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REVIEW ARTICLE

The legume pod borer, *Maruca vitrata* Fabricius (Lepidoptera: Crambidae), an important insect pest of cowpea: a review emphasizing West Africa

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Abstract

The legume pod borer *Maruca vitrata* Fabricius (Lepidoptera: Crambidae) is a pantropical insect pest of legumes. In West Africa *M. vitrata* is the most devastating insect pest of cowpea, a food crop providing much-needed, inexpensive protein to farmers and consumers. Various approaches to controlling this pest have been tried, including cultural management, host plant resistance and use of synthetic and botanical pesticides, all with limited success. In this review we present information on the distribution, morphology, molecular characteristics, behavior and host plants of *M. vitrata*. We give especial attention to innovative management tactics being developed for West Africa, including genetically engineered *Bt* cowpea, new biopesticides and use of exotic parasitoids. We discuss research needs for enhancing integrated pest management (IPM) for *M. vitrata* in Africa.

Keywords *Maruca vitrata* · Africa · Pest management · Cowpea · Migration · Crop losses

Introduction

Legumes such as beans and peas are major sources of protein for poor people in the tropics. Production of these legumes is limited by several constraints, among which insect pests are the most important. The legume pod borer, *Maruca vitrata* Fabricius (Lepidoptera: Crambidae), is the key pest of legume crops in the tropics and sub-tropics (Singh and Van Emden 1979; Singh and Allen 1980; Singh and Jackai 1988; Jackai and Daoust 1986; Sharma 1998). In West Africa, *M. vitrata* causes devastating damage to cowpea (Singh et al. 1990).

Several approaches have been developed to control *M. vitrata* on cowpea, including host plant resistance, biological control and use of synthetic or biological pesticides (Adati et al. 2008). Those efforts have had limited success, in part because the cowpea gene pool contains few if any genes conferring strong resistance to *M. vitrata*, but also because of the cost, safety and limited availability of pesticides. Consequently, scientists concerned about the Africa region are continuing to search for better tools and strategies for managing *M. vitrata*. These include biological control using exotic parasitoids (Dannon et al. 2010a, b; Tamò et al. 2016), biopesticides (Sokame et al. 2015), as well as development and deployment of *Bt* cowpea expressing the Cry1Ab toxin of *Bacillus thuringiensis* Berliner (Huesing et al. 2011). Irrespective of the management tools deployed, success requires a sound knowledge of the pest insect biology and ecology. The present review paper summarizes available information on *M. vitrata* and identifies gaps that need to be filled by further research.

Economic importance

M. vitrata causes devastating damage to mungbean, *Vigna radiata* (L.) R.Wilczek (Fabaceae), and black gram, *Vigna mungo* (L.) Hepper (Fabaceae), in Asia, and to pigeonpea,

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Cajanus cajan (L.) Huth (Fabaceae), in Asia and East Africa. In West Africa it is a major constraint to cowpea production. The extent of losses caused by *M. vitrata* is difficult to assess since several other insects feed simultaneously on the crops. However, an estimate of US$ 30 million economic loss in the semi-arid tropics annually due to *M. vitrata* has been reported (ICRISAT 1992). There are reports of 100% loss of flower buds and pods of black gram (Giraddi et al. 2000) and damage to 50–60% of pigeonpea plants (Singh 1997) due to *M. vitrata*. In Tanzania losses on common bean due to the combined effects of *M. vitrata* and *Helicoverpa armigera* Hübner, were estimated at 33–53% (Karel 1985). Damage to a single cowpea flower by *M. vitrata* can lead to the loss of an entire potential pod. Larval density of one per flower is enough to cause significant yield losses (Atachi and Ahohuendo 1989). An action threshold of 40% larval infestation in flowers of cowpea was established in Nigeria (Ogunwolu 1990). Yield losses of cowpea range from 25 to 85% depending on the country and the variety (Singh et al. 1990; Echendu and Akingbohungbe 1989).

Origin of *M. vitrata*

Maruca vitrata Fabricius (1787*)* was long known as *Maruca testulalis* until it received its current name (Heppner 1995). *M. vitrata* belongs to the order Lepidoptera, the Pyraloidae superfamily and the Crambidae family. In addition to *M. vitrata*, the genus *Maruca* includes *Maruca amboinalis* Felder and *Maruca nigroapicalis* De Joannis (Tamò et al. 1997). There are references in the literature to other *Maruca* species, *Maruca fuscalis* Yamanaka, *Maruca aquitilis* Guerin-Meneville, *Maruca bifenestralis* Mabile and *Maruca simialis* Snellen (Myers et al. 2013) but it is unclear if they are distinct species or subspecies of *M. vitrata*, *M. amboinalis* and *M. nigroapicalis*. Recent molecular characterization indicates differences between *M. vitrata* specimens suggesting there are subspecies (Margam et al. 2011a). *M. amboinalis* and *M. nigroapicalis* have been observed only in the Indo-Malaysian and Australia area (Rose and Singh 1989) while *M. vitrata* is pan-tropical. The geographic origin of *M. vitrata* has remained unclear for long time. The Indo-Malaysian region appeared to be the most probable area of origin of the genus *Maruca*, including *M. vitrata,* because of the larger diversity of natural enemies encountered there (Tamò et al. 1997). More recent phylogeographic studies involving *M. vitrata* strongly support a possible South East Asian origin of this pest (Periasamy et al. 2015).

