained, from success in impeding male location of baited traps and reducing fruit infestation in treated vineyards (Taschenberg and Roelofs 1977), to unsuccessful in reducing pest pressure in treated vineyard edges (Trimble et al. 1991, Trimble 1993). Several reasons could account for the failure of mating disruption at the edge of vineyards: improved survival of grape berry moth along borders, adjacent habitats serving as refuges during pesticide applications, higher wind velocity near the vineyard edges lowering pheromone concentration in these areas, and the influx of gravid females from wild areas (Trimble et al. 1991) as was also proposed for *L. botrana* (Cardé and Minks 1995, Karg and Sauer 1997). Schmitz et al. (1995) proposed that higher *L. botrana* larval densities at edges corresponded with higher mating success due to lower mobility in searching males. Lewis and Johnson (1999) concluded from their pheromone disruption experiments that this practice needs to be accompanied by insecticide applications and must only be used in low to moderate-risk vineyards (Dennehy et al. 1990a, b) exceeding 2 ha (5 acres) in area. In vineyards with high pest pressure and small area (more border area than interior) pheromone disruption is likely to fail due to the reasons stated above (Trimble et al. 1991).

Biever and Hostetter (1989) used pheromone-baited traps in a study carried out in Missouri, and concluded it was a potential aid in the improvement of pest management programs, when these were tailored to specific vineyards. However, it became obvious before long that although grape berry moth phenology might be well described by trap captures early in the season, the same did not occur later on during the 2nd and 3rd flights (Dennehy et al. 1990b). These researchers noted that moth captures did not correlate with egg-laying in vineyards, possibly because of competition from calling females.

Dennehy et al. (1990b) reported that before the 1980s, only 40-70% of New York vineyards required insecticide applications, which were mainly prophylactic owning to the low cost of chemical products and high prices paid for grapes. Methods to control the grape berry moth had focused on the use of insecticides such as methyl-parathion, azinphosmethyl, and carbaryl (Dennehy et al. 1990b, Nagarkatti et al. 2002b). However, the Food Quality Protection Act of 1996 brought about the loss of registrations for some of the most important insecticides. In Michigan, current (2003) recommended sprays against grape berry moth for conventionally-managed vineyards (Table 1.1) include azinphosmethyl, phosmet, methomyl, carbaryl, methoxyfenozide (Wise et al. 2003). Higher prices of the newer insecticide products have prompted grape growers to increasingly consider the integrated pest management (IPM) approach which focuses on a combination of strategies, including pest monitoring, biological and cultural control (sanitation), new chemical products with different modes of action, less harmful to the environment and directed more selectively to the pest. Promising reduced-risk insecticides include methoxyfenozide, spinosad, and acetamiprid.

Table 1.1. Typical spray program for insect management in conventionally-managed vineyards in Southwest Michigan, indicating the phenological state of grapes at the time pests should be targeted.

Grape Phenology	Pests Controlled	Insecticide
Bud Break If scouting reveals significant damage.	Climbing Cutworm Grape Flea Beetle	Chlorpyrifos or Fenpropathrin.
Pre-bloom	Rose Chafer Grape Berry Moth	Carbaryl, methomyl, fenpropathrin or azinphosmethyl.
Post-bloom *(1st Cover)* - 10-14 days after pre-bloom spray.	Grape Berry Moth	Carbaryl, methomyl, fenpropathrin or azinphosmethyl.
	Grape Leafhopper	Methomyl, imidacloprid or fenpropathrin.
Bunch closing *(3rd Cover)* - 4 weeks after post-bloom spray, if scouting reveals a need for treatment.	Grape berry moth	Carbaryl, methomyl, methoxyfenozide or phosmet.
	Grape Leafhopper	Methomyl, imidacloprid or fenpropathrin.
Post-veraison *(5th Cover)* if scouting reveals a need for treatment.	Grape berry moth	Carbaryl, methomyl or phosmet.

CHAPTER 2:

DISTRIBUTION OF MALE GRAPE BERRY MOTH, *ENDOPIZA VITEANA*, IN NATURAL AND CULTIVATED HABITATS

INTRODUCTION

Studies of grape berry moth distribution have usually centered on determining moth abundance in the vineyard with the help of pheromone traps, and counting infested grape clusters. Hoffman and Dennehy (1989) found that infestation by *Endopiza viteana* was unpredictable from year to year, from vineyard to vineyard, and within vineyards. Biever and Hostetter (1989) suggested this was due to 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, and this is assumed to be because they harbor wild grape and are associated with greater vineyard infestations than at sites where no woods are found (Dennehy et al. 1990b). However, woods containing *Vitis* spp. may also provide shelter and food sources for parasitoids of *E. viteana* (Seaman et al. 1990, Dennehy et al. 1990b).

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 on the basis of damage assessments (Dennehy et al. 1990b, 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 towards 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 caught a greater proportion of moths 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 less than 2 m high whereas in woods they climb primarily on deciduous trees up to 25 m. Thus, a response to habitat structure may 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 1-1.5 to 3.0 m high 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); 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 *C. pomonella,* though these studies differ in their conclusions. Howell et al. (1990) did not find 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, recorded maximum captures of *C. pomonella* 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". They compared catches of traps placed at 0.4 and 1.2 m, heights in accordance to vine trunk height. No significant difference was found between these two heights, but for both species, more moths were captured at 1.2 m (Gabel and Renczés 1985).

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 ecosystem, 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, Michigan. 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, Oregon) each baited with a lure containing 0.1 μg 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 weekly and the number of grape berry moth males recorded. Vineyard management was conventional, following recommended practices for management of insect pests (Table 1.1).

Vertical distribution

To determine variation in *E. viteana* abundance with 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 to position. 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. This area is used by growers to manoeuver machinery. Two 10 m tall PVC poles were placed at least 3 m from the woods edge at each of four vineyard-woods interfaces. Each pole was constructed from PVC pipe, using a 3.3 m x 10.4 cm inside diameter (i.d.) piece connected to two 3.3 m x 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, North Carolina) 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 (Figure 2.1). 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. Traps were also hung further up, at 12.2, and 15.2 m above the ground, using loops of rope 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 non-normal, and so all data were transformed (log n+1) to meet the criteria of normality and homogenous variance 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 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), taking 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.

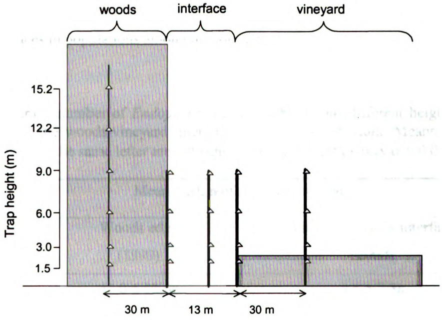

Figure 2.1. Schematic representation (not to scale) of a study site in 2001. Pheromone traps (triangles) were hung at different heights on poles or ropes in five positions across the vineyard-woods habitats. Grey boxes represent the extent of the two habitats.

RESULTS

Vertical distribution

Throughout this experiment, 3,434 moths were trapped at the edge of the woods moreover moth captures varied significantly with height ($F_{3,25}$ = 31.37, $P < 0.0001$) (Table 2.1). Traps at 9.0 m caught significantly more moths than traps at lower heights ($P < 0.0001$); more than 61% of all moths caught at 9.0 m. This compared to 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 2.1). The variability in these data reflects differences in populations among the four farms.

Table 2.1. Average number of *Endopiza viteana* caught at four different heights at the woods edge and the woods-vineyard interface in two different years. Means within a column followed by the same letter are not significantly different (Tukey α = 0.05).

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

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 more moths (23,275) were caught in the woods than in the vineyard (8,453). During Flight 1, 84% of moths were caught in the woods, whereas 52% and 49% were trapped in the woods in flights 2 and 3, respectively, indicating variation in distribution between habitats over time. Twelve thousand and fifty eight moths (38% of the moths trapped all season) were 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 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 2.2). 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 2.2).

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, $P < 0.0001$) (Figure 2.2), while the interaction between position and flight was significant ($F_{38,206}$ = 4.04, $P < 0.0001$). Combining captures of *E. viteana* between 1.5 and 9.0 m, I observed 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) (Table 2.3). During Flight 1, 86% of the moths were caught in the woods habitat (both inside and edge) compared to 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 2000. Captures in the interface were low throughout the season (Figure 2.2), and more moths were trapped inside the vineyard than at the edges. This difference was significant in Flights 2 and 3 (Table 2.3).

Table 2.2. Average number of *Endopiza viteana* caught per flight in traps placed at a height of 1.5 m in four different positions within the habitats sampled during 2000. Means within a row followed by the same letter are not significantly different (Tukey α = 0.05).

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

Table 2.3. Average number of *Endopiza viteana* caught in traps per position (1.5-9.0 m heights pooled), during three flights sampled during 2001. Means within a row followed by the same letter are not significantly different (Tukey α = 0.05).

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

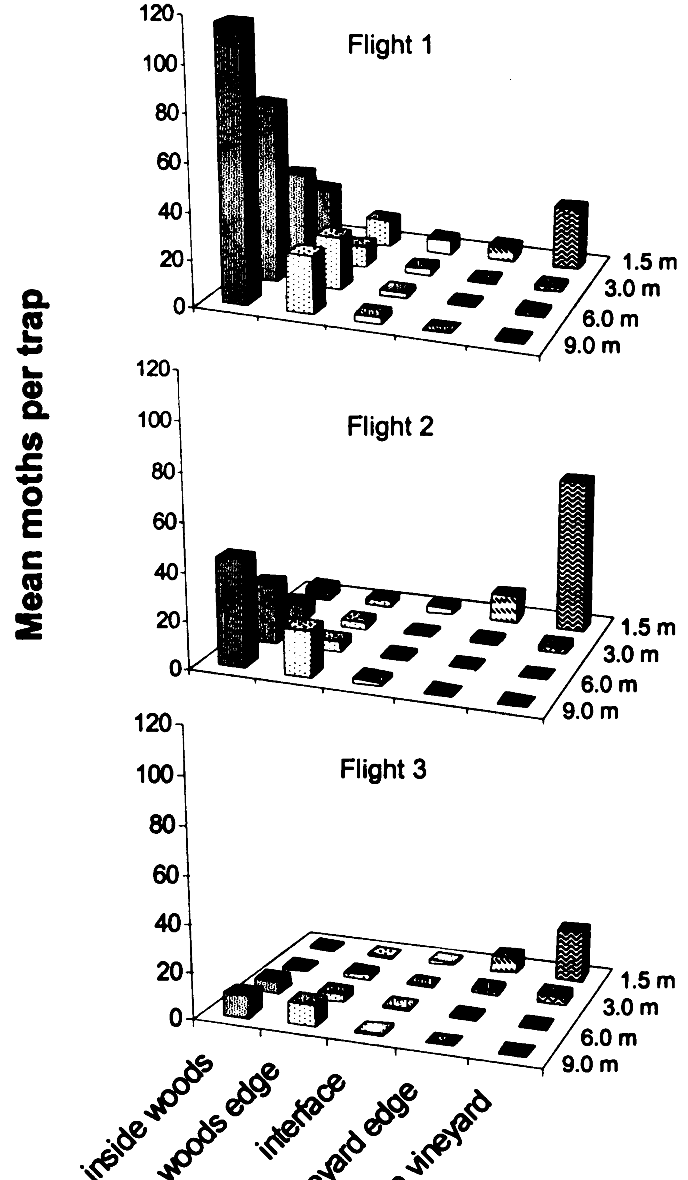

Figure 2.2. Average number of male *Endopiza viteana* caught per trap during each flight in 2001, trapped at four heights across five positions in the vineyard-woods agroecosystem.

When relative abundance was compared among heights, some clear patterns were seen (Figure 2.2). 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 $F_{3,97} = 73.96$; $P < 0.0001$); the greatest number of moths was caught in the higher traps in the woods habitat and in the lowest traps in the vineyard habitat (Figure 2.2).

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 (Figure 2.2), though this 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 (Figure 2.2). 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 high. 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 (Figure 2.3). This change in relative abundance with height in the woods was consistent across flights (Figure 2.3), and the change among flights was consistent with results during 2000 (Table 2.2).

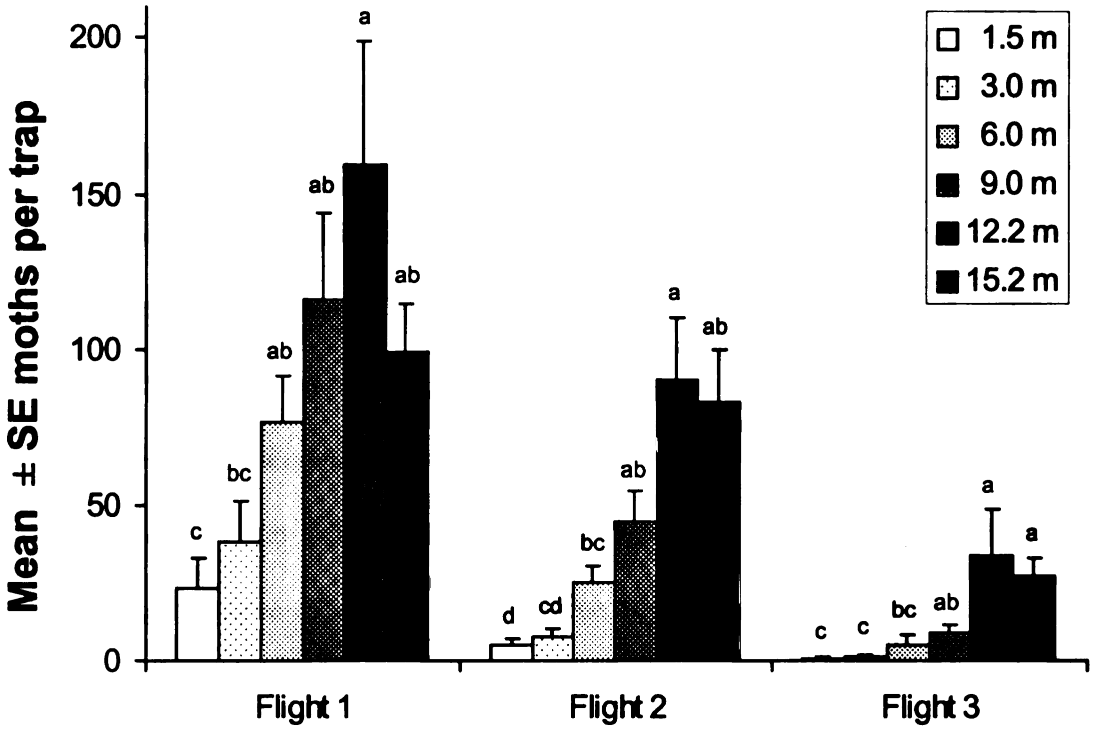

Figure 2.3. Average number of male *Endopiza viteana* per trap during each flight, trapped at six heights inside woods adjacent to vineyards during 2001. Within each flight, bars with the same letters are not significantly different (Tukey $\alpha = 0.05$).

DISCUSSION

This study found differential spatial and temporal distribution of grape berry moth across the vineyard and woods ecosystems. 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 and captures decreased for successive flights. There are several possible explanations for this reduction. 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 June 25 (Flight 2 and 3) as day length 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. 1990b, 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 is likely due to the response of this species to the structure and composition of its habitat. My results obtained from traps at 1.5 m agree with previous findings (Hoffman and Dennehy 1989, Lewis and Johnson 1999), but by placing traps between 1.5 and 9.0 m above the ground in these different habitats, I 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; Figures 2.2 and 2.3). Hoffman and Dennehy (1989) found that pheromone traps placed at wooded 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 my 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 caught more moths high in the woods than did 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, abundance is greatest in the higher canopy. Relative abundance between habitats is greatest 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; Figure 2.2.) indicate that the lack of host plants in this position provided no host substrate to which the moths could respond. In vineyards, the greatest moth captures were consistently within the canopy; few moths were captured above 1.5 m. Taken together with the results in woods described above, these results agree strongly with the suggestion of Hoffman and Dennehy (1989), that *E. viteana* distribution is tightly coupled to the structure of the habitat where its host is present.

Four species of wild *Vitis* are commonly found throughout wild and perturbed habitats in the Eastern United States (Morano and Walker 1995). I took samples from the sites studied and followed a simple key by Voss (1985) which showed the wild grape species present were principally *V. riparia*, *V. labrusca* and *V. aestivalis*. 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 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. Botero-Garcés, 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, b) 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 to those placed outside the canopy (Howell et al. 1990). Riedl et al. (1979) argued that more *C. pomonella* males were caught in traps placed in the higher tree canopy because mating occurred 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.

My 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. 1990b, 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). My 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 due to 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.

CHAPTER 3:

INFLUENCE OF UNCULTIVATED HABITATS AND NATURAL HOST PLANTS ON CLUSTER INFESTATION BY GRAPE BERRY MOTH, *ENDOPIZA VITEANA*, IN MICHIGAN VINEYARDS

INTRODUCTION

Insects require varied resources, such as food, water, oviposition substrates, shelter, and overwintering hosts, and these may not be available within a single habitat (Kareiva 1983, Toepfer et al. 2002). An ecosystem comprised of multiple habitats will be required for growth of insect populations that need multiple resources to complete development. Habitat heterogeneity is not only important for resource availability and consequently insect conservation (Welch 1990, Woiwod and Stewart 1990), it may also contribute to keeping insect pest populations below economic thresholds within agricultural landscapes (Altieri 1983, Macdonald and Smith 1990, Welch 1990, Banks 2000, Ekbom 2000) by increasing the effectiveness of natural enemies (Wratten and Thomas 1990, Williams and Martinson 2000). However, uncultivated habitats may also harbor insect pests and disease due to movement from wild hosts (Barrett 2000, Jeanneret 2000). Thus, pest management strategies that consider movement of insects within this habitat mosaic may be more effective than those designed solely for the agricultural setting (Landis 1994).

