Journal of Integrated Pest Management (*2016*) 7(1): 2; 1–12
doi: 10.1093/jipm/pmv023
Profile

OXFORD

Natural History, Ecology, and Management of the Mexican Bean Beetle (Coleoptera: Coccinellidae) in the United States

L. B. Nottingham,[1,2] G. P. Dively,[3] P. B. Schultz,[4] D. A. Herbert,[5] and T. P. Kuhar[1]

[1]Department of Entomology, Virginia Tech, 170 Drillfield Dr., 216 Price Hall, Blacksburg, VA 24061-0319 (louisn@vt.edu; tkuhar@vt.edu), [2]Corresponding author, e-mail: louisn@vt.edu, [3]Department of Entomology, University of Maryland, 4112A Plant Sciences Bldg., College Park, MD 20742-4454 (galen@umd.edu), [4]Department of Entomology, Virginia Tech, Hampton Roads AREC, 1444 Diamond Springs Rd., Virginia Beach, VA 23455 (schultzp@vt.edu), and [5]Department of Entomology, Virginia Tech, Tidewater AREC, 6321 Holland Rd., Suffolk, VA 23437 (herbert@vt.edu)

Received 1 October 2015; Accepted 13 November 2015

Abstract

Mexican bean beetle, *Epilachna varivestis* Mulsant, is an invasive, phytophagous ladybeetle that has occurred in the United States since the late 1800s. In the 1970s, it was a major defoliating pest of soybeans in the eastern United States, before populations mysteriously crashed. Today, the insect remains a devastating pest of *Phaseolus* species, such as common bean, *P. vulgaris*, and lima bean, *P. lunatus*, in geographic locations with moderate summer temperatures and regular rainfall, such as the Mid-Atlantic and southern Appalachian Mountain regions of the United States. Larvae and adults injure plants by consuming leaf tissue, which promotes desiccation and decreases photosynthetic activity. Beetle damage can be successfully mitigated with various insecticides (both conventional and organic), or via augmentative releases of the biological control agent, *Pediobius foveolatus* (Crawford). Various cultural and mechanical management tactics also exhibit management potential; however, more research is necessary to determine specific criteria for effective implementation of these strategies. This paper will review the general biology of Mexican bean beetle, management options to mitigate crop damage, and its historical timeline as a pest in the United States.

Key words: Mexican bean beetle, *Phaseolus*, Coccinellidae, pest management, biology

Mexican bean beetle, *Epilachna varivestis* Mulsant, is an above-ground chewing pest of many commercially grown legumes (Fabaceae). Hosts may include tepary beans (*Phaseolus acutifolius*), common beans (*Phaseolus vulgaris*), lima beans (*Phaseolus lunatus*), soybeans (*Glycine max*), alfalfa (*Medicago sativa*), beggarweed (*Desmodium incanum*), and cowpea (*Vigna unguiculata*); however, this insect survives and reproduces most successfully on bean species in the genus *Phaseolus* (Friend and Turner 1931, Bernhardt and Shepard 1978). The native range of Mexican bean beetle is thought to be in the high elevations of western Mexico and Central America, though the exact distribution is unknown (Howard and English 1924). The current range includes most of the United States and southern Canada (Marcovitch and Stanley 1930, Nicholas and Kogan 1972, Fess 2008). Damaging populations are most common in the Mid-Atlantic and southern Appalachian Mountain regions of the United States (Nottingham and Kuhar 2013, 2014a), due to moderate summer temperatures (high, day-time temperatures between 25 and 29.5°C [77 and 85°F]) and regular summer rainfall (Marcovitch and Stanley 1930, Sweetman 1932).

Beetles overwinter as adults and emerge in the late spring or early summer to feed and mate (Friend and Turner 1931, Howard 1941; Fig. 1). Oviposition may occur from spring until fall (Howard and English 1924). All lifestages of this insect occur within the canopy of host plants, making this pest easy to find and identify. Larvae and adults feed primarily on the soft leaf tissue of hosts plants, resulting in leaves that appear lacy and skeletonized (Howard 1941; Fig. 2). Larvae and adults also feed on pods as a secondary option (Howard 1924). Although past documents suggest that pod damage occurs after plants are severely defoliated (Howard and English 1924, Capinera 2001), our observations in Virginia indicate that it is fairly common for beetles to damage pods, even while leaf matter is available (Fig. 3; L. B. N., unpublished data).

Description and Life Cycle

Adult

Like many coccinellids, Mexican bean beetle adults have a round body shape, a concealed head, and black dorsal spots. Immediately

Fig. 1. Mexican bean beetle adult (right) and eggs (left) on a snap bean leaf. (Photo by L. B. Nottingham)

Fig. 2. Skeletonized snap bean leaf from Mexican bean beetle feeding. (Photo by L. B. Nottingham)

following eclosion from the pupal stage, the visible cuticle of the adult is bright yellow and often without spots. Spots generally develop within minutes or hours, and the cuticle will gradually darken to a copper color within two to three weeks (Fig. 4; Friend and Turner 1931). Each elytron has eight black spots in three horizontal rows. Adults are 6–8 mm (0.24–0.31 in) long and 4–6 mm (0.16–0.24 in) wide, though size varies based on their diet and sex (Friend and Turner 1931). Males are usually smaller than females, and can be distinguished by a notch at the end of the last abdominal segment (Fig. 5; Capinera 2001). Adults can walk and fly, but often remain in one location once they have found a suitable host. Adults spend much of their time feeding and mating within the plant canopy; however, adults can fly long distances to find host plants after overwintering, disperse when populations become crowded, or when locating overwintering sites (Howard and English 1924, Auclair 1959).

Fig. 3. Mexican bean beetle larva feeding on a snap bean pod, despite availability of sufficient leaf matter. (Photo by L. B. Nottingham)

Egg

Eggs are light yellow when first deposited (Fig. 1), but darken when they are close to hatching (Capinera 2001). They are 1.2 mm (0.05 in) long and 0.6 mm (0.02 in) wide. Clusters of 30–70 eggs are deposited on the undersides of leaves to avoid direct sunlight, which increases egg mortality (Howard and English 1924, Miller 1930, Barrigossi 1997). Eggs typically hatch within seven days (Capinera 2001). Eggs can hatch sooner as temperatures increase; however, total hatch is generally reduced in warmer conditions (Howard and English 1924).

Larva

Larvae are cylindrical and soft bodied. The cuticle is yellow and covered in spines that are either black, or yellow with black tips (Fig. 6). Mexican bean beetle larvae are stout and sluggish, compared with the larvae of predatory lady beetles. They generally remain on the undersides of leaves where they continuously feed on leaf tissue (Friend and Turner 1931). Larvae undergo four instars in ∼20 d, growing from 1.5 mm (0.06 in) to 8.5 mm (0.33 in) long. First instars develop in 4–6 d; second instars in 2–4 d; third instars in 3–5 d; and fourth instars in 6–10 d (Friend and Turner 1931).

