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Emergence of *Maruca vitrata* as a Major Pest of Food Legumes and Evolution of Management Practices in Asia and Africa

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Abstract

Legume pod borer, *Maruca vitrata*, has emerged as a major pest on food legumes in Asia and Africa. It is an oligophagous pest, feeding on over 70 species in Fabaceae. We examine the species complex in Asia, Africa, Oceania, and the Americas, with an emphasis on molecular taxonomy. Studies on pheromone production and perception suggest the existence of pheromone polymorphism, especially in Asia and Africa. No *Maruca*-resistant varieties are available in the major food legumes including cowpea, pigeonpea, mungbean, and yard-long bean. Legume growers use chemical pesticides indiscriminately, leading to the development of pesticide resistance. However recent developments in habitat management, classical biocontrol with more efficient parasitoids, biopesticides, and judicious use of insecticides pave the way for sustainable management of *M. vitrata*, which can reduce the pesticide misuse. Active engagement of the private sector and policy makers can increase the adoption of integrated pest management approaches in food legumes.

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INTRODUCTION

Legume pod borer, *Maruca vitrata* Fab. (Lepidoptera: Crambidae), is the most devastating pest on food legumes in tropical Asia and sub-Saharan Africa, and it also occurs in the Americas, Australia, and the Pacific (110). Besides *M. vitrata*, three other *Maruca* species have been described (132, 146). Recent studies have suggested the presence of multiple species in *Maruca* and subspecies of *M. vitrata* in different geographical regions (66, 69, 71), which is quite important in the context of its management. The species mostly infest the reproductive parts in at least 73 host plant species, mostly legumes, with up to 72% yield losses (110). It has been reported as a major pest on at least nine cultivated legumes in Asia, with cowpea as the predominant cultivated host in Africa. Legume farmers in Asia and Africa rely on chemical insecticides to produce blemish-free beans.

Indiscriminate insecticide use has been recorded in most legume production systems. For instance, in Cambodia, applicators mixed an average of four pesticides together in a single spray on yard-long bean (108). Such use of pesticides has contributed to the development of resistance (32, 119), besides its impact on human and environmental health. The only available review on *M. vitrata* globally was published two decades ago (110), with a recent review emphasizing only West Africa (10). In this article, we review and summarize recent research on this complex species, including research on the damage that it causes, its pheromones, biocontrol, biopesticides, and integrated pest management (IPM).

TAXONOMY AND DISTRIBUTION

The Indo-Malaysian region is considered the center of origin for the genus *Maruca* (19). Eight *Maruca* species, *Maruca amboinalis* Felder, *Maruca aquitilis* Guérin-Ménéville, *Maruca bifenestralis* Mabilie, *Maruca fuscalis* Yamanaka, *Maruca nigroapicalis* Joannis, *Maruca simialis* Snellen, *Maruca testulalis* Geyer, and *M. vitrata* Fabricius, have been listed (<https://animaldiversity.org>); *M. testulalis* is a junior synonym of *M. vitrata*. *M. aquitilis* and *M. bifenestralis* are also synonyms of *M. vitrata* (28). Besides *M. vitrata*, only *M. amboinalis*, *M. nigroapicalis*, and *M. fuscalis* have been formally described (132, 146). *M. amboinalis* was described based on male and female genitalia (59, 99) and *M. nigroapicalis* was described from Vietnam but has not been reported since the first description (132). *M. fuscalis* was reported from Indonesia, Australia, and Madagascar (63, 146). We can find no information on the description of *M. simialis*. Thus, only four species are formally described and recognized in the genus *Maruca*.

Differential responses of *M. vitrata* male moths to the same sex pheromone blends were reported within West Africa (31) and Asia (107, 124), suggesting the presence of different species or subspecies in *Maruca*. Phylogenetic analysis of *Maruca* populations using the *mitochondrial cytochrome c oxidase-I (cox1)* gene indicated the presence of multiple putative *Maruca* species or subspecies (71). Subsequent study involving *Maruca* populations from different continents using *cox1* sequences confirmed the presence of three putative *Maruca* species [one each in Latin America and Oceania (including Indonesia) and *M. vitrata*] (66). Further investigations using the internal transcribed spacer 2 (ITS2) region confirmed the separate grouping of *M. vitrata* populations from Asia and Africa (67). A recent study using pheromone-binding protein (PBP) genes suggests the occurrence of a putative *Maruca* species in South America and two putative subspecies, one in Asia and the other in Africa (69). Interestingly, this study found that *M. vitrata* is the predominant species in Papua New Guinea, where populations were collected from different locations, but earlier evidence showed the presence of another *Maruca* species in this country (66). Thus, molecular studies suggest the distribution of several putative *Maruca* species in Asia–Africa, Oceania, and the Americas. *M. vitrata* in Asia and Africa seem to be the same species, as many populations from the two continents are morphologically indistinguishable. However, genome-wide analyses

of the *Maruca* populations from different geographical regions (continents) should be conducted in future studies to understand the exact patterns of admixture and complex demographic history, given the limitations associated with the nuclear and mitochondrial markers in molecular taxonomy. Such analyses will not only validate the results from previous *cox1* or nuclear marker based studies, but also confirm whether any of these species or subspecies are synonymous, as documented for *Bemisia tabaci* in a recent study (35). In addition, more adult specimens need to be collected from Oceania and the Americas to characterize and identify the species of *Maruca* present.