Studies on the grape berry moth, *E. viteana* have used pheromone traps as a tool to understand pest behavior and phenology. Comparisons of relative moth captures at different positions within vineyards have been reported by several researchers

(Taschenberg et al. 1974, Biever and Hostetter 1989) who pointed out that more *E. viteana* males are typically caught at borders versus interiors of vineyards. Hoffman and Dennehy (1989) used 15 traps to sample moths in two vineyards and two types of adjacent habitats (two woodlots and one alfalfa field). They found more moths were captured in the woods but only at the beginning of the season, since by mid-June, male moth abundance in the vineyard had increased and exceeded abundance in woodlots. In contrast, few moths were caught in alfalfa fields nearby (Hoffman and Dennehy 1989). This study also noted that infestation of grapes by *E. viteana* larvae seemed greater at vineyard edges than interiors, as reported elsewhere by Biever and Hostetter (1989) and Trimble et al. (1991). Taschenberg et al. (1974) first suggested this could be due to immigration of gravid females from wild areas, thus proposing a link between managed and uncultivated (or wild) habitats. Based on this, Dennehy et al. (1990a) developed a risk assessment program for New York state vineyards, in which risk from grape berry moth was based partly on the proximity to woods or tree rows (Hoffman and Dennehy 1989, Dennehy et al. 1990a, b, Martinson et al. 1991).

Vineyards across Eastern North America are surrounded by a range of different uncultivated habitats. Most of them are suitable for wild grapevines, yet the effect of these habitats on vineyard cluster infestation by *E. viteana* larvae has not been reported previously. There is also little information on how abundance of wild grape varies with uncultivated habitat type, and the relationship between these wild grapevines and vineyard infestation by grape berry moth. The goal of the present study was to determine the relationship between the type of adjacent uncultivated habitat and vineyard infestation by *E. viteana*, focusing on the role of wild grapevines. Specific objectives were to compare the relative abundance of grape berry moth across habitat types, determine the effect of habitat type on abundance of wild grape, and determine whether vineyard infestation by this insect is predicted by the presence, density, or fruiting of wild grapevines in adjacent habitats.

MATERIALS AND METHODS

This study was conducted in commercial juice grape (*Vitis labrusca,* var. Concord and Niagara) vineyards in Van Buren County, Michigan, during 2001 and 2002. All vineyards were approximately 1.6 ha, with at least one side bordered by an uncultivated habitat that was one of the following four types: deciduous woods, coniferous woods, a single row of mixed trees (a tree row) 8-12 m wide, or grasses. All uncultivated habitats sampled, except for the grasses, consisted of mostly mature trees established at least 20 years earlier. The number of replicated sites (vineyard with adjacent uncultivated habitat) for each habitat type ranged from four to eight in 2001 and from seven to nine in 2002. Conventional vineyard management practices were implemented by the growers at all sites following recommended management measures against insect pests (Table 1.1).

Vineyard infestation

Infestation by grape berry moth was assessed non-destructively by visual inspection of grape clusters once a month during July, August, and September of 2001 and 2002. A cluster was considered infested if one or more grapes was observed with symptoms (entrance hole, frass, webbing, larvae) of grape berry moth. Percent cluster infestation was determined by examining 20 clusters per vine, on five vines at the vineyard border (100 clusters) and five vines at the interior (another 100 clusters), for a total of 200 clusters per site (Martinson et al. 1991). This procedure was carried out in the 26 vineyards studied in 2001 and the 30 vineyards in 2002.

Moth abundance

At each site, relative moth abundance was measured using four large plastic delta traps (Suterra LLC, Bend, Oregon) baited with lures containing 0.1 μg of synthetic sex pheromone of *E. viteana* (90:10 ratio of (Z)-9-12Ac and (Z)-11-14Ac), lined with sticky inserts. At each site, a trap was placed 1.5 m high at a position 30 m inside the vineyard, at the edge of the vineyard, at the edge of the uncultivated habitat, and 30 m inside it (Figure 3.1). Since tree row habitats were long and narrow (8-12 m width), only one trap was deployed in this habitat and the position was considered a border. Trap inserts were replaced as needed and pheromone lures were changed monthly using the same batch of lures for all traps. Traps were set before the first grape berry moth flight and checked weekly for the number of moths caught until vineyards were harvested in September. The cumulative total capture of male *E. viteana* was determined for each trap at each date that infestation was assessed.

Wild grape survey

During 2001 and 2002, the presence (or absence) of wild grapevines and wild grape clusters within the uncultivated habitat was determined in an area 38 m wide by 63 m deep in woods and grasses (2,394 m^2), and 15 m deep in tree row habitats (570 m^2). This was done by examining the vegetation in the uncultivated habitats and rating each site with 1 for present or 0 for absent. In 2002, a more extensive survey was carried out to measure the relative abundance of wild grapevines within the uncultivated habitats studied, adapting methods of Matteucci and Colma (1982) for vegetation sampling. At each site (Figure 3.1), five trained observers were spaced 8 m apart along the edge of the uncultivated habitat, so that the middle observer was standing next to the pheromone trap placed at the border. Each observer recorded wild grape presence (1) or absence (0) by looking in three directions (samples): to their left, in front of them, and to their right, including the tree canopy, within a 3 m radius. Measurements were taken every 6 m (a station) until observers reached 60 m inside the uncultivated habitat, for a total of 165 samples (11 stations x 3 samples per observer). In the case of tree rows, the maximum depth sampled was 18 m, to ensure that both sides of each row were inspected.

A wild grape index describing the abundance of wild grapevines in the uncultivated habitats was calculated by adding numbers recorded at each station (minimum 0 and maximum 3 per station) to provide a measure of the number of times wild grape was observed in each uncultivated habitat site. This sampling was only carried out in 2002 because wild grapes are perennial and their presence was unlikely to change in consecutive years.

To determine whether the risk of infestation by grape berry moth could be predicted by sampling wild grapevine abundance only at the borders of uncultivated habitats, part of the above data was used to calculate a restricted wild grape index for each site. This was based on the samples collected within a 38 m wide x 15 m deep area of each adjacent border habitat (45 samples per site), providing a standard sampling area to adequately compare uncultivated habitats.

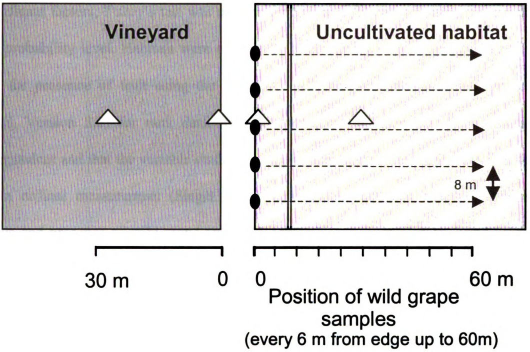

Figure 3.1. Schematic representation of an experimental site (not to scale), with pheromone traps (triangles) at four positions across the vineyard-uncultivated habitat transect. The vertical double line indicates the width of the tree row habitat; the interface width ranged from 5-10 m depending on the vineyard. Wild grape surveys were done by five observers (black ovals) following a 60 m transect (horizontal dotted lines). Counts of wild grape were recorded every 6 m along these transects.

Data analysis

One way ANOVA was used to test the effect of uncultivated habitat type on cluster infestation by *E. viteana* and the cumulative number of moths trapped at each position on each sampling date, using PROC GLM (SAS, Version 8.0). Moth counts were log (n+1)-transformed and values of percent cluster infestation were arcsine-transformed to homogenize variance between treatments. Wild grape indices were compared between habitat types with the GLM Procedure (SAS, Version 8.0). For all significant factors, Tukey's test was used to determine differences between means at the 5% probability level. Habitats were compared for frequency of wild grapevine presence and for presence of fruit using the Kruskal-Wallis nonparametric one-way procedure (SAS, Version 8.0) for rank data. This test's assumptions are that the samples are independent and that the variable studied has a continuous distribution and requires that it is an ordinal measurement (Siegel 1956). Correlations between vineyard infestation levels and presence of wild grape and wild grape clusters were also analyzed using the Kruskal-Wallis test (SAS, Version 8.0). Regressions between vineyard cluster infestation and cumulative moth captures in vineyards and habitats adjacent to them, and between cluster infestation and wild grape indices were obtained with the REG Procedure (Model 1) (SAS, Version 8.0). All analyses were performed with the SAS program (SAS Institute, 1996).

RESULTS

Vineyard infestation by **E. viteana**

In 2001, levels of infestation by grape berry moth at vineyard borders varied significantly depending on the type of neighboring uncultivated habitat in July ($F_{3,22}$ = 3.71, P = 0.03), August ($F_{3,22}$ = 5.69, P = 0.005) and September ($F_{3,22}$ = 4.46, P = 0.01) (Table 3.1). Percent larval infestation was significantly greater in vineyards near deciduous woods than near grasses (P = 0.02, P = 0.003, and P = 0.01, for each month respectively). Vineyard interior infestation levels showed similar trend (Table 3.1), but with no significant difference between habitats ($F_{3,22}$ = 1.43, P = 0.26 for July; $F_{3,22}$ = 1.43, P = 0.26 for August; $F_{3,22}$ = 1.24, P = 0.32 for September).

Table 3.1. Infestation of grape clusters by *Endopiza viteana* larvae at border and interior positions of vineyards adjacent to four types of uncultivated habitats. Samples were taken at three times of the year during 2001 and 2002. For each year, means within a column followed by the same letter are not significantly different (Tukey $\alpha = 0.05$).

Year and Adjacent Habitat:	n	Mean (± SE) cluster infestation (%) in vineyards					
		July		August		September	
		Border	Interior	Border	Interior	Border	Interior
2001							
Deciduous woods	8	26.0 ± 6.9**a**	10.8 ± 2.6**a**	46.2 ± 4.5**a**	23.6 ± 5.3**a**	78.2 ± 6.3**a**	37.2 ± 9.5**a**
Coniferous woods	7	12.1 ± 1.4**ab**	6.3 ± 2.3**a**	28.9 ± 4.3**ab**	15.0 ± 6.0**a**	60.0 ± 7.2**ab**	26.1 ± 6.9**a**
Tree row	4	8.5 ± 0.7**ab**	8.0 ± 2.1**a**	33.2 ± 11.6**ab**	12.5 ± 2.9**a**	71.2 ± 11.3**ab**	40.7 ± 9.9**a**
Grasses	7	8.4 ± 2.6**b**	4.7 ± 0.7**a**	18.4 ± 3.3**b**	9.4 ± 1.6**a**	41.9 ± 7.3**b**	21.1 ± 6.6**a**
2002							
Deciduous woods	8	72.4 ± 5.1**a**	39.5 ± 5.4**a**	79.4 ± 11.3**a**	62.7 ± 7.8**a**	99.2 ± 0.6**a**	78.6 ± 4.3**a**
Coniferous woods	6	30.5 ± 5.1**b**	13.0 ± 2.8**b**	86.8 ± 2.4**a**	55.2 ± 6.6**a**	92.3 ± 5.1**ab**	65.1 ± 10.0**a**
Tree row	7	34.6 ± 8.4**b**	20.6 ± 6.2**ab**	75.3 ± 8.5**a**	56.9 ± 7.3**a**	93.9 ± 1.8**ab**	71.9 ± 8.0**a**
Grasses	9	29.2 ± 4.9**b**	21.8 ± 5.4**ab**	61.3 ± 9.8**a**	40.1 ± 8.7**a**	78.3 ± 9.1**b**	56.2 ± 11.1**a**

In July 2002 border infestation levels were significantly affected by the type of neighboring habitat ($F_{3,26} = 10.24$, $P < 0.0001$) as in the previous year, and in addition, the interior infestation in July varied with adjacent habitat ($F_{3,26} = 4.05$, $P = 0.02$) (Table 3.1). Vineyards near deciduous woods had more infested grape clusters at borders than vineyards near grasses ($P = 0.0003$), tree rows ($P = 0.001$), or coniferous woods ($P = 0.001$). The difference between the two types of woods also was significant in interior levels of infestation ($P = 0.02$). In August, uncultivated habitats had no significant effect on either border ($F_{3,26} = 1.33$, $P = 0.28$) or interior ($F_{3,26} = 1.83$, $P = 0.17$) vineyard infestation levels. In September, as in the previous year, vineyard borders had significantly higher infestation levels near deciduous woods than near grasses ($P = 0.02$) ($F_{3,26} = 3.20$, $P = 0.04$), but this effect was not found at vineyard interiors ($F_{3,26} = 1.11$, $P = 0.36$).

Abundance of male **E. viteana**

Moth abundance accumulated through the season was similar in all vineyards regardless of the type of uncultivated habitat adjacent to it, both in borders ($F_{3,22} = 0.30$, $P = 0.83$ in 2001; $F_{3,26} = 0.96$, $P = 0.43$ in 2002) and interiors ($F_{3,22} = 0.84$, $P = 0.54$ in 2001; $F_{3,26} = 0.24$, $P = 0.87$ in 2002) (data not shown). Data analyzed individually by month showed no significance either ($P > 0.63$ for borders and $P > 0.27$ for interiors in 2001, $P > 0.33$ for borders and $P > 0.41$ for interiors in 2002).

Table 3.2. Relative abundance of male *Endopiza viteana* adults during 2001 and 2002 at border and interior positions of four types of uncultivated habitats adjacent to commercial vineyards. Samples were taken weekly during each season, and cumulative values are reported for the three dates infestation was sampled on. For each year, means within a column followed by the same letter are not significantly different (Tukey $\alpha = 0.05$).

Year and Adjacent Habitat	n	Mean (± SE) cumulative number of moths trapped					
		July		August		September	
		Border	Interior	Border	Interior	Border	Interior
2001							
Deciduous woods	8	41.0 ± 25.3**ab**	56.1 ± 33.2**ab**	41.2 ± 25.3**ab**	56.9 ± 33.5**ab**	49.1 ± 30.1**ab**	56.1 ± 33.2**a**
Coniferous woods	7	24.0 ± 6.3**a**	37.7 ± 5.0**a**	25.1 ± 6.4**a**	38.4 ± 5.2**a**	45.1 ± 18.7**a**	37.7 ± 5.0**a**
Tree row	4	18.2 ± 2.4**ab**	-	19.5 ± 2.7**ab**	-	41.7 ± 12.0**ab**	-
Grasses	7	4.6 ± 5.2**b**	6.1 ± 3.4**b**	4.9 ± 5.1**b**	6.1 ± 3.4**b**	7.1 ± 5.9**b**	7.9 ± 4.2**a**
2002							
Deciduous woods	8	101.6 ± 19.3**a**	255.4 ± 74.2**a**	104.7 ± 19.6**a**	260.1 ± 76.8**a**	120.5 ± 25.0**a**	284.9 ± 90.4**a**
Coniferous woods	6	196.8 ± 63.8**a**	211.5 ± 14.4**a**	207.7 ± 67.7**a**	214.0 ± 15.4**a**	226.7 ± 74.1**a**	249.7 ± 34.4**a**
Tree row	7	191.0 ± 64.7**b**	-	213.1 ± 71.5**a**	-	284.6 ± 84.8**a**	-
Grasses	9	8.2 ± 2.5**b**	10.7 ± 3.8**b**	9.8 ± 3.7**b**	11.1 ± 3.9**b**	11.7 ± 4.9**b**	11.3 ± 4.0**b**

However, moth abundance varied significantly among the uncultivated habitats (Table 3.2). In July 2001, moth captures at the border ($F_{3,22} = 3.63$, $P = 0.03$) and interior ($F_{2,22} = 5.06$, $P = 0.02$) of uncultivated habitats were significantly different according to habitat type, similar to August ($F_{3,22} = 3.83$, $P = 0.02$; $F_{2,22} = 5.14$, $P = 0.02$, respectively) and September ($F_{3,22} = 3.28$, $P = 0.04$; $F_{2,22} = 5.02$, $P = 0.02$). Fewer moths were caught in borders of grasses near vineyards than in borders of coniferous woods ($P = 0.04$ in July, $P = 0.03$ in August) (Table 3.2). Similarly, in 2002 moth captures at borders and interiors of uncultivated habitats varied significantly (borders: $F = 27.59$ for July, $F = 26.03$ for August, $F = 26.86$, for September with df = 3,26 and $P < 0.0001$ for all; interiors: $F = 43.09$, $F = 41.88$, $F = 40.31$, respectively, df = 2,26 and $P < 0.0001$ for all). The lowest moth abundance was in grasses compared to the other uncultivated habitats ($P < 0.0001$ for each comparison in July, August and September) (Table 3.2).

A regression analysis between the total moth captures in uncultivated habitats and mean vineyard infestation (average of border and interior levels) showed a positive but weak relationship in September 2001 and August and September 2002 (Table 3.3a). There also was a weak negative relationship between mean vineyard infestation and moth abundance in vineyards (Table 3.3b) during both years, except in July 2001.