Fig. 4. Mexican bean beetle adults form spots and darken with age. Youngest (far left) to oldest (far right). (Photos by L. B. Nottingham)

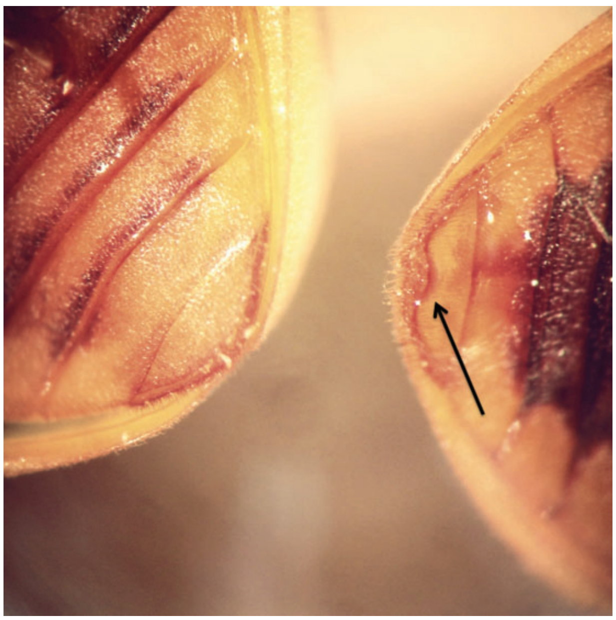

Fig. 5. Sex distinction among adults. Male (on right with arrow) exhibits a small, concave notch on the posterior end of the abdomen. Notch is not present on the female (left). (Photo by L. B. Nottingham)

Fig. 6. Mexican bean beetle larva. (Photo by Taliaferro Trope)

Fig. 7. Mexican bean beetle pupae in aggregation. (Photo by L. B. Nottingham)

Pupa

Pupae are similar in general appearance to larvae; however, at this stage, the beetle attaches to a plant by its posterior end and becomes immobile (Friend and Turner 1931). Pupae are often found aggregated on a single leaf (Howard and English 1924) in the lower half of the plant canopy (Fig. 7). Within the first couple of days as a pupa, the spiny cuticle turns pale and recedes to the posterior end of the insect. The rest of the pupa is yellow and relatively smooth. Pupation lasts about 9 d (Friend and Turner 1931, Capinera 2001).

Overwintering

Mexican bean beetle overwinters as an adult and emerges in the late spring to early summer, after 238–277 degree days baseline temperature: 10°C [50°F]; (Fess 2008). Higher levels of precipitation during overwintering months can increase survival and emergence of overwintering adults (Douglass 1933, Auclair 1959). Beetles generally overwinter in groups, and in areas with well-draining soils and leaf cover (Howard and English 1924, Friend and Turner 1931). Leaf litter such as pine needles was shown to provide the highest quality substrate for beetle survival, rather than open fields or crop debris (Thomas 1924).

Feeding and Injury

Adults and larvae feed on plant tissue with chewing mouthparts; however, Howard (1941) described the mechanism as being unique, and more similar to the rasping and sucking technique used by thrips. Beetles use their mandibles to scrape the leaf surface, piling plant tissue together. The mandibles then compress the dislodged tissue, extracting plant juices. Plant juices are ingested, while solid matter is discarded.

The majority of feeding injury occurs from third and fourth instars (McAvoy and Smith 1979). Beetles generally feed on the lower leaf surface while avoiding veins, creating a lacy, skeletonized appearance of the remaining leaf (Howard 1941; Fig. 2). Foliar feeding injury results in decreased photosynthetic activity and desiccation of the plant (Peterson et al. 1998). Though beetles feed primarily on the foliage, they will also feed on pods and flowers once they become present (Howard and English 1924, Capinera 2001). Even minor pod feeding can render the fruit unmarketable, as well as increasing opportunity for plant pathogen entry (Krupke et al. 2015).

When other environmental conditions are favorable (particularly adequate rainfall), beans can tolerate a fair amount of pest injury (Haile et al. 1998). Common beans and soybeans can withstand 45–80% defoliation at vegetative stages, and 20–60% at flowering and pod fill stages before yields decrease (Capinera et al. 1987, Schaafsma and Ablett 1994, Haile et al. 1998). Unfortunately, Mexican bean beetle also prevails under moist conditions. Consistent rainfall increases survivorship of all life stages (Marcovitch and Stanley 1930, Miller 1930, Sweetman 1932, Kitayama et al. 1979, Wilson et al. 1982) as well as larval feeding (McAvoy and Smith 1979).

Because environmental conditions can affect the fitness of both pest and host, economic injury levels and treatment recommendations can be dubious, or even misleading. For instance, while beans may be capable of tolerating more foliar feeding in high precipitation years, densities of Mexican bean beetle may be higher under those conditions as well. Moreover, larger pest populations are more likely to damage pods. Also, the larger the pest population, the higher the number of individuals that will go into overwintering and emerge the following spring. During dry conditions, Mexican bean beetle populations may stay below threshold levels; however, beans will be more sensitive to desiccation from feeding injury. For these reasons, it is important to consider the weather when making pest management decisions. See section "Management" (Chemical) for thresholds and treatment recommendations.

Colonization of Host Plants

In the eastern United States, spring-planted snap beans (stringless common beans sold for fresh market consumption) and lima beans are typically already growing when beetles emerge from overwintering, allowing beetles to move directly into these crops (Fess 2008, Gatton 2008). If preferred hosts are not initially available, emerging beetles may occupy less preferred legumes, such as kudzu, *Pueraria lobate*, alfalfa, *Medicago sativa*, cowpea, *Vigna unguiculata*, and beggarweed, *Desmodium incanum* (Howard 1924, Friend and Turner 1931, Barrigossi 1997). Overwintered adults are capable of flying long distances to find host plants (Auclair 1959). Once a host is located, females will feed for ~12 d before depositing their eggs (Bernhardt and Shepard 1979). Females lay eggs throughout the season, producing between 500–1,200 eggs per female (Friend and Turner 1931, Sweetman 1932, Capinera 2001).

Snap beans are usually harvested in mid to late summer, at which point beetles may move into less preferred crops (often soybeans) if snap or lima beans are no longer available. In some cases, especially in cool and wet conditions, beetles may cause economic damage to these secondary hosts (Howard and English 1924, Wilson et al. 1982).

Susceptibility and Resistance Among Host Plants

Like most herbivorous insects, Mexican bean beetle experiences variable developmental and reproductive success when feeding on different host plants. Snap beans and lima beans are the most *susceptible* host species of Mexican bean beetle (tepary bean, *Phaseolus acutifolius*, is also highly susceptible, but is rarely grown commercially in the eastern United States; Friend and Turner 1931). Plants of these species are likely to experience significant feeding damage because they provide optimal nutrition and physical habitat, while lacking strong defensive qualities. Varieties such as 'Spartan arrow' snap bean, 'Jackson Wonder' lima, and nearly all "wax" bean varieties (snap beans with yellow pods) are among the most susceptible to Mexican bean beetle (Campbell and Brett 1966, Raina et al. 1978).

Varieties such as 'Regal' snap bean, 'Idaho Refugee' snap bean, 'Baby Fordhook' lima bean, and 'Baby White' lima bean exhibit high levels of *resistance* to Mexican bean beetle feeding and development. When raised on these varieties, beetles consumed less plant matter, gained less weight, and laid fewer eggs, relative to other varieties (Campbell and Brett 1966, Raina et al. 1978). Overall, wax bean varieties rank among the most susceptible, while lima bean varieties often exhibit resistance to Mexican bean beetle (Campbell and Brett 1966, Raina et al. 1978). Variety trials in Virginia agree with similar findings, in which wax varieties incur greater beetle densities and damage than lima beans and green snap beans (Nottingham 2014; Fig. 8).