HOST PLANTS AND POPULATION DYNAMICS

Wild and Cultivated Host Plants

M. vitrata primarily feeds on plants in the Fabaceae and was reported on 39 plant species, including two non-leguminous plants (*Sesamum* sp. and *Hibiscus* sp.) (110). However, there were no reports of *M. vitrata* feeding on non-leguminous plants after the first report from Africa. Interestingly, when sesame was evaluated as an intercrop with mungbean to manage *M. vitrata* in Bangladesh, *M. vitrata* did not feed on it (44). A recent review listed 28 new wild host plants from Africa (10). In addition, *Maruca* spp. were reported on *Canavalia* sp., *Dioclea guianensis*, *Dioclea trujellensis*, *Millettia pinnata*, *Sesbania cannabina*, *Sesbania grandiflora*, and *Sesbania rostrata* (25, 46, 66, 69), giving a total of 73 legume host plant species, with the genus *Vigna* (11 species) being predominant, followed by *Crotalaria* (9 species) and *Tephrosia* (6 species). Of the cultivated legumes, *Vigna unguiculata*, *V. unguiculata* subsp. *sesquipedalis*, *Vigna radiata*, *Vigna mungo*, *Cajanus cajan*, *Dolichos lablab*, *Lablab purpureus*, *Phaseolus vulgaris*, and *Glycine max* are the most important host plants.

Host Shifts

Unlike in Asia, very few cultivated host plants are available for *M. vitrata* in Africa, with cowpea being the predominant host in West Africa and pigeonpea in Eastern and Southern Africa (10). *M. vitrata* populations thrive exclusively on perennial leguminous hosts during the long dry, main rainy, and short wet seasons (7) in West Africa; however, similar information is lacking for Eastern and Southern Africa. In contrast, several cultivated legumes sustain *M. vitrata* populations in different seasons in Asia (110), except during the brief off season when, for instance, feeding was recorded during summer in Taiwan on *S. cannabina*, which has not been recorded as a host outside of Taiwan (47). Although a seed pod borer, *M. vitrata* feeds on *S. cannabina* by folding the leaflets, tying them with silken thread, and remaining concealed inside (45). However, the population densities dropped to zero in January due to inferior quality of *S. cannabina* (46), when it moved to *S. grandiflora* flowers. Thus, *M. vitrata* can shift between cultivated and wild host plants, and even to nonreproductive parts of an unusual host plant, resulting in the maintenance of populations year-round, except during periods with subzero temperatures (55). The diversity of wild and cultivated legumes in an area should be considered when designing management strategies.

Host Plant Races?

M. vitrata is oligophagous, feeding on Fabaceae, and multiple generations occur on cultivated and wild host plants. The different feeding patterns on some hosts and differential responses of male moths to the same sex pheromone blends in Asia and Africa led to speculation of host-associated genetic variation, as reported in another Crambidae, *Ostrinia nubilalis* (136). *M. vitrata* collected

from cultivated and wild hosts did not show host-associated genetic structure in Asia and Africa (3, 66), except for one study in India based on collections from five cultivated legumes in a single location (104). The latter study needs to be validated.

Host Plant Volatile–Mediated Interactions

Host selection by phytophagous insects is partly mediated by host plant volatiles. Female *M. vitrata* moths show oviposition preference for floral parts, since bioactive compounds are present in its host plant flowers (88, 142). Higher electrophysiological responses of female *M. vitrata* moths to *S. grandiflora* and *V. unguiculata* flower and pod extracts (39, 88) and increased mating due to 1-octen-3-ol in cowpea volatiles (13) can be exploited in pest management, since trapping of female moths or moths of both sexes can be more effective in reducing crop damage than trapping of male moths alone using pheromone traps. For instance, lures made up of host-floral volatiles demonstrated effective attraction to *M. vitrata* female moths (151). In addition, *M. vitrata* larval feeding induced cowpea volatiles that acted as an oviposition repellent but attracted the parasitoids (88). Thus, host plant chemicals provide a platform for developing semiochemical-based management strategies against *M. vitrata*.

NATURE AND EXTENT OF DAMAGE

How larvae of *M. vitrata* feed on and cause damage to food legumes was summarized in two earlier reviews (10, 110). Larvae usually feed on reproductive parts, with flowers being the most preferred (110). Young larvae create webs on buds, blossoms, flowers, and pods with adjacent leaves, and bore into buds and pods to feed on developing seeds. However, an unusual feeding on *S. cannabina* leaves over flowers or pods was observed in Taiwan (47). In contrast, *M. vitrata* feeds preferentially on *S. grandiflora* flowers over leaves or pods. Thus, *M. vitrata* shows plasticity in its feeding habits on unusual host plants. Up to 72% of yield loss due to *M. vitrata* has been reported for cowpea and pigeonpea (110). Without any control measures, reported pod yield losses ranged from 17% to 53% in Taiwan for cowpea (62); from 25% to 40% for yard-long bean in Cambodia, Indonesia, and Thailand (43, 125, 149); and from 10% to 45% for mungbean in Bangladesh (150). Yield losses due to *M. vitrata* can be high depending on the crop, season, location, level of pest control efforts, and incidence of natural mortality factors. If the crop is left unprotected, close-to-complete crop failure is a possibility, which forces the growers to apply pesticides, often indiscriminately.

MANAGEMENT

Host Plant Resistance

Current approaches in host plant resistance are guided by the nature of crop–pest interactions, pest ecology, and the availability of novel resistance genes discovered with modern genomic tools. In the case of *M. vitrata*, resistance genes have been identified in cultivated legumes and their wild relatives. In addition, operational levels of resistance have been obtained in cowpea, which was transformed with genes encoding insecticidal proteins from the soil microorganism *Bacillus thuringiensis* (*Bt*). We summarize and discuss present knowledge on host plant resistance in major grain and vegetable legumes to *M. vitrata*.