Survey of wild grape

The probability of wild grapevines being present was similar among the different uncultivated habitats (Kruskal-Wallis $\chi^2 = 1.78$, df = 3, $P = 0.65$ for 2001; $\chi^2 = 4.11$, df = 3, $P = 0.25$ for 2002) (Table 3.4). However, the frequency with which wild grapevines bore clusters in these uncultivated habitats varied with habitat type (Table 3.4) ($\chi^2 = 14.0$, df = 3, P = 0.003 for 2001; χ^2 = 10.07, df = 3, P = 0.02 for 2002). As measured by Wilcoxon rankings, wild grapevines with fruit clusters were more frequently found in deciduous woods, followed by tree rows then coniferous woods (where no fruit clusters were found in 2001). Wild grapevines in grasses were never observed with fruit clusters.

Table 3.3. Values obtained for regression analysis of cluster infestation in vineyards and cumulative number of male *Endopiza viteana* adults captured in a) uncultivated habitats and b) in vineyards. Significant regressions are displayed in bold.

a)

Year	df	*F*	*P*	r^2	Slope
2001					
July	1,46	0.73	0.39	0.02	-0.03
August	1,46	1.42	0.24	0.03	0.05
September	1,46	14.91	**0.0004**	**0.24**	0.20
2002					
July	1,51	2.91	0.09	0.05	0.07
August	1,51	14.14	**0.0004**	**0.22**	0.15
September	1,51	10.93	**0.002**	**0.18**	0.14

b)

Year	df	*F*	*P*	r^2	Slope
2001					
July	1,50	3.27	0.08	0.06	-0.06
August	1,50	5.53	**0.02**	**0.10**	-0.11
September	1,50	8.85	**0.004**	**0.15**	-0.22
2002					
July	1,58	23.14	**0.0001**	**0.28**	-0.32
August	1,58	4.84	**0.03**	**0.08**	-0.23
September	1,58	8.36	**0.005**	**0.13**	-0.30

Wild grape index (WGI) values varied significantly among habitats ($F_{3,22}$= 7.81, $P = 0.001$ in 2001, and $F_{3,26} = 7.21$, $P = 0.001$ in 2002, Table 3.4). There were more wild grapevines in deciduous woods compared to tree rows ($P = 0.007$ in 2001, $P = 0.001$ in 2002) and grasses ($P = 0.001$ in 2001, $P = 0.006$ in 2002). Although the difference in WGI values was not significant between the two types of woods ($P = 0.10$ in 2001, and $P = 0.34$ in 2002), wild grapevine abundance was greater in deciduous woods (Table 3.4). The restricted wild grape index (RWGI) values showed a similar trend to the WGI values, but with a lower magnitude (Table 3.4). Values varied significantly between habitats ($F_{3,22}$= 3.28, $P = 0.04$ in 2001, and $F_{3,26} = 4.31$, $P = 0.01$ in 2002) and there were more wild grapevines in deciduous woods than any other habitat, though it was only significant when compared to grasses (Table 3.4).

Table 3.4. Parameters measured in the 2002 survey of wild grape, *Vitis* spp., within four types of uncultivated habitats adjacent to vineyards. For wild grape indices, means within a column followed by the same letter are not significantly different (Tukey $\alpha = 0.05$).

Type of uncultivated habitat	n	Wild grape presence	Wild grape clusters presence	Wild grape index (WGI)	Restricted wild grape index (RWGI)
Deciduous woods	8	100%	75%	45.0**a**	12.4**a**
Coniferous woods	6	100%	33%	29.0**ab**	8.5**ab**
Tree row	7	71%	43%	7.1**b**	6.7**ab**
Grasses	9	89%	0%	14.0**b**	2.1**b**

Relationship between wild grape and grape berry moth infestation

The presence or absence of wild grapevines in uncultivated habitats was not predictive of vineyard infestation during any of the sampling times in this study, neither at vineyard borders (Kruskal-Wallis df = 1, $P > 0.21$ in 2001; df = 1, $P > 0.36$ in 2002) nor vineyard interiors (df = 1, $P > 0.33$ in 2001; df = 1, $P > 0.08$ in 2002). On the other hand, the presence of fruit clusters on wild grapevines in uncultivated habitats was found to be related to vineyard infestation by grape berry moth larvae during some of the sampling times of both years (Figure 3.2, Table 3.5). In 2001, infestation levels in vineyards were not correlated with WGI of the uncultivated habitat adjacent to them, neither at borders (df = 1,24: $F = 4.14$, $P = 0.05$ for July; $F = 3.50$, $P = 0.07$ for August; $F = 1.30$, $P = 0.27$ for September) nor at interiors (df = 1,24: $F = 0.93$, $P = 0.34$ for July; $F = 1.60$, $P = 0.22$ for August; $F = 0$, $P = 0.95$ for September). In contrast, in July 2002, there were significantly greater infestation levels at vineyard borders when the adjacent uncultivated habitat had greater WGI ($F_{1,28} = 7.93$, $P = 0.009$) (Figure 3.3) but not for the following months (df = 1,28: $F = 2.29$, $P = 0.14$ for August; $F = 3.10$, $P = 0.09$ for September). That same year, no significant relationship was observed between WGI of uncultivated habitat and vineyard interior levels of infestation (Figure 3.3) (df = 1,28: $F = 1.38$, $P = 0.25$ for July; $F = 0.02$, $P = 0.89$ for August; $F = 0.38$, $P = 0.54$, for September). Regression analysis using RWGI did not show significant correlations in 2002. The only positive significant correlation was obtained in July 2001 between RWGI and infestation levels at the border of vineyards ($F = 4.86$, df = 1,24, $P = 0.04$) (Figure 3.3).

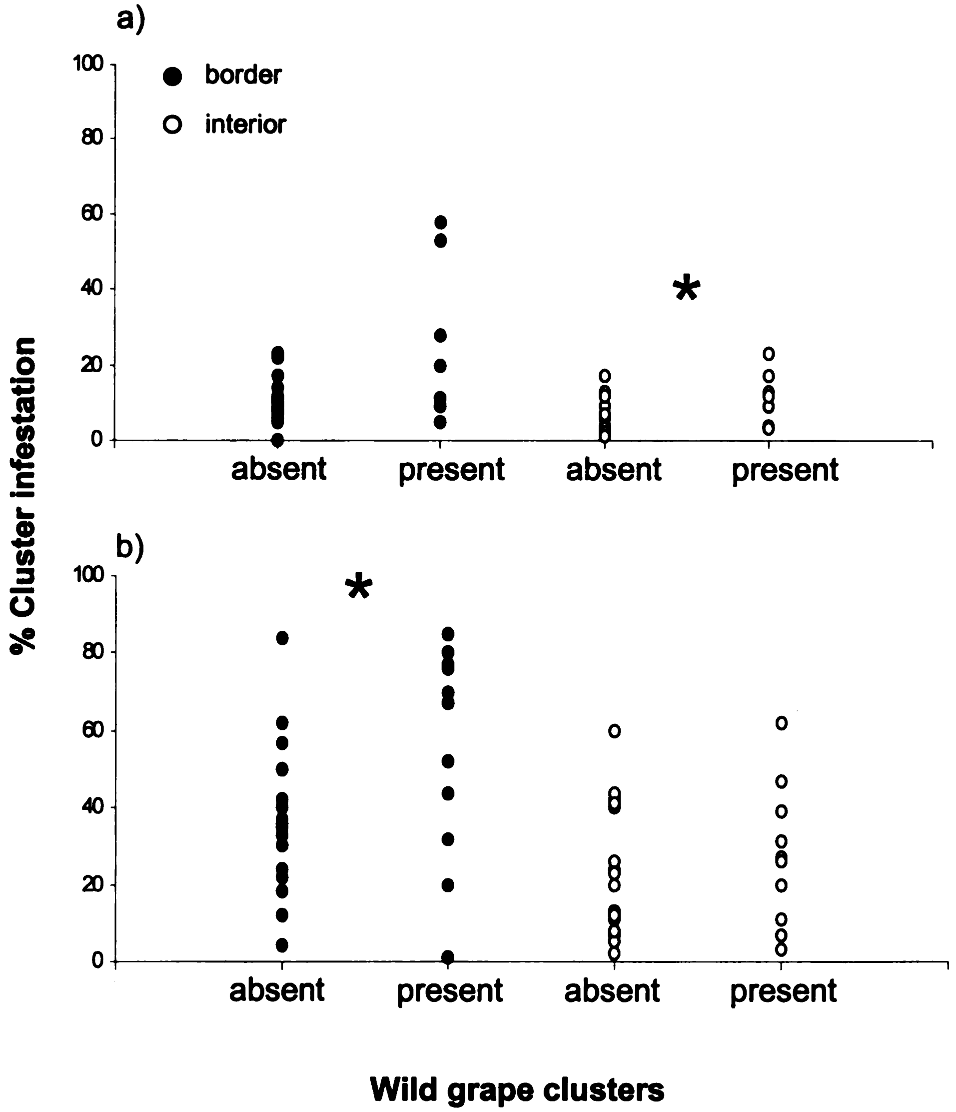

Figure 3.2. Infestation levels by *Endopiza viteana* larvae in vineyard borders (dark) and interiors (white) adjacent to habitats where wild grape clusters were present or not. a) July 2001, b) July 2002. The asterisk indicates a significant difference between sites with wild grape clusters absent or present.

Table 3.5. Correlation between vineyard percent cluster infestation by *Endopiza viteana* larvae at vineyard borders and interiors, and the incidence of wild grapevines bearing fruit clusters in the uncultivated habitat adjacent to the vineyard. Significant Kruskal-Wallis-test CHI-square and *P*-values are in bold.

		Vineyard border		Vineyard interior	
Year	df	χ^2	*P*	χ^2	*P*
2001					
July	1	3.02	0.08	**4.03**	**0.04**
August	1	3.32	0.07	0.30	0.58
September	1	1.08	0.30	0.66	0.42
2002					
July	1	**4.18**	**0.04**	0.47	0.49
August	1	2.49	0.11	0.15	0.70
September	1	0.70	0.40	0.05	0.83

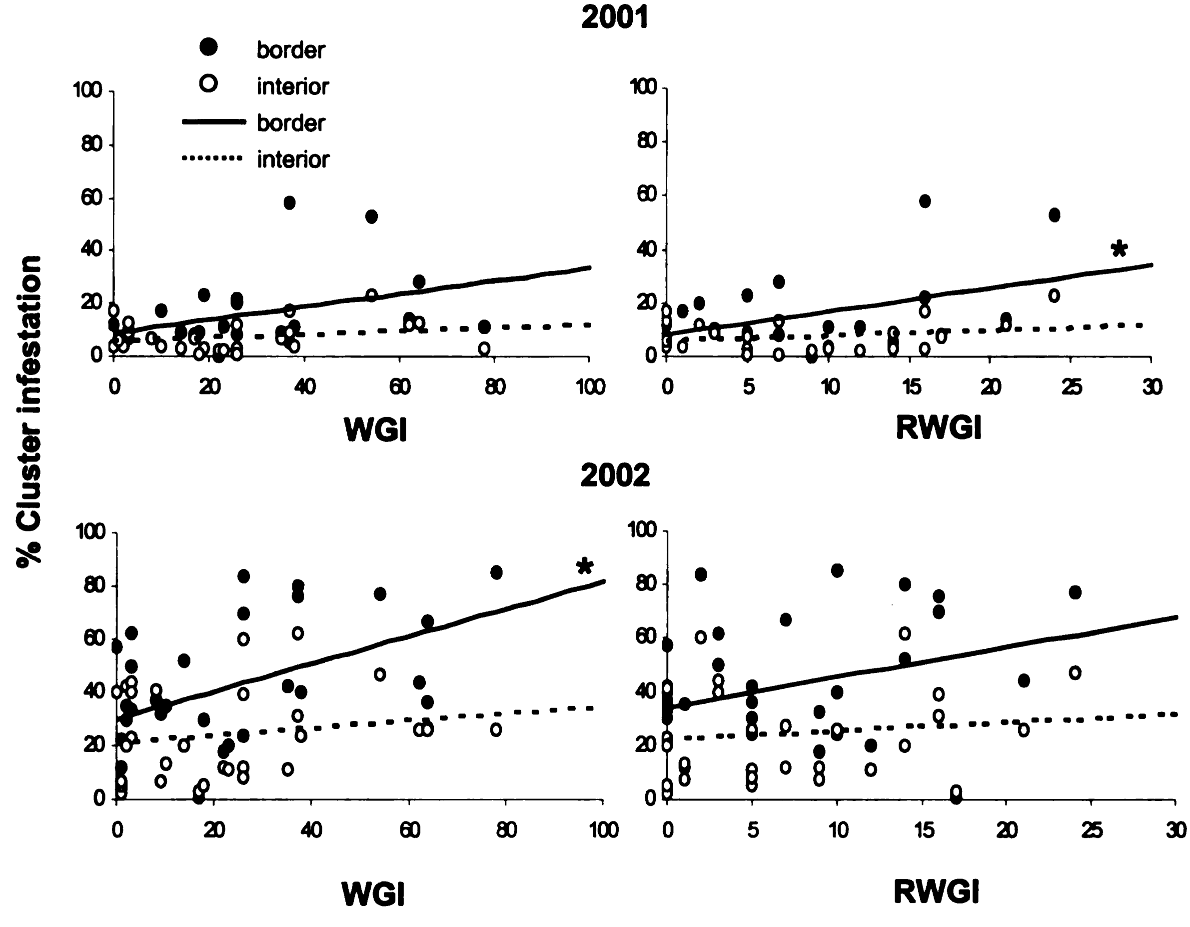

Figure 3.3. Relationship between percent cluster infestation in vineyards by *Endopiza viteana* larvae in July 2001 (top) and July 2002 (bottom) and wild grape index (WGI) or restricted wild grape index (RWGI) values of the adjacent habitats. Cluster infestation at the borders is shown by dark circles and solid lines, and infestation at the interiors is shown by open circles and dashed lines. The asterisk denotes significance.

DISCUSSION

This study showed that uncultivated habitats adjacent to vineyards in Michigan influenced cluster infestation by grape berry moth larvae, and that the effect is most evident at vineyard borders. Greater larval infestation by *E. viteana* at vineyard borders than interiors has been reported previously in other Eastern US grape production regions in studies of vineyards along wooded borders (Biever and Hostetter 1989, Hoffman and Dennehy 1989, Trimble et al. 1991). The greater infestation at borders could be due to improved overwintering survival of pupae at borders as opposed to interiors (Trimble et al. 1991), immigration by gravid females from woods (Trimble et al. 1991, Trimble 1993), *E. viteana* possibly favoring woods in which it has evolved over cultivated vineyards (Nagarkatti et al. 2002a), or because borders provide a restricted area for movement by females to lay eggs in comparison to vineyard interiors, making egg deposition more likely at borders.

Comparisons among vineyards with different neighboring habitats revealed that the greatest infestation was observed near deciduous woods, whereas the lowest infestation was observed in vineyards near grasses (Table 3.1). The presence of nearby woods was previously reported to pose a risk of grape berry moth larval infestation in vineyards (Hoffman and Dennehy 1989). Potential explanations included the observation that wild grapes were usually (though not always) present in wooded habitats, and that *E. viteana* could be responding to structural characteristics of wooded edges (Hoffman and Dennehy 1989, Martinson et al. 1991). The study reported here separated woods into two types according to their primary vegetation, and separated uncultivated habitats into three different structure types; woods, a single row of trees, and grasses. Deciduous vegetation in woods presents a greater risk than coniferous vegetation (Table 3.1), and that trees, whether as part of a forest or in a single row, are sufficient to provide greater risk of infestation than habitats without trees. Herbivores have been shown to respond in a significant way to landscape complexity within a 1.5 km radius, particularly because of mortality effects caused by parasitoids that are especially sensitive to this landscape context (Thies et al. 2003).

Although vineyard infestation levels varied among vineyards with different adjacent habitats, the abundance of moths in vineyards did not vary in a similar pattern, and no positive relationship between the level of cluster infestation by larvae and moth abundance was detected. Rather, the relationship was often negative (Table 3.3b) indicating that moth captures should not be taken as a predictor of the risk of cluster infestation in the vicinity. This corroborates studies conducted on the European grape berry moth *Lobesia botrana* (Karg and Sauer 1995) and earlier studies on *E. viteana* (Dennehy et al. 1990b). Although abundance of male moths in vineyards did not vary significantly in relation to the type of adjacent uncultivated habitat, there was significant variation when abundance of these moths was sampled within these uncultivated habitats (Table 3.2). Male moth abundance in uncultivated habitats was positively correlated with vineyard infestation in August 2002 and September of both years (Table 3.3a). By comparing data in Tables 3.1 and 3.2, it is clear that the greatest infestations were found in vineyards near those deciduous woods that contained the greatest numbers of male moths, and that lower levels of vineyard infestation occurred near grasses in which the fewest moths were captured. Sciarretta et al. (2001) similarly showed that in the plum fruit moth, *Cydia funebrana,* catches were insignificant in landscapes other than orchards where their food substrate was present, and in their studies of *E. viteana* Hoffman and Dennehy (1989) demonstrated that this species was more abundant in woods and vineyards containing grapes than in neighboring alfalfa fields. In a recent study (Chapter 2), male moth abundance in deciduous woods increased with height of trap, with more than 76% of the moths being caught in the tree canopy at and above 9 m, further emphasizing that the distribution of *E. viteana* is related to that of its host.