Host plant physiology plays an important role in their resistance and susceptibility to Mexican bean beetle. Internal sugar concentrations are known to dictate how attractive plants are to their attackers. Bean plants with greater concentrations of sucrose and fructose are shown to be more attractive to Mexican bean beetle (Augustine et al. 1964). Among the legumes (Fabaceae), *Phaseolus* beans tend to contain the highest concentration of these sugars, which may explain, at least partially, why they are the most preferred hosts of Mexican bean beetle (LaPidus et al. 1963, Augustine et al. 1964).

Certain physiological components of host plants can aid in defense against Mexican bean beetle. Most beans, and many other plant groups, contain chemical compounds called cyanogenic glycosides (Vetter 1999). Although these chemicals are actually sugar compounds, they play an important role in a host plant's ability to

Fig. 8. Susceptible vs. tolerant host beans. Wax snap bean variety 'Dragon's Tongue' (bottom right plot) showing more visible injury than lima bean variety 'Fordhook' (bottom left plot) and nonwax snap bean varieties (above plots). (Photo by L. B. Nottingham)

deter insect pests, including Mexican bean beetle (Ballhorn and Lieberei 2006). In response to pest feeding, cyanogenic glycosides are converted into toxic hydrogen cyanide, which can either poison the attacker, or at least halt feeding (Gleadow and Woodrow 2002, Ballhorn et al. 2009). Because cyanogenic glycosides occur at varying concentrations in most *Phaseolus* beans, some varieties are well protected from attack, while others remain susceptible (Nayar and Fraenkel 1963, Ballhorn and Lieberei 2006). For instance, cyanogenic glycosides are more likely to occur at significant levels in lima beans than snap beans, which may explain why many lima bean varieties exhibit resistance to Mexican bean beetle (Viehoever 1940). Interestingly, at low concentrations, these compounds are not poisonous, and actually stimulate Mexican bean beetle feeding (Nayar and Fraenkel 1963).

Management

Cultural

Cultural pest management is the manipulation of an agricultural system, without the use of chemical inputs, in order to prevent or interfere with a pest's ability to damage the crop(s) (Ferro 1987). Examples include crop-rotation, trap cropping, using resistant plant varieties, and adjusting planting dates. From an integrated pest management (IPM) stand-point, cultural practices should be the first line of defense for managing insect pests (Groves 2014). Developing cultural management strategies requires a thorough understanding of the biology of pests and their hosts.

Cultural management strategies for Mexican bean beetle are understudied and deserve greater consideration. Grower surveys convey that Mexican bean beetle is a greater challenge in pesticide-free operations, and therefore, the continued pursuit of effective cultural strategies should be a top priority (Nottingham and Kuhar 2014a).

Reflective Plastic Mulch

Planting beans on plastic (polyethylene) mulches that reflect sunlight (specifically, metalized and white-colored plastic) has shown potential as a cultural strategy to mitigate damage from Mexican bean beetle (Nottingham and Kuhar 2015). Mexican bean beetle adults and larvae are deterred by direct light (Howard and English 1924, Miller 1930), and are less likely to survive when forced to remain in direct light (Howard and English 1924). Metalized (reflective aluminum top and black bottom) and white plastic mulches can significantly increase shortwave light intensity (300–1,100 nm), even on cloudy days (Ham et al. 1993). Field experiments at Virginia Tech have shown that Mexican bean beetle are less likely to colonize and deposit eggs on beans planted on metalized and white plastic mulches, compared to bare ground and black plastic (Nottingham and Kuhar 2015). Beans planted on metalized and white plastic mulches also had less foliar damage (Fig. 9), less pod damage, and significantly greater yields than beans grown on black plastic and bare ground (Nottingham and Kuhar 2015).

Timed Planting

Planting beans early in the spring, or late in the summer, can mitigate Mexican bean beetle damage (Howard and English 1924, Thomas 1924). This method encompasses various mechanisms. Overwintering Mexican bean beetles normally emerge early in the summer, after 238–277 degree days (baseline temperature: 10°C [50°F]) (Fess 2008), and remain active until early fall, when they begin searching for overwintering habitat. Planting bean crops as early as possible, or as late as possible, can reduce the overlap of crop development and peak beetle activity (Howard and English 1924). Also, most life stages of Mexican bean beetle consume less foliage and develop slower at temperatures between 20 and 24°C (68–75°F), usually occurring in the late spring and early fall (McAvoy and Smith 1979, Fan et al. 1992).

There are two potential drawbacks to this method. First, planting beans when soil and air temperatures are still cool often results in slower germination and smaller stands (Relf and McDaniel 2015). Second, planting early or late increases the risk that crops may get exposed to frost, which can damage or kill plants (Reiter et al. 2014).

Trap Crops

Rust (1977) tested the efficacy of trap cropping for Mexican bean beetle. This study reported control in systems where snap beans were used as trap crop for adjacent soybeans. However, there were no successful attempts to mitigate damage to snap or lima beans using trap crops. There is no evidence, to date, suggesting that trap crop methods can protect *Phaseolus* beans from Mexican bean beetle.

Resistant Crops

The work of Campbell and Brett (1966) and Raina et al. (1978) suggests that Mexican bean beetle damage may be reduced by simply growing more resistant bean varieties, such as 'Regal' snap bean, 'Idaho Refugee' snap bean, 'Baby Fordhook' lima bean, and 'Baby White' lima bean, and/or avoiding susceptible varieties, such as 'Spartan arrow' snap bean, 'Jackson Wonder' lima bean, and nearly all "wax" bean varieties.

Staggered Planting Dates

Mexican bean beetle management using staggered plantings of snap beans was explored by Fess (2008). This method attempts to contain beetle populations to plants from one planting group, while the rest of the crop is ignored. Though no consistent level of control was detected throughout this experiment, certain plantings in the staggered treatments did exhibit fewer Mexican bean beetle, as well as reduced damage. Staggered planting may in fact be a viable management strategy for Mexican bean beetle, but more research is needed to obtain specific implementation guidelines.

Physical/Mechanical

Row Covers

Fess (2008) found that polyester row covers successfully reduced abundance of Mexican bean beetle adults, larvae, and pupae on snap beans in West Virginia. Many smaller farms use this method;

Fig. 9. Planting beans on reflective polyethylene mulch may be an effective cultural management strategy for Mexican bean beetle. Greater levels of feeding injury were detected on beans grown on bare ground (left) and black plastic (middle) than metallic plastic (right) and white plastic (not pictured). (Photos by L. B. Nottingham)

however, some downfalls include increased labor, materials, and the risk of excluding beneficial insects.

Mechanical Removal

Small farms and gardens commonly use mechanical (by-hand) removal to reduce injury from Mexican bean beetle (Nottingham and Kuhar 2014). Because beetles complete their entire life cycle within the crop canopy, this simple strategy can adequately protect crops. The feasibility of this tactic, however, is highly reliant on the scale of the operation and the amount of labor available.

Biological Control

Predators

Mexican bean beetles are well protected from predatory organisms. In addition to the spines that adorn the larvae (Fig. 6), larvae, pupae, and adults all produce toxic, alkaloid secretions that are known to deter many arthropod predators upon contact (Happ and Eisner 1961, Eisner et al. 1986, Attygalle et al. 1993, Eisner and Meinwald 1995).