Geographical distribution

The wider distribution of *M. vitrata* extends from the Cape Verde Island in West Africa to Fiji and Samoa in the Far East including Hawaii, Australia and South-East Asia (Hopkins 1927; Garthwaite 1940; Caldwell 1945; Holdaway and Wiujam 1942). It has also been reported in the neotropics, which include South and Central America, the Caribbean islands and southern Florida (Heppner 1995). It has been observed in Western Europe (Goater 1986; Karsholt and Razowski 1996), however, this probably represents an accidental introduction as there is no record of any established population in Europe.

Morphological description

The adult *M. vitrata* moth has a wingspan of 13–25 mm and a dark brown body. Females weigh more than males (Jackai and Inang 1992). The abdomen has nine segments. Adult females usually have a blunt tipped abdomen. A sharp or forked hairy abdominal tip (male genitalia) is the distinguishing character of the adult male. The male abdomen is longer than that of the female.

Newly laid eggs are greenish white in color and later become yellow. Eggs are oval and translucent, with faint reticulate sculpturing on the chorion, and measure 0.65 × 0.45 mm (Taylor 1967; Okeyo-Owuor and Ochieng 1981).

The larvae are tube shaped, with slender heads. The larval body is translucent with a pair of dark brown spots on each segment (Okeyo-Owuor and Ochieng 1981). The intensity of spotting varies with the host plant; sometimes no spots are present. Larval color ranges from greenish to brown, depending on the food. The larval stage consists of five instars, the mature fifth instar larva measuring 11–12 mm long and 2.1–2.4 mm wide (Taylor 1967; Nyiira 1971; Akinfenwa 1975). The larval instar can be identified by measuring the width of the head capsule; 1st instar: 0.16–0.19 mm; 2nd: 0.31–0.38 mm; 3rd: 0.50–0.63 mm; 4th: 0.75–1.00 mm; 5th: 1.25–1.38 mm (Adati et al. 2004).

The pupa progressively changes color, from light brown to red brown and finally to dark brown, which becomes mottled with black and yellow just before adult emergence. Male pupae have a small distinct ring on the last abdominal segment; in females this ring is absent (Hassan 2007). The pupa loses weight and length during the first days of pupation (Okeyo-Owuor and Ochieng 1981).

Molecular characterization

Near-complete sequencing of the mitochondrial genome of *M. vitrata* (14,054 bp) has revealed that the arrangement and orientation of the 13 protein-coding, two rRNA and 19 tRNA genes is typical of an insect mitochondrial genome. There was a high A + T content of 80.1% and a bias for the use of codons with A or T nucleotides in the 3rd position (Margam et al. 2011b).

Phylogenetic analysis of a mitochondrial cytochrome c oxidase I gene (COX1) fragment indicates that three *Maruca* sp. mitochondrial lineages have unique geographic distributions. Lineages 1 and 2 are found in Australia, Taiwan, and West Africa (Niger, Nigeria, and Burkina Faso) and lineage 3 is found in Puerto Rico. Phylogenetic reconstruction based upon ribosomal DNA internal transcribed spacer-2 sequences provided additional evidence for three *Maruca* sp. clades, suggesting that multiple unique *Maruca* species or subspecies are present worldwide. Phylogenetic analysis indicates the highest nucleotide diversity among samples from West Africa (Margam et al. 2011a). Analysis of *M. vitrata* single nucleotide polymorphism (SNP) markers suggests that genetic structuring may occur within West Africa populations (Burkina Faso, Niger and Nigeria), there being significant levels of differentiation between eastern and western sample sites of the West Africa sub-regions (Margam et al. 2011c). SNP analysis of West Africa samples indicated that 67.3% level of the genetic variation was within individuals compared to 17.3% among populations (Agunbiade et al. 2012). It appears that three divergent genotypes exist within West Africa indicating three distinct populations (Agunbiade et al. 2012).

Phylogenetic analyses of *M. vitrata* populations on cultivated cowpea *V. unguiculata* and three wild host plants (*Pueraria phaseoloides* (Roxb.) Benth., *Lonchocarpus sericeus* (Poir) H.B.K and *Tephrosia candida* (Roxb.) DC.) revealed two genotypic clusters (co-ancestries) on the four host plants across three geographic locations, but there was little geographic variation predicted among genotypes from different geographic locations (Agunbiade et al. 2014). Variation among host plants at a location and host plants among locations showed no consistent evidence for *M. vitrata* population subdivision. This suggests that host plants do not significantly influence the genetic structure of *M. vitrata* (Agunbiade et al. 2014). This has potentially broad implications for insect resistance management (IRM) plans for trangennic *Bt* cowpea useful in the control of *M. vitrata*. Such mixing of *M. vitrata* populations with wild alternative hosts has positive implications for an IRM plan in West Africa that relies at least partially on the presence of the wild alternative hosts near fields of *Bt* transgenic cowpeas (Onstad et al. 2012).