The variation in abundance of adult *E. viteana* among different habitats suggests that the suitability of these habitats for this pest is not identical. This study focused on variation in the host plant within these habitats as a potential explanation for the difference in captures of *E. viteana* males. When wild grape vines were sampled, the plants were equally likely to be present in each adjacent habitat (Table 3.4). Those wild grapevines were identified to species following a taxonomic key by Voss (1985) and corresponded to *V. labrusca*, *V. riparia* and *V. aestivalis*. This is in agreement with observations that appropriate habitats for wild grapevines, particularly *V. riparia*, are relatively continuous across Eastern North America (Morano and Walker 1995, Downie and Granett 2000). The habitats did, however, differ in the likelihood of the wild vines having clusters. These were most commonly observed in the deciduous woods sites, although never observed in grasses, which could be because wild grapes are poor competitors of weeds and shrubs when they lack structural support, but also because grapevines are likely to be mowed with the grass. In addition, Mullins et al. (1992) report that horizontally-trained shoots of some varieties of cultivated grapes are less fruitful than vertically-trained ones.

As measured by WGI values, deciduous woods had six times more wild grapevines on average than tree rows, three times more than grass fields, and almost twice as many as coniferous woods (Table 3.4). Although the lower WGI values of tree rows were a direct result of the smaller area that a single row of trees occupies, they reflect the total amount of wild grapevines in an uncultivated habitat. On the other hand, the RWGI quantified wild grape presence within a standard area neighboring vineyards. Both indices revealed significant differences in wild grapevine abundance among habitats, with highest values of both indices for deciduous woods.

The presence of woods *per se* did not create equal risk of pest infestation, because the two types of woods differed significantly in their impact on vineyard infestation, male moth abundance, and likelihood of containing grape clusters. Indeed, wild grapevines were in 75% of deciduous woods sites and only at 33% of coniferous woods sites studied. The lower fruit production of grapevines in coniferous woods has not been documented previously, but increased soil acidity (pH < 6.5) can sometimes limit commercial grape production. Pine needles on the ground affect soil acidity, inhibit germination of new grapevines, and decrease the number of flowers available for cross pollination which is necessary for the primarily dioecious wild grapes (Mullins et al. 1992). The most important factor affecting the suitability of this habitat for vines is that coniferous woods have dense canopies throughout the year, reducing light penetration to the forest floor and creating less favorable mesoclimatic conditions than those found in deciduous woods (Mullins et al. 1992). I am not aware of studies that describe wild grape fruiting distribution or abundance in any geographical range, but personal observations of wild grapevines show that inside deciduous woods, the majority of fruiting typically occurs higher than 12 m within the woods canopy, while at the edges of woods and along tree rows, fruit clusters are found from low near the ground to high into the tree canopies (N. Botero-Garcés, unpublished data).

Fruiting frequency and wild grape indices were both related to infestation by grape berry moth in vineyards. Fruiting was significantly correlated with cluster infestation in July 2001 (interiors) and July 2002 (borders) (Figure 3.2, Table 3.5), probably because the presence of wild fruit clusters in the uncultivated habitat improved the quality of the overall landscape for *E. viteana*. This result agrees with the "ideal free distribution" prediction in which herbivores distribute themselves so that they utilize resources optimally (Williams et al. 2001). Indeed, Nagarkatti et al. (2002a) postulate that females of *E. viteana* prefer wild grapes over cultivated ones and are better adapted to densely wooded habitats with varied vegetation. Research in vineyards and neighboring deciduous woods (Chapter 2) suggests that *E. viteana* distribution throughout this agrolandscape is tightly correlated to the vertical and horizontal distribution of *Vitis* host plants. It may be possible that moths are attracted to wild grape clusters in greater numbers than can be supported, and in such cases females unable to lay eggs in wild grapes may disperse to locate new hosts in the nearby vineyards.

In July 2002, unprecedented levels of infestation by grape berry moth were observed, particularly at vineyard borders (Table 3.1, Figure 3.2b). This cluster infestation tended to be greater when the uncultivated habitat contained fruit clusters or wherever WGI values were highest, as suggested by the positive correlation between vineyard infestation and WGI and border infestation and RWGI (Figure 3.3). This result may have been because wild grape clusters were abundant in the uncultivated habitats, though this can only be inferred from this data and should be tested in another study. The low predictive power of these three wild grape parameters might be because *E. viteana* do not depend on the presence or abundance of wild grapevines, but on the presence and abundance of wild grape berries for development. It is possible that by factoring presence of fruit clusters in adjacent sites into any wild grape index we may achieve a better predictor of vineyard infestation.

This study highlights the importance of landscape management for manipulation of crop pest populations. Typically, descriptions of the influence of adjacent habitats on crops have addressed whether the effect is negative due to pest immigration, or positive because of movement of natural enemies (Seaman et al. 1990, Dorn et al. 1999) and the availability of alternate insect hosts for pest parasitoids (Dennehy et al. 1990a). The grape berry moth, a specialist pest species that dwells in native habitats next to cultivated grapes, may be able to cross the area between habitats to colonize vineyards, much like codling moth, *C. pomonella* (Dorn et al. 1999). Intercrop movement of insect pests is not uncommon, as reviewed by Sciarretta et al. (2001) for both large and small spatial scales. In some cases, the pest's biology depends on inter-habitat movement, as with *Ostrinia nubilalis* which need to fly to grassy surrounding areas in order to mate and rest (Derrick et al. 1992). In other systems, the incidence of uncultivated habitats neighboring cultivated land affects pest pressure due to immigration, as occurs with a complex of thrips in British Columbia, Canada, moving in and out of nectarine orchards (Pearsall and Myers 2001). Nagarkatti et al. (2002a) argue that inter-habitat movement by *E. viteana* may occur only within the immediate vicinity, due to the insect's lack of flight vigor.

Future studies should address potential dispersal capacity of this species and factors affecting potential inter-habitat movement (Hughes and Dorn 2002).

Integrated pest management (IPM) programs may be more effective against grape berry moth by accounting for the wild grape abundance and fruiting in neighboring habitats. Future trapping strategies, that may include female baits such as the one developed for *C. pomonella* (Light et al. 2001), should consider sampling in uncultivated habitats, since these appear to be influential to grape berry moth populations. The removal of wild grapevines in habitats neighboring vineyards may reduce the impact of this pest by decreasing the amount of larval food substrate available for developing generations of *E. viteana*. However, as our analyses of the relationship between wild grape indices and vineyard infestation by *E. viteana* show, the area of influence of wild grapevines is not limited to a border area so vineyard managers may need to consider the whole uncultivated habitat when considering cultural control practices. A study of the landscape context over different (or larger than the one described here) spatial scales, similar to the research by Thies et al. (2003) could help identify critical landscape factors for grape berry moth infestation in vineyards.

The immediate effects of removing wild hosts could also include increased pest pressure, since it is not unusual for a portion of a resident population to migrate in response to environmental cues and selection pressure (Hughes and Dorn 2002). Further studies should address the effect of wild host removal on associated populations of parasitoids of *E. viteana*, as Dennehy et al. (1990a) have indicated that wild hosts are a "source and refuge for natural enemy populations" in a study in which egg parasitoids accounted for the greatest *E. viteana* mortality. Wild hosts in combination with the diverse vegetation that characterizes natural or undisturbed land make up a habitat that is favored by parasitoids, as discussed by Nagarkatti et al. (2002a). Since Williams and Martinson (2000) have shown that leafhopper parasitoids are better able to successfully colonize New York vineyards when alternate hosts are present within uncultivated (wooded) habitats, parasitoids of *E. viteana* may also require these resources adjacent to vineyards. The benefits of maintaining a complex landscape (preserving woods and riparian vegetation) or simplifying it (removal of woods and wild grapevines) should be further studied in this system before any management plans are implemented, since differential impacts on parasitoid communities have been demonstrated (Mellaned et al. 1999, Thies and Tscarntke 1999).

CHAPTER 4:

MOVEMENT OF GRAPE BERRY MOTH IN VINEYARD AGROECOSYSTEMS

INTRODUCTION

Insect populations are capable of movement from one habitat to another both in space and time (Wratten and Thomas 1990, Landis 1994, Drake and Gatehouse 1995). These movements may be related to the need for food or oviposition substrates, mating sites or refugia, all of which are usually distributed in a patchy pattern (Miller and Strickler 1984, Denno and Roderick 1991). Herbivorous insects can potentially survive with these patchy resources available to them in two basic ways: by accepting different foods (polyphagy) or dispersing in the environment in search of their host.

Within a complex environment, mono- and oligophagous insects are better suited for finding and accepting the right host than polyphagous ones, due to finely-tuned mechanisms in their nervous system that govern host selection (Bernays 2001). Some specialist Lepidoptera, in particular, have coevolved with plant taxa that produce compounds useful to them in host identification or that convey protection to their larvae (Dethier 1941, Ehrlich and Raven 1964, Rosenthal and Janzen 1979, Bernays 2001).

The grape berry moth is a monophagous herbivore whose hosts, *Vitis* spp. vines, have no known chemical defense against infestation by this insect. Nevertheless, this association of pest and host may have led to the evolution of fine-tuned host-finding behaviors that have not yet been studied in detail. This gap in understanding includes moth movement within and between habitats containing grapes. In Michigan, the grape agroecosystem is comprised of relatively small (< 2 ha) vineyards interspersed with remnants of woods, windbreaks (single rows of trees) and other crops, where wild grapevines grow both with and without support (Chapter 3). There are three very common species of wild vines in Michigan: *V. riparia, V. labrusca*, and *V. aestivalis* (Chapters 2 and 3). Woods are one of the main uncultivated habitats present in Michigan and across Eastern North America, and are a significant reservoir for grape berry moth (Chapter 2).

One of the most important but often overlooked characteristics of those woods is the space occupied by the canopy (branches, leaves) as opposed to the forest floor within human reach. This three-dimensional structure both determines the distribution of epiphytes (and vines) and their availability to herbivores (Richards 1983) and creates a habitat in which some flying insects are more abundant in the tree canopy (Rees 1983, Sutton 1983, Su and Woods 2001). In the case of *E. viteana*, which is most abundant above 9 m in the tree canopy, the distribution is tied to its host's vertical distribution, probably in response to fruit cluster distribution (Chapter 2). This effect of food resource distribution has also been observed in predators that at different life stages forage in separate host strata for their particular prey (Cisneros and Rosenheim 1998) and also in insect parasitoids whose abundance is tied to structurally complex habitats (Roland and Taylor 1997, Thies and Tscharntke 1999). This complies with the ideal free distribution theory, which predicts that herbivores will be distributed so as to optimally exploit resources (Williams et al. 2001).

According to the distribution of its host plant, the three life stages of *E. viteana* are likely to follow different dispersion patterns in this agrolandscape (Schowalter 1996). Adult male moth distribution has been assessed, as was mentioned above, but gaps in knowledge exist regarding distribution of female moths. Larval distribution within diverse plant communities such as deciduous woods is likely aggregated on grapevines, whereas within homogenous habitats (such as vineyards) distribution might be throughout the habitat. It is expected that pupae follow these distribution patterns, as fourth instars seek grape leaves to cut crescent-shaped sections in order to spin a cocoon (Chapter 1). However, in the overwintering generation, diapausing pupae are inside cocoons spun on vine leaves and these leaves fall to the ground during leaf senescence and remain nearby the grapevine during the winter. Another way that movement may occur is when (or if) leaves are carried by the wind or rain, and therefore pupae are transported within them. This type of passive dispersion has never been identified or studied in the grape berry moth system. Elucidating whether this passive transport takes place could perhaps shed light on certain peculiarities of patterns of distribution of adults in the spring, particularly the greater abundance of moths in the woods in spring.

Another possibility is that there are two different populations of *E. viteana,* one in uncultivated habitats, spatially separated from the other vineyard population. However, trapping data (Chapter 2) seem to indicate that these populations mix, either actively by interchange of adults, or passively by pupae on leaves being taken by winds to the edge of woods. Indeed, some have proposed that *E. viteana* abundance is high at the woods edge in the spring due to improved survival of pupae at vineyard borders (Martinson et al. 1990). Adult trapping studies by Trimble (1993) and Hoffman and Dennehy (1989) suggest that the uncultivated and cultivated habitats are linked by dispersal of this pest between these habitats. There is no direct supporting data for this dispersal between habitats, however.

Uncultivated habitats within agricultural landscapes may have positive or negative impacts on crop pests and beneficial insects (van Emden 1965, Solomon 1981, Ekbom 2000) (Chapter 3). Others have addressed patterns of insect distribution caused by winds interacting with these habitats, and have related it to pest impact on crops (Pasek 1988). However, direct insect movement has been more difficult to study, although both laboratory and field methods are available.

Laboratory methods for measuring flight capacity

Flight of insects has been studied using flight mills, in which an arm of known length rotates around an axis carrying an insect glued to it by the thorax. During flight, the arm revolves around the center and by doing so, cyclically interrupts the light on a sensor that allows automated recording of flight frequency and duration, allowing calculation of flight velocity, duration of flight bouts, distance flown per bout, and assessment of the tendency to undertake long (migratory) or short (appetitive) flights (Beerwinkle et al. 1995).

Flight mills have been used to show that low temperatures limit flight onset and flight ability, while increasing temperatures in general cause increased locomotory activity (Sanders et al. 1978, Fasoranti et al. 1982, Taylor and Shields 1990). Differences between sexes in how temperature, relative humidity, and diet affect flight ability have also been documented (Sharp et al. 1976, Taylor and Shields 1990, Sappington and Showers 1993) using this method.

However, flight mills may present misleading information. Sharp et al. (1976) stated that the soybean looper, a Noctuid, was a poor flyer in flight mills whilst they were supposed to be strong fliers in the wild. Sappington and Showers (1992) working with black cutworm, *Agrotis ipsilon*, also stated that data obtained from flight mills ought to be interpreted with caution since the experimental conditions were "inherently intrusive" to the moths and therefore very stringent criteria should be applied to experiments. Cooter and Armes (1993) recommend that flight mill data be used only to compare estimates of flight performance and not be extrapolated to the moth's behavior in the field. Because of the limitations of the flight mill approach, studies of insect movement have also been carried out directly under field conditions. These methods have centered on direct observation (night goggles, binoculars) and different variations of mark-release-recapture methods.

Methods for marking insects

Mark-release-recapture studies use a mark of some kind that has been put on the insect beforehand, which is then used to identify marked insects in subsequent samples of the population. This mark can be a tag, a body mutilation of some sort, a paint mark, a genetic marker, a radioactive-isotope mark, an element mark, or more recently, a protein mark or some genetically engineered mark (Hagler and Jackson 2001). Recognition of the mark can be achieved through several techniques such as harmonic radars, radiotelemetry, radio-activity and metal detectors (Piper and Compton 2002). Of the simpler available methods, incorporating dyes into meridic diets has been shown to work well (Showers et al. 1989) but some mortality may occur and a colony must be at hand.

Marking with fluorescent pigment dusts depends on insect morphology and has been shown to be successful for marking minute insects (García-Salazar and Landis 1997, Cronin et al. 2001) including moths, without affecting survival or ability to find pheromone traps (Mo et al. 2003).

Mark-release-recapture methods have been used to show that the codling moth, *C. pomonella*, has the capacity to engage in long-range flights up to 11 km, preferably in the 2nd to 7th day of life (Schumacher et al. 1997). Females first oviposited before engaging in long (between-habitat) flights (Schumacher et al. 1997), in contradiction with the oogenesis-flight syndrome (Johnson 1969). The oriental fruit moth, *C. molesta*, tended to be sedentary and had lower flight capacity than *C. pomonella* (approximately 1 km), although a small proportion of the population, most likely gravid females, ventured into long flights (Hughes and Dorn 2002).

Methods for insect recapture under field conditions

Insect recapture depends on the use of some sort of trap suited to the insect's environment and behavior (Juillet 1963, Muirhead-Thomson 1991). Food baits and pheromone traps are usually employed because of their efficacy (higher recapture rates) but they bias insect movement (Weissling and Knight 1994). Traps without attractants can give an indication of natural dispersal and flight patterns of foraging insects and they are generally called passive or interception traps or both (Muirhead-Thomson 1991). They include the Malaise trap, which can be in many forms and modifications, but generally consists of a frame on which a vertical fabric has been stretched so as to interfere with flying insects. When the insect makes contact with the trap it climbs up towards a container that captures it. A killing agent inside the container will ensure that specimens will not be destroyed by other trapped more robust species. An important quality of this trap is that direction of flight can be inferred since the trap is mechanically intercepting insects flying in a given direction. By modifying the trap (a screen in the middle) or joining two of them, with two different containers at the top, insects flying in opposite directions can be sampled. In a comparative study, Juillet (1963) found that the Malaise trap was the second best device for capturing flying insects, including Lepidoptera species. Passive interception traps can be constructed of transparent plastic panes coated with sticky material. These are usually hung on tree canopies, and have been successful in trapping both sexes of codling moth, *C. pomonella* (Weissling and Knight 1994, Knight 2000).

Muirhead-Thomson (1991) recommends that at least two types of traps with different principles of capture and attraction be used when studying insect flight, since interpretation of only one capturing technique can be "difficult or speculative". The limitations of mark-release-recapture methods lie in the possibility of using inadequate marks (not in accordance with the life stage or morphology of the insect), losing the marked population (no recapture of any individual), or not recognizing it as marked (tag lost, color faded). This is why the species considered for these studies needs to be studied beforehand, so that the marking method is appropriate for the behavior and morphology of the organism (Hagler and Jackson 2001).