Although many arthropods are known to prey upon Mexican bean beetle, few native predators have proven effective at reducing population levels of this pest (Howard and Landis 1936). The most common predators of Mexican bean beetle include predatory stink bugs such as *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) (Waddill and Shepard 1975) and ladybeetles (Coleoptera: Coccinellidae). Others predators are found in the families Anthocoridae (Hemiptera), Nabidae (Hemiptera), and Chrysopidae (Neuroptera) (Howard and Landis 1936).

In Virginia, we commonly observed ladybeetles feeding on Mexican bean beetle eggs, while hemipteran predators, especially *Podisus maculiventris* (Say), were more likely to feed on larvae and adults (Fig. 10; L. B. N., unpublished data). To further explore this predator–prey complex, numerous predator arthropods were brought to the laboratory and offered different life stages of Mexican bean beetle. Chewing predators, including ladybeetles and ground beetles, only fed on eggs, while ignoring other life stages. Piercing–sucking predators, including damsel bugs (Hemiptera: Nabidae), assassin bugs (Hemiptera: Reduviidae), and stink bugs, readily fed upon all life stages (L. B. N., unpublished data). These observations suggest that piercing–sucking predators may be less sensitive to the chemical defenses of Mexican bean beetle than chewing predators.

Parasitoids

Several native, North American tachinid flies are known to parasitize Mexican bean beetle adults (Howard and Landis 1936). One notable species that occurs throughout the eastern United States is *Phorocera claripennis* Macquart (Diptera: Tachinidae) (Howard and Landis 1936). Unfortunately, these flies occur in densities that are too low to naturally limit Mexican bean beetle populations; parasitism levels only range from one to three percent (Howard and Landis 1936).

Landis and Howard (1940) discussed another tachinid species, *Paradexodes epilachnae* Aldrich, which is known to parasitize Mexican bean beetle at a rate of 16–54% in its native range of central Mexico. Because of its importance in the native range, this parasitoid was reared and released in 19 U.S. states from 1930–1935. Though the fly successfully reduced local populations of Mexican bean beetle and dispersed, no individuals were able to survive winters in the eastern United States (Landis and Howard 1940). This classical biological control initiative was eventually abandoned.

The most successful classical biological control method for control of Mexican bean beetle utilizes the eulophid wasp, *Pediobius foveolatus* (Crawford) (Hymenoptera: Eulophidae; Fig. 11) (Stevens et al. 1975, Fess 2008). This parasitoid was discovered in India, and is native to most of southern Asia and Japan (Angalet et al. 1968). Initial screenings of this wasp showed that it was unable to harm native coccinellids other than Mexican bean beetle and Squash beetle, *Epilachna borealis* (F.) (Angalet et al. 1968, Schaefer et al. 1983). Female wasps lay around 20 eggs in a single beetle larva, from which most will emerge as adults (Stoner 2002). Adult wasps then mate and search for more beetle larvae.

In their native range, *P. foveolatus* overwinters in host larvae (Ghani and Mohyuddin 1982) or does not overwinter at all due to

Fig. 10. Predators of Mexican bean beetle. Predatory stink bug nymph (Hemiptera: Pentatomidae) (left) feeding on Mexican bean beetle adult. Ladybird beetle larva (Coleoptera: Coccinellidae) (right) feeding on Mexican bean beetle eggs. (Photos by L. B. Nottingham)

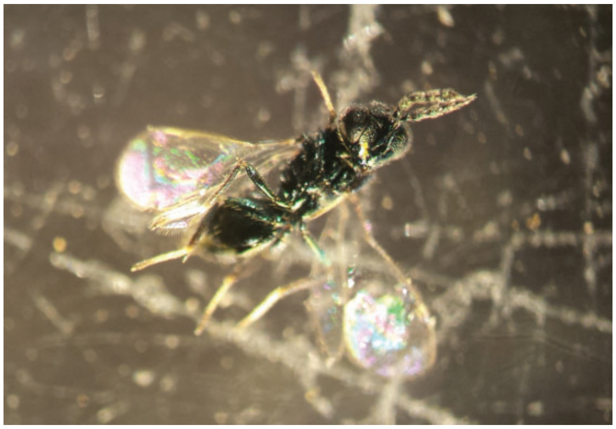

Fig. 11. *Pediobius foveolatus* (Hymenoptera: Eulophidae) adult. An exotic, parasitoid wasp of the Mexican bean beetle. (Photo by L. B. Nottingham)

the lack of a cold season. In the United States, however, *P. foveolatus* cannot survive cold winter months because all North American *Epilachna* hosts overwinter as adults, not larvae (Schaefer et al. 1983). Therefore, these wasps must be released annually in the United States in order to provide control of Mexican bean beetle (Stevens et al. 1975).

To successfully manage Mexican bean beetle using *P. foveolatus*, it is crucial to properly schedule the release. Ideally, wasps should be released at both one and two weeks after first-instar beetles are discovered in beans (Stoner 2002). Accurate scouting and timing of release is necessary because wasps reproduce most successfully within third- and fourth-instar larvae (Angalet et al. 1968), so it is imperative that those Mexican bean beetle instars are present at wasp release. It is also important not to release wasps when it is raining or cold, as they are not well adapted to these conditions (Stoner 2002). Release wasps at a rate of 1,000 wasps (or 50 mummies) per 3,600 square feet of beans (Stoner 2002). Successful parasitism and emergence of the next generation of wasps can be visibly monitored by the presence of dark-brown, dead Mexican bean beetle larvae (mummies) with one small hole, from where adult wasps exited (Fig. 12; Stoner 2002).

When considering an augmentative release of *P. foveolatus*, it is important to remember that wasps must be ordered from a vendor, and that delivery may take anywhere from one day to three weeks. Once the eggs of Mexican bean beetle are first discovered, the grower should contact vendors for expected delivery times. *P. foveolatus* wasps can be purchased from the New Jersey Department of Agriculture and other commercial insectaries.

Chemical Control

In the 1960s and 1970s, Mexican bean beetle was effectively controlled with foliar-spray applications or in-furrow systemic applications of many of the organophosphates, carbamates, or chlorinated hydrocarbons registered at the time (Webster and Smith 1962, Judge et al. 1970). Today, very few of these insecticides are registered for use on edible beans. However, numerous other insecticides including pyrethroids, neonicotinoids, and combination insecticide products provide effective control of this pest when applied as a foliar spray (Nault and Speese 2001, Kuhar et al. 2012). The pyrethroid bifenthrin was shown to be more efficacious than the organophosphate acephate or the carbamates methomyl and carbaryl at reducing beetle damage to snap bean pods in Virginia (Nault and Speese 2001). In a recent insecticide efficacy test in which soybeans were sprayed with various insecticides in the field and then leaves were excised and exposed to Mexican bean beetle adults, several insecticides including the pyrethroids bifenthrin, lambda-cyhalothrin, zeta cypermethrin as well as acephate, methomyl, and combination products containing lambda-cyhalothrin plus the neonicotinoid thiamethoxam or beta cyfluthrin plus imidacloprid, all provided up to 90% control for 10 d after application (T. P. K., unpublished data). Patton et al. (2003) evaluated a number of organic insecticides, and showed that azadirachtins, pyrethrins, and spinosad all provided significant control of Mexican bean beetle compared to an untreated control.