Cowpea. In West Africa, developing *M. vitrata*–resistant cowpea varieties was a major endeavor in the late 1970s. Although a few varieties exhibiting some levels of field resistance or tolerance

to *M. vitrata* were identified (84, 85), after extensive screening of the International Institute of Tropical Agriculture (IITA) cowpea germplasm, it became clear that no cultivated cowpea would be able to provide operational levels of resistance to *M. vitrata* (10). In Asia, cowpea accessions with high phenol and flavonoid contents (53) or high trichome density in pods (82) show some resistance to *M. vitrata*. Although wild *Vigna* species displaying high levels of resistance to *M. vitrata* (37, 49, 86) raised hopes for interspecific crosses, these efforts were abandoned due to their strong cross-incompatibility with cowpea (36). Cowpea has been transformed with the *cry1Ab* gene construct from *B. thuringiensis*, which was highly toxic to *M. vitrata* (94). The development of transgenic cowpea was accompanied by complementary studies targeting its environmental (48) and non-target organism risk assessment (11), as well as by insect resistance management (87). Since *Bt*-cowpea with a single gene would inevitably lead to resistance in *M. vitrata*, the possibility of stacking the *vegetative insecticidal protein* (*vip*) gene from *B. thuringiensis* with a dissimilar mode of action than *cry1Ab* was assessed (14). Apart from regulatory approval, large-scale deployment of *Bt*-cowpea in the field will depend on production and distribution of the huge quantity of transgenic seeds required and convincing both farmers to grow them and consumers of their food safety.

Pigeonpea. Screening pigeonpea varieties for *M. vitrata* resistance was a major focus at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (110), but only low to moderate levels of resistance or tolerance were found. Generally, *M. vitrata* preferred short-duration and determinate lines with clustered inflorescences (105), while high phenol concentrations in flowers and pods imparted resistance (131). Since yield increased synergistically when these moderate resistance levels were deployed with newer synthetic or biopesticides (111), partial resistance in pigeonpea is still an advantage.

Mungbean. Among over 10,000 germplasm accessions at World Vegetable Center (WorldVeg), four mungbean accessions were identified as *M. vitrata*-resistant sources (22). In India, direct field screening resulted in 4–5 moderately resistant or tolerant accessions (112, 116). Tolerant accessions suffered the highest flower infestation but had higher yields due to flower compensation. As in pigeonpea, higher phenol content in mungbean pods offered some resistance to *M. vitrata* (54). However, spatial and temporal variation were reported in *M. vitrata* resistance in mungbean genotypes when tested based on field performance (22, 23). Thus, no mungbean varieties displaying operational levels of resistance to *M. vitrata* are currently available.

Yard-long bean. Attempts to identify host plant resistance are scant for yard-long bean. Only 50 yard-long bean accessions to *M. vitrata* resistance have been screened in India, and none exhibited exceptional levels of resistance (141), although tolerance was a possibility (90). A recent field screening attempt in Bangladesh identified one commercial genotype (Long Red Mollika) as moderately resistant to *M. vitrata* (6). However, low infestation was significantly correlated with lower protein content in flowers and pods, making this variety unsuitable for further development as an *M. vitrata*-resistant cultivar because high protein content is essential in commercial varieties.

Sex Pheromone

M. vitrata produces a three-component sex pheromone, with (*E,E*)-10,12-hexadecadienal (*EE*10,12–16:Ald) as the major compound (2) and (*E,E*)-10,12-hexadecadienol (*EE*10,12–16:OH) and (*E*)-10-hexadecenal (*E*10–16:Ald) as the minor compounds (30). Synthetic sex pheromone

consisting of major and minor compounds in a 100:5:5 ratio attracted male *M. vitrata* moths in Benin and Ghana, whereas *EE*10,12–16:Ald alone was most effective in Burkina Faso (30, 31). However, none of these blends attracted male moths in Mauritius (140), Taiwan (107), Thailand, and Vietnam (124). The different responses of *M. vitrata* male moths to pheromone blends suggest the possible existence of geographic variation in Asia and Africa. Interestingly, *EE*10,12–16:Ald and *EE*10,12–16:OH were present in female moths from Benin, Taiwan, Thailand, and Vietnam, but *E*10–16:Ald was absent in all four populations (106). These results are in striking contrast with earlier studies, which reported the presence of *E*10–16:Ald as a minor component (30, 64). In fact, *E*10–16:Ald was the major compound in female *M. vitrata* moths from Wuhan (64). Thus, it is possible that variation exists in the number, quantity, and proportion of *M. vitrata* pheromone compounds among geographically distant populations. As indicated in the molecular studies, genetic differences within *M. vitrata* populations could lead to such variations in pheromones. Heritable intrapopulation variation and changes in activity of desaturase enzymes altering the ratio of components in the moth sex pheromone have been reported (42). The biosynthesis pathway for *M. vitrata* pheromone is initiated from C16:CoA, with fatty acid desaturases converting the substrate into intermediate products, which are reduced by pheromone gland-specific fatty acyl-CoA reductase (20). Determining the expression levels of desaturase enzymes in pheromone glands of geographically distant *M. vitrata* and mapping desaturase genes onto the linkage map will provide additional insights into the variation in pheromone components.