Life history

The complete life cycle of *M. vitrata* requires from 22 to 25 days (Singh and Jackai 1988) depending on the temperature. Adults are nocturnal (Taylor 1967; Usua and Singh 1979; Lu et al. 2007). They are inactive during the day and can be found at rest under the lower leaves of the host plant (Lu et al. 2007). Depending on the temperature and food quality adult lifespan ranges between 3 to 10 days (Taylor 1967; Huang and Peng 2001; Ramasubramanian and Babu 1989; Naveen et al. 2009). However, longevity of 29 or more days has been recorded in laboratory conditions (Chi et al. 2005). Females usually have a longer lifespan (Taylor 1967; Atachi and Ahounou 1995; Huang and Peng 2001; Naveen et al. 2009). Adults emerge from pupae throughout the day but the greatest emergence occurs at night (Huang and Peng 2001; Lu et al. 2007). Adult emergence of both sexes is almost synchronous and the sex ratio is 1:1 in the laboratory. However, light trap catches indicate that sex ratios in nature may differ under different conditions (Taylor 1967; Huang and Peng 2001; Huang et al. 2003; Ba et al. 2009; Traore et al. 2014). Recently Adati et al. (2012) demonstrated that the sex ratio is seasonal and location- related. In the northern Sahelian area of West Africa the sex ratio switched from being female-biased early in the season to an equilibrium during the rest of the season. In the southern coastal area of West-Africa the sex-ratio changed from male-biased to female-biased during the year. Adult mating reaches its peak three days after female emergence from pupation (Huang and Peng 2001; Lu et al. 2007). Mating activity takes place between the fourth and twelfth hour of darkness when temperatures range between 20 and 25 °C and relative humidity is greater than 80% (Jackai et al. 1990; Hassan 2007). Females typically only mate once (IITA 1981; Atachi and Gnanvossou 1989) while males may have multiple matings (Jackai et al. 1990). On cowpea plants, gravid females deposit eggs on all aerial parts (leaves, vegetative buds, flowers leaf axils) but lower surfaces of leaves are the most preferred (Okeyo-Owuor and Ochieng 1981). Eggs are deposited singly or in batches of 2–6 (Bruner 1930; Wolcott 1933; Krishnamurthy 1936; Taylor 1967, 1978). The female has a pre-ovipositional period of 3 to 4 days and the peak of oviposition occurs on the sixth to eighth days after pairing (Ke et al. 1985). One female may lay from 200 to more than 800 eggs within 3 to 14 days depending on environmental conditions (Taylor 1967, 1978; Akinfenwa 1975; Huang and Peng 2001; Chi et al. 2005; Naveen et al. 2009). Hatching occurs 3 to 5 days after eggs are laid (Singh and Jackai 1988; Chang and Chen 1989; Ramasubramanian and Babu 1989). Temperatures below 10.5 °C and above 34.3 °C are less suitable for egg development (Adati et al. 2004). Larvae emerge early in the evening and are mainly nocturnal (Usua and Singh 1979). Larval development is completed within 8 to 14 days depending on the environmental conditions (Adati et al. 2004; Singh and Allen 1980; Okeyo-Owuor and Ochieng 1981; Atachi and Gnanvossou 1989; Singh and Jackai 1985; Ramasubramanian and Babu 1989), but larval development requiring up to 24 days or more has been reported (Chang and Chen 1989). Temperatures between 19.5 °C and 29.3 °C seem most suitable for the development of *M. vitrata* larvae (Jackai and Inang 1992; Adati et al. 2004). There is a pre-pupal stage of 1–2 days (Taylor 1978;

Ramasubramanian and Babu 1989). Pupation occurs in a silken cocoon attached to the plant or within pods or in the soil near the host plant (Okeyo-Owuor and Ochieng 1981). The pupal stage lasts 3.3–14 days (Ramasubramanian and Babu 1989; Ochieng et al. 1981; Jackai and Inang 1992; Chang and Chen 1989; Adati et al. 2004), depending on temperature. In Africa *M. vitrata* does not undergo diapause (Adati et al. 2012; Arodokoun et al. 2003; Bottenberg et al. 1997; Okeyo-Owuor and Ochieng 1981; Taylor 1967) and the populations of the insect during the off-season are maintained on a wide range of host plants (Tamò et al. 2002; Arodokoun et al. 2003).

Host plants

Cultivated host plants

M. vitrata has been recorded on more than 15 cultivated crops, most frequently on cowpea, pigeonpea and mung bean (Table 1). Pigeonpea, mung bean and yard long bean are the most important host plants of *M. vitrata* in Asia. In West Africa, the most important cultivated host plant is cowpea, while in Eastern and Southern Africa pigeonpea is the major host. In the Americas, the most important host plant is lima bean. Host plant preference experiments suggest that cowpea is the most preferred host plant for oviposition and larval development (Ntonifor et al. 1996; Chi et al. 2003; Chandrayudu et al. 2005).

Non-cultivated host plants in West-Africa

Wild alternate host plants of *M. vitrata* in West Africa were first reported by Taylor (1967, 1978). Subsequently, Atachi and Djihou (1994) gave a more comprehensive list of wild hosts in Africa. However, according to Tamò et al. (2002), only Zenz (1999) and Arodokoun et al. (2003) provide an accurate list of *M. vitrata* hosts as they reared the larvae collected on the plants to adult emergence to confirm species identity. So far, 23 host plants have been recorded in Benin, all belonging to the Fabaceae family (Arodokoun et al. 2003). In addition, nine other species have been recorded in Burkina Faso (Ba et al. 2009; Traore et al. 2014), resulting in a total of 32 host species in West Africa (Table 2).

