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ORIGINAL RESEARCH ARTICLE

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Distribution and diversity of alternate hosts of *Maruca vitrata* Fabricius in three West African countries

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Abstract

The evolution of resistance to the *Bacillus thuringiensis* (*Bt*) toxins by insect pests is a major threat to *Bt* technology. However, the rate of resistance can be slowed with appropriate integrated insect resistance management (IRM) strategies. Surveys were conducted to identify alternate host species for *Maruca vitrata* (commonly called the legume pod borer or *Maruca*) that could serve as refuges for Pod-Borer Resistant (PBR) cowpea in three West African countries (Ghana, Nigeria, and Burkina Faso). Survey sites included 25 in northern Ghana, 44 in northern Nigeria, and 52 in north-central and southwestern Burkina Faso. Alternate hosts of *Maruca* identified from plant species belonging to the *Fabaceae* family that showed signs of *Maruca* damage on cowpea tissues were collected and dissected. Larvae that were found during these dissections were reared to adult moths in the laboratory then identified to species. The alternate host plants including species of *Crotolaria*, *Sesbania*, *Tephrosia*, and *Vigna* were the most frequently encountered among sites and locations. Flowering and podding of these plants overlapped with flowering and podding of the nearby (~200 m) cowpea crop. Abundance of these wild hosts and overlapping flowering patterns with the cowpea crop in most locations have the potential to sustain ample numbers of *Bt* susceptible *Maruca* that will mate with possible resistant *Maruca* and deter resistance development. Further quantitative studies, however, are required from each location to determine if actual *Maruca* production from alternate hosts is sufficient for a PBR IRM strategy. If verified, this approach would be compatible with the high dose/refuge IRM strategy that includes alternate hosts and non-*Bt* crops as refuges.

Keywords Cowpea · *Fabaceae* plants · *Bt* · IRM

Introduction

Cowpea, *Vigna unguiculata* (L) Walp., is an important food for people and feed for livestock in Sub-Saharan Africa. However, cowpea production has major insect pest constraints especially by *Maruca vitrata* Fabricius (Lep. *Crambidae*) (commonly called the legume pod borer or *Maruca*; latter used hereafter), which can reduce yields 20–80% (Singh et al. 1990). Controlling *Maruca* is a challenge for smallholder farmers (Jackai

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and Adalla 1997). Many growers cannot afford chemical insecticides and when some synthetic insecticides, such as cypermethrin, dimethoate, and endosulfan have been used, *Maruca* populations have evolved resistance (Bottenberg 1995; Ekesi 1999). Also, many growers lack the proper safety equipment and, because of literacy challenges, do not know how to handle these compounds safely (Onstad et al. 2012; Jepson et al. 2014). Moreover, despite years of research, no cowpea varieties with natural resistance to *Maruca* have been identified and, when chemical insecticides are used, often 5–8 sprays are required in one cropping season (Fatokun 2002). The chemical insecticide-use challenge and the possibility that *Maruca* could evolve resistance to available insecticides require other options for pest control in cowpea.

One promising solution to control *Maruca* is to use genetically engineered (GE) cowpea varieties that provide protection against insects. The lepidopteran specific *cry1Ab* gene expressed in Pod-Borer Resistant (PBR) cowpea, also known as *Bacillus thuringiensis* (*Bt*) cowpea, has demonstrated near-complete control of *Maruca* in field trials in West Africa (Ba et al. 2019; Addae et al. 2020). *Bt* cowpea has now been approved by regulators for commercial release in Nigeria (NBMA 2019).

Insect resistance to GE plants in other parts of the world, however, suggests that an insect resistance management (IRM) plan is necessary to protect PBR cowpea from selecting for resistance in *Maruca* populations (Addae et al. 2020). The African stalk borer, *Busseola fusca* (Fuller), has evolved resistance to *Bt* maize in South Africa (Van Rensburgh 2007). Also, other moths (Lepidoptera) have evolved resistance to GE crops, for example, the fall armyworm, *Spodoptera frugiperda* (J.E. Smith), to *Bt* maize in Puerto Rico, Brazil, and United States (Tabashnik et al. 2009; Storer et al. 2010; Huang et al. 2011). Developing an integrated IRM plan that includes high-dose expression of the trait and use of refuges is recommended as an effective strategy for preventing insect resistance (Carrière et al. 2010; Campagne et al. 2016). The size of the refuge will depend on the distribution of alternate hosts of *Maruca* in the locations where the PBR cowpea will be grown. Therefore, the objective for this study was to identify the distribution and diversity of alternate hosts in West Africa, specifically Ghana, Nigeria, and Burkina Faso, where cowpea is commonly grown. Determination of alternate hosts will provide essential parameters for developing an IRM strategy that will delay the evolution of resistance to the *Bt* toxin in *Maruca* populations.

Materials and methods

Surveys of alternate hosts were conducted in Ghana, Nigeria, and Burkina Faso during October 2014, which is within the cowpea cropping season. There were 25 sites in the Tolon-Kumbungu location in northern Ghana; 25 sites near Bunkure, Kano State and 19 sites near Bomo, Kaduna State in northern Nigeria (44 total sites); 12 sites near Ziniaré, Oubritenga Province in north-central Burkina Faso and 40 sites near Bobo Dioulasso, Houet Province in southwestern Burkina Faso (52 total sites). The surveys were carried out in three agro-ecological zones, which in some cases overlap: Guinea Savanna (Tolon-Kumbungu and Bomo), Sudan Savanna (Bunkure, Ziniaré, and Bobo Dioulasso), and Sahel Savanna (Ziniaré).

Survey sites were non-systematically selected at each location. Global Positioning System (GPS) coordinates using decimal degrees (DD) were used to identify the location of the alternate hosts. Assessment of alternate hosts within 200 m of cultivated cowpea farms began by using the transect intercept method of sampling vegetation as described by Greig-Smith (1983). At the beginning of each sampling point, a 200 m line, referred to as baseline, was established in a designated direction, south-north in this example (Fig. 1). The baseline (200 m) was divided into ten equal parts (marks) starting from 0 to the 10th mark (the end of 200 m length). Three sets of numbers from the ten designated marks were randomly generated and then allocated to each baseline. Three line transects (transects 1, 2, and 3) of 50 m each were established starting at the marked points, running perpendicular to the baseline and parallel to one another, in this example a west–east direction. Sampling was done along each transect for terminal shoots, flower buds, flowers, or pods of all *Fabaceae* plant species. These plants were carefully examined for the presence of *Maruca* larvae or *Maruca*-like damage. This procedure was repeated at all the survey points, that is, 25 times in Ghana, 44 in Nigeria, and 52 in Burkina Faso. This resulted in an assessment of alternate hosts in areas within 200 m of cultivated cowpea that included grazing lands, forests, and other cultivated crops (Fig. 2).