Besides variation in *M. vitrata* pheromone composition across geographic locations, differential male pheromone response behavior can be linked to the alteration in the pheromone-binding proteins (PBP). Pheromone reception in male moths is mediated by PBPs, which bind to the pheromone compounds and carry them to the receptor cells. Two PBPs (MvitPBP1 and MvitPBP2) were identified from male *M. vitrata* moths (65), and MvitPBP3 was identified from female moths. Two general odorant-binding proteins (MvitGOBP1 and MvitGOBP2) were also identified (151). Binding affinities of MvitPBPs with the sex pheromones (70) and MvitGOBPs with host-floral volatiles (151) confirmed their importance. In fact, the binding capacity of a MvitPBP with host plant volatiles similar to MvitGOBP2 confirmed the presence of identical key binding sites and similar protein pocket structure around the binding cavity (70). The differences in sex-linked loci can be associated with differential pheromone response behavior in male moths, as the gene loci conferring specificity in pheromone communication systems showed fixed amino acid differences between strains or species (144). Amino acid changes at critical locations of the MvitPBPs among *Maruca* populations from Asia, Africa, Oceania, and South America were found (69), which warrants further analysis to understand whether these amino acid differences in PBP contribute to the reported differential responses to *M. vitrata* pheromone blends, or whether they indicate species differences.

The isomer (*Z,E*)-10,12-hexadecadienal, when blended with *EE*10,12–16:OH and *E*10–16:Ald in a 100:10:5 ratio, elicited responses in *M. vitrata* male moths (15). This study also confirmed the attraction of *M. vitrata* pheromone compounds and their isomers with host plant volatiles. This lure attracted a significantly higher number of male *M. vitrata* moths in India and Cambodia (15, 57), but failed to attract moths in yard-long bean fields in Laos, Taiwan, Thailand, and Vietnam (122). If this variation in response to pheromone blend(s) coincides with geographic variation in the female pheromone composition, then geographic differentiation between *M. vitrata* populations is a possibility. Thus, additional studies on female pheromone composition are necessary in those countries where no male response to pheromone blend(s) is recorded. In addition, further improvement to increase the efficacy of *M. vitrata* pheromone lures is required to use them for monitoring or mass trapping.

Habitat Management

Food legumes are mostly cultivated in cereal-based production systems in Asia and Africa. When cereal crops are grown as intercrops—maize with cowpea (139) and rice with pigeonpea (29) in Nigeria, maize and sorghum with mungbean and black gram (27), sorghum and pearl millet with pigeonpea (38), and sorghum and groundnut with black gram (115) in India—*M. vitrata* damage is effectively reduced. However, maize or sorghum was not an effective intercrop in every legume production system (29, 81). In most of the studies, intercrops were shown to be effective in reducing *M. vitrata* damage in grain legumes, but studies are lacking for vegetable legumes, especially in Southeast Asia. In general, intercrops were effective when they were grown with the grain legumes in 1:3 to 1:1 ratio. However, vegetable farmers may not be able to afford using 33–50% of their land for intercrops, since it could drastically reduce their income, which might be the reason for the lack of research on or adoption of intercrops in vegetable legumes. The intercrops may limit the dispersal of *M. vitrata* into and within the legume crop habitat, besides favoring the proliferation of natural enemies (97). Altered microclimate, especially relative humidity within the crop canopy, also reduced the incidence of *M. vitrata* (98). Thus, efficacy of intercropping varies with the cropping systems, type, and host or nonhost status of the intercrop; the phenological synchrony of the main and intercrops; and the microclimate. Local validation is required to optimize the intercrop, which should have an economic value besides reducing *M. vitrata* damage on the main crop so that the growers are more likely to be convinced to spare some area for intercrops.

A trap-cropping strategy has not been given much emphasis for managing *M. vitrata*. An early study found that sunn hemp (*Crotalaria juncea*) can be used as a trap crop to manage *M. vitrata* (52). Female *M. vitrata* moths preferred to lay eggs on *C. juncea* (51), but >80% larval mortality with the lowest growth index for surviving larvae was recorded on *C. juncea* (52). Although *C. juncea* became an ideal candidate for dead-end trap-cropping against *M. vitrata*, further research on establishing the most effective model for deploying *C. juncea* with legumes was not pursued, and thus it is worth testing. Another attempt evaluated the potential of pigeonpea as a trap crop with cowpea, but it failed against *M. vitrata* (9). Considering the smallholder production systems in Asia and Africa, where mixed cropping including legumes is a common practice, and where trap-cropping is a natural fit, more research emphasis should be given on trap-cropping strategies for managing *M. vitrata*.

Biological Control

Several predators and parasitoids are reported to attack various life stages of *M. vitrata*. Among these natural enemies, parasitoids are the most widely studied, and the majority of them attack the larvae of *M. vitrata*. In this section, we briefly describe the use of predators and parasitoids to control *M. vitrata*, including the recent emphasis on classical biological control.