Fig. 12. Mexican bean beetle larva, parasitized by *Pediobius foveolatus*. (Photo by L. B. Nottingham)

The economic threshold for this pest can vary greatly depending on environmental conditions (temperature, amount of rainfall, and the use of irrigation), time of year, host species or variety, plant maturity, etc. Guidelines for pesticide use found in state extension publications provide current and detailed information explaining both when to spray, what to spray, and how to safely apply these insecticides. Most current recommendations suggest treating snap beans at 20% defoliation pre-bloom, and 10% at bloom to pod stage (Flood and Wyman 2005, Reiter et al. 2014). Soybeans should be treated at 40% defoliation pre-bloom, and at 15% bloom to pod stage (Krupke et al. 2015).

Historical Perspective

Native Range and Spread

Mexican bean beetle was first described by Mulsant (1850) from specimens in Mexico. The original name was *Epilachna corrupta*, but it was later changed to *Epilachna varivestis*. The native range of this beetle is thought to be a region of western Mexico known as "The Plateau," referring to its high elevation of 1,219–2,438 m (4,000–8,000 ft; Friend and Turner 1931). Unlike the hot and dry climate that is characteristic to a large portion of Mexico, the Plateau region is more cool and moist. Daily high temperatures in the summer average around 25°C (77°F), and summer rainfall averages 40 cm (16 in; Marcovitch and Stanley 1930). The exact parameters and extent of Mexican bean beetle's native range are unknown, but it is possible that its original territory stretched across Central America and into the Andes Mountains of South America, where there is a great diversity of *Epilachna* species (Howard and English 1924, Gordon 1975).

The earliest records of Mexican bean beetle in the United States date back to 1864. It was first recognized as an economic pest in 1883, when severe damage to wax beans (varieties of common beans that are yellow and stingless) was reported in Colorado (Chittenden 1919). The first sighting of this pest east of Texas was in 1918, near Birmingham, Alabama (Thomas 1924). It is assumed that beetles were transported there, from the Southwest, in cut alfalfa (Friend and Turner 1931). By the late 1920s the beetle spread north to southern Canada, and west to Michigan (Harding 1933).

Mexican bean beetle populations are currently found throughout the United States; however, economic populations are most common in the Mid-Atlantic and southern Appalachian Mountain regions (Nottingham and Kuhar 2014). This beetle is greatly limited by summer rainfall, humidity, and temperature (Marcovitch and Stanley 1930, Sweetman 1932, Kitayama et al. 1979, Wilson et al. 1982, Mellors and Bassow 1983). The regions where Mexican bean beetle is most severe are characterized by summers with regular rainfall, high humidity, and daily high temperatures ranging from 25 to 29.5°C (77–85°F) (Marcovitch and Stanley 1930, Sweetman 1932, Fess 2008, Nottingham and Kuhar 2014). Though this beetle is also found in the Southwest and Great Plains, populations in these regions are mostly limited to irrigated croplands, and rarely reach economic levels (Barrigossi 1997).

Fluctuations in Pest Status

Mexican bean beetle received little attention until the mid-1920s, when it became well established in all but seven states east of the Mississippi River (Tissot 1943). The subsequent torrent of scientific publications on this beetle is indicative of its breakthrough into economic importance in the 1920s and 1930s. For example, the Bibliography of American Economic Entomology lists 213 publications referencing Mexican bean beetle from the years 1930–1939 (Tissot 1943).

Friend and Turner (1931) performed damage trials on numerous legumes to determine which were most susceptible to beetle feeding, and found that only *Phaseolus* species were severely damaged. Though this study suggests that Mexican bean beetle was only economically threatening to *Phaseolus* crops, some growers from southeastern states reported Mexican bean beetle infesting and damaging soybean crops (Howard and English 1924). This was said to occur in situations where populations of Mexican bean beetle were allowed to grow very large within snap beans, then populations would migrate to adjacent soybean fields after snap beans were destroyed (Howard and English 1924). It is unclear whether it was a true threat to soybeans, or any crops other than snap bean, dry bean, and lima bean, during the 1920–1940 time-period.

By the 1940s and into the 1950s, there was a substantial decrease in the number of Mexican bean beetle publications (Nichols and Kogan 1972), which suggests that there was a decline in this pest's occurrence and severity. Whether populations actually subsided is undocumented.

In the mid-1960s, the beetle once again emerged as a major pest, with economic damage reported throughout most agricultural regions of the eastern United States. This resurgence was unique, in that Mexican bean beetle was also causing widespread damage to soybean, as well as *Phaseolus* bean species. The beetle was also reported outside of its normal range, reaching the Piedmont and Coastal Plain regions of Virginia, North Carolina, and South Carolina, as well as mid-western states including Indiana and Ohio (Nichols and Kogan 1972, Hallman et al. 1977, Hammond 1984, Metterhouse et al. 1989). This pest once again became a prominent subject in research publications by the late-1960s (Nichols and Kogan 1972), and through to the mid-1980s (Nottingham and Kuhar 2014). Also, due to its conspicuous nature in the field, and suitability for laboratory rearing and experimentation, Mexican bean beetle gained considerable popularity among various groups of scientists as a practical research specimen (Nichols and Kogan 1972).

1979 to 1981 was the height of Mexican bean beetle pest pressure in United States history, especially for soybean (Metterhouse et al. 1989, Hudson et al. 2013; G. P. D., unpublished data). Nearly every soybean field in the Delmarva region of Virginia, Delaware, and Maryland was severely damaged (G. P. Dively, personal communication). However, by the mid-1980s, occurrences of Mexican bean beetle declined, especially in soybean (Hudson et al. 2013). To date, Mexican bean beetle is rarely a pest of any legume species outside of the genus *Phaseolus*. Even in that host, Mexican bean beetle is generally only a concern in smaller, organic operations (Nottingham and Kuhar 2014).

Cause for Pest Decline

The cause of Mexican bean beetle's decline is still undetermined. Some resolve that classical biological control is responsible for the suppression of this pest. *Pediobius foveolatus* has been used since the 1960s to control Mexican bean beetle, and was released in mass quantities across multiple Mid-Atlantic states during the 1960s and 1970s (*P. foveolatus* is still released annually by the state of New Jersey).

Climate change is also a common theory for the decline. Compared to century averages, the weather during Mexican bean beetle's peak in the 1960s and 1970s was considerably cooler, and with more precipitation (NOAA-CAG 2014, NOAA-DATM 2014). Because cool, wet weather generally aides beetle survival, climate may have been the key factor that permitted beetles to flourish and attack the less suitable host, soybean, during this time-period. These two theories are explored below.

Parasitoid (*Pediobius foveolatus*) Releases

Beginning in 1966, *P. foveolatus*, a parasitoid wasp originally discovered in India, was imported to the United States to be tested for potential control of Mexican bean beetle (Angalet et al. 1968). Initial testing determined that *P. foveolatus* would readily parasitize the larvae of Mexican bean beetle, while leaving native, predatory coccinellids unharmed (Angalet et al. 1968). In 1972, Maryland, then other states, began releasing these wasps to control Mexican bean beetle (Schaefer et al. 1983). USDA branches in New Jersey, Maryland, Delaware, and Virginia released wasps throughout these states, focusing on areas with large soybean acreage and high Mexican bean beetle populations (Reichelderfer 1979).