All species belonging to the *Fabaceae* intercepting the transects were recorded. Crown cover estimates (proportion of the ground cover occupied by a perpendicular projection of the individual plant species) of each plant intercepting the transects were recorded (Greig-Smith 1983). The intercept lengths for each species were summed and each of these values was divided by the total length of the transect. These values then were converted to coverage percentages for each species.

The formula used for calculating plant cover was:

$$\text{Plant cover\%} = \Sigma i / Tl \times 100$$

Σi = sum of individual plant intercept lengths

Tl=Total length of the transect line

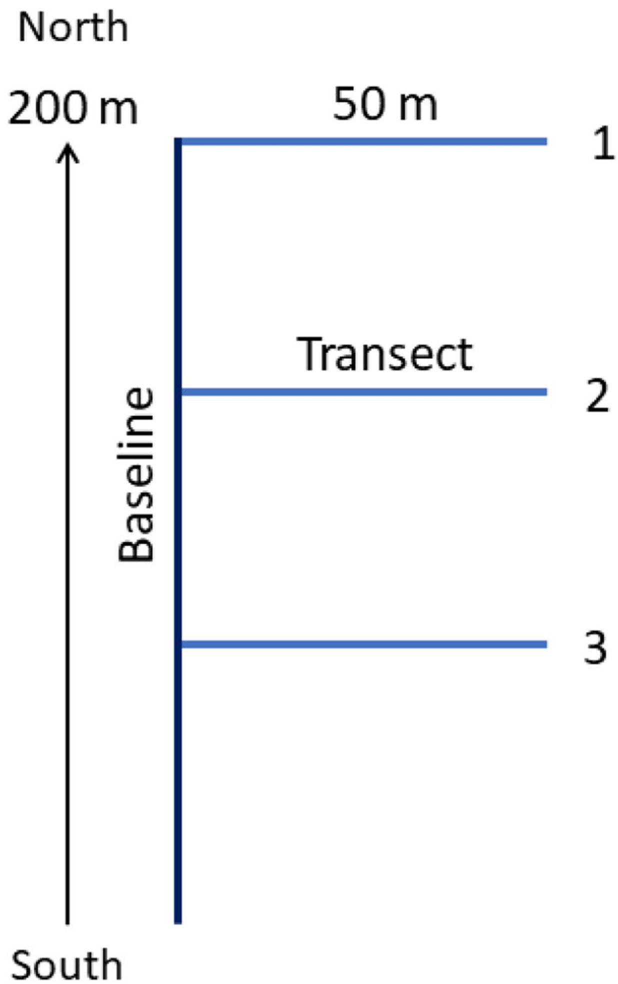

Fig. 1 Three 50 m transects were established from a 200 m baseline that extended from a cowpea farm at each survey site

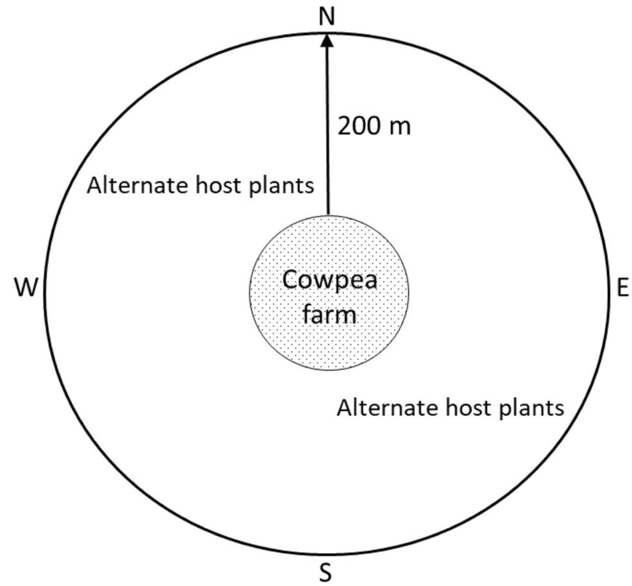

Fig. 2 Diagram of the surveys for alternate host plants within 200 m of cowpea farms used at each location

Samples of potential alternate hosts found within 200 m from the border of cultivated cowpea fields were examined for *Maruca* damage symptoms on terminal shoots, flower buds, flowers, and pods, which included feeding scars, tunnels, and evidence of frass. Infested plants were dissected for recovery of *Maruca* larvae. Plants from which the larvae were collected were then identified to species. The larvae were identified by the characteristic translucent, shining body with six rows of black spots running from thorax to abdomen and a dark brown head. The adults were identified by three white patches with black margins on the brown forewings (Sharma et al. 1999). In cases where the infested plants could not be identified readily in the field, voucher specimens were collected, wrapped in tissue paper, placed in plastic bags, and then sent to the authors' respective research institutes for identification. Plants were identified to genera and, if possible, species using the following references: Akobundu 1987; Akobundu and Agyakwa 1987. Cowpea field infestations were estimated in Ghana and Nigeria by inspecting 100 randomly distributed cowpea plants for *Maruc*a infestation damage on terminal shoots, flower buds, flowers, and pods. Sampling of *Maruca* larvae on cowpea farms was timed generally to coincide with flowering. Cowpea plants can compensate for flower removal, so gently removing flowers during sampling reduces plant destruction and limits yield loss (Abudulai and Shepard 2003).