Feeding behavior

Initial infestation of cowpea plants begins with adults that have emerged from alternate hosts (Taylor 1967). Larvae feed

Table 1 Worldwide cultivated host plants of *Maruca vitrata* F

Host plants	Countries or region	References
Vigna unguiculata (cowpea)	Brazil; West, central, East and southern Africa	Quintela et al. (1991); Jackai and Daoust (1986); Singh and Allen (1980)
Vigna sesquipedalis (long bean)	South Asia, East Asia, Australia	Dean (1978); Caldwell (1945); Ke et al. (1985); Chang and Chen (1989)
Vigna radiata (mung bean)	South Asia	Krishnamurthy (1936); Litsinger and Cowell (1978)
Vigna mungo (blackgram)	South-Asia	Dhuri and Singh 1983
Vigna angularis (adzuki bean)	East Asia	Chi et al. (2003); Jung et al. (2009)
Cajanus cajan (pigeonpea)	Indian subcontinent; East and Southern Africa	Bhagwat et al. (1996); Minja et al. (1999)
Phaseolus vulgaris (common bean)	South-East Asia, East Asia, Pacific Islands, Hawaii, Australia Central and Southern America, East and Southern Africa	Chang and Chen (1989); Hopkins (1927); Passlow (1969); Holdaway and Wiujam (1942); Leonard and Mills (1931); Minja et al. (1999); Chi et al. (2003)
Phaseolus lunatus (lima bean)	Central Americas	Bruner (1930); Leonard and Mills (1931)
Dolichos lablab (field bean)	South Asia, East Asia, Australia,	Lal (1985); Passlow (1969); Ke et al. (1985)
Glycine max (soybean)	East Asia, Ecuador	Chang and Chen (1989); Kogan and Turnipseed (1976); Chi et al. (2003)
Pisum sativum (pea)	Thailand	Fang (1994)
Arachis hypogea (groundnut)	Myanmar; Mauritius	Ghosh (1923); Dove and Williams (1971)
Canavalia gladiata (sword bean), *C. ensiformis* (jack bean)	Australia	Passlow (1969)
Pueraria phaseoloides (tropical kudzu)	Australia	Cameron (1986)
Sphenostylis stenocarpa (African yam bean)	Nigeria	Ogah and Ogah (2012)
Psophocarpus tetragonolobus (winged bean)	Ghana	Afreh-Nuamah (1983)

Table 2 Wild host plants of *M. vitrata* in Africa (Updated from Arodokoun et al. 2003; Ba et al. 2009, Pittendrigh et al. 2012)

Families	Species	Countries
Fabaceae	*Afromosia laxiflora* (Benth) Harms	Benin
	Andira inernis (Wright) D.C.	Benin
	Carnavalia ensiformis (L.) D.C.	Benin
	Carnavalia virosa (Roxb.)	Benin
	Centrosema pubescens	Benin
	Crotalaria naragutensis Hutch.	Burkina Faso
	Crotalaria ochroleuca G. Don	Burkina Faso
	Daniella oliveri (Rolfe.) Hutch. & Dalziel	Burkina Faso
	Esclerotona dolabriformis (coll.)	Benin
	Lonchocarpus sericeus (Poir) H.B.K	Benin
	Lonchocarpus cyanescens (Schum & Thonn)	Benin
	Milletia thonningii	Benin
	Mucuna poggei Taub.	Burkina Faso
	Pacchyrrhizus angulatus (Rich.)	Benin
	Pterocarpus erinaceus (Poir)	Benin
	Pterocarpus santalinoïdes (l'Her. ex D.C.)	Benin
	Psophocarpus palustris (Deso.)	Benin
	Rhynchosia hirta (Andrews) Meikle and Verdc.	Burkina Faso
	Rhynchosia pycnostachya (DC) Meikle	Burkina Faso
	Sesbania pachycarpa DC.	Benin, Burkina Faso, Niger
	Tephrosia bracteolata (Guill. & Perr.)	Burkina Faso
	Tephrosia candida (Roxb.) DC.	Burkina Faso
	Tephrosia humilis (Guill. & Perr.)	Benin
	Tephrosia nana Schweinf	Burkina Faso
	Tephrosia platycarpa Guill. & Perr.	Benin
	Vigna gracilis (Guill. & Perr.) Hook.f.	Burkina Faso
	Vigna nigritia Hook.f.	Burkina Faso
	Vigna racemosa (G.Don) Hutch. & Dalziel	Benin
	Xerroderri sulthmanii (Taub.) Mend & Sous.	Benin

on the tender parts of stems, peduncles, flowers, flower buds and young pods (Atachi and Gnanvossou 1989) but they prefer the floral parts (Karel 1985; Liao and Lin 2000; Chi et al. 2003). Within the flower, the larvae feed preferentially on stamens and pistils (Traore et al. 2013). Larvae are dispersed randomly on cowpea flowers (Firempong and Mangalit 1990; Liao and Lin 2000). The vertical distribution of larvae on plants did not significantly differ among the strata of the flowers and pods (Liao and Lin 2000). Several first-instar larvae may be found together within individual flowers (Traore et al. 2013), but later they disperse, moving singly from one flower to another. Each larva may consume four to six flowers before larval development is completed (Gblagada 1982). First, second and third instar larvae are less mobile than fourth and fifth instars (Jackai and Daoust 1986). Most of the 1st and 2nd instar larvae are observed on flowers (Okeyo-Owuor et al. 1983; Liao and Lin 2000), while the majority of the 4th to 5th instars are found on pods (Okeyo-Owuor and Ochieng 1981; Okeyo-Owuor et al. 1983; Liao and Lin 2000). However, first instar larvae may be found within newly formed pods (Traore et al. 2013). Third to fifth-instar larvae are capable of boring into the pods, and occasionally into the peduncle and stems (Taylor 1967).