Inoculative releases yielded positive results; parasitism rates of 80–100% of Mexican bean beetle larvae were commonly documented near release sites (Stevens et al. 1975, Barrows and Hooker 1981). However, Stevens et al. (1975) also reported slow parasitoid population dispersal from these sites. Also, *P. foveolatus* cannot overwinter in the United States due to cold winters and the lack of an overwintering host (Schaefer et al. 1983). In the wasps' native territory, the weather either is conducive for year-round exposure, or wasps overwinter in their hosts, which overwinter as larvae. Because Mexican bean beetle overwinter as adults, wasps are without adequate winter refuge in the United States (Schaefer et al. 1983). Because *P. foveolatus* can neither overwinter successfully nor spread rapidly, management with this wasp requires yearly releases in more locations than is practical for widespread control of Mexican bean beetle.

By the mid-1980s, all states except New Jersey had discontinued state-run releases of *P. foveolatus* (G. P. Dively and P. Schultz, personal communication). At this time, pest pressure from Mexican bean beetle began its sharp decline as well, especially in soybean (Hudson et al. 2013; G. P. D., unpublished data).

The short-comings of this biological control agent make it an unlikely cause for the wide-spread decline of Mexican bean beetle in the eastern United States. None-the-less, annual releases of *P. foveolatus* are still carried out by the State of New Jersey, as well as many individual farmers and gardeners, and can be a very effective tool for localized management (Fess 2008, Hudson et al. 2013).

Climate Change

Climate shifts are likely a major cause of Mexican bean beetle's fluctuating severity. Like most insects, this beetle's ability to feed and thrive is heavily dependent on temperature and moisture. Numerous studies describe the relative inability of this insect to tolerate temperatures increasing beyond 30°C (80°F) with low relative moisture (Marcovitch and Stanley 1930, Miller 1930, Sweetman 1932, Kitayama et al. 1970, Wilson et al. 1982, Mellors and Bassow 1983, Mellors et al. 1984). Wilson et al. (1982) also witnessed that beetles were only able to feed and survive on soybean under temperature and humidity conditions that were considered to be optimal.

Marcovitch and Stanley (1930) developed a climatic index that accurately predicts the potential for Mexican bean beetle pest pressure for specific locations (assuming the presence of plant hosts) based on temperature and rainfall. The formula reads:

$$L \times \left(\frac{L}{2}\right) \times \left(\frac{100}{R}\right)^2$$

where L = the successive number of days above 32.2°C (90°F) and R = total rainfall (inches) from June through September. Localities that consistently produce low values (below 2000) are considered "optimal" for Mexican bean beetle. The model works on a continuous scale, so increasing index values suggest relative decreases in habitability for the beetle. For instance, Norfolk, VA, produced an index level of 284 in 1925, when the area experienced severe Mexican bean beetle outbreaks in local host crops; meanwhile, locations in western Tennessee had values around 15,000, and little to no beetle pressure observed (Marcovitch and Stanley 1930).

From 1950 to 1987, the University of Maryland rated Mexican bean beetle damage in soybean crops in Maryland, Delaware, and Virginia, and calculated climate index values using Marcovitch and Stanley's (1930) formula. Their findings show cool and wet weather persisting throughout the 1960s and 1970s, compared to the overall average, and that Mexican bean beetle damage to soybean was most severe during this time (Nottingham and Kuhar 2014, G. P. D., unpublished data). Historical weather data from the National Oceanic and Atmospheric Administration (NOAA) validate the University of Maryland's weather data. Temperatures across most of the eastern United States were below the century average in both the 1960s and 1970s (NOAA-DATM 2014). Furthermore, the Palmer drought severity index for Virginia depicts consistently high climatic moisture levels during most of the 1970s, when pest pressure reached all-time highs (NOAA-CAG 2014). After 1980, hotter and dryer weather returned, and Mexican bean beetle severity decreased (Nottingham and Kuhar 2014, G. P. D., unpublished data).

Concluding Remarks

Recognition of Mexican bean beetle as a significant agricultural pest has greatly decreased over the past thirty years; yet it remains a devastating pest to edible bean crops throughout large portions of the United States. Within its range, outbreaks reach economic levels on an annual basis, especially for snap bean growers who attempt to minimize, or forgo, the use of chemical insecticides (Nottingham and Kuhar 2014). Mexican bean beetle is easily controlled with insecticides in conventional bean production, but little effort has been made to study progressive management strategies. The authors of this manuscript hope this profile on Mexican bean beetle will provide the necessary information to aid in, and encourage, the development of an integrated pest management approach to controlling this pest.

Acknowledgments

We thank Robert Trumbule, USDA Maryland, for insight and support; Thomas Dorsey, USDA New Jersey, for contributions to our research; and Taliaferro Trope for donating photographs. Substantial funding for our research on Mexican bean beetle was provided by Southern Sustainable Agricultural Research and Education (SARE), project number GS13-120.

References Cited

Angalet, G. W., L. W. Coles, and J. A. Stewart. 1968. Two potential parasites of the Mexican bean beetle from India. J. Econ. Entomol. 61: 1073–1075.

Attygalle, A. B., K. D. McCormick, C. L. Blankespoor, T. Eisner, and J. Meinwald. 1993. Azamacrolides: a family of alkaloids from the pupal defensive secretion of a ladybird beetle (*Epilachna varivestis*). Proc. Natl. Acad. Sci. Chem. 90: 5204–5208.

Auclair, J. L. 1959. Life-history, effects of temperature and relative humidity, and distribution of the Mexican bean beetle, *Epilachna varivestis* Mulsant, (Coleoptera: Coccinellidae) in Quebec, with a review of the pertinent literature in North America. Ann. Entomol. Soc. Quebec 5: 18–43.

Augustine, M. G., F. W. Fisk, R. H. Davidson, J. B. LaPidus, and R. W. Cleary. 1964. Host-plant Selection by the Mexican bean beetle, *Epilachna varivestis*. Ann. Entomol. Soc. Am. 57: 127–134.

Ballhorn, D. J., and R. Lieberei. 2006. Oviposition choice of Mexican bean beetle (*Epilachna varivestis*) depends on host plants cyanogenic capacity. J. Chem. Ecol. 32: 1861–1865.

Ballhorn, D. J., S. Kautz, M. Heil, and A. D. Hegeman. 2009. Cyanogenesis of wild lima bean (*Phaseolus lunatus* L.) is an efficient direct defense in nature. PLoS ONE 4: e5450.

Barrigossi, J. A. F. 1997. Development of IPM systems for the Mexican bean beetle (*Epilachna varivestis* Mulsant) as a pest of dry bean (*Phaseolus vulgaris* L.). Ph.D dissertation, University of Nebraska, Lincoln.

Barrows, E. M., and M. E. Hooker. 1981. Parasitism of the Mexican bean beetle by *Pediobius foveolatus* in urban vegetable gardens. Environ. Entomol. 10: 782–786.

Bernhardt, J. L., and M. Shepard. 1978. Overwintered Mexican bean beetles: emergence from overwintered sites, fecundity, fertility, and longevity. Ann. Entomol. Soc. Am. 71: 724–727.

Campbell, W. V., and C. H. Brett. 1966. Varietal resistance of beans to the Mexican bean beetle. J. Econ. Entomol. 59: 899–902.