Laboratory rearing and identification of *Maruca*

The *Maruca* larvae collected were sent to the laboratory for rearing and identification. Each specimen was placed in a glass vial containing artificial diet made from a modified *Ostrinia nubilalis* Hübner diet obtained commercially from Bio-Serv Company, Flemington, NJ. USA (Bio-Serv product No. F9478B-M) without corncob grits but supplemented with cowpea flour. The vials were plugged with cotton wool, labeled, and incubated at 25 ± 1 °C and 60–70% relative humidity (RH) until adult (moths) emergence. *Maruca* moths were identified by entomologists at each institute. If a *Maruca* adult was confirmed then the host plant was recorded; otherwise, the plant was not recorded.

Results

The results for distribution and diversity of alternate hosts of *Maruca* in five locations within three countries in West Africa are presented in Tables 1–5. The survey found many *Fabaceae* plant species in areas where cowpea and

Table 1 Tolon-Kumbungu, Ghana: Distribution, alternate hosts species of *Maruca vitrata*, plant growth stage, number of plants, total number of plants, percentage plant cover, total percentage plant cover, and number of *Maruca* larvae/100 cowpea plants at Tolon-Kumbungu location in Ghana

Site ID	Latitude	Longitude	Plant Species	*Plant Stage	[a]*Maruca* Larvae/Damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)	*Maruca*/100 Cultivated Cowpea Plants
1	9.58362	-1.06601	*Stylosantes* spp	V	Damage	4	10.0	0.3	0.8	92
			Senna obtusifolia	F, P	Damage	6		0.5		
2	9.48082	-1.14034	*Corchorus olitorius*	F, P	Damage	2	10.0	0.3	4.8	66
			Senna obtusifolia	F, P	Damage	3		4.0		
			Tephrosia linearis	P	Damage	5		0.5		
3	9.65729	-1.04056	*Corchorus olitorius*	P	Larvae	1	10.0	0.3	2.1	0
			Senna obtusifolia	F, P	Larvae	3		0.8		
			Tephrosia linearis	P	Larvae	6		1.0		
4	9.50641	-0.90020	No plants		None	0	0	0	0	
5	9.39680	-1.12069	*Tephrosia linearis*	P	Larvae	10	10.0	1.0	1.0	161
6	9.62311	-1.11845	*Senna obtusifolia*	F, P	Larvae	5	14.0	0.9	2.3	70
			Tephrosia bracteolata	P	Larvae	5		1.0		
			Cajanus cajan	P	Larvae	4		0.4		
7	9.35141	-0.94192	*Pueraria phaseoloides*	P	Damage	3	9.0	0.5	1.4	0
			Senna obtusifolia	F, P	Damage	6		0.9		
8	9.49730	-1.08123	*Corchorus olitorius*	F, P	Larvae	2	12.0	0.5	2.2	12
			Senna obtusifolia	F, P	Larvae	4		0.8		
			Tephrosia linearis	P	Larvae	6		0.9		
9	9.51486	-0.98796	*Senna obtusifolia*	F, P	Damage	6	6.0	0.7	0.7	223
10	9.55297	-1.22093	*Senna obtusifolia*	F, P	Damage	7	7.0	0.8	0.8	15
11	9.59153	-1.00675	*Senna obtusifolia*	F, P	Larvae	4	10.0	0.7	1.7	143
			Tephrosia linearis	P	Larvae	6		1.0		
12	9.60278	-0.91893	*Senna obtusifolia*	F, P	Damage	6	6.0	0.7	0.7	201
13	9.48085	-1.01690	*Senna obtusifolia*	F, P	Damage	7	7.0	0.9	0.9	360
14	9.44947	-1.13075	*Tephrosia linearis*	P	Larvae	6	6.0	1.0	1.0	276
15	9.36689	-1.05412	*Tephrosia linearis*	P	Larvae	7	7.0	0.9	0.9	242
16	9.41265	-0.97896	*Pueraria phaseoloides*	P	Larvae	2	14.0	0.6	3.1	1
			Crotalaria retusa	P	Larvae	5		0.9		
			Tephrosia linearis	P	Larvae	3		1.0		
			Senna obtusifolia	F, P	Larvae	4		0.6		
17	9.54248	-1.11272	*Corchorus olitorius*	P	Damage	1	8.0	0.3	1.7	17
			Senna obtusifolia	F, P	Damage	5		0.8		
			Stylosantes spp	V	Damage	2		0.6		
18	9.55013	-0.94211	*Senna obtusifolia*	F, P	Damage	8	8.0	0.9	0.9	198
19			*Senna obtusifolia*	F, P	Larvae	8	24.0	1.0	1.5	84
			Tephrosia linearis	P	Larvae	16		0.5		
20	9.53071	-1.15888	*Corchorus olitorius*	P	Damage	2	12.0	0.3	1.6	21
			Senna obtusifolia	F, P	Damage	5		0.9		
			Stylosantes spp	V	Damage	5		0.4		

Table 1 (continued)

Site ID	Latitude	Longitude	Plant Species	*Plant Stage	[a]*Maruca* Larvae/Damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)	*Maruca*/100 Cultivated Cowpea Plants
21	9.47037	-1.126208	*Crotalaria quinquefolia*	P	Larvae	4	10.0	1.1	1.8	88
			Tephrosia bracteolata	P	Larvae	6		0.7		
22	9.60475	-1.19699	*Senna obtusifolia*	F, P	Larvae	3	7.0	0.8	1.3	10
			Tephrosia linearis	P	Larvae	4		0.5		
23	9.65951	-1.29041	*Senna obtusifolia*	F, P	Larvae	4	9.0	0.9	1.9	44
			Tephrosia bracteolata	P	Larvae	5		1.0		
24	9.61829	-1.00704	*Senna obtusifolia*	F, P	Larvae	3	7.0	0.8	1.8	208
			Tephrosia bracteolata	P	Larvae	4		1.0		
25	9.66633	-1.18758	*Senna obtusifolia*	F, P	Larvae	4	10.0	0.8	1.7	23
			Tephrosia bracteolata	P	Larvae	6		0.9		
					Mean	4.8	9.3	0.8	1.5	106.3
					Standard Error	0.37	0.84	0.08	0.19	21.18

**V* Vegetative, *F* Flowering, and *P* Podding

[a]*Maruca* larvae or *Maruca*-like damage found, plants classified as alternate or potential alternate hosts, respectively

Maruca coexist. The *Fabaceae* plant species found in the survey areas were classified into three categories based on: 1) presence of *Maruca* larvae on the plants classified as alternate host, 2) only *Maruca*-like damage found (potential alternate host), and 3) none, where neither *Maruca* nor *Maruca*-like damage, was found. These three categories (larvae, damage, and none) are presented in the Tables 1–5.