Adult migration patterns in West-Africa

In the humid zone of southern West Africa adult *M. vitrata* moths are caught in light traps throughout the year but there are two peak periods, from mid May to mid August and from mid October to mid February (Bottenberg et al. 1997). When cowpea is not present the insect develops on wild alternate host plants (Tamò et al. 2002). In southern Benin, most *M. vitrata* flight activity occurs after cowpea cultivation has been completed, and at a time when abundant major alternate hosts found in the forest and along streams start flowering (Bottenberg et al. 1997). The insect has been considered endemic only in the coastal areas of Southern Benin, Nigeria and Ghana (Bottenberg et al. 1997; Tamò et al. 2002). However, more recent observations indicate it also survives the dry season in northern areas like Bobo-Dioulasso in Southern Burkina Faso along river streams (Ba et al. 2009; Traore et al. 2014), although in this region the flight activity of moths is only observed during the rainy season when cowpea is flowering (Ba et al. 2009; Baoua et al. 2011). In areas where feral host plants are uncommon or absent *M. vitrata* is only a migratory pest, annually invading cowpea fields during the rainy season. In West Africa, *M. vitrata* migrates from the southern coastal area (6° 25'N latitude) to northward (as far as 13° 48' N latitude), pushed by favorable monsoon winds (Adati et al. 2012). In the Kano area in northern Nigeria *M. vitrata* invades cowpea fields during the rainy season (July to October); three generations occur there during the year (Bottenberg et al. 1997). In the more northern and drier areas of Niamey (Niger) and Kamboinsé (Burkina Faso), only one generation of *M. vitrata* has been observed during the year (Bottenberg et al. 1997; Ba et al. 2009). During their south-to-north migration *M. vitrata* find favorable feeding and reproductive conditions on a succession of different host plants and, thereby, increase their population size and density with each successive generation. There is so far no report of any Southward migration of *M. vitrata*.

Natural enemies

There is a diversity of natural enemies associated with *M. vitrata* (Table 3). Natural enemies fall into three categories: predators, entomopathogenic organisms, and parasitoids. The predators include mites, spiders, ants and mantids.

Entomopathogenic organisms include bacteria, fungi, protozoans and viruses (Table 3) that have been found infecting *M. vitrata* larvae in the field in Africa (Otieno et al. 1983; Tamò et al. 2003).

The parasitoid fauna in Africa include over 20 species of wasps from the Eulophidae, Braconidae, Scelionidae, Ichneumonidae, Pteromalidae, Chalcididae and Trichogramatoidae families and dipteran parasitoids from the Tachinidae families. According to Okeyo-Owuor et al. (1991), total mortality due to all natural enemies in Kenya is greater than 50%. Many studies have been made on *M. vitrata* natural enemies with emphasis on parasitoids. The rate of parasitism is estimated to be less than 10% on cultivated cowpea in Africa (Taylor 1967; Akinfenwa 1975; Gblagada 1982; Okeyo-Owuor et al. 1991; Bottenberg et al. 1998; Arodokoun et al. 2006; Traore et al. 2014) while on alternate host plants in southern Benin the parasitism rate reached 35% (Arodokoun et al. 2006).

Control of *Maruca vitrata* on cowpea

Control with synthetic insecticides

Chemical control of *M. vitrata* on cowpea has been used extensively (Jerath 1968; Taylor 1968a; Dina and Medaiye 1976). The great majority of chemical insecticides shown to be effective against *M. vitrata* are no longer used; most having been banned. Recent research on chemical control of *M. vitrata* indicates that several pyrethroids (cypermethrin, deltamethrin, lambda cyhalothrin) were effective at the time they were tested (Attachi and Sourokou 1989; Amatobi 1994; Amatobi 1995; Liao and Lin 2000). The organophosphate dimethoate was also effective (Attachi and Sourokou 1989; Amatobi 1995). In Nigeria, two sprays of lambda-cyhalothrin or cypermethrin combined with dimethoate was considered the most cost-effective approach for controlling *M. vitrata* and increasing cowpea yield (Amatobi 1994, 1995). In Benin, a combination of deltamethrin and dimethoate was considered, at the time of testing, effective for controlling the pest on cowpea (Attachi and Sourokou 1989). However, laboratory bioassays with strains of *M. vitrata* in Nigeria indicated the potential for the insect to evolve resistance to pyrethroids (Ekesi 1999). Moreover, with the new restrictions on the use of dimethoate in many countries, its use on a food crop like cowpea should be considered with caution.

Control with biopesticides

Biopesticides are pesticides derived from natural materials, such as plants (botanicals), fungi, bacteria and viruses (micropesticides).

Neem-based preparations are the major botanical tested thus far for controlling *M. vitrata* on cowpea. Preparations (1) made from leaves, (2) seed aqueous extracts and (3) neem oil have been reported to be effective for controlling *M. vitrata* (Jackai and Oyediran 1991; Tanzubil 2000). Neem reduces *M. vitrata* feeding, thus resulting in less seed damage (Jackai et al. 1992). In addition to controlling *M. vitrata,* neem based sprays increase pod yield (Cobbinah and Osei-Owusu 1988; Ivbijaro and Bolaji 1990; Emosairue and Ubana 1998). However, as reported by Bottenberg and Singh (1996) the effectiveness of neem is variable from year to year. This should not be surprising since the concentration of active chemicals might be expected to vary from plant to plant, vary with the season and maturity of the source material, vary based on how the extracts are performed, and perhaps vary geographically as well.