Capinera, J. L. 2001. Handbook of vegetable pests. University of Florida Academic Press, San Diego, CA.

Capinera, J. L., D. R. Horton, N. D. Epsky, and P. L. Chapman. 1987. Effects of plant density and late-season defoliation on yield of field beans. Environ. Entomol. 16: 274–280.

Chittenden, F. H. 1919. The bean ladybird and its control. US Department of Agriculture Farmers Bulletin 1074–1081, Washington D. C.

Douglass, J. R. 1933. Habits, life history, and control of Mexican bean beetle in New Mexico. USDA Technical Bulletin 376–422, Washington D. C.

Eisner, T., and J. Meinwald. 1995. Chemical ecology: the chemistry of biotic interaction, p. 33. National Academy of Science, Washington DC.

Eisner, T., M. Goetz, D. Aneshansley, G. Ferstandig-Arnold, and J. Meinwald. 1986. Defensive alkaloid blood of the Mexican bean beetle (*Epilachna varivestis*). Experientia 42: 204–207.

Fan, Y., E. Groden, and F. A. Drummond. 1992. Temperature-dependent development of Mexican bean beetle (Coleoptera: Coccinellidae) under constant and variable temperatures. J. Econ. Entomol. 85: 1762–1770.

Ferro, D. N. 2013. IPM world textbook: Cultural Control. University of Minnesota, Department of Entomology. (http://ipmworld.umn.edu/ferro) (accessed 11 January 2016).

Fess, T. L. 2008. Organic management of Mexican bean beetle (*Epilachna varivestis*) in snap bean (*Phaseolus vulgaris* L.). M.S. thesis, West Virginia University, Morgantown.

Flood, B. R., and J. A. Wyman. 2005. Beans, pp. 66–80. *In* R. Foster and B. R. Flood (eds.), Vegetable insect management, Meister Media Worldwide, Willoughby, OH.

Friend, R. B., and N. Turner. 1931. The Mexican bean beetle in Connecticut. Conn. Agric. Exp. Stat. Bull. 332: 71–108.

Gatton, H. 2008. Snap bean pest management strategic plan for Virginia. North Carolina and Delaware, Southern Region IPM Workshop, Blacksburg, VA (http://www.ipmcenters.org/pmsp/pdf/VA-NC-DEsnapbeanPMSP.pdf) (accessed 11 January 2016).

Ghani, M. A. and A. I. Mohyuddin. 1982. Investigations on the natural enemies of *Epilachna* spp. in Pakistan. Commonwealth Institute of Biological Control, Pakistan Station.

Gleadow, R. M., and I. E. Woodrow. 2002. Constraints on effectiveness of cyanogenic glycosides in herbivore defense. J. Chem. Ecol. 28: 1301–1313.

Gordon, R. D. 1975. A Revision of the Epilachninae of the Western Hemisphere (Coleoptera: Coccinellidae). Agricultural Research Service USDA Technical Bulletin No. 1493. Washington D. C.

Groves, R. 2014. Integrated pest management: cultural control. University of Wisconsin Extension. (http://labs.russell.wisc.edu/vegento/crops-and-insects/ipm-integrated-pest-management/cultural-control/) (accessed 11 January 2016).

Haile, F. J., L. G. Higley, and J. E. Specht. 1998. Soybean cultivars and insect defoliation: yield loss and economic injury levels. Agron. J. 90: 344–352.

Hallman, G. J., C. R. Edwards, and J. E. Foster. 1977. Soybean cultivars evaluated for Resistance to Mexican bean beetle in southern Indiana. J. Econ. Entomol. 70: 316–318.

Ham, J. M., G. J. Kluitenberg, and W. J. Lamont. 1993. Optical properties of plastic mulch affect the field temperature regime. J. Am. Soc. Horticultural Sci. 118: 188–193.

Hammond, R. B. 1984. Development and survival of Mexican bean beetle, *Epilachna varivestis* Mulsant, on two host plants. J. Kansas Entomol. Soc. 54: 695–699.

Happ, G. M., and T. Eisner. 1961. Hemorrhage in a coccinellid beetle and its repellent effects on ants. Science 134: 329–331.

Harding, G. E. 1933. Distribution of the Mexican bean beetle. Econ Geogr 9: 273–278.

Howard, N. F. 1924. The Mexican bean beetle in the East. USDA Agricultural Bulletin No. 1407. Washington D. C.

Howard, N. F. 1941. Feeding of the Mexican bean beetle larva. Ann. Entomol. Soc. Am. 34: 766–769.

Howard, N. F., and L. L. English. 1924. Studies of the Mexican bean beetle in the Southeast. USDA Agricultural Bulletin No. 1243. Washington D. C.

Howard, N. F., and B. J. Landis. 1936. Parasites and Predators of the Mexican bean beetle in the United States. USDA, Circular Bulletin 418: 1–12.

Hudson, W., G. Robbins, M. Mayer, T. Dorsey, E. Rooney, and L. Bronhard. 2013. Biological control of Mexican bean beetle, *Epilachna varivestis*, using the parasitic wasp, *Pediobius foveolatus*. New Jersey Department of Agriculture, Beneficial Insect Laboratory. (http://www.nj.gov/agriculture/divisions/pi/pdf/mexicanbeanbeetle.pdf) (accessed 11 January 2016).

Judge, F. D., F. L. McEwan, and H. B. Rinick. 1970. Field testing candidate insecticides on beans and alfalfa for control of Mexican bean beetle, potato leaf hopper, and plant bugs in New York State. J. Econ. Entomol. 63: 58–62.

Kitayama, K., R. E. Stinner, and R. L. Rabb. 1979. Effects of temperature, humidity and soybean maturity on longevity and fecundity of the adult Mexican bean beetle, *Epilachna varivestis*. Environ. Entomol. 8: 458–464.

Krupke, C. H., J. L. Obermeyer, and L. W. Bledsoe. 2015. Soybean insect control recommendations. Purdue Extension Publication No. E-77-W West Lafayette, IN (http://extension.entm.purdue.edu/publications/E-77.pdf) (accessed 11 January 2016).

Kuhar, T. P., H. Doughty, K. Kamminga, A. Wallingford, C. Phillips, and J. Aigner. 2012. Evaluation of foliar insecticides for the control of foliar insects in snap beans in Virginia, 2011. Arthropod Management Tests 31(E2): 1–2.

Landis, B. J., and N. F. Howard. 1940. *Paradexodes epilachnae*, a Techinid parasite of the Mexican bean beetle. USDA Technical Bulletin No. 721. 32p. Washington D. C.

LaPidus, J. B., R. W. Cleary, R. H. Davidson, F. W. Risk, and M. G. Augustine. 1963. Plant susceptibility to insects: chemical factors influencing host selection by the Mexican bean beetle, *Epilachna varivestis* Mulsant. Agric. Food Chem. 11: 462–463.

Marcovitch, S., and W. W. Stanley. 1930. The climatic limitations of the Mexican bean beetle. Ann. Entomol. Soc. Am. 23: 666–686

McAvoy, T. J., and J. C. Smith. 1979. Feeding and development rates of the Mexican bean beetle on soybeans. J. Econ. Entomol. 72: 835–836.

Mellors, W. K., and F. E. Bassow. 1983. Temperature-dependent development of Mexican bean beetle (Coleoptera: Coccinellidae) immatures on snap bean and soybean foliage. Ann. Entomol. Soc. Am. 76: 692–698.