At the Tolon-Kumbungu location in Ghana, nine taxa of plants—namely, *Senna obtusifolia* L., *Tephrosia linearis* (Willd.) Pers., *Tephrosia bracteolata* Guill. & Perr., *Corchorus olitorius* L., *Stylosanthes* spp., *Pueraria phaseoloides* (Roxb.) Benth., *Crotalaria quinquefolia* L., *Cajanus cajan* (L.) Millsp., and *Crotalaria retusa* L. or combinations of them—were found at 24 of the 25 survey sites (Table 1). Most of the plant species were at flowering or podding stages except *Stylosanthes* spp. that was at the vegetative stage. Besides *Stylosanthes* spp, all of them had either only *Maruca* damage symptoms or presence of *Maruca* larvae. No alternate host plants were found at site 4. Numbers and mean cover percentages (n, $\bar{x} \pm$ SE) for the four most common plant species found at this location were *S. obtusifolia* (20, 0.96 ± 0.16), *T. linearis* (9, 0.83 ± 0.08), *T. bracteolate* (5, 0.92 ± 0.06), and *Corchorus olitorius* (5, 0.34 ± 0.04). The average number of potential host plants (larvae, damage, and none) found along the three transects for each site was 9.3 with 1.5% average plant cover (Table 1). The average number of *Maruca* larvae on 100 cowpea plants growing in cultivated cowpea fields was 106.3.

Five plant species—namely, *Sesbania sesban* (L.) Merr., *Crotalaria senegalensis* (Pers.), *Tephrosia bracteolata, Vigna racemosa* (G. Don) Hutch. & Dalziel, *T. platycarpa* Guill. & Perr., and combinations of them—were found at 22 of the 25 survey sites at the Bunkure location in Nigeria (Table 2). Only two locations had the latter two species. Most of the plant species were at flowering or podding stages except *C. senegalensis* species that was at vegetative stage. All the plant species found had either presence of *Maruca* larvae or only damage symptoms. No alternate host plants were found at sites 8, 9 and 16. The most common species found at this location were *S. sesban* (12, 1.29 ± 0.21), *C. senegalensis* (10, 1.35 ± 0.19), and *T. bracteolata* (8, 0.81 ± 0.17). The mean number of host plants found along the three transects for each site was 8.4 with 1.5% average plant cover (Table 2). The average number of *Maruca* larvae on 100 cowpea plants growing in cultivated cowpea fields was 7.5.

At the Bomo location in Nigeria, four plant species—namely, *V. racemosa*, *C. senegalensis*, *Centrosema pubescens* Benth., and *Sesbania sesban,* or combinations of them—were found in 11 of the 19 survey sites (Table 3). All the plant species were at flowering or podding

Table 2 Bunkure, Nigeria: Distribution, alternate hosts species of *Maruca vitrata*, plant growth stage, number of plants, total number of plants, percentage plant cover, total percentage plant cover, and number of *Maruca* larvae/100 cowpea plants at Bunkure location in Nigeria

Site ID	Latitude	Longitude	Plant Species	*Plant Stage	[a]*Maruca* larvae/damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)	*Maruca*/100 Cultivated Cowpea Plants
1	11.64036442	8.53500009	*Vigna racemosa*	F, P	Larvae	4	17	0.5	2.5	6
			Sesbania sesban	F, P	Larvae	3		0.6		
			Tephrosia bracteolata	F, P	Larvae	5		0.8		
			Crotalaria senegalensis	F, P	Larvae	5		0.6		
2	11.61781923	8.68227965	*Sesbania sesban*	F, P	Larvae	2	2	0.8	0.8	6
3	11.64021299	8.67552034	*Crotalaria senegalensis*	V	None	7	7	0.9	0.9	6
4	11.70545070	8.63737061	*Crotalaria senegalensis*	V	None	8	8	2.2	2.2	6
5	11.70603367	8.60894575	*Crotalaria senegalensis*	F, P	Larvae	9	9	1.1	1.1	
6	11.69757320	8.56319127	*Sesbania sesban*	F	Larvae	5	10	0.9	1.4	5
			Crotalaria senegalensis	F	Larvae	5		0.5		
7	11.71013698	8.53350067	*Tephrosia pachycarpa*	F, P	Larvae	4	4	0.9	0.9	
8	11.72034553	8.50993629	No plants			0	0	0	0	
9	11.60849065	8.48749779	No plants			0	0	0	0	
10	11.65962024	8.48592655	*Crotalaria senegalensis*	F, P	Larvae	7	11	2.1	4.1	4
			Sesbania sesban	F	Larvae	4		2.0		
11	11.66747623	8.50880198	*Vigna racemosa*	F, P	Larvae	5	7	0.7	1.2	8
			Sesbania sesban	F	Larvae	2		0.5		
12	11.61648761	8.55753370	*Sesbania sesban*	F, P	Larvae	6	6	1.9	1.9	
13	11.64471471	8.55240856	*Sesbania sesban*	F, P	Larvae	13	13	3.0	3.0	11
14	11.72368847	8.53695549	*Tephrosia bracteolata*	F	None	3	3	0.2	0.2	
15	11.75688541	8.53241275	*Tephrosia bracteolata*	F	Damage	3	3	0.3	0.3	14
16	11.66158183	8.66675412	No plants			0	0	0	0	
17	11.64613670	8.65819845	*Crotalaria senegalensis*	V, F	None	9	9	1.6	1.6	7
18	11.63127192	8.63893415	*Crotalaria senegalensis*	V	None	6	6	1.0	1.0	
19	11.61391721	8.62249678	*Crotalaria senegalensis*	F, P	None	9	9	1.8	1.8	
20	11.65876976	8.75347867	*Tephrosia bracteolata*	F	Damage	6	16	1.3	2.6	6
			Sesbania sesban	F, P	Larvae	10		1.4		
21	11.67271553	8.73205067	*Sesbania sesban*	F, P	Damage	9	14	1.0	1.7	11
			Tephrosia bracteolata	F	Damage	5		0.8		
22	11.68522105	8.71908848	*Tephrosia bracteolata*	F	Larvae	9	27	1.7	5.0	
			Sesbania sesban	F, P	Larvae	10		1.7		
			Crotalaria senegalensis	F	Larvae	8		1.7		
23	11.70977543	8.73345578	*Sesbania sesban*	F, P	Larvae	6	10	0.9	1.6	
			Tephrosia bracteolata	F, P	Larvae	4		0.7		
24	11.70868647	8.71455698	*Sesbania sesban*	F, P	Larvae	7	7	1.0	1.0	