Predators. Twenty-one predatory species, including 14 insects from Dermaptera, Coleoptera, Hemiptera, Hymenoptera, and Mantodea and 7 spiders from Selenopidae, Araneidae, Oxyopidae, Salticidae, and Sparassidae, were reported to feed on *M. vitrata* (110). Of the 21 predators, only 6 species were reported from Africa (10) (**Table 1**). While most of the insect predators preferred to attack *M. vitrata* larvae, spiders and praying mantids preferentially attacked the moths. Apart from the studies listed in the previous two review papers (10, 110), very few studies have reported the predators of *M. vitrata* (16, 47, 83, 102) (**Table 1**). Most of these predators are generalists feeding on a wide variety of host insects in natural field conditions (83, 102). Predators may occasionally reduce the *M. vitrata* larval population, depending on the nature and density of

Table 1 List of predators and parasitoids attacking *Maruca vitrata* in Asia, Africa, and the Americas

Natural enemy	Country or Region	Reference(s)
Predators		
Spider (<i>Selenops radiatus</i>) Ants (<i>Camponotus sericeus</i> , <i>Camponotus rufoglaucus</i>) Praying mantids (<i>Polyspilota aeruginosa</i> , <i>Spodromantis lineola</i>) Earwig (<i>Diaperasticus erythrocephala</i>)	Africa	10
Potter wasps (<i>Delta conoideum</i> , <i>Delta campaniforme esuriens</i> , <i>Delta pyriforme</i>)	India (Odisha)	102
Pyrrhocorid (<i>Antilochus coquebertii</i>) Spiders (<i>Oxyopes shweta</i> , <i>Thomisus katrajghatus</i> , other <i>Thomisus</i> sp., <i>Salticus</i> sp.)	India (Assam)	16
Unidentified predatory staphylinid	Taiwan	47
Predatory bug (<i>Eocantbecona furcellata</i>)	India (Uttarakhand)	83
Parasitoids		
<i>Apanteles</i> sp., <i>Microbracon thurberiphae</i> , <i>Brachymeria ovata</i> , <i>Nemorilla floralis</i> , <i>Argyrophylax (Sturmia) albincisa</i>	Central America	58
<i>Apanteles taragamae</i>	India (Odisha), Taiwan	47, 102
<i>Caenopimpla</i> sp., <i>Temelucha</i> sp.	India (Assam)	17
<i>Bassus asper</i> , <i>Exorista xanthaspis</i> , <i>Peribaea orbata</i>	Philippines, Taiwan	47, 138
<i>Bassus javanicus</i>	Southeast Asia	134
<i>Trichomma</i> sp., <i>Triclistus</i> sp., <i>Plectochorus</i> sp.	Taiwan	47

co-occurring pest organisms in legume production systems, but they cannot be solely relied on as an effective *M. vitrata* control component.

Parasitoids. Five parasitoid species were recorded in Central America (58) (Table 1). Subsequently, a list of 33 parasitoids, predominantly hymenopterans (Braconidae, Bethyridae, and Ichneumonidae) that are native but also including those introduced for biological control of *M. vitrata* in the Americas and the Caribbean, Asia, Africa, and France, was compiled (143). Another list of 26 Hymenoptera parasitoids (Braconidae, Chalcididae, Ichneumonidae, Eulophidae, Pteromalidae, and Scelionidae) and 10 Tachinidae (Diptera) were added (110). A recent review (10) emphasizing West Africa reported a total of 24 parasitoids (native or introduced), including 5 dipterans and 19 hymenopteran wasps, infesting *M. vitrata*; five of these were new records (10). Outside of the above lists, a few additional parasitoids have been reported in Asia (17, 47, 102, 134, 138). Thus, at least 98 parasitoid species have been reported attacking *M. vitrata* life stages; most of them are braconid wasps attacking the larvae, but none of them are specific for *M. vitrata* (8, 68).

Despite the lack of specificity, some of these parasitoids were explored for classical biocontrol. Of the parasitoids introduced from Trinidad to Mauritius, only *Bracon cajani* and *Eiphosoma dentator* became established (40), and they were ineffective. Subsequently, they were introduced into Hawaii, Sri Lanka, and Fiji (24), but all of these attempts failed (143). In recent decades, *Apanteles taragamae* was introduced into Benin from Taiwan (26). *A. taragamae* was reported to be gregarious and parasitized five other Pyraloidea species in India (75, 92). However, *A. taragamae* in Taiwan was considered a different strain, since it was strictly solitary with a maximum of 63% *M. vitrata* parasitism in field conditions (47), and was thus imported into Africa. However, it failed to establish due to poor ecological adaptation (10, 133).

Because of the lack of species-specific parasitoids of *M. vitrata*, explorations were made in Southeast Asia, the believed origin of *Maruca*, which resulted in the identification of three more parasitoids—*Phanerotoma syleptae* (egg-larval), *Therophilus javanus*, and *Therophilus maruca* (larval parasitoids) (128). *P. syleptae* and *T. javanus* were later introduced into Benin. After two years of

confined experimentation, they were released more widely in Benin and Burkina Faso in 2016, and their establishment and successful survival during the long dry season on *M. vitrata* on alternative host plants in the absence of cowpea was confirmed in mid-2017 (10, 133). As egg-larval and larval parasitoids, respectively, the species will complement each other in field conditions, and thus these two species may improve the biological control of *M. vitrata* in Asia and Africa. Future IPM programs should integrate these two parasitoids as components for managing *M. vitrata*.

Entomopathogens

In this section, we summarize available information on the use of entomopathogenic fungi, bacteria, and viruses in the management of *M. vitrata*. Entomopathogens are known to infect and kill *M. vitrata*. Entomopathogenic organisms have been isolated, tested, and formulated for use against *M. vitrata*. Commercially available microbial pesticides have also been tested for controlling *M. vitrata*.