Mellors, W. K., A. Allegro, and A. M. Wilson. 1984. Temperature dependent simulation of the effects of detrimental high temperatures on the survival of Mexican bean beetle eggs (Coleoptera: Coccinellidae). Environ. Entomol. 13: 86–94.

Metterhouse, W., T. Burger, M. Grulich, A. Hamilton, G. Zehnder, D. H. Kludy, F. R. Brush, P. B. Schultz, J. Keeling, and J. Tate. 1989. The use of beneficial insects in Virginia. Report of the Virginia Department of Agriculture and Consumer Affairs, House Document No. 34, Richmond, VA.

Miller, D. F. 1930. The effect of temperature, relative humidity and exposure to sunlight upon the Mexican bean beetle. J. Econ. Entomol. 23: 945–955.

Mulsant, M. E. 1850. Species des C'oleopieres trimeres seciiripalpes. Annals des Sciences, Physiques et Naturelles. p. 815–817.

Nault, B. A., and J. Speese. 2001. Evaluation of insecticides for control of insect pests of snap bean, 2000. Arthropod Management Tests 26 (E5): 1–2.

Nayar, J. K., and G. Fraenkel. 1963. The chemical basis of the host selection in the Mexican bean beetle, *Epilachna varivestis* (Coleoptera, Coccinellidae). Ann. Entomol. Soc. Am. 56: 174–178.

Nichols, M. P. and M. Kogan. 1972. A bibliography of the Mexican Bean Beetle, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae). Literature of Arthropods Associated with Soybeans. Illinois Natural History Survey, Biological Notes No. 77.

NOAA-CAG. 2014. Climate at a glance. (http://www.ncdc.noaa.gov/cag/) (accessed 11 January 2016).

NOAA-DATM. 2014. Decadal average temperature maps. (http://www.ncdc.noaa.gov/temp-and-precip/state-temps/) (accessed 11 January 2016).

Nottingham, L. 2014. Investigating the movement and host selection of Mexican bean beetle, *Epilachna varivestis* Mulsant, among five host plants using mark-release-recapture. V. J. Sci. 65: p. 11.

Nottingham, L., and T. Kuhar. 2013. Mexican bean beetle. Virginia Cooperative Extension Publication ENTO-51NP. Blacksburg, VA (http://pubs.ext.vt.edu/ENTO/ENTO-51/ENTO-51-pdf.pdf) (accessed 11 January 2016).

Nottingham, L., and T. Kuhar. 2014. History, distribution and pest status of the Mexican bean beetle. Virginia Cooperative Extension Publication ENTO-62NP. Blacksburg, VA (http://pubs.ext.vt.edu/ENTO/ENTO-62/ENTO-62-pdf.pdf) (accessed 11 January 2016).

Nottingham, L., and T. Kuhar. 2015. Management of Mexican bean beetle, *Epilachna varivestis Mulsant*, in snap beans using cultural control strategies. Southern SARE Graduate Student Project GS13-120. (http://mysare.sare.org/MySare/ProjectReport.aspx?do=viewRept&pn=GS13-120&y=2015&t=1) (accessed 11 January 2016).

Patton, T. W., G. P. Dively, and A. K. Miller. 2003. Evaluation of organic insecticides for control of Mexican bean beetle, 2002. Arthropod Management Tests 28(E3): 1–2.

Peterson, R., L. G. Higley, F. G. Haile, and J. A. Barrigossi. 1998. Mexican bean beetle (Coleoptera: Coccinellidae) injury effects photosynthesis of *Glycine Max* and *Phaseolus vulgaris*. Environmental Entomology 27: 373–381.

Raina, A. K., P. S. Benepal, and A. Q. Sheikh. 1978. Evaluation of bean varieties for resistance to Mexican bean beetle. J. Econ. Entomol. 71: 313–314.

Reichelderfer, K. H. 1979. Economic feasibility of biological control technology: using a parasitic wasp, *Pediobius foveolatus*, to manage Mexican bean beetle on soybeans. USDA Agricultural Economic Report No. 430. Washington D. C.

Reiter, M. S., S. T. Rideout, T. P. Kuhar, H. P. Wilson, J. H. Freeman, J. A. Parkhurst, R. A. Straw, J. Samtani, G. Gu, and C. D. Mullins. 2014. Commercial vegetable production recommendations. Virginia Cooperative Extension Publication No. 456–420. Blacksburg, VA.

Relf, D., and A. McDaniel. 2015. Beans. Virginia Cooperative Extension Publication No. 426-402. Blacksburg, VA. (https://pubs.ext.vt.edu/426/426-402/426-402_pdf.pdf) (accessed 11 January 2016).

Rust, R. W. 1977. Evaluation of trap crop procedures for control of Mexican bean beetle in soybeans and lima beans. J. Econ. Entomol. 70: 630–632.

Schaafsma, A. W., and G. R. Ablett. 1994. Yield loss response of navy bean to partial or total defoliation. J Prod Agric. 7: 202–205.

Schaefer, P. W., R. J. Dysart, R. V. Flanders, T. L. Burger, and K. Ikebp. 1983. Mexican bean beetle (Coleoptera: Coccinellidae) larval parasite *Pediobius foveolatus* (Hymenoptera: Eulophidae) from Japan: field release in the United States. Environ. Entomol. 12: 852–854.

Stevens, L. M., A. L. Steinhauer, and J. R. Coulson. 1975. Suppression of Mexican bean beetle on soybeans with inoculative releases of *Pediobius foveolatus*. Environ. Entomol. 4: 947–952.

Stoner, K. A. 2002. Using *Pediobius foveolatus* as biological control for Mexican bean beetle on organic vegetable farms. Connecticut Agricultural Experiment Station No. ENO22. New Haven, CT. (http://www.ct.gov/caes/cwp/view.asp?a=2815&q=376726) (accessed 11 January 2016).

Sweetman, H. L. 1932. The effects of temperature and moisture on the distribution of the Mexican bean beetle, *Epilachna corrupta*, Mulsant. Ann. Entomol. Soc. Am. 25: 224–240.

Tissot, A. N. 1943. The Mexican bean beetle in Florida. Fla. Entomol. 26: 1–8.

Thomas, F. L. 1924. Life history and control of the Mexican bean beetle. Alabama Polytechnic Institute Agricultural Experiment Station Bulletin 221. Auburn, AL.

Vetter, J. 1999. Plant cyanogenic glycosides. Toxicon 38 (2000): 11–36.

Viehoever, A. 1940. Edible poisonous beans of the lima type (*Phaseolus lunatus*). Thai. Sci. Bull. 2: 1–99.

Waddill, V., and M. Shepard. 1975. A comparison of predation by the pentatomids, *Podisus maculiventris* (Say) and *Stiretrus anchorago* (F.), on the Mexican bean beetle, *Epilachna varivestis* Mulsant. Ann. Entomol. Soc. Am. 68: 1023–1027.

Webster, R. E., and F. F. Smith. 1962. Systemic insecticides for Mexican bean beetle control. J. Agric. Chem. 17: 44.

Wilson, K. G., R. E. Stinner, and R. L. Rabb. 1982. Effects of temperature, relative humidity, and host plant on larval survival of the Mexican bean beetle, *Epilachna varivestis* Mulsant. Environ. Entomol. 11 (2000): 121–126.