Table 2 (continued)

Site ID	Latitude	Longitude	Plant Species	*Plant Stage	[a]*Maruca* larvae/damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)	*Maruca*/100 Cultivated Cowpea Plants
25	11.73461084	8.74487234	*Tephrosia bracteolata*	V, F	Damage	12	12	0.7	0.7	
					Mean	5.8	8.4	1.0	1.5	7.5
					Standard Error	0.54	1.23	0.12	0.25	0.86

**V* Vegetative, *F* Flowering, and *P* Podding

[a] *Maruca* larvae or *Maruca*-like damage found, plants classified as alternate or potential alternate hosts, respectively

stages except *C. pubescens* that was at the vegetative stage. Also, all the plant species found had either presence of *Maruca* larvae or only damage symptoms with the exception of two species, *C. senegalensis*, and *C. pubescens,* where neither larvae nor *Maruca*-like damage were found. No alternate host plants were found at sites 1, 4, 5, 9, 10, 12, and 13. The numbers and mean cover percentages for the most common plant species found at this location were *V. racemosa* (7, 0.86 ± 0.14) and *Crotalaria senegalensis* (4, 0.63 ± 0.06). The mean number of potential host plants found along the three transects for each site was 4.5 with 1.3% average plant cover (Table 3). The average number of *Maruca* larvae found on 100 cowpea plants growing in cultivated cowpea fields was 5.2.

Three species of alternate hosts—namely, *C. retusa, S. pachycarpa,* and *T. bracteolata*, all of which had *Maruca* larvae present—were found at the Ziniaré location in Burkina Faso (Table 4). *T. bracteolata* was found only in two locations. The other two species either occurred alone or at two locations in combination. Numbers and mean cover percentages for the most common plant species found at this location were *C. retusa* (8, 5.1 ± 2.20) and *S. pachycarpa* (4, 3.1 ± 1.77). The mean number of host plants where *Maruca* was found along the three transects for each site was 5.1 with 7.6% plant coverage. Most of the plant species were at the flowering stage with a few also at the podding stage. *Maruca* larvae were not counted in cultivated cowpea fields in Burkina Faso.

At the Bobo Dioulasso location in Burkina Faso, six plant species—namely, *Tephrosia nana* Kotschy & Schweinf., *Vigna* spp., *T. bracteolata, C. retusa, S. pachycarpa,* and *Crotalaria goreensis* Guill. & Perr.—were verified with *Maruca* larvae present and classified as alternate hosts (Table 5 and 6). Some plant species occurred either singly or in combination in some locations. All plant species were either at flowering/podding stages except *C. retusa* and *C. goreensis* that were only flowering. The mean cover percentages for the most common plant species found at this location are: *T. nana* (33, 9.4 ± 1.67), *Vigna* spp., (20, 8.8 ± 1.55), *T. bracteolate* (12, 6.9 ± 2.10), *C. retusa* (9, 5.3 ± 2.23), and *S. pachycarpa* (7, 2.9 ± 1.04). Overall, the average number of host plants where *Maruca* was found along the three transects for each site was 14.0 with 17.9% plant coverage. Similarly, the number of *Maruca* larvae was not counted in cultivated cowpea fields.

Discussion

Our study aimed to assess the distribution and diversity of alternate host plants for *Maruca* in selected, important cowpea-growing countries in West Africa. Generally, the alternate host plants including *Crotolaria*, *Sesbania*, *Tephrosia*, and *Vigna*, species were the most frequently

Table 3 Bomo, Nigeria: Distribution, diversity of alternate hosts species of *Maruca vitrata*, plant growth stage, number of plants, total number of plants, percentage plant cover, total percentage plant cover, and number of *Maruca* larvae/100 cowpea plants at Bomo location in Nigeria

Site ID	Latitude	Longitude	Plant Species	*Plant Stage	[a]*Maruca* Larvae/damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)	*Maruca*/100 Cultivated Cowpea Plants
1	11.13999287	7.7559723	No plants			0	0	0	0	
2	11.17953789	7.7689160	*Crotalaria senegalensis*	F	None	5	5	0.5	0.5	4
3	11.17129300	7.7436321	*Vigna racemosa*	F, P	Larvae	5	5	1.5	1.5	6
4	11.19391765	7.7324808	No plants			0	0	0	0	
5	11.21473073	7.7339301	No plants			0	0	0	0	
6	11.14786319	7.7162571	*Vigna racemosa*	F, P	None	6	6	1.1	1.1	
7	11.16452975	7.7127145	*Crotalaria senegalensis*	F	None	6	6	0.6	0.6	
8	11.19234762	7.7093731	*Vigna racemosa*	F, P	Larvae	6	11	0.5	1.1	9
			Crotalaria senegalensis	F, P	Larvae	5		0.6		
9	11.21251657	7.7070784	No plants			0	0	0	0	
10	11.15914819	7.6809331	No plants			0	0	0	0	
11	11.17509588	7.6662540	*Vigna racemosa*	F, P	Larvae	6	6	0.4	0.4	
12	11.18538938	7.6830715	No plants			0	0	0	0	
13	11.18658545	7.6674138	No plants			0	0	0	0	
14	11.22572976	7.6515024	*Crotalaria senegalensis*	F	Larvae	6	6	0.8	0.8	2
15	11.21043449	7.6540033	*Vigna racemosa*	F, P	Larvae	6	6	1.0	1.0	5
16	11.19310951	7.6292119	*Vigna racemosa*	F, P	Larvae	6	6	0.8	0.8	
17	11.16617967	7.5955768	No plants			0	0	0	0	
18	11.17995267	7.6108720	*Sesbania sesban*	F, P	Larvae	7	16	0.6	14.3	
			Vigna racemosa	F, P	Larvae	6		0.7		
			Centrosema pubescens	V	None	3		13.0		
19	11.19049989	7.5831448	*Sesbania sesban*	F, P	Larvae	6	12	0.8	1.8	
			Centrosema pubescens	V	None	6		1.0		
					Mean	3.7	4.5	1.0	1.3	5.2
					Standard Error	0.59	1.09	0.55	0.74	1.16