Entomopathogenic fungi. Various isolates and formulations of entomopathogenic fungi have been evaluated against *M. vitrata* under laboratory and field conditions. In particular, *Beauveria bassiana* and *Metarhizium anisopliae* isolates were moderately to highly pathogenic to *M. vitrata* in Nigeria (34), Benin (74), India (123), and Kenya (137). However, locally available formulations of *B. bassiana* and/or *M. anisopliae* were less effective against *M. vitrata* in India (130) and Thailand (149), whereas they were highly effective in Vietnam (123) in laboratory conditions. The results of field trials using formulations of entomopathogenic fungi against *M. vitrata* on food legumes are summarized in **Table 2**. In the majority of the studies, the efficacy was low, and very few studies demonstrated high reductions in pod damage. Field trials in India (Karnataka) and Cambodia with *M. anisopliae* showed the highest pod damage reduction, which can be linked to the favorable weather conditions (high relative humidity and average temperature of approximately 30°C) (125). The combination of these two factors needs to be considered when assessing entomopathogenic fungal formulations for managing *M. vitrata*. Since entomopathogenic fungal formulations can be effective against a range of pests (125), they could be used in IPM programs targeting food legumes in Asian and African humid tropics.

Entomopathogenic viruses. Entomopathogenic viruses are one of the most viable tools in eco-friendly pest management approaches because of their species specificity. Until recently, only *Galleria mellonella* nucleopolyhedrovirus (NPV) could elicit infections of *M. vitrata* larvae in the laboratory, but there was little prospect for field applications (91). Although cypovirus and granulovirus were reported infecting *M. vitrata* in China and Kenya (89, 147, 148), their sublethal nature precluded any further applications. A highly virulent NPV infecting *M. vitrata* was identified in Taiwan, confirmed to be unique and named as *M. vitrata* multiple nucleocapsid nucleopolyhedrovirus (MaviMNPV), which is closely related to *Bombyx mori* NPV but distant from the *Autographa californica* multicapsid nucleopolyhedrovirus (61). Since MaviMNPV is highly effective against *M. vitrata* larvae of early larval instars (61), which feed on the surfaces of flowers and pods, it has become an ideal component for killing the caterpillars before they enter inside these reproductive organs. MaviMNPV formulations reduced *M. vitrata* damage on hyacinth bean in Taiwan by 46–54% (127).

MaviMNPV was introduced into Benin by IITA and was confirmed to cause 88% larval mortality (127, 135). MaviMNPV biopesticide was effective in controlling *M. vitrata*, resulting in up to 34% cowpea yield gain in Benin, Burkina Faso, Niger (135), and Nigeria (78). The grain yield can be increased further if MaviMNPV formulations are improved or combined with botanicals.

MaviMNPV in combination with neem or *Jatropha* oils resulted in lower cowpea pod damage, leading to higher yield (73, 113). Production, formulation, and marketing of MaviMNPV require attention if this component is to be included in *M. vitrata* IPM packages. In general, production of baculoviruses using host larvae is laborious, time consuming, and difficult to scale up, in addition to issues of product quality and profitability. A community-based pilot production model is being tried in Benin with a cheaper *M. vitrata* mass-production method, using cowpea sprout diet, developed by IITA-Benin. Thus, large-scale *M. vitrata* larval production was possible, leading to lower MaviMNPV production costs (126), but the active involvement of the private sector will be the key to launching large-scale quality formulations of MaviMNPV. Finally, a unique association was found between *A. taragamae* and MaviMNPV, with *A. taragamae* transmitting MaviMNPV to *M. vitrata* larvae over generations (26, 127), which can favor rapid spread of MaviMNPV in field conditions. However, further research is needed to understand the additive, synergistic, or antagonistic interactions of MaviMNPV and *A. taragamae* when combined in an IPM package.

Entomopathogenic bacteria. *Bacillus cereus*, *B. thuringiensis*, *Streptococcus faecalis*, and *Serratia marcescens* were reported to be naturally infecting bacteria on *M. vitrata* in Kenya (89). *M. vitrata* was highly susceptible to Cry1Ab and Cry1Ca toxins in West Africa and Taiwan (121), to *B. thuringiensis* subsp. *kurstaki* formulations in Thailand (60, 149), and to *B. thuringiensis* subsp. *aizawai* formulations in Vietnam and Taiwan (123). The differential susceptibility pattern of various *M. vitrata* populations can be attributed to their previous level of exposure to *B. thuringiensis* formulations, which contain Cry1A or Cry1Ca toxins, and to the quality of the formulations.

Under field conditions, variable effectiveness of *B. thuringiensis* formulations against *M. vitrata* has been reported from different countries (Table 2), with a reduction in pod damage ranging from 35% to 75% after applying *B. thuringiensis* formulations in Cambodia, India, and Thailand. However, most field trials were conducted without previous assessment of the baseline susceptibility of *M. vitrata* field populations and used doses recommended for other lepidopteran pests. Thus, future studies should establish the baseline susceptibility of *M. vitrata* to *B. thuringiensis* formulations in a region first, before conducting field efficacy trials. This will enable confirmation of whether the first and second instar larvae are susceptible to *B. thuringiensis* formulations, which is critical since it is imperative to kill the *M. vitrata* caterpillars before they bore inside the floral and fruiting bodies.

Botanical pesticides. Botanical pesticides have been widely evaluated against *M. vitrata*. Leaf, seed, or bark extracts of at least eight different plant species were tested against *M. vitrata* in Asia and Africa (Table 2). Neem (*Azadirachta indica*) has been tested in field conditions more widely than other botanical pesticides. In laboratory studies, results of neem pesticides were highly variable, mainly because of the varying concentration of azadirachtin. For instance, neem oil formulations exhibited a high degree of insecticidal activity to *M. vitrata* larvae only at higher concentrations (50, 130, 149); significant larval mortality with a commercial neem formulation was recorded at a dose of 3,000 ppm (60). One laboratory study in Africa documented substantial reduction in *M. vitrata* egg hatch by *Piper guineense* and *Allium sativum* extracts (33), although this result has not been replicated.