Movement by E. viteana

Sampling for adult *E. viteana* typically relies on the use of pheromone traps which attract only males. These are usually placed at 1.5 m above the ground at vineyard borders. Male abundance within vineyards has been studied in order to identify patterns of spatial distribution that could help predict vineyard infestation, but without much success (Trimble 1993). Several authors have noted that greater grape cluster infestation at vineyard borders usually corresponds to lower moth captures and have explained this by suggesting that wild females may be moving from woods to lay their eggs in vineyard grapes during the growing season (Taschenberg et al. 1974, Hoffman and Dennehy 1989, Trimble 1991, 1993). Data presented in Chapter 2 show that moth captures continue throughout the season when the woods canopy is sampled, indicating that the woods population may be expanding and subsequently colonizing vineyards.

Elucidating *E. viteana* movement behavior will potentially improve our knowledge of the insect's ability to survive in deteriorating environments or it's ability to colonize new ones. It will also help in improving pest management strategies, since mating disruption, for example, is less effective if gravid females immigrate from wild areas into vineyards (Trimble 1993). The goal of this study was to determine the capacity of *E. viteana* adult moths for movement within vineyards, and to determine whether this species can move from woods to adjacent vineyards. Three different methods for studying movement of this species were used: mark-release-recapture of fluorescent dust-treated moths, bi-directional Malaise traps for monitoring movement of adult moths, and tracking winter movement of pupae using recapture of painted leaves.

METHODS

Mark-Release-Recapture study

This study was conducted in a four-year old experimental vineyard (*Vitis labrusca*, var. Niagara), at the Trevor Nichols Research Complex, Allegan Co., Michigan, during 2001 and 2002. The vineyard consisted of three parallel blocks, each of 32 rows and seven vines, with a total of 672 vines. This vineyard was bordered by another vineyard on its eastern side, by woods to the west, an apple orchard to the south, and a grassy field to the north. Vineyard management was conventional, following recommendations for treating insect pests (Table 1.1).

Traps used for recapture

Two different kinds of traps were used to capture grape berry moths: pheromone traps for males and passive-interception pane traps for both sexes. The first were large plastic delta traps (Suterra LLC, Bend, Oregon), baited with lures containing 0.1 µg of synthetic sex pheromone of *E. viteana* (90:10 ratio of (Z)-9-12Ac and (Z)-11-14Ac), and lined with sticky inserts. New inserts were used every time moths were found in traps upon being checked, and lures inside pheromone traps were replaced every month from the same batch of lures. The passive interception traps were made of 380 x 280 x 3 mm Plexiglas panes, coated on both sides with tangle trap paste (The Tanglefoot Company, Grand Rapids, MI). All traps were hung from the trellis at approximately 1.5 m high, and the plastic panes were secured to the ground by strings to maintain their vertical position. A total of 33 panes and 56 pheromone traps was deployed during 2001, and 31 panes and 56 pheromone traps during 2002, in a pattern of concentric circles, radiating from the middle to the periphery of the vineyard (Figure 4.1). The first circle of pane traps was 2-3.30 m away from the central point of release, and consisted of four panes, while the peripheral ring of traps consisted of pheromone traps positioned around the vineyard and entering the four adjacent habitats. Traps were placed at the edge of each of these four habitats separated 20 m from each other: two were within the edge of the grassy field to the north, two on the first row of trees in an orchard to the south, two on the first row of vines of the adjacent vineyard to the east, and two at the edge of the woods to the west. Eight pheromone traps and four pane traps were placed inside the woods (Figure 4.1).

Marking moths

Newly emerged adult grape berry moths were taken from the *E. viteana* colony at the Small Fruit Entomology Laboratory, Michigan State University, established in 2000 using larvae collected in infested grapes from a commercial vineyard in Van Buren Co., Michigan. The colony was kept in two sets of conditions, according to phenological state. Adult moths were maintained at 26°C and 70-80% RH, and a photoperiod 16:8 (L:D) h. Some larvae were reared on commercial table grapes in the laboratory under 22-25°C and 16:8 (L:D) h, 30% RH, or in a meridic diet (Nagarkatti et al. 2000) inside an environmental chamber at the same conditions except that temperature was 25° C. To help preserve wild traits, moths reared from grapes collected in the same vineyard were added to the colony at the end of the first year.

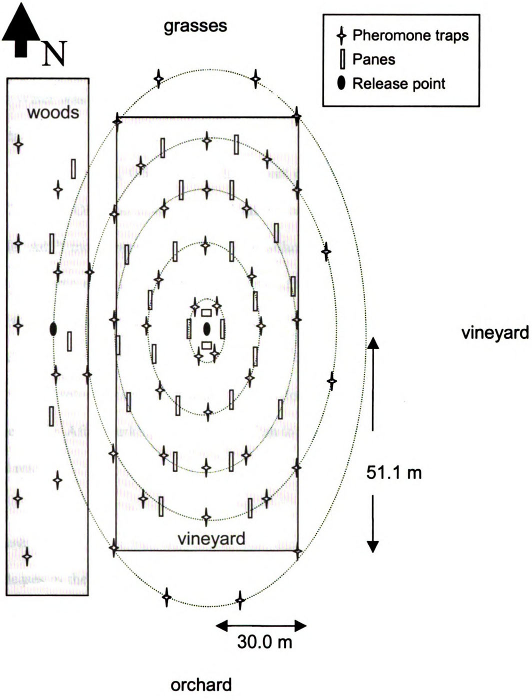

Figure 4.1. Schematic representation (not to scale) of the experimental vineyard-woods set up where marked moths releases took place. Pheromone and pane traps were arranged around a central vineyard release point in concentric circles; a release point inside the woods was also used to determine extent of movement between woods and vineyards.

The moths were held in groups of ~400 in 3.8 L white utility pails (Holiday Housewares Inc., Leominster, MA), covered on the top with white tulle veil held in place by a rubber band. A 12 cm-diameter opening was drilled on the side; a white cotton sleeve was attached to allow the operator's arm to be introduced without the insects flying out. Water was provided by placing damp dental cotton wicks either fixed to the bottom of the cages or on top of the tulle covering it.

To mark the moths, 0.5 g of dry fluorescent dust dye (Dayglo Color Division, Switzer, Cleveland, OH) was dissolved in 75 ml of acetone (99.9%) in a small cosmetic spray bottle. Adult moths were sprayed with the solution through the veil. However, it was noted that some excess drops of solution tended to form at the bottom of the cage and catch the wings of moths and pin them to the cage surface. To avoid this, after removing the cotton wick, the cage was inverted, tapped once so that moths landed on the veil and then the solution was sprayed through it. Moths on the tulle were marked and dried immediately. After marking, moths were taken to the release point and placed in the shade until release.

Moth releases

Releases in the vineyard were made at its central point, at row 16, at the base of vine 11. Releases took place between 1700-1900 h, when winds were low, it was not raining, and air temperature was approximately 25 ° C. The weather report was checked prior to release so that no rain or storms were expected for the following day(s). To release the moths, the bucket was placed on its side and the rubber band holding the veil was carefully cut off so that moths could fly out. All live moths had escaped the cage by the next day, when the number of moths released was determined by subtracting the number of moths found dead inside the bucket from the original number in the bucket.

Moths were released four times in each of 2001 and 2002 during July, August and September, using moths at a 1:1 sex ratio, as maintained in the colony. During 2002, a total of 850 moths was released in the adjacent woods during the last three vineyard releases.

Moth recapture

All traps were checked at regular intervals after release from 12 h to 300 h after release. Pheromone trap inserts with moths were taken to the laboratory and examined by illuminating the moths with a UV light under a microscope for presence of fluorescent dust. Moths captured on sticky panes were removed from the panes with a spatula and taken individually to the laboratory where they were observed in the same way.

Weather data

Weather data were gathered from the Michigan Automated Weather Network (MAWN) (http://www.agweather.geo.msu.edu/mawn) station at the Trevor Nichols Research Complex (42.59°, -86.16°) for hourly averages of wind speed, wind direction, relative humidity, precipitation and air temperature. Hourly averages of these weather factors were selected for every day between 1 July and 21 September for each year. Average values of weather factors from 1700 and 2200 h were calculated, since this is the period during which the grape berry moth flies (G. English-Loeb, pers. comm.). Data from this activity period for each day was again averaged over the period of days from release to recapture (the day before traps were checked) for each recaptured moth.

Data analysis

In order to evaluate the direction of moth flight in relation to wind direction, and to compare differences in flight directions between sexes and trap types, the data on individual moths were analyzed using Oriana software (Version 1.06, 1994). Calculations of Watson's *F*-test were conducted to compare pairs of circular means because this test is particularly powerful for samples of small size (Batschelet 1981). Circular histograms, in which 0° corresponds to the actual North of the spatial location, were produced to show the mean angle direction (MAD) comprising the mean angle (vector) and 95% confidence intervals for each of the wind and moth direction samples. The data on individual moths recaptured were analyzed using the REG procedure (Model 1) (SAS, Version 8.0, SAS Institute 1996) to determine the relationship between weather factors and the distance flown by moths. To determine differences in flight distance between sexes or between moths released in the vineyard and moths released in the woods, the NPAR1WAY procedure (SAS, Version 8.0) was used with a Kruskal-Wallis test (SAS Institute 1996).

Malaise traps to measure movement in and out of vineyards

This study was conducted at three juice grape (*Vitis labrusca*, var. Concord and Niagara) farms in Van Buren Co, Michigan, during 2000. At each farm, two vineyards bordered by deciduous woods on at least one side were selected for deployment of Malaise traps.

Each bi-directional Malaise trap consisted of two traps next to each other facing opposite directions. Each was made of ½ inch and ¾ inch PVC, held together by bolts and covered by white tulle, following the design of Isard et al. (2000) for studies of western corn rootworm. A container made of two similar clear plastic 2 liter soda bottles was placed at the top of each trap to collect flying insects (Figure 4.2a). One of the bottles was cut in two and its upper half was used as a funnel lodged into the upper half of the other cut bottle. The lid of this latter bottle was filled with paradichlorobenzene (PDB) as killing agent, covered with tulle, and screwed back.

Traps were deployed at a wooded edge of each vineyard, within the end row of cultivated grapes (Figure 4.2b), with the vertical poles placed 30 cm into the ground for support, and standing 2.15 m tall. One side faced the inside of the vineyard and the other faced the woods. A second bi-directional Malaise trap was placed across from the first at the edge of the woods with one side open to the woods and the other to the vineyard. Finally, a third bi-directional Malaise trap was placed at a height of 9.0 m directly above the second, so that one side faced the woods canopy and the other faced out from the woods (Figure 4.2b). A PVC pole as described in Chapter 1 was used to place a Malaise trap 9.0 m above the ground. Traps were lifted to the top of the pole with the help of pulleys hung from loop bolts and 30 m long nylon ropes, which were secured to the side of the pole. Each week, when collecting insect samples, traps were pulled down and the contents of the containers were examined. The dead insects trapped in the upper section of the trap were poured into one or several 5 oz. plastic cups labeled with trap number, location, and direction (of insect flight). The cups were then taken to the laboratory in a cooler. Specimens were frozen, to be sorted and counted during the winter. The number of grape berry moths captured in traps, their sex, and the direction of their flight was recorded.

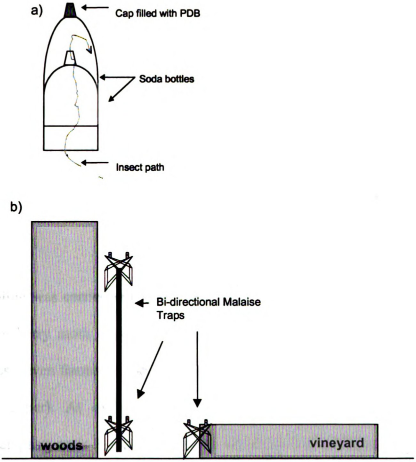

Figure 4.2. a) Detail of the Malaise trap insect collecting containers, made of two tops of 2 liter soda bottles encased in one another, with a lid full of a killing agent. b) Schematic representation of the vineyard set up with two bi-directional Malaise traps placed at the edge of woods and vineyard (gray boxes) at 1.5 m high, and one bi-directional Malaise trap placed 9.0 m high near the woods canopy.

Painted leaves study

This study was conducted after harvest in the fall of 2002 in four juice grape (*V. labrusca*, var. Niagara and Concord) vineyards in Van Buren Co., Michigan. All of the vineyards had deciduous woods to the north and east of the vineyard tested. At each vineyard, two sets of vines were painted; one set on the north of the vineyard (*N-S*), and the second set on the east (*E-W*) (Figure 4.3, lower). Within each set, I painted the leaves on three adjacent border vines located either at the end of three rows or in the middle of one, and three vines in the same position but located 30 m inside the vineyard. Leaves were painted with one of four bright colors (blue, red, orange and neon yellow) using Specialty Lacquer spray (Rust-Oleum Corporation, Vernon Hills, IL) before leaf senescence in October. Paint was applied to the majority of leaves of each vine by spray-painting the top and underside of the vines. Vines in each of the four positions were painted with different colors, to differentiate among leaves from each painted area.

Sampling

Sampling was carried out in the spring after snow melt (April and May) at the time of grape berry moth emergence from diapause. For each set (*N-S* and *E-W*) of colored leaves, seven transects were delineated using a measuring tape and colored flags (Figure 4.3, upper). At each transect, leaves were sampled from ten contiguous rectangular sampling areas 3.0 x 1.5 m (inside area 4.5 m^2) that ran parallel to the woods and vineyard edges, with the mid-point of the sampling in line with the middle painted vine. Transect 1 was inside the woods, Transect 2 was at the edge of the woods, Transect 3 was in the middle of the interface between woods and vineyard (6.1-14.5 m wide), Transect 4 was at the edge of the vineyard near to the border painted vines, Transects 5, 6 and 7 were 15, 30 and 45 m inside the vineyard, with Transect 6 running over the interior painted vines (Figure 4.3). The number of colored leaves inside each rectangle was recorded for each sample, with a separate record made for the different colors applied to vines in each of the *N-S* and *E-W* sets.

Data analysis

The NPAR1WAY procedure (SAS, Version 8.0) was used in a Kruskal-Wallis test to establish differences between sets, between positions and among transects for each set, and between the number of leaves of each color found per transect, including pair-wise comparisons (SAS Institute, 1996).

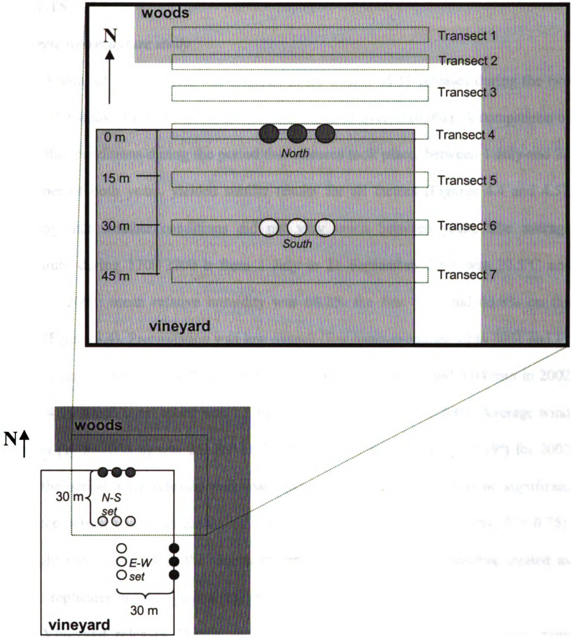

Figure 4.3. Schematic representation (not to scale) of the arrangement of painted vines in the leaf dispersal experiment. Grapevines (circles) at the border and interior of the vineyard in two positions per set (N-S and E-W) were spray-painted with four different colors (lower). The sampling transects are shown by seven parallel transects from the inside of the woods to 45 m inside the vineyard (upper).

RESULTS

Mark-release-recapture study

A total of 3,505 moths was released in the course of 11 releases during the two years of the study (Table 4.1), and 246 were recaptured overall (6.9%). A comparison of the weather conditions during the period that releases took place, between 1 July and 21 September of both years, yielded similar results for all factors (Figures 4.4 and 4.5), indicating that weather conditions did not vary much between years. The average temperature during 1700-2200 h from 1 July to 21 September 2001 was 22.3°C and 24.1°C in 2002; mean relative humidity was 68.2% the first year and 63.8% on the second (Figure 4.4). Precipitation was low overall (few rainy evenings, 10 in 2001 and 12 in 2002 over 83 evenings) with a mean 0.09 mm per day in 2001, and 0.04 mm in 2002 (Figure 4.5). Mean wind speed was 1.2 m/s in 2001 and 1.1 m/s in 2002. Average wind direction (1700-2200 h) was 252.88° (± 7.99°) for 2001 and 249.62° (± 7.19°) for 2002 during the period when releases were made (83 d) (Figure 4.5); there was no significant difference between years as shown by Watson's *F*-test ($F = 0.10$, df = 164, $P = 0.75$). The eight moth releases in the vineyards across both years were therefore treated as separate replicates in subsequent analyses.

Vineyard releases. Within the eight vineyard releases, about nine times more male moths were recaptured than females in 2001, and eight times more in 2002 (Table 4.1), a clear effect of pheromone trap efficacy compared to passive interception traps. In pheromone traps, 173 males were recaptured over the eight releases, while in pane traps the total number of moths recaptured was 29. Of these, 69.1% were females (20).