**V* Vegetative, *F* Flowering, and *P* Podding

[a] *Maruca* larvae found, plants classified as alternate hosts

Table 4 Ziniare, Burkina Faso: Distribution, diversity of alternate hosts species of *Maruca vitrata*, plant growth stage, number of plants, total number of plants, percentage plant cover, and total percentage plant cover at Ziniare location in Burkina Faso

Site ID	Latitude	Longitude	Plant Species	*Plant Stage	[a]*Maruca* Larvae/Damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)
1	12.602711	1.440205	*Crotalaria retusa*	F	Larvae	5	16	0.3	0.8
			Sesbania pachycarpa	F, P	Larvae	11		0.5	
2	12.538133	1.387176	*Crotalaria retusa*	F	Larvae	2	2	0.3	0.3
3	12.522327	1.370214	*Crotalaria retusa*	F	Larvae	3	3	15.4	15.4
4	12.653579	1.320516	*Sesbania pachycarpa*	F, P	Larvae	7	7	4.4	4.4
5	12.579998	1.333505	*Crotalaria retusa*	F	Larvae	3	11	1.6	1.6
			Sesbania pachycarpa	F, P	Larvae	8		0.01	
6	12.582069	1.358098	*Crotalaria retusa*	F	Larvae	4	4	14.1	14.1
7	12.583691	1.360641	*Crotalaria retusa*	F	Larvae	1	1	3.7	3.7
8	12.583260	1.375090	*Crotalaria retusa*	F	Larvae	5	5	5.2	5.2
9	12.583545	1.376891	*Sesbania pachycarpa*	F, P	Larvae	4	4	7.5	7.5
10	12.583858	1.378756	*Tephrosia bracteolata*	F, P	Larvae	3	3	30.1	30.1
11	12.583924	1.378775	*Crotalaria retusa*	F	Larvae	1	1	0.3	0.3
12	12.583216	1.378859	*Tephrosia bracteolata*	F, P	Larvae	4	4	8.2	8.2
					Mean	4.4	5.1	6.5	7.6
					Standard Error	0.74	1.27	2.26	2.51

**F* Flowering and *P* Podding

[a] *Maruca* larvae found, plants classified as alternate hosts

encountered among sites and locations. *Crotalaria* species were commonly found in all the five survey locations in Ghana, Nigeria, and Burkina Faso. *Tephrosia* species were found mostly at Tolon-Kumbungu (Ghana), Bunkure (Nigeria), and Bobo Dioulasso (Burkina Faso). *Sesbania* species were found at Bomo (Nigeria) and the two locations in Burkina Faso. *Vigna* species were found at both Bunkure and Bomo (Nigeria), and Bobo Dioulasso (Burkina Faso). *Senna obtusifolia* was especially prominent in Tolon-Kumbungu (Ghana). Previous studies have identified most of these species as alternate hosts of *Maruca* (Tamò et al. 2002; Arodokoun et al. 2003), corroborating our findings. There were instances where only damage symptoms were observed on the plants and those plants were classified as potential alternate hosts of *Maruca*. Also, there were plants where neither *Maruca* larvae nor *Maruca*-like damage were found. This occurred especially at the Bomo (Nigeria) location. These same plant species, however, except for *Centrosema pubescens*, had *Maruca* larvae or damage at other locations. There were sites where no plant species were found because of scarce vegetation or poor accessibility, especially at Bomo. Unlike the higher numbers of *Maruca* larvae found on the cowpea plants in Ghana, few *Maruca* larvae were found on cowpea plants in Nigeria because the growers had sprayed their crops with chemical insecticides prior to conducting the survey or the pest pressure was low that year. Another challenge was sorting through the many plant species that were encountered during the surveys. Future studies could address this by focusing on the major known alternate species at a location.

The extensive distribution and diversity of the alternate plant species within the surveyed locations indicate that they could be used as refuges when *Bt* cowpea is introduced. Many *Maruca* larvae were found on both cowpea plants on the farms and alternate hosts growing within 200 m of the farms in Tolon-Kumbungu (Ghana), and Bunkure (Nigeria) locations. While the presence of *Maruca* larvae on cowpea plants was not determined in Burkina Faso, earlier studies by Traore et al. (2014) reported that *Maruca* populations overlapped on cultivated cowpea and alternate hosts plants during the rainy season in southwestern Burkina Faso. These observations suggest that adult *Maruca* emerging from cultivated cowpea and alternate host plants in close vicinity are very likely to mix and mate. Small farms embedded in areas with alternate hosts particularly could benefit. For example, a one-hectare farm (10,000 m^2) potentially could attract *Maruca* from a radius of 200 m (or more). In this case, *Maruca* would be attracted from a minimum area of 125,600 m^2, which is more than 12 times the size of the farm. Likewise, half, quarter, and one-tenth hectare farms would attract *Maruca* from proportionally larger areas, that is, more than 25, 50, and 125 times larger, respectively. Consequently, when *Bt* cowpea is planted in similar environments, resistant moths could mate with susceptible moths, which lowers the frequency of the resistance alleles

Table 5 Distribution, diversity of alternate hosts species of *Maruca vitrata*, plant growth stage, number of plants, and percentage plant cover at Bobo Dioulasso location in Burkina Faso (Part 1)