In field studies, neem was evaluated in the forms of seed or leaf extract, oil, soap, or other commercial formulations on different food legumes. The results were not consistent, most likely due to factors including the variation in the types of spray solutions containing different concentrations of azadirachtin, temperature and sunlight, and physiology of *M. vitrata*. The pod damage reduction by neem treatments was 50% or more over the untreated fields, but only in half of the studies (Table 2). In addition to neem, a limited number of studies have been conducted using

Table 2 Summary of results of biopesticide trials against *Maruca vitrata* in terms of damage reduction in food legumes in Asia and Africa

Location	Crop	Formulation	Reduction in pod damage over untreated plants	Reference(s)
Entomopathogenic fungi				
Karnataka (India)	Cowpea	<i>Metarbizium anisopliae</i> , 1–2 × 10 ¹² conidia/ha	45–68%	95
Tamil Nadu (India)	Black gram	<i>Beauveria bassiana</i> , 2.8 × 10 ⁶ CFU/g	0–50%	114
Uttarakhand, Andhra Pradesh (India)	Pigeonpea	<i>B. bassiana</i> (Biosoft [®] , Toxin WP 1.15%)	26–53%	93, 117, 118
Nakhon Pathom (Thailand)	Yard-long bean	<i>B. bassiana</i>	17–23%	149
		<i>M. anisopliae</i>	20–23%	
Southern provinces (Cambodia)	Yard-long bean	<i>M. anisopliae</i> (Real M-62 [®] , Real M-69 [®])	48–77%	125
Cotonou (Benin)	Cowpea	<i>B. bassiana</i> (oil-based formulation)	52%	73
Entomopathogenic bacteria				
Andhra Pradesh (India)	Cowpea	<i>B. thuringiensis</i> subsp. <i>kurstaki</i> (Delfin [®])	70%	21
Andhra Pradesh (India)	Pigeonpea	<i>Bacillus thuringiensis</i> (Bt-1)	40%	117
Uttar Pradesh (India)	Mungbean	<i>B. thuringiensis</i>	58%	145
Uttarakhand (India)	Pigeonpea	<i>B. thuringiensis</i> subsp. <i>kurstaki</i> (Halt [®])	32%	93
Andhra Pradesh (India)	Pigeonpea	Project Directorate of Biological Control <i>B. thuringiensis</i> -1, National Bureau of Agriculturally Important Insects <i>B. thuringiensis</i> -G4	48–62%	118
Nakhon Pathom (Thailand)	Yard-long bean	<i>B. thuringiensis</i> subsp. <i>aizawai</i> (Zitarback F.C. [®])	36–52%	149
		<i>B. thuringiensis</i> subsp. <i>kurstaki</i> (Redcat [®])	36–45%	
Southern provinces (Cambodia)	Yard-long bean	<i>B. thuringiensis</i> subsp. <i>aizawai</i> (Xentari [®])	46–72%	125
		<i>B. thuringiensis</i> subsp. <i>kurstaki</i> (Crymax [®] , E911 [®])	48–75%	
Botanical pesticides				
Andhra Pradesh (India)	Cowpea	Neem, 1,500 ppm	53%	21
Andhra Pradesh, Karnataka, Uttar Pradesh (India)	Pigeonpea	Neem Seed Kernel Extract (NSKE), 5%	5–54%	38, 77, 117
Gujarat (India)	Cowpea	NSKE, 5%	40%	56
		Azadirachtin, 0.001%	36%	
Uttarakhand (India)	Pigeonpea	Jatropha oil, 1–2%	47–75%	93
		NSKE, 5%	46%	
		Black cumin seed extract, 2%	39%	
Uttar Pradesh (India)	Mungbean	Azadirachtin, 1l/ha	45%	145

(Continued)

Table 2 (Continued)

Location	Crop	Formulation	Reduction in pod damage over untreated plants	Reference(s)
Tamil Nadu (India)	Pigeonpea	Neem soap, 1 %	63%	103
		Pongamia soap, 1 %	57%	
		NSKE, 5 %	54%	
Andhra Pradesh (India)		Neem, 1,500 ppm	26%	118
Jessore (Bangladesh)	<i>Lablab purpureus</i>	Neem seed extract, 10–15%	18–46%	100
Mahogany seed extract, 10%		24–63%		
Gazipur (Bangladesh)		Neem oil, 0.5%	44–57%	5
		Neem leaf extract, 2%	26–34%	
		Chili extract, 2%	48–51%	
		Mahogany oil, 0.5%	47–51%	
Nakhon Pathom, Pathum Thani (Thailand)	Yard-long bean	Neem formulations (Thai neem [®] , NeemBaan [®])	11–75%	60, 149
Southern provinces (Cambodia)	Yard-long bean	Neem leaf extract, 5%	37–52%	125
Zaria (Nigeria)	Cowpea	<i>Azadirachta indica</i> , 10%	69%	72
		<i>Artocarpus altilis</i> , 10%	66%	
		<i>Manibot esculenta</i> , 10%	59%	
Nyankpala (Ghana)	Cowpea	Neem seed extract, 5–20%	54–83%	12
Cotonou (Benin)	Cowpea	Neem oil emulsion, 0.25 %	32–41%	113
		Jatropha oil emulsion, 0.25 %	22–35%	