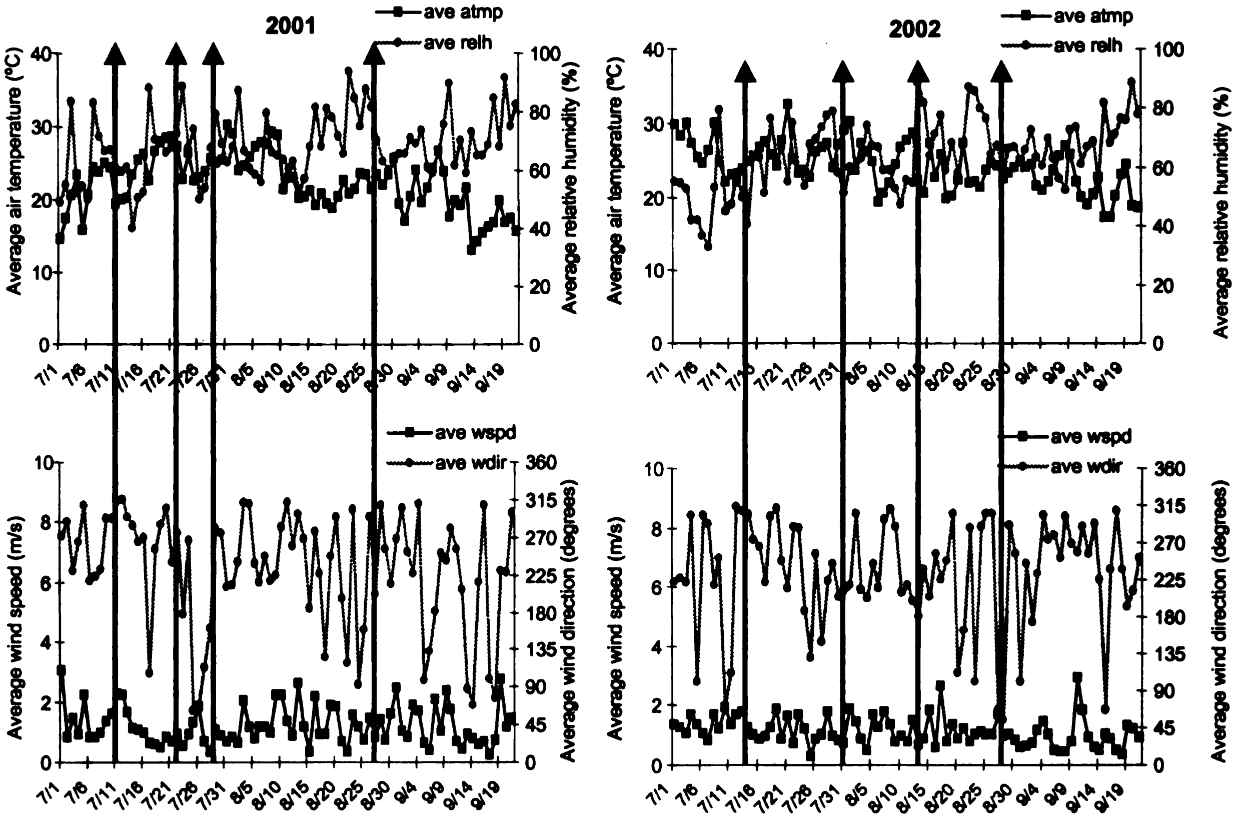

Figure 4.4. Weather conditions during the period between 1 July and 21 September of 2001 and 2002; wind, temperature, and relative humidity. Data were obtained by averaging values between 1700 and 2200 h (moth active time) for each day. Vertical arrows represent releases for each year.

The highest recapture rate was achieved in the release of 31 July 2001, when almost 32% of the estimated males released (210) were recaptured, for a total of 17.1% adult moths recaptured overall (including females) (Table 4.1).

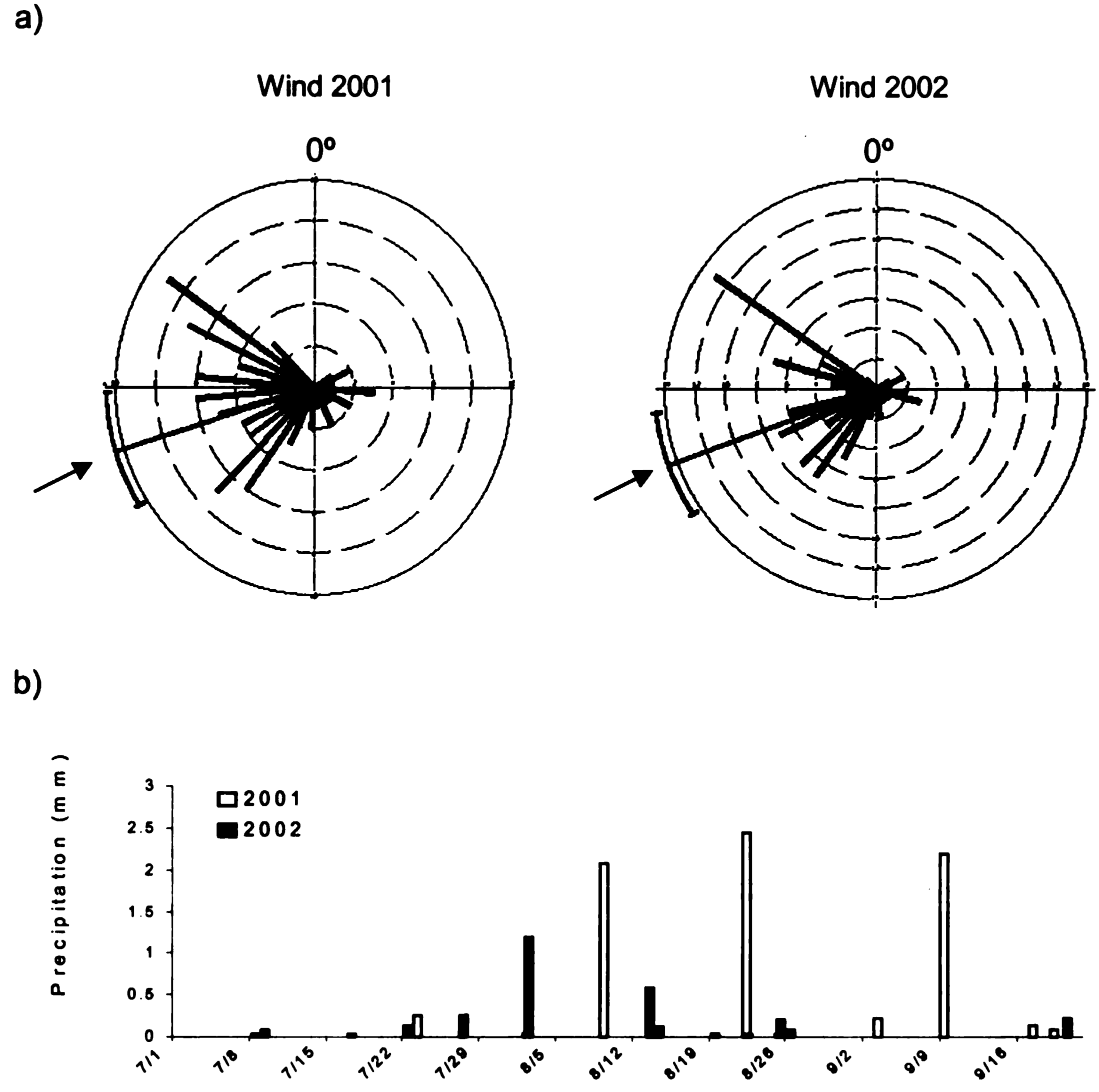

Figure 4.5. Weather conditions during the period between 1 July and 21 September of 2001 and 2002. Data were obtained by averaging values between 1700 and 2200 h (moth active time) for each day. a) Circular histograms with mean angular vector and 95% confidence limits for wind direction for each year. The arrows represent the average wind direction. b) Daily precipitation during moth active time during the period of releases.

The maximum displacement recorded from a vineyard release was that of a male moth captured in a pheromone trap 58.2 m from the central release point (Table 4.2). The maximum distance a female moth moved after being released in the middle of the vineyard was 41.2 m (2001) but the mode for the eight releases was 3.2 m from the central release point. The average displacement of male moths was more than twice that of females, although one female (from a woods release) flew almost twice as far as the average maximum distance male moths flew when released in the vineyard (Table 4.2).

Table 4.1. Total number of marked and recaptured *Endopiza viteana* moths released and recaptured in two habitats. Percentages were calculated for each sex based on a 1:1 sex ratio of released moths.

	Marked *E. viteana* moths				
	# released	# recaptured		% recaptured	
		males	females	males	females
Releases in the vineyard					
12 July 2001	350	11	3	6.3	1.7
24 July 2001	500	40	4	16.0	1.6
31 July 2001	420	67	5	31.9	2.4
31 August 2001	365	26	1	14.3	0.6
17 July 2002	300	24	3	16.0	2.0
1 August 2002	280	2	0	1.4	0.0
15 August 2002	200	15	3	15.0	3.0
28 August 2002	240	17	1	14.2	0.8
Total	**2655**	**202**	**20**	**15.2**	**1.5**
Releases in the woods					
1 August 2002	240	4	1	3.3	0.8
15 August 2002	300	19	0	12.7	0.0
28 August 2002	310	0	0	0.0	0.0
Total	**850**	**23**	**1**	**5.4**	**0.2**

Table 4.2. Maximum and mean distances flown by marked and recaptured *Endopiza viteana* moths released in two habitats, and mean angle of direction flown.

	Max displacement (m)		Mean ± SE displacement (m)		Mean ± SE direction (degrees)	
	males	females	males	females	males	females
Releases in vineyard						
12 July 2001	33.7	18.4	12.4 ± 3.0	7.6 ± 3.6	147.3 ± 28.3	277.5 ± 2.5
24 July 2001	58.2	41.2	14.4 ± 2.1	19.5 ± 3.6	134.3 ± 15.4	130.0 ± 15.8
31 July 2001	58.2	41.2	14.1 ± 1.5	23.1 ± 9.6	184.9 ± 8.2	149.0 ± 51.0
31 August 2001	35.6	3.2	10.4 ± 1.4	3.2 ± 0.0	178.7 ± 18.2	90.0 ± 0.0
17 July 2002	19.3	3.3	8.4 ± 0.7	3.3 ± 0.1	154.4 ± 20.2	33.3 ± 28.3
1 August 2002	7.3	-	7.3 ± 0.0	-	330.0 ± 0.0	-
15 August 2002	53.4	4.0	19.7 ± 3.7	3.5 ± 0.2	162.0 ± 28.1	125.0 ± 81.3
28 August 2002	52.3	3.2	17.1 ± 3.8	3.2 ± 0.0	17.1 ± 3.8	90.0 ± 0.0
Average/moth	**39.7± 6.7**	**19.1± 3.0**	**13.8 ± 0.8**	**11.4 ± 6.7**	**163.6 ± 30.2**	**127.8 ± 28.7**
Releases in woods						
1 August 2002	109.3	79.4	90.6 ± 8.3	-	73.3 ± 4.9	-
15 August 2002	101.5	-	58.5 ± 6.5	-	83.6 ± 7.8	-
28 August 2002	-	-	-	-	-	-
Average/moth	**105.4 ± 3.9**	**79.4 ± 0.0**	**64.1 ± 6.1**		**81.8 ± 6.5**	

Table 4.3. Regression analysis of distance flown by vineyard-released marked *Endopiza viteana* moths against time to recapture and average weather conditions for periods of flight activity between release and recapture of each moth. Significant regressions are in bold.

				Weather factor			
			Time	Wind speed	Air temperature	Rel. humidity	Precipitation
Moths recaptured:		df	(h)	(m/s)	(° C)	(% RH)	(mm)
In pheromone traps							
	F	1,194	8.05	0.98	0.02	1.24	0.02
	P	1,194	**0.005**	0.32	0.88	0.27	0.90
	r^2	1,194	0.04	0.005	0.0001	0.006	0.0001
In pane traps							
	F	1, 27	2.79	4.64	4.65	0.60	1.26
	P	1,27	0.11	**0.04**	**0.04**	0.44	0.27
	r^2	1,27	0.09	0.15	0.15	0.02	0.04
Males							
	F	1,7	108.0	0.93	0.21	0.05	0.03
	P	1,7	**< 0.0001**	0.37	0.66	0.83	0.87
	r^2	1,7	0.94	0.12	0.03	0.007	0.004
Females							
	F	1,18	0.10	3.22	5.07	0.74	1.40
	P	1,18	0.76	0.09	**0.04**	0.40	0.25
	r^2	1,18	0.005	0.15	0.22	0.04	0.07

During the first four releases in the vineyard, variability in mean direction in which moths flew were small, ranging from 134-185 degrees (Table 4.2). Male moths flew on average at a direction of 163.6 degrees (SSE) and females 127.8 degrees (ESE).

Data were split according to the type of trap used. Regression analysis indicated that for moths caught in pheromone traps, the distance flown was positively correlated with time after release (Table 4.3). Since this relationship was not significant for pane trap moths, these were separated by sex, and regression was performed on each sex separately. No significance was found between distance flown and time elapsed from release for females. However, the distances flown by the nine male moths captured in pane traps were positively related to the time after release, with a highly significant coefficient of determination of 0.94. A Kruskal-Wallis test was used to determine differences between sexes for mean distance flown before landing on panes, but no significant difference was found ($X^2 = 0.33$, df = 1, $P = 0.57$).

Weather factors affected the distance flown by moths, in particular the wind speed and air temperature (Table 4.3). For moths caught in panes, distance flown was significantly and negatively correlated with wind speed (Distance flown = – 15.50 Windspeed + 28.99, Table 4.3). The same was true for moths caught in pheromone traps, though not significantly (Distance flown = – 2.61 Windspeed + 16.51, Table 4.3). Air temperature apparently affected female movement more than male movement, which was also reflected in pane traps (Distance flown = 1.55 Temperature – 27.59, Table 4.3).

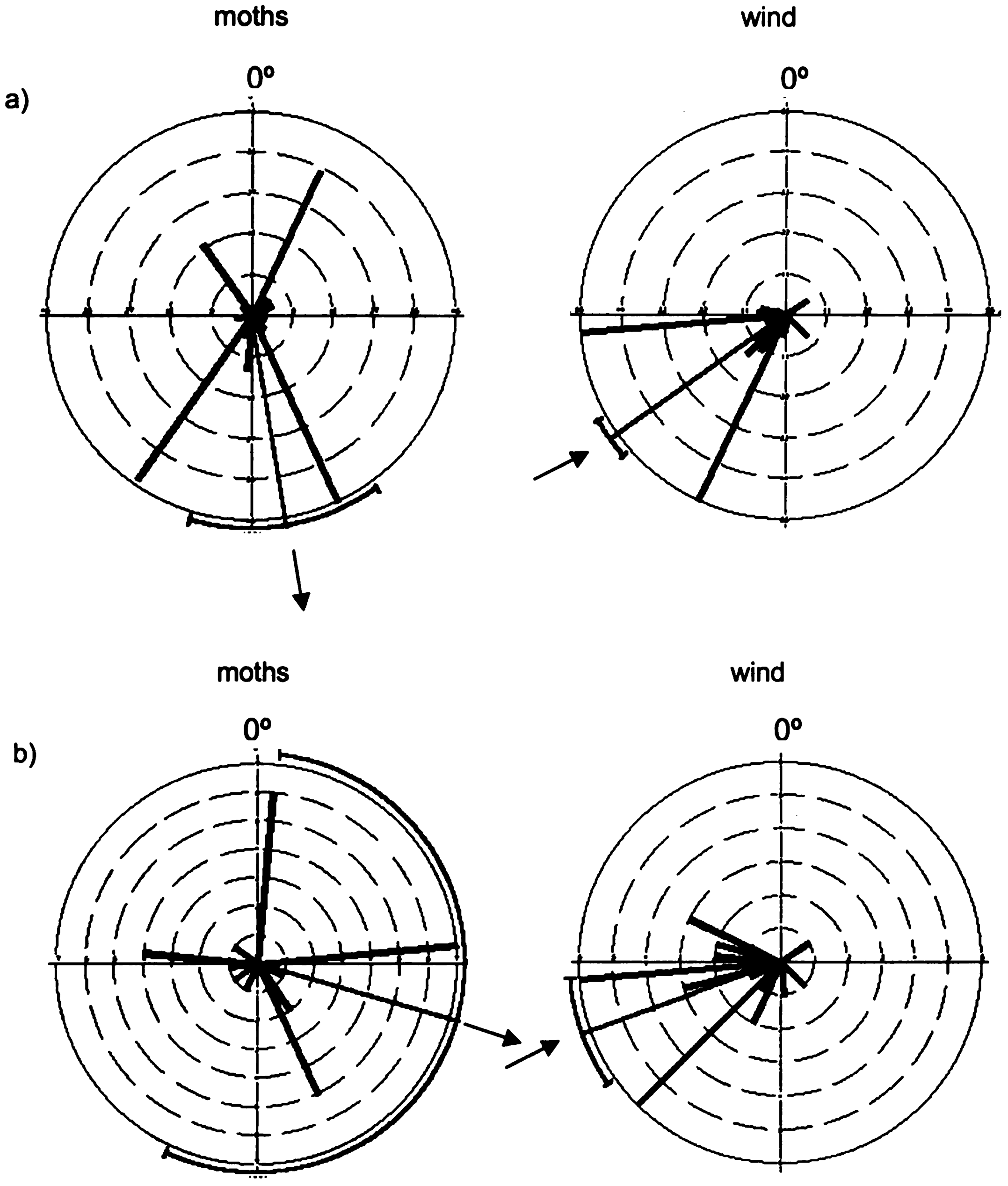

Figure 4.6. Circular histograms of the frequency and distribution of vectors of moths and wind direction for the period that moths were flying between release and recapture in a) pheromone traps and b) pane traps. The mean angular vector with 95% confidence limits runs beyond the outermost circle; the 0° corresponds to the vineyard North and the center of the histogram the vineyard release point, while the arrows represent the average directions taken by the moths and the wind.