In addition to neem, several other botanicals have shown insecticidal effects against *M. vitrata* in cowpea fields, including *Pepper guineense* Schum & Thonn, *Artocarpus altilis* Park, *Aframomum melegueta* Roscoe, and papaya leaves (Ivbijaro and Bolaji 1990; Oparaeke et al. 2005; Adetonah

Table 3 Natural enemies of *Maruca vitrata* in Africa (Update from Usua and Singh 1978; Agyen-Sampong 1978; Otieno et al. 1983; Okeyo-Owuor et al. 1991; Ezueh, 1991; Bottenberg et al. 1998; Tamò et al. 2003, 2016; Arodokoun et al. 2006; Adati et al. 2008; Traore et al. 2014)

Type	Order	Family	Species	Stage	Location
Parasitoids	Diptera	Tachinidae	*Aplomya metallica*	L	Gh
			Cadurcia sp.	L	Be
			Pseudoperichaeta laevis	L	Gh, Ng
			Thecocarcelia incedens	L	Gh
			Thelairosoma palposum	L	Ng
	Hymenoptera	Trichogrammatidae	*Trichogrammatoidea eldanae*	E	Be
		Braconidae	*Apanteles* sp.	L	Ke
			Bassus bruesi	L	Be
			Bracon sp.	L	Be, BF, Ke
			Braunsia kriegeri; Braunsia sp.	L, P	Be, BF, Ke, Ng
			Cardiochiles philippinensis	L	Gh
			Chelonus sp.	L	Ke
			Dolichogenidea sp.	L	Be
			Phanerotoma sp. *P. leucobasis, P. syleptae*	L	Be
			Pristomerus sp.	L	Be
			Therophilus javanus,	L	Be
			Testudobracon sp.	L	Be
		Chalcididae	*Antrocephalus* sp.	P	Ke
			Brachymeria sp.	L, P	Be
		Eulophidae	*Tetrastichus sesamiae,*	P	Ke
			Tetrastichus sp.	L	Ng
Parasitic Mites		Acari	*Dinothrombius* sp.	L	Gh
Predators	Araneae	Selenopidae	*Selenops radiates*	L,A	Ng
	Hymenoptera	Formicidae	*Camponotus sericeus* *C. rufoglaucus*	L	Ng, Ke
	Neoptera	Mantidae	*Polyspilota aeruginosa Spodromantis lineola*	A	Ng
	Dermaptera	Forficulidae	*Diaperasticus erythrocephala*	L,P	Ke
Pathogens		Protozoa	*Mettesia* sp. *Nosema marucae* sp. n.	L,P L,P	Ke
		Bacteria	*Bacillus* sp. *Colostridium* sp.	L,P	Ke
		Virus	CPV, Granulovirus	L	Be, Ke

A = Adult; E = Eggs; L = Larva; P=Pupa,

Be = Benin; BF = Burkina Faso; Gh = Ghana; Ke = Kenya; Ng = Nigeria

et al. 2005; Oparaeke 2006). These preparations likewise may affect insects in addition to *M. vitrata*.

Microbial pesticides have been tested for controlling *M. vitrata*. Laboratory bioassays with isolates from *Beauveria bassiana* (CPD 3 and 10) and *Metarhizium anisopliae* (CPD 5 and 12) were found to be highly pathogenic to eggs of *M. vitrata*, achieving 89–100% mortality (Ekesi et al. 2002). In addition isolates from *M. anisopliae* (ICIPE 18 and ICIPE 69) caused larval mortality of 91 and 81% (Tumuhaise et al. 2015). Also, *Bt* δ-endotoxins (Cry proteins) of the soil bacterium *Bacillus thuringiensis* Berliner are highly toxic against *M. vitrata* early instars larvae (Taylor 1968b; Murdock et al. 2008).

More recently, a *M. vitrata* specific baculovirus, was identified in Taiwan (Lee et al. 2007), and has been introduced into West Africa for controlling this pest in the field (see 13.1).

Cultural control

Different cultural approaches have been tested for reducing *M. vitrata* infestations on cowpea fields including, different planting dates, use of fertilizers, plant spacing, trap crops, and crop associations. In Northern Nigeria, early planting of cowpea (first to second week of July) significantly reduced the *M. vitrata* infestation (Ekesi et al. 1996). However, the applicability of a planting date approach is not feasible because of unpredictable rainy seasons. There is no convincing evidence that mineral fertilizers affect *M. vitrata* infestations (Atachi et al. 1998; Asiwe 2009). Cowpea plant spacing likewise do not significantly influence *M. vitrata* infestation (Alghali 1991; Asiwe et al. 2005). Intercropping of cowpea with other crops (maize, sorghum, peppers, cassava, pigeonpea, and *Sesbania*) did not show clear evidence of reduction of *M. vitrata* infestations (Ezueh and Taylor 1984; Dissemon and Hindorf 1990; Gethi et al. 1993; Emeasor and Ezueh 1997; Bottenberg et al. 1998; Capo-Chichi et al. 2008).

Host-plant resistance

Screening of cowpea varieties for resistance to *M. vitrata* has been extensive, with several hundred germplasm accessions evaluated at the International Institute of Tropical Agriculture (IITA) and in the research institutes of the National Agriculture Research Systems (NARS). Numerous resistance sources have been reported from cultivated land races, but none had high levels of resistance (IITA 1984). As a result, the search for resistance was extended to wild relatives of cowpea. Resistance to *M. vitrata* was found in some wild *Vigna vexillata* accessions (Jackai 1991; Jackai et al. 1996). Pod trichome density, higher phenol and tannin content were identified as the main mechanism of resistance (Jackai and Oghiakhe 1989; Oghiakhe 1995; Oghiakhe et al. 1992; Oghiakhe 1996). However, attempts to transfer resistance genes from *V. vexillata* to cultivated cowpea by means of wide crosses were unsuccessful (Fatokun 2002).