Site ID	Latitude	Longitude	Plant Species	Plant Stage	[a]*Maruca* Larvae/Damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)
1	11.363926	-4.357493	*Crotalaria retusa*	F	Larvae	10	10	21.6	21.6
2	11.401730	-4.059483	*Vigna* spp.	F, P	Larvae	7	12	22.7	30.9
			Vigna spp.	F, P	Larvae	5		8.2	
3	11.523662	-3.988279	*Tephrosia nana*	F, P	Larvae	21	28	15.8	17.2
4	11.495369	-4.007024	*Sesbania pachycarpa*	F, P	Larvae	7		1.4	
5	11.383900	-4.078004	*Tephrosia nana*	F, P	Larvae	8	23	3.2	3.3
			Tephrosia nana	F, P	Larvae	15		0.1	
6	11.351522	-4.120257	*Sesbania pachycarpa*	F, P	Larvae	5	14	5.3	5.5
			Tephrosia bracteolata	F, P	Larvae	9		0.2	
7	11.294763	-4.201514	*Tephrosia nana*	F, P	Larvae	11	24	30.2	75.7
			Tephrosia nana	F, P	Larvae	6		15.4	
			Tephrosia nana	F, P	Larvae	7		30.1	
8	11.193713	-3.981966	*Tephrosia nana*	F, P	Larvae	10	13	0.7	4.6
			Crotalaria retusa	F	Larvae	3		3.9	
9	10.847111	-4.610803	*Crotalaria goreensis*	F	Larvae	2	8	0.003	1.0
			Tephrosia nana	F, P	Larvae	6		1.0	
10	10.756940	-4.718950	*Sesbania pachycarpa*	F, P	Larvae	5	16	7.7	15.1
			Tephrosia nana	F	Larvae	11		7.4	
11	10.784480	-4.695112	*Tephrosia nana*	F, P	Larvae	17	22	3.9	11.5
			Tephrosia bracteolata	F, P	Larvae	5		7.6	
12	10.783881	-4.694111	*Vigna* spp.	F, P	Larvae	1	29	15.5	52.3
13	10.851357	-4.608559	*Crotalaria goreensis*	F	Larvae	6		15.5	
			Tephrosia nana	F, P	Larvae	9		1.0	
			Crotalaria retusa	F	Larvae	4		6.1	
			Tephrosia bracteolata	F, P	Larvae	6		0.001	
			Vigna spp.	F, P	Larvae	3		14.2	
14	10.960695	-4.449583	*Vigna* spp.	F, P	Larvae	6	17	0.003	14.5
			Tephrosia bracteolata	F, P	Larvae	5		3.0	
			Tephrosia nana	F, P	Larvae	6		11.5	
15	11.013442	-4.397813	*Vigna* spp.	F, P	Larvae	5	24	0.003	32.6
			Tephrosia nana	F, P	Larvae	10		11.5	
			Vigna spp.	F, P	Larvae	3		15.6	
			Crotalaria goreensis	F	Larvae	6		5.5	
16	11.097236	-4.315528	*Crotalaria goreensis*	F	Larvae	5	8	21.6	40.3
			Tephrosia nana	F, P	Larvae	3		18.7	
17	11.096933	-4.614221	*Vigna* spp.	F, P	Larvae	4	13	3.5	4.2
			Tephrosia nana	F, P	Larvae	9		0.7	
18	11.068907	-4.772015	*Tephrosia bracteolata*	F, P	Larvae	6	15	3.2	23.7
			Vigna spp.	F, P	Larvae	5		0.9	
			Tephrosia bracteolata	F, P	Larvae	4		19.6	
19	10.985292	-4.837563	*Sesbania pachycarpa*	F, P	Larvae	8	29	2.8	6.6
			Tephrosia bracteolata	F, P	Larvae	11		0.003	
			Tephrosia bracteolata	F, P	Larvae	10		3.8	
20	10.978962	-4.848805	*Vigna* spp.	F, P	Larvae	6	6	3.0	3.0

**F* Flowering and *P* Podding

[a] *Maruca* larvae found, plants classified as alternate hosts

Table 6 Distribution, diversity of alternate hosts species of *Maruca vitrata*, plant growth stage, number of plants, and percentage plant cover at Bobo Dioulasso location in Burkina Faso (Part 2 with means)

Site ID	Latitude	Longitude	Plant Species	Plant Stage	[a]*Maruca* Larvae/Damage	# Plants	Total # Plants	Plant Cover (%)	Total Plant Cover (%)
21	11.083893	-4.663021	*Tephrosia bracteolata*	F, P	Larvae	5	12	4.2	23.6
			Vigna spp.	F, P	Larvae	7		19.4	
22	11.121591	-4.492918	*Tephrosia nana*	F, P	Larvae	4	34	0.8	33.0
			Crotalaria retusa	F	Larvae	10		7.5	
			Vigna spp.	F, P	Larvae	2		13.2	
			Crotalaria retusa	F	Larvae	9		0.005	
			Tephrosia nana	F, P	Larvae	9		11.5	
23	11.203598	-4.398504	*Tephrosia nana*	F, P	Larvae	14	14	31.1	31.1
24	11.417590	-4.436721	*Tephrosia nana*	F, P	Larvae	5	5	30.1	30.1
25	11.618431	-4.577209	*Sesbania pachycarpa*	F, P	Larvae	2	6	2.5	4.5
			Crotalaria retusa	F, P	Larvae	4		2.0	
26	11.620683	-4.564374	*Tephrosia nana*	F, P	Larvae	8	8	10.2	10.2
27	11.691362	-4.527594	*Tephrosia nana*	F	Larvae	1	4	6.8	10.9
			Tephrosia nana	F, P	Larvae	3		4.1	
28	11.690357	-4.526324	*Sesbania pachycarpa*	F, P	Larvae	4	4	0.006	0.006
29	11.780450	-4.516463	*Tephrosia nana*	F, P	Larvae	8	20	1.1	30
			Tephrosia nana	F, P	Larvae	1		14.3	
			Tephrosia nana	F	Larvae	6		13.8	
			Crotalaria retusa	F	Larvae	5		0.8	
30	11.512473	-4.490122	*Sesbania pachycarpa*	F, P	Larvae	10	10	0.5	0.5
31	11.513628	-4.490196	*Crotalaria retusa*	F	Larvae	8	13	0.3	3.3
			Vigna spp.	F, P	Larvae	5		3.0	
32	11.192714	-3.896319	*Vigna* spp.	F, P	Larvae	5	5	4.2	4.2
33	11.192781	-3.896094	*Vigna* spp.	F, P	Larvae	4	11	14.2	24.5
			Tephrosia bracteolata	F, P	Larvae	7		10.3	
34	11.193407	-3.896113	*Vigna* spp.	F, P	Larvae	5	5	3.5	3.5
35	11.205040	-3.822919	*Vigna* spp.	F, P	Larvae	3	4	3.2	4.0
			Tephrosia nana	F, P	Larvae	1		0.8	
36	11.202236	-3.793131	*Tephrosia nana*	F, P	Larvae	5	11	1.0	9.5
			Tephrosia nana	F, P	Larvae	1		0.002	
			Tephrosia nana	F, P	Larvae	5		8.5	
37	11.222421	-3.726286	*Tephrosia nana*	F, P	Larvae	3	12	1.2	20.4
			Crotalaria retusa	F	Larvae	2		5.5	
			Tephrosia nana	F, P	Larvae	6		8.3	
			Vigna spp.	F, P	Larvae	1		5.4	
38	11.230347	-3.716379	*Tephrosia nana*	F, P	Larvae	16	16	10.2	10.2
39	11.193137	-3.998305	*Vigna* spp.	F, P	Larvae	2	18	12.7	40.9
			Tephrosia nana	F, P	Larvae	5		5.1	
			Vigna spp.	F, P	Larvae	2		13.6	
			Tephrosia bracteolata	F, P	Larvae	9		9.5	
40	11.221571	-4.472499	*Tephrosia bracteolata*	F, P	Larvae	10	10	21.6	21.6
					Mean	6.3	14.0	8.0	17.9
					Standard Error	0.41	1.28	0.88	2.67