Direction of movement by moths captured in pheromone traps was also analyzed separately from moths caught in pane traps. For each case, the direction flown by the moth was compared with the average wind direction during the period the moth flew, to determine whether moth flight was directly influenced by wind direction. For male moths captured in pheromone traps, there was a significant difference between their mean direction and wind direction ($F = 47.01$, df = 390, $P < 0.01$). The mean direction vector for male moths in pheromone traps was 170.34° (± 13.58°) and for wind 234.63° (± 3.00°), indicating that moths moved generally at a tangent to the wind (Figure 4.6a). For the 29 moths captured in pane traps, the difference between average wind direction and moth direction increased and was significant ($F = 16.96$, df = 56, $P < 0.01$), with a mean direction vector for moths of 105.87° (± 50.92°) and for wind of 250.02° (± 7.89°) (Figure 4.5b). When females were analyzed alone against the average wind direction, the difference was again significant ($F = 5.43$, df = 38, $P < 0.03$). Females moved in more different directions overall, with a greater variability between individuals and a mean vector of 88.84° (± 131.52°). Wind direction was much less variable at 243.86° (± 10.92°) (Figure 4.7a). Males caught in panes also had a significantly different flight direction from the mean wind direction ($F = 12.30$, df = 16, $P < 0.01$) with a mean vector of 113.65° (± 53.73°) for males and 260.50° (± 9.78°) for the wind (Figure 4.7b). There was no difference in flight direction between females and males caught in panes ($F = 0.10$, df = 27, $P = 0.76$). No moths released in the vineyard were ever recaptured in the woods or outside the vineyard.

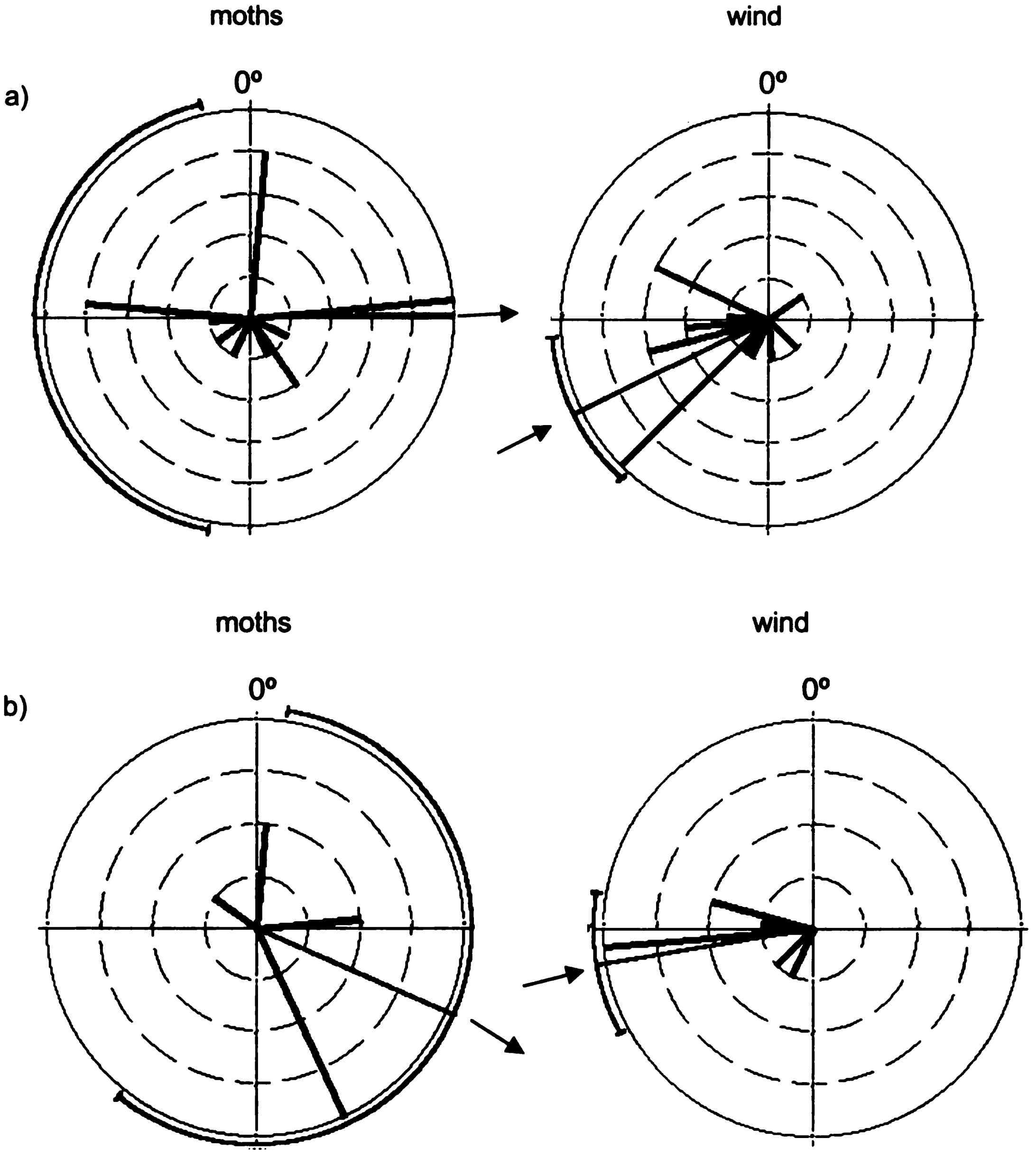

Figure 4.7. Circular histograms of the frequency and distribution of vectors of a) female moths and wind direction and b) male moths and wind direction for the period that moths were flying between release and recapture in pane traps. The mean angular vector with 95% confidence limits runs beyond the outermost circle with 0° corresponding to the vineyard North. The center of the histogram is the vineyard release point, and the arrows represent the directions taken by the moths and the wind.

Woods releases. Of the 850 moths released in the woods, 24 were recaptured, 18 of them in the vineyard and the other six in one pheromone trap at the edge of the woods, facing the vineyard. Male moths released in the woods flew further overall: 64.1 m on average, compared to 13.8 m for males released in the vineyard (Table 4.2). This difference was significant by Kruskal-Wallis ($X^2 = 51.24$, df = 1, $P < 0.0001$). Too few females were recaptured from woods releases to analyze their flight parameters.

A regression analysis of the distance flown by moths released in the woods and the time it took to fly that distance (Table 4.3) yielded a significant relationship ($F_{1,22} = 4.46$, $P = 0.046$) with a coefficient of determination of 0.17 %. Of the four weather factors compared, mean wind speed ($F_{1,22} = 4.51$, $P = 0.05$, $r^2 = 0.17$) and mean precipitation ($F_{1,22} = 4.48$, $P = 0.05$, $r^2 = 0.17$) were not significantly associated with distance flown by moths released in the woods, though these regressions were close to the critical P-value (= 0.0459). Neither relative humidity ($F_{1,22} = 0.09$, $P = 0.77$, $r^2 = 0.04$) nor air temperature ($F_{1,22} = 1.62$, $P = 0.22$, $r^2 = 0.07$) were significantly correlated with distance flown by moths released in the woods. There was a significant difference between the mean angle of moth direction and the mean wind direction ($F = 348.53$, df = 46, $P < 0.01$) with a mean vector for moths of 81.68° (± 6.20°) and 225.34° (± 3.06) for the wind (Figure 4.8). This shows that woods-released moths moved toward the vineyard in preference to any other direction.

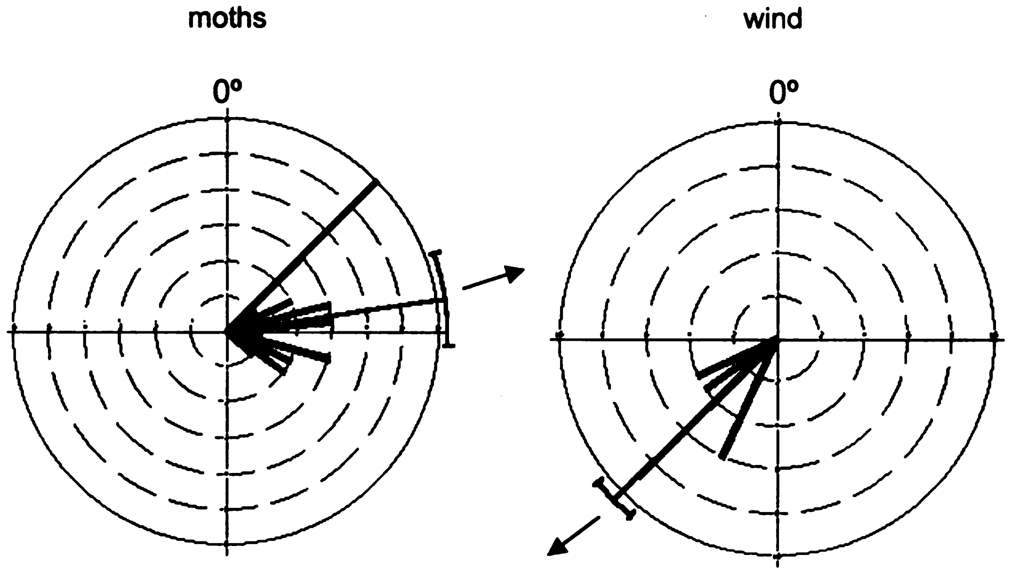

Figure 4.8. Circular histograms of the frequency and distribution of vectors of moths released from the woods and wind direction for the period that moths were flying between release and recapture in vineyard traps. The mean angular vector with 95% confidence limits runs beyond the outermost circle. The 0° corresponds to the vineyard North and the center of the histogram is the vineyard release point. The arrows represent the average direction taken by the moths and the wind.

Malaise trap study

Only five specimens of *E. viteana* were captured with the bi-directional Malaise traps. All five moths were found to be leaving the vineyard at 1.5 m high. This experiment was not repeated after 2000.

Painted leaves study

After seven months in the field, and after the winter snow cover melted, a total of 2,377 painted leaves was found on the ground of the vineyards. Painted leaves were observed as far as 60 m from the point of release (painted vines) in the case of a north painted border leaf that was found on the north-east woods edge of the vineyard. A border leaf painted on the east of the vineyard was observed 29 m away to the northeast, also at the woods edge. A very similar number of leaves was recovered from the N-S set: 1,249 (53%) and the E-W set 1,128 (47%), but more of them came from border vines than from interior ones; the total for the border colors was 1,548 (65.5%) leaves and 829 (34.5%) leaves for the interior colors. A Kruskal-Wallis test determined both sets (N-S and E-W) were not significantly different in the number of leaves recovered, whether these had come from border vines ($X^2 = 0.33$, df = 1, $P = 0.56$) or interior vines ($X^2 = 0.71$, df = 1, $P = 0.39$). An individual analysis of each set suggested border leaves were not distributed evenly across transects ($X^2 = 19.06$, df = 6, $P = 0.004$ for N-S, and $X^2 = 17.13$, df = 6, $P = 0.009$ for E-W) and neither were interior leaves ($X^2 = 12.64$, df = 6, $P = 0.049$ for N-S, $X^2 = 18.10$, df = 6, $P = 0.006$ for E-W). To test whether transect orientation had any effect on leaf distribution, another Kruskal-Wallis tested differences between sets (N-S and E-W) by comparing transect per transect, the number of leaves recovered. No significant difference between sets ($P > 0.08$ for border leaves and $P > 0.16$ for interiors) was found, so they were analyzed together in subsequent analyses.

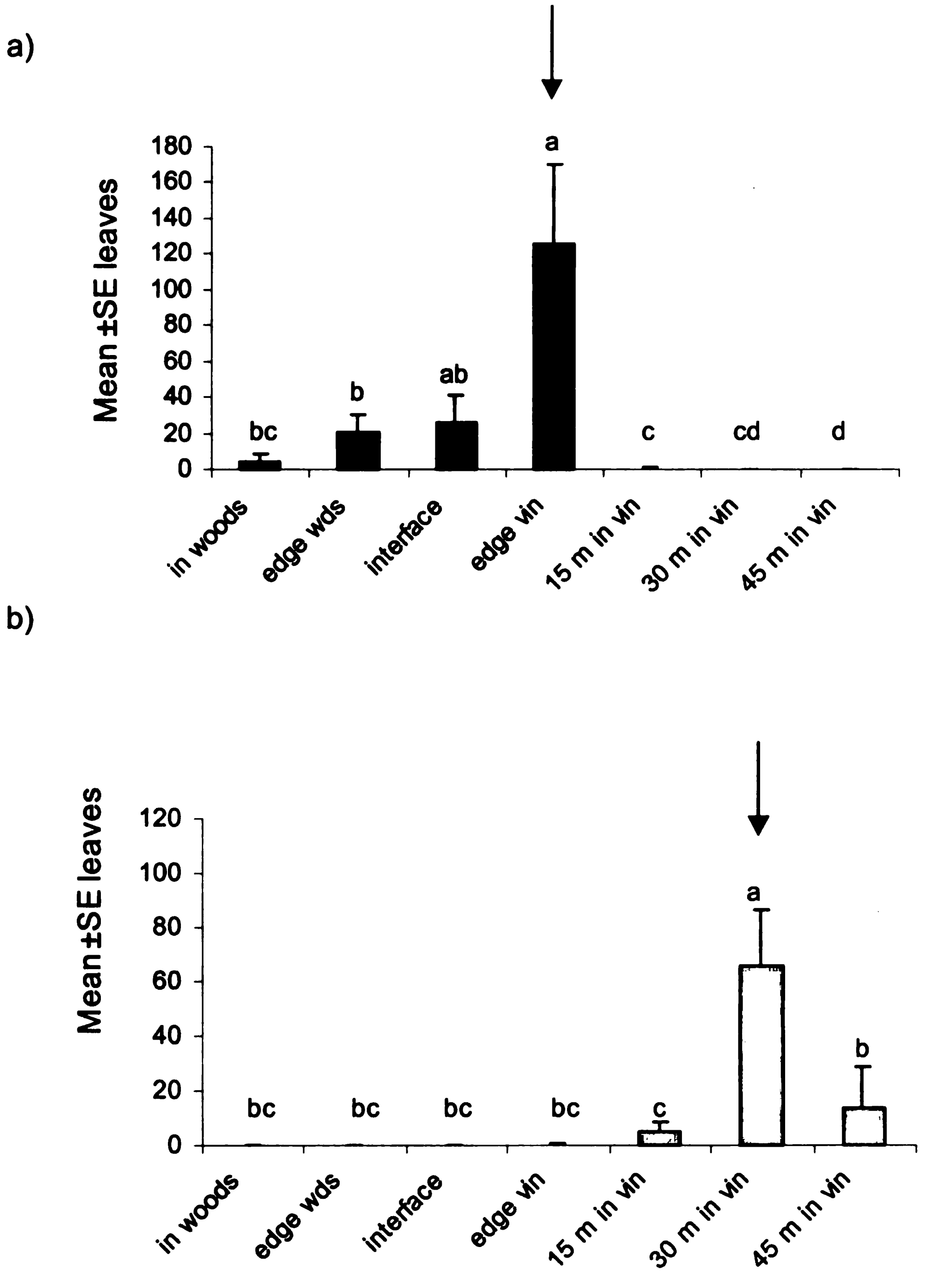

Figure 4.9. Mean ± SE number of leaves counted per transect (45 m^2) from inside the woods habitat to 45 m inside the vineyard, for leaves that were painted on a) border vines and b) interior vines. The arrows indicate the locations of painted vines.

The number of border and interior painted leaves varied significantly among transects (Kruskal-Wallis $X^2 = 35.24$, df = 6, $P < 0.0001$ for border leaves, and $X^2 = 29.83$, df = 6, $P < 0.0001$ for interior leaves). Therefore, pair-wise comparisons between transects were made (Figure 4.9a). Significant differences among transects indicated that the trend of leaf movement was skewed towards the exterior of the vineyard. This was more noticeable for border leaves but also for interior ones (Figure 4.9b).

DISCUSSION

Adult **E. viteana** *movement*

The different sections of this study show the capacity for different methods of dispersal by grape berry moth. The mark-release-recapture method used was successful and suitable for studying *E. viteana* flight behavior in the field, which had not previously been done. I assume that the flight capacity of the moths used, which had been reared in the laboratory, was similar and not different from that of wild moths. This is because the colony was two years old (about 21 generations) but new genes from the original population had been added twice, at approximately the 9th and 21st generation to help conserve feral traits. Given the weather factors of southwest Michigan during the summer months and the proximity of woodlots (24 m in this case) to vineyards, grape berry moth adults are able to immigrate into cultivated grapes up to 109 m away from their point of departure. Although only one female released in the woods was recaptured in the vineyard, it is nonetheless proof that they are able to move beyond a single habitat in their search for their host. It is possible to extrapolate this field study to other field conditions and state that moths within uncultivated habitats such as woods are able to fly from these wild habitats to cultivated grapes. Gravid or virgin female moths can immigrate to vineyards since there was no significant difference between sexes in the distance flown. This coincides with the general knowledge on other species such as the codling moth, *C. pomonella*, which are able to move between distant orchards (Dorn et al. 1999, Keil et al. 2001).