Biological control

Initial attempts to use biological control to manage *M. vitrata* on pigeonpea were made in Mauritius during the 1950s by introducing, from Trinidad, natural enemies of the related species, *Ancylostomia stercorea*. Seven parasitoid species were released and two became established, *Bracon cajani* and *Eiphosoma dentator*. Early claims were made that these two parasitoids increased the harvestable crop of pigeon pea from 40 to 70% (Greathead 2003) but these claims were disputed when the pests continued to be a problem on the island.

In West Africa biological control of *M. vitrata* with releases of parasitoid is being explored and is detailed below.

Effectiveness of pheromone traps in IPM

Investigations on the use of pheromones for monitoring *M. vitrata* populations as part of an IPM program have been attempted in West-Africa. Sex pheromones were successfully extracted by Adati and Tatsuki (1999) and further studies confirmed the presence of EE10,12–16:Ald and EE10,12–16:OH as major and minor blend components, respectively, together with a third component (*E*)-10-hexadecenal (E10–16:Ald) (Downham et al. 2003). Successful trapping of *M. vitrata* was accomplished using a synthetic pheromone blend containing the three aforementioned components (Downham et al. 2003). A water-trap made from a 5 l plastic jerry-can placed at 120 cm height was the most effective trapping system, and the lure remained attractive for at least 4 weeks (Downham et al. 2004). Pheromone trap catches were observed up to 12 days before larval infestations in flowers and a week or more in advance of flowering within cowpea fields (Adati et al. 2008). Thus, trap catches can signal impending infestations and provide an earlier warning than the appearance of flowers.

Even so, the limited geographical effectiveness of the lures has slowed the use of pheromone traps in IPM. Low pheromone trap catches were observed with all synthetic pheromone lures in northern Nigeria while in Burkina Faso high pheromone trap catches were obtained with lures containing the single major component alone and not with the three-component blend found to be effective in southern Benin (Downham et al. 2003; Adati et al. 2008). Possible explanations of this phenomenon include the observation that most female *M. vitrata* migrating to the North are already mated, and even their offspring seem to be sexually inactive in the dryer areas. The reasons for this are yet to be elucidated (Adati et al. 2012).

On-going efforts for controlling *Maruca* on cowpea in West-Africa and further research needs

Current efforts for controlling *M. vitrata* on cowpea in West Africa include biological control with parasitoids and viruses and genetically engineered *Bt* cowpea. Further research is essential for these control approaches to become fully developed and sustainable.

Biological control with parasitoid wasps and viruses

Biological control of *M. vitrata* with parasitoid wasps was attempted at IITA over several years. Indigenous parasitoids were not highly effective for controlling *M. vitrata* on cowpea because they are more location-specific than host specific, and cannot cope with high *M. vitrata* population densities (Arodokoun et al. 2006). This resulted in a search for more effective parasitoids in Southeast Asia, the putative area of origin of *M. vitrata* (Periasamy et al. 2015). One interesting parasitoid species, *Apanteles taragamae* Viereck (Hymenoptera: Braconidae), was imported in 2007 from the World Vegetable Center (AVRDC) in Taiwan to investigate its potential as a biological control candidate against *M. vitrata*. Colonies were established in the laboratory of IITA in Cotonou, Benin, where the parasitoid was assessed in the laboratory (Dannon et al. 2010a, b; Dannon et al. 2012a, b) and in small-scale experimental releases (Tamò et al. 2012). Although the results showed that *A. taragamae* was effective in targeting *M. vitrata* in the field and disperses effectively, recovery rates were very low, pointing to poor ecological adaptation. However, this first introduction represented a good case study for developing a biological control pipeline (Tamò et al. 2016). In fact, as more efficient parasitoids were identified by AVRDC (Srinivasan et al. 2012), the two most promising ones, *Therophilus javanus* and *Phanerotoma syleptae* (Hymenoptera, Braconidae), were subsequently introduced to the rearing labs of IITA-Benin. After 2 years of confined testing, and upon obtainment of release permits by the respective national authorities, a total of 101,600 adult parasitoids – 60,100 in Benin (30,300 *T. javanus* and 29,800 *P. syleptae*) and 41,500 in Burkina Faso (23,000 *T. javanus* and 18,500 *P. syleptae*) – were released with participation of local communities. A few months after releases, both parasitoids were recovered from the field and from wild host plants in both countries. In Benin, surveys carried out in February/March 2017 indicate with certitude that both species have successfully survived the long dry season on alternative host plants in the absence of cowpea, nearly 1 year after initial experimental releases (Tamò, unpublished data).