other plant species, such as mahogany in Bangladesh, Pongamia in India, and various plant species in Nigeria. Unlike *B. thuringiensis* pesticides, botanical pesticides were tried in various African countries, especially Ghana and Nigeria, and their effectiveness in reducing *M. vitrata* damage on cowpea was found to be significantly higher than in untreated fields. Most of the species were local plants and were tested in few studies (Table 2). These plants may not be available in large quantities, and thus exploiting them on commercial scale will be a challenge. In general, neem is the most widely used botanical pesticide against *M. vitrata* in both Asia and Africa. If formulated and used properly, neem is able to reduce *M. vitrata* damage significantly. Since neem has antifeedant and repellent properties, application of neem products at the early flowering stage can reduce the incidence of *M. vitrata*. In addition, neem can elicit a synergistic effect in combination with microbial pesticides, since microbial pesticides can kill larvae more rapidly if they are stressed due to neem (76). Neem formulations can be effective against different pests on food legumes, so farmers might be easily convinced to use them in IPM packages targeting *M. vitrata*.

Insecticides and Resistance to Insecticides

Insecticides are the predominant control approach used by legume producers globally to tackle *M. vitrata*. Although statistics on the pesticide quantity used specifically against *M. vitrata* are absent, some studies document the pesticide types and quantity used to manage pests in yard-long bean including *M. vitrata*. Farmers in Thailand and Vietnam solely relied on synthetic pesticides in yard-long bean, with an average of 16.3 kg/ha of formulated pesticides per cropping cycle (109).

Farmers in Laos sprayed pesticides more frequently than did farmers in Cambodia and Vietnam, and in Cambodia, applicators mixed an average of four pesticides in a single spray (108). Pesticide use against *M. vitrata* has been similar in Africa, with resistance to organochlorines, organophosphates, and synthetic pyrethroids documented two decades ago (32). Resistance to organophosphates and pyrethroids was reported in India (119). However, there were no further follow-up studies on these resistant populations to document the development of resistance to other pesticides, despite the indiscriminate use of pesticides against this pest in Asia and Africa. Recent studies have attempted to screen chemical pesticides against *M. vitrata* on pigeonpea, cowpea, and black gram in India (96, 101, 120). In Brazil, where *M. vitrata* is considered a seasonal pest of soybean, pesticides were found to reduce *M. vitrata* damage significantly (41). The use of pesticide combinations might exacerbate the development of resistance, and thus it is imperative to have pesticide resistance monitoring programs in *M. vitrata*.

Integrated Pest Management

IPM in cowpea was recommended as an *M. vitrata* control option more than 30 years ago, but its implementation continued to rely largely on the intensive utilization of chemical pesticides for many years. A review of IPM in cowpea-cereal systems in West Africa (1) reemphasized the need to sensitize farmers to refrain from using pesticides and to invest more efforts into developing bio-control and habitat management approaches. These recommendations were put into practice by subsequent projects, which have been using multi-pronged strategies, including farmer field fora, digital approaches, women's cooperatives, and partnerships with small-scale industries in West Africa. One of those digital approaches was the development of a prototype Farmer Interface Application (FIA), in collaboration with the Scientific Animations Without Borders program. FIA is a simple app running on Android systems to empower low-literacy farmers to make informed decisions about *M. vitrata* control; it has been field-tested in Benin and can be used on simple smartphones (4).

IPM approaches targeting legume pests including *M. vitrata* were attempted sporadically in East Africa and Asia, but they were not piloted or implemented on a large-scale. For instance, an IPM package based on cowpea and sorghum intercropping with carbofuran seed dressing and insecticide spraying once each at the budding, flowering, and podding stages increased cowpea grain yields in eastern Uganda (80). In the same region, another IPM package that combined early planting, close spacing, and insecticide applications once each at the budding, flowering, and podding stages was suggested (79). Similarly, IPM modules for pigeonpea were developed for different agroclimatic zones in India (129). An IPM package based on sequential application of biopesticides (*B. thuringiensis*, *M. anisopliae*, and neem) and a chemical pesticide was developed and piloted in Cambodia; this package reduced the infestation by aphids, thrips, and *M. vitrata* without compromising yield in yard-long bean (125). However, IPM showed variable effectiveness in different regions and seasons. Control of *M. vitrata* is a major challenge for IPM in summer grain legumes in Australia (18). IPM packages should be adjusted to the local cropping systems and environment and then scaled up. It has become imperative to ensure the availability of IPM component technologies at affordable costs within the reach of the legume growers in Asia and Africa, and an enabling policy environment is necessary for large-scale promotion and adoption of IPM (1).

CONCLUSIONS AND FUTURE ISSUES

The genus *Maruca* has four described species, with *M. vitrata* being the predominant pest species feeding on 73 plant species in Fabaceae. Presence of subspecies and pheromone polymorphism complicates its management, which requires further studies for the better understanding and

refinement of IPM. Although host plant resistance does not seem to be promising, transgenic approaches in cowpea offer hope in limited geographic locations due to nonuniform policies and regulatory frameworks in Asia and Africa. Recent advances in biopesticides and classical biocontrol make them strong candidate components of IPM. However, simple and cheaper MaviMNPV production techniques and quality formulations of *B. thuringiensis* and entomopathogenic fungi need to be scaled up through the private sector. Since neem is synergistic with microbial pesticides, it should form a key component of IPM. It is unlikely that any single method of pest management can achieve a level of *M. vitrata* control acceptable to producers, which warrants the promotion of IPM packages for the sustainable management of legume pests including *M. vitrata*.

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