Environmental conditions often determine the extent and occurrence of flight. The average weather conditions between 1700 and 2200 h during the months this study took place were amenable to moth flight (Figure 4.4). Wind speed was the most important abiotic factor affecting moth dispersal (Table 4.3) but the average speed was 1.2 m/s in 2001 and 1.1 m/s in 2002, well into the range of 0.5-2 m/s cited as the range for take off for many insects (Pasek 1988, Colvin 1995). Researchers in New York (G. English-Loeb, pers. comm.) have studied grape berry moth flight in wind tunnels and noted that this species engages in flight at wind speeds of 0.5-1.0 m/s, suggesting that *E. viteana* are not strong fliers. The negative correlation between wind speed and the distance flown by moths before landing on a pane trap was weak ($r^2 = 0.15$) but this was expected given that wind speeds around 3.0 m/s inhibit flight in small insects (Kisimoto and Sogawa 1995). Wind speed and precipitation had a greater influence on moths released in the woods than relative humidity or air temperature, probably because greater distances of dispersal require more effort than short intra-habitat movements. It is noteworthy to find that there could be differences in flight capacity or flight direction between different generations of this species, perhaps in response to vine phenology, though there are no studies on *E. viteana* to indicate this.

The difference in direction of moth movement and wind shown above indicates that moths have some control over their dispersal. Pheromone trap-recaptured moths generally flew south when they were released at the vineyard center (Figure 4.6a), at a tangent from where the wind direction. Male moths exhibited more directed flight than females (Figure 4.7) who were distributed in many directions. Perhaps this is because males fly across oncoming wind in order to catch pheromone plumes from females as they are emitted further downwind, whereas females are moving to locate oviposition substrate. The case for a directed flight in grape berry moth can be better made with the example of moths released in the woods (Figure 4.8). In this case, regardless of the presence of pheromone traps located in directions from 135-360° from the woods release point, moths flew east towards the vineyard. This would signify that pheromone plumes were not responsible for driving the movement, but rather that moths were flying towards hosts. Because six of these moths were recaptured in the woods before crossing the interface towards the vineyard, it is to be expected that they encountered the pheromone plume and were diverted from their direction. An important finding is that moths released in the woods flew significantly greater distances than moths released in the middle of the vineyard, which is perhaps a sign that *E. viteana* is able to exhibit short and long-range flights.

Pheromone traps were successful at re-capturing marked male moths and passive-interception traps proved useful in capturing moths of both sexes. Special attention should be given to pane trap placement, since they need to be sufficiently within the grape canopy so as to interfere with moth flight, but yet leaves should not stick to them.

The fact that more females than males were captured in pane traps suggests a difference in flight strategies between sexes. For example, females tend to fly inside the canopy, where clusters are located, and hit the pane traps located within the leaves and fruit more easily than males who are flying more externally to catch pheromone drift. A difference in flight movement between sexes may also be indicated by the fact that time between release and recapture was positively correlated with distance flown for males captured in pane traps but not females (Table 4.3). Females released in the vineyard did not fly long distances before their recapture (Table 4.2). This could mean that females move in short bouts and displace little in a given amount of time, whereas males engage in more prolonged flights and therefore reach farther distances sooner. The difference in female and male maximum displacement was somewhat consistent throughout eight releases, with males displacing farther (Table 4.2) which may be due to difference in behaviors of each sex while searching for virgin mates or oviposition substrate.

The data obtained are the first record of displacement for *E. viteana* of either sex, and it will be important to follow with studies on maximum flight capacity in this species. The average maximum displacement of female *E. viteana* was ten times lower than for the oriental fruit moth, *C. molesta* (Hughes and Dorn 2002), but more studies are necessary to assess how this translates into flight ability and capacity. This species may be poor fliers as has been suggested by Nagarkatti et al. (2002a), or short fliers that make repetitive bouts of movement.

Malaise trapping

Malaise trapping was not an effective passive method for capturing *E. viteana,* although the traps themselves may be useful for other species. Multiple non-target specimens were collected, mainly Diptera, some Hymenoptera and a few Lepidoptera. However, *E. viteana* did not appear to respond to the trap at the rate expected (only five moths captured), perhaps because the grape berry moth is not a very good flier and because flight takes place mostly within the canopy of the vines which are not thoroughly sampled by the trap. In addition to the behavioral aspect, several physical factors contributed to the failure of the Malaise trapping experiment. Powerful winds exerted excessive force against the bi-directional Malaise traps at the top of the poles, made more susceptible by the fact they stood 9.0 m high. Several of the poles bent and/or fell apart, bringing down the Malaise traps with them. The traps had sturdy and flexible PVC frames that never broke, but the veil (tulle) ripped and the insect collectors fell apart from the impact, scattering the insects collected during the week. Samples from different sites and different weeks were thus lost, in addition to the fact that some insect containers of the ground traps (at 2.15 m high) disappeared. The experiment was kept going nonetheless all through the summer, but because of the missing samples, it was deemed incomplete.

Passive movement of E. viteana

The study on leaf movement yielded interesting results regarding the potential for passive movement of the overwintering stage of *E. viteana*. This showed that there is movement of dead leaves in vineyards during the winter season, and that this movement is away from the vine on which the leaf grew. Furthermore, this movement is directed towards the exterior of the vineyard toward adjacent habitats. This movement may potentially affect the distribution and survival of overwintering grape berry moths that pupate in leaves. The position of painted leaves in the spring indicated that leaves on border vines disperse during the winter months towards the woods more than into the vineyard (Figure 4.9), while interior leaves disperse less and tend to stay near the vines from which they fall (Figure 9). Sampling along the woods transects for the N-S sets indicated that leaf movement not only occurred towards the north, it also tended towards the east, to distances up to 29 m away from the vine of origin. Likewise, sampling for the E-W sets yielded painted leaves 60 m away to the north of the vine they dropped from. This reveals not only a considerable capacity for dispersal of a passively moving pupa, but also that winds may be a factor to take into consideration when assessing the impact of grape berry moth on a vineyard. Wind direction will influence dead leaf transport during the winter months. The impact of snow cover and rain and patterns of water drainage should be explored further to see if it has any impact on leaf dispersal during the winter months. However, it is important to state that I do not know whether a painted leaf moves as would an unpainted leaf. I assume that they do, and that it is likely the paint did not hamper the passive transportation of the leaves. Likewise, I do not know how long pupae stay on the leaves before these rot, since painted and unpainted leaves were found in varying levels of decomposition. It would be necessary to address these questions in order to confirm movement of pupae within the vineyard.

There are several final points to be made about *E. viteana* movement within the grape system of Michigan. The displacement distances observed in this study would suggest that *E. viteana* does not move too far within the grape agroecosystem. On the other hand, we do not know whether this species undertakes long flights because the farthest trap in this study was located less than 150 m from moth origin. It is important to study flight capacity in the grape berry moth, to determine expected distances covered by moths moving between habitats, the propensity for long-range flights in *E. viteana,* and whether this dispersal is affected by age, sex or physiological state. Afterwards, it will be important to remember that some exchange of moths between cultivated and wild grapes can be favorable to growers because the exchange of genes may help delay development of resistance (Nagarkatti et al. 2002b). The studies described here demonstrate that moths can move between wild and cultivated habitats by both active and passive transport.

CHAPTER 5:

CONCLUSIONS AND FUTURE RESEARCH NEEDS

Research presented in this thesis helps to explain why pheromone traps, helpful in determining the onset of grape berry moth flight, fail to provide accurate information on the pest pressure in vineyards later in the season. These traps attract only males, and may lose attractiveness as the season progresses due to competition with virgin females, as has been found for codling moth (Howell 1974) and the sunflower moth (Pyralidae) (Aslam et al. 1990). Traps placed at 1.5 m height in the woods near vineyards may misrepresent the degree of pest pressure expected from the surrounding habitat because they would underestimate the population size in the latter part of the season. The findings in Chapter 2 suggest that male moths preferably fly in the woods canopy, and they may aggregate in areas where females are more likely to be, near fruit clusters where oviposition must take place. Wild grapes seldom fruit in the shade of the woods under a dense canopy, and grapevines are more likely to survive by climbing on trees to reach sunlight. High male abundance in the woods canopy therefore could indicate that females are present near fruit clusters, similar to males of the webbing clothes moth (Tineidae) that are more likely to successfully mate if they first find adequate larval substrate for females (Takacs et al. 2002). Future studies should verify the distribution of female moths in this system, and understand the mechanisms that trigger grape berry moth attraction to grapes. The development of attract and kill strategies for grape berry moth would be improved if we knew more about mating behavior (e.g. how many times *E. viteana* mates), since there is the possibility that males that have contacted a toxicant may pass it along to the female during mating.

The data in Chapter 3 demonstrate that high levels of infestation in vineyard borders are largely influenced by the proximity of the vineyard to habitats containing wild grape. The area of influence of these adjacent habitats would be a suitable object of future studies, similar to landscape context research of Thies et al. (2003). We need to find out if the effect of deciduous woods, for example, varies with distance from the vineyard. We need to explore the effect that woods size and density of woodlots at the landscape level may have on grape berry moth pest pressure. This can and should all be linked to studies on grape berry moth flight capacity, because the spatial context should take into consideration the dispersal capacity of the insect. Ultimately, these studies could help elucidate why mating disruption practices have failed in some areas (Dennehy et al. 1990, R. Isaacs, pers. comm.), or have great potential in others (Trimble et al. 1993).

The ability to predict deleterious pest impact on a vineyard may depend on more than one parameter of the wild grape or its habitat near to a vineyard. Presence of wild grape fruit clusters in woods were found to be insufficient for reliable prediction of pest impact in adjacent vineyards (Chapter 3), and the same was found for grapevine abundance. However, improved predictive power may be possible if these two parameters could be combined to develop a factor representing the abundance of fruiting vines. To illustrate this, results from Chapter 3 were combined so that sites where wild fruit clusters were observed would carry greater weight than sites where clusters were not observed, independent of each site's wild grape index. The following equation was applied to calculate a combined predictor (CP):

$$CP = WGI + (F \times WGI)$$

where WGI = sum of vines observed at the site (same as in Chapter 3) and F = fruit presence at the site (0 or 1). Taking July of 2001 as an example, by using CP values in a regression analysis (REG PROCEDURE, SAS Institute, 1996) with cluster infestation levels in vineyard, coefficients of determination increased while significance was observed for both borders ($P = 0.004$, $r^2 = 0.30$) and interiors ($P = 0.04$, $r^2 = 0.17$), compared to data from Chapter 3 (Figures 3.2 and 3.3). This example illustrates the possibilities of being able to better predict *E. viteana* pest impact on a given month through the use of a new wild host parameter.

Having determined at least that the presence of wild grapevines in adjacent habitats can be injurious to neighboring vineyards; the removal of wild vines may decrease pressure from this pest. However, removing wild hosts may be deleterious to natural enemies of *E. viteana* (Seaman et al. 1990, Landis 1994, Nagarkatti et al. 2002a). Future research should focus on a thorough survey of parasitoids and other natural enemies of this species in Michigan, to compare with the studies of Slingerland (1904), Seaman et al. (1990), and Nagarkatti et al. (2002a) and determine how much they benefit grape culture by reducing the incidence of pest insects.

Another topic that should be addressed in the future is how different species of *Vitis* are used by grape berry moths. We do not know whether *E. viteana* prefer a particular species of wild vines, but there are reports of some varieties of cultivated *labrusca* (e.g. Catawba) that are less susceptible to this insect (B. Blum, pers. comm.). These studies should include female moth preference for these different species of wild grapes and also survival rates of the several stages from 1st instar to adult. The results of such studies should then be linked to studies on natural enemies, to determine whether *E.*

viteana population dynamics differ not only according at the vineyard-uncultivated habitat scale, but also within uncultivated habitats.

Movement of gravid females from woods into vineyards to lay eggs on cultivated grapes is a significant possibility (Dennehy et al. 1990, Trimble 1993) as was concluded in Chapter 4. Future research should address flight capacity of the grape berry moth as conducted previously with other fruit pests (Dorn et al. 1999) to determine differences between sexes, age, and mating status. Flight behavior data can then be joined with information on landscape context studies to be able to rationally assess grape berry moth impact on vineyards in a certain region. It is also important to consider the possibility that different races of *E. viteana* (proposed by Tobin et al. 2002) have different strategies and may behave differently in different grape agroecosystems.

Although not presented in this thesis, I often detected moth presence in the woods traps when vineyard traps did not catch any. Consequently, one implication of this research for grape growers is that by monitoring moth presence in uncultivated habitats, the quality of the information (e.g. onset of flight, hotspots of abundance near vineyards) would greatly improve if growing degree day models are shown to help predict optimal spray timings with more accuracy. Pheromone traps should be placed inside and at the edge of woods, at the highest level the scout can reach without it taking too much time to check the traps. Secondly, these studies indicate the need to take the entire habitat into consideration when selecting a site for vineyard establishment. Uncultivated habitats nearby may cause future pest pressure on the grapes, as is the case with deciduous woods. Increasing the distance between these areas and the prospective vineyard should serve as a preventive measure in pest management, though there is still a need to determine this minimum distance. Cultivation of other crops around grapes can serve as a 'safety belt' against immigration by the grape berry moth, and casual observations of vineyards in SW Michigan indicate that these buffers are highly effective in maintaining a low population of grape berry moth.

Some of the vineyards studied indicated very high pest pressure, pointing to the need for integrated strategies to reduce grape berry moth populations in and around vineyards. This includes, as stated above, locating uncultivated areas, and within these, sampling for wild grape and determining the potential risk they pose for grape berry moth infestation (i.e. presence of clusters). Deciduous woods and fruiting wild vines will be the most important factors to sample. Wild grape clusters and clusters in the vineyard border should be examined for presence of natural enemies. Finally, returning to cultural practices implemented in the 1800s and early 1900s, such as raking and chopping of leaves in the fall would be advisable, since this would help destroy part of the population that is overwintering in the vineyard.

The conclusions of this study are a lesson in not underestimating nature. Grape berry moth populations have been affected by the removal of woodlots and their replacement with crops of different kinds, but they have been able to colonize vineyards and flourish in the wood fragments left within this landscape mosaic. Uncultivated habitats are typically considered beneficial to agriculture by their provision of refuges for parasitoids and predators (e.g. Kareiva 1983). However, when they harbor pest insects and allow them to escape management practices applied to the vineyard crop, they can be detrimental to the production of grapes. Insects have dynamic populations that thrive to occupy every possible niche present in agroecosystems, and this research shows that this is true for *E. viteana* in the grape growing regions of Michigan.

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APPENDICES

APPENDIX 1

Taxonomic note on *Endopiza viteana* Clemens.

As described in Chapter 1, there has been some confusion regarding the taxonomy of *E. viteana*. In Clemens' (1860) description of *viteana*, he placed a question mark next to the genus to which he assigned the species, *Endopiza*. In point of fact, *Endopiza* is a misspelling of *Endopisa* (J. Brown[1], pers. comm.), which is now considered a synonym of *Grapholita* (Poole and Gentili 1996). When Obraztsov revised the group in 1953, he recognized that *viteana* and relatives did not belong in the same genus as *botrana* (i.e., *Lobesia*), nor did they belong in *Endopisa;* hence, he described *Paralobesia* to accommodate these species (J. Brown, pers. comm.). Diakonoff in 1973 interpreted Clemens' *Endopiza* as a valid genus (with the type species of *viteana*), rather than a misspelling, and relegated *Paralobesia* to the status of a junior synonym of *Endopiza* (i.e., *Endopiza* is the senior synonym by priority) (Hodges 1983). Powell in 1983 followed Diakonoff, recognizing *Endopiza* as a valid genus, and since the mid-1980s the species has been referred to most frequently in the literature as *Endopiza viteana* Clemens. However, according to J. Brown (pers. comm.) Diakonoff was incorrect in resurrecting *Endopiza* because a misspelling cannot be interpreted as the proposal of a new genus. For this reason, the Obraztsov genus *Paralobesia* is valid and the correct name should be *Paralobesia viteana* (Clemens). This is the name that Brown uses in the new World Catalogue on Tortricids to be published in spring of 2004 (J. Brown, pers. comm.); however, until then and for simplicity, I refer to this species by the name in the title of this dissertation.

[1] Systematic Entomology Laboratory, USDA, c/o National Museum of Natural History, Washington D.C.

APPENDIX 2

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2003-07

Title of thesis or dissertation (or other research projects):

BEHAVIORAL ECOLOGY OF THE GRAPE BERRY MOTH, *ENDOPIZA VITEANA* CLEMENS, IN MICHIGAN AGROECOSYSTEMS

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s)
Natalia Botero-Garcés................

Date August 22, 2003

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America.
Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:
Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Appendix 2.1

Voucher Specimen Data

Page 1 of 1 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults	Adults	Other	Museum where deposited
Endopiza viteana Clemens	MI, Ingham Co., East Lansing Natalia Botero-Garcés various dates 1999-2001 from Grape Berry Moth colony					7	9		
	MI, Van Buren Co., Paw Paw Natalia Botero-Garcés various dates 1999-2000					2	1		
	MI, Van Buren Co., Lawton Natalia Botero-Garcés 15-Aug-2000						1		
	MI, Berrien Co. Zsofia Szendrei 18-Jul-2000					1			

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Natalia Botero-Garcés

Date 22 August 2003

Voucher No. 2003-07

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

22 AUG 2003

Curator Date