**F* Flowering and *P* Podding

[a] *Maruca* larvae found, plants classified as alternate hosts

(Roush 1997; Gould 1998). This random mating of moths will help delay and perhaps prevent *Maruca* from developing resistance to the *Bt* toxin.

In this study, many *Maruca* larvae were found on alternate hosts during the rainy season. Traore et al. (2014) reported that during the dry season, *Maruca* maintained a permanent population on the wild host plants *Mucuna poggei* Taub. and *Daniella oliveri* Rolfe in Burkina Faso. Arodokoun et al. (2003) also found *Maruca* in the dry season in southern and central Benin. There is evidence that *Maruca* moths migrate to the north during the rainy season and disperse from local wild hosts (Bottenberg et al. 1997; Ba et al. 2009; Margam et al. 2010).

Utilization of wild hosts plants can be an effective component of IRM strategies for transgenic crops (Jackson et al. 2008). Establishing refuges, however, will be required at some locations where alternate hosts plants are not found or production is low. In fact, Margam et al. (2010) after surveying a total of 67 sites in proximity to cowpea fields in the Sudan Savannah (Kano, Nigeria), the Northern Guinea Savannah (Zaria, Nigeria), and the Sahel Savannah (Maradi, Niger) ecological zones, indicated that alternate host plants for *Maruca* are scarce or absent during the cowpea-growing season in these areas. Their findings were inconsistent with earlier studies that showed an abundance of alternate hosts in West Africa (Atachi and Djihou 1994; Tamò et al. 2002; Arodokoun et al. 2003). They hypothesized that the lack of alternate hosts in their survey was likely due to the northerly arid region of the survey. They concluded that since *Maruca* is migratory into those northerly arid regions and becomes locally extinct at the end of each growing season, the lack of alternate hosts would not impact IRM strategies (Margam et al. 2010). While our study had some geographical overlap with the Margam et al. (2010) study, our survey areas were focused more in the semi-arid cowpea zones where more alternate hosts would be expected (Ba et al. 2019). It is noteworthy that our study was qualitative and only identified the potential for *Maruca* production. Further quantitative studies are needed to determine *Maruca* population sizes that originate from alternate hosts relative to those that originate from cultivated cowpea in order to model their potential for use in an IRM plan.

Another way to increase the number of *Maruca* that originate from alternate hosts includes the use of a cultivated crop, e.g., pigeon pea, *Cajanus cajan*. This crop is an alternate host for *Maruca* in Ghana and could be planted as a refuge as well as food for the growers. The refuge can be comprised of cultivated non-transgenic crop plants or perhaps any other host plants that can support significant population sizes for the targeted insect pest species (Agunbiade et al. 2014). Vacher et al. (2003) suggested refuge fractions of less than 25% will minimize pest density while efficiently delaying resistance. Further studies should be done to ascertain the appropriate refuge percentage required for *Bt* cowpea to ensure effective insect resistance management. The high dose/refuge strategy is considered central to managing resistance to *Bt* toxins (Carrière et al. 2010; Campagne et al. 2016). Pod-borer Resistant cowpea has near complete control of *Maruca* in field tests in West Africa (Addae et al. 2020). Breeding is currently in progress to introduce a second *Bt* gene in addition to the *cry1Ab* gene at research institutes in West Africa (Bett et al. 2017). Two or more genes in a crop has been reported to delay development of resistance to *Bt* toxins better than a single gene. The second gene, however, does not need to be high dose (Head and Greenplate 2012; Onstad et al. 2012). Other information required for fine-tuning an IRM strategy should include a better understanding of pest biology/ecology including interactions with biocontrol agents, product deployment patterns, local cropping systems, and plans for insect susceptibility monitoring, grower communications on compliance, and remedial action should resistance occur.

Conclusion

There are abundant and diverse alternate hosts for *Maruca* in the surveyed locations where cowpea is grown in Ghana, Nigeria, and Burkina Faso. The alternate hosts with their flowering and podding patterns may be adequate for most of the sites in each location to serve as a refuge to delay *Maruca* from developing resistance to the *Bt* toxin until a *Bt* cowpea variety with two insecticidal genes is deployed. This qualitative study suggests there is potential for adequate refuge from alternate hosts, but follow-up quantitative studies are necessary to verify this. Refuges should be established where alternate hosts are not available or uncertain. A robust IRM strategy is required for growing Pod-borer Resistant *Bt* cowpea. This strategy should include abundant alternate hosts for *Maruca*. However, in areas where alternate hosts are limited or missing, growers' compliance to produce non-*Bt* cowpea will be needed. Future studies could determine better estimates of the population size of *Maruca* in the refuge as compared to those of *Bt* cowpea. Such insights would allow effective modeling to understand the long-term potential for the evolution of resistance in *Maruca* populations in *Bt* cowpea.

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Declarations

Conflict of interest The authors declare that they have no conflict of interests.

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