In addition to exploring the use of parasitoid wasps, experiments with the *M. vitrata* Multi-NucleoPolyhedroVirus (MaviMNPV) imported from Taiwan have been conducted in West Africa (Pittendrigh et al. 2012). MaviMNPV was found to be highly effective against *M. vitrata* in Taiwan (Lee et al. 2007). The virus has acute toxicity and kills almost 100% of the larvae 5–7 days after spraying of the virus preparation (Lee et al. 2007). Trials with strains of *M. vitrata* in Benin suggested that sprays of the pesticides are highly effective, achieving more than 95% larval mortality (Tamò et al. 2012). Moreover, field trials in Benin, Burkina Faso and Niger suggest that the viral biopesticide could be as effective as conventional insecticides in controlling *M. vitrata*, with an estimated 26–34% grain yield gain as compared with the control non-sprayed plots (Tamò et al. 2012). In more recent field trials, mixtures of MaviMNPV and neem oil were able to control cowpea pests beyond *M. vitrata*, thereby increasing yields above those obtained by standard synthetic pesticides (Sokame et al. 2015).

Genetically engineered *Bt* cowpea

Many years of classical screening of cowpea germplasm for *M. vitrata* resistance has failed to identify material that can be used in a breeding program. Accordingly, based on decades of success in controlling other lepidopteran pests, a biotechnology solution was developed using *Bacillus thuringiensis* δ-endotoxins (Popelka et al. 2006; Murdock et al. 2008). Early bioassay work established that the Cry1Ab class of *Bt* proteins commonly used in *Bt* maize was very effective in controlling *M. vitrata* (Popelka et al. 2006; P. C. Addae et al. unpublished data). Bioassays with transgenic lines, in particular event 709A, encoding a Cry1Ab toxin resulted in 100% mortality of *M. vitrata* larvae after 3 days of feeding tests (P. C. Addae et al. unpublished data). No less than 20 Confined Field Trial (CFT) of transgenic events of the cowpea variety IT86-D1010 expressing a Cry1Ab protein have been conducted starting in 2008 in Puerto-Rico and extending to Nigeria in 2009 and later to Burkina Faso, Ghana and Malawi. Lines with high levels of resistance to *M. vitrata* were identified under heavy artificial infestation with first instar *M. vitrata* larvae. Seeds and pods were all heavily damaged (100%) on the non-transgenic control variety while seed damage was negligible on the best transgenic counterpart. The most promising lines out-yielded the controls by 4 to 75-fold depending on level of insect infestation, year and location (P. C. Addae et al. unpublished data). Lines such as event 709A meet all the standard international regulatory requirements, e.g. single copy of the transgene, and free of vector backbone sequences. Event 709A is being introgressed into farmer preferred varieties in Burkina Faso, Ghana and Nigeria.

Further research needs

Food and Feed and Environmental Risk Assessments will be used to establish the safety of *Bt* cowpea before commercial release. An expert panel was convened in 2009 to assess the current state of regulatory safety data and identifying any additional research needs (Huesing et al. 2011). The review included an assessment of (1) non-target organisms (NTOs), (2) Insect Resistance Management (IRM) and (3) gene flow. The panel determined that for NTOs, more detailed knowledge of insects associated with wild/weedy cowpea was needed to ensure that the *Bt* trait would not increase the fitness of wild/weedy cowpea and allow it to become an invasive species. In addition, the panel determined that more information on NTOs associated with wild/weedy cowpea were necessary to support the wealth of information showing that *Bt* toxins have no unintended effects on NTOs, including those associated with the wild/weedy cowpea. Also needed was a comprehensive list of all the non-target arthropods (especially beneficial organisms) associated with cultivated cowpea to allow an assessment of potential harm that might result from the *Bt* toxin. Regarding IRM, Onstad et al. (2012) concluded that if *Bt* cowpea is deployed only into regions where *M. vitrata* is not endemic, i.e. northern Nigeria, then there is little concern with resistance emerging in the *M. vitrata* population. However, given the efficacy of the *Bt* cowpea it is anticipated that cultivation will extend to all West-African *Bt* cowpea growing regions. An IRM strategy is accordingly being developed by working with global experts in academia, government and industry standards organizations (http://www.

excellencethroughstewardship.org/). The resulting IRM plan will include (i) short-term approaches for use of a single *Bt* gene and (ii) development plans for use of a second generation currently under development of *Bt* cowpea expressing two Cry genes with different modes of action. With regard to IRM, more work is needed to measure the contribution of refugia (wild host plants or cultivated non-*Bt* cowpea) on *M. vitrata* populations especially their value in providing a source of susceptible adults.

As stated earlier, the current efforts for biological control of *M. vitrata* include use of exotic parasitoids and pathogenic viral pesticides. Regarding the use of parasitoids, the more critical issue is to develop a parasitoid delivery strategy so that they become established. Two options can be explored. The first would consist of releases of parasitoid wasps in endemic areas of *M. vitrata* in the southern coast of West Africa. It is crucial to identify nursery plots of *M. vitrata* host plants on which the parasitoid could be released. If the parasitoids establish then it is conceivable that they could control the population of *M. vitrata* in a way that could limit population buildup and northward migration during the rainy season. The second option would be to explore the possibility of inundative releases of the parasitoids during the rainy season in the migration zone of *M. vitrata*. Since those areas do not have an endemic population of *M. vitrata*, the challenges will be to develop parasitoid production units for annual releases of the parasitoids before pest outbreak.

Summary

Over the past 50 years significant efforts have been made to control damage on cowpea in West Africa due to *M. vitrata*. Breakthroughs have been recently made with the development of *Bt* cowpea. However, for *Bt* cowpea to be successful and sustainable it should be considered within an IPM approach that includes host plant resistance (*Bt* cowpea), biological control and effective pest scouting. With a regional approach involving biological control of *M. vitrata* combined with *Bt* cowpea deployment, improved and sustainable control of *Maruca vitrata* might be achieved.

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