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Feeding preferences of the legume pod borer, *Maruca vitrata* Fab. (Lepidoptera: Crambidae) larvae and suitability of different flower parts for larvae development

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Running Title: *M. vitrata* feeding preferences

Abstract. With the advent of transgenic *Bt*-cowpea, there is a need to identify the feeding preferences of *Maruca vitrata* Fab., in order to determine which component of the plant the expression of the toxin needs to be the highest in order to ensure the greatest efficacy of the insecticidal *Bt* proteins. In the current study we examined the feeding preferences of *M. vitrata* larvae in a naturally infested cowpea field. We also tested, in the laboratory, the suitability of different flower components for the larval development of *M. vitrata*. Our results indicated that in the field, all types of flowers, regardless of their age, were infested with *M. vitrata* larvae. The reproductive organs, in the flowers, were the preferred feeding diet for the larvae. Laboratory bioassays confirmed that the reproductive organs were the optimal tissues for *M. vitrata* larval development. The implications of these findings for transgenic *Bt*-cowpea are discussed.

Keywords: cowpea, flower components, larval development

Introduction

Cowpea is the major legume grain crop in Sub-Saharan Africa and the main protein source for many rural people in this area of the world. However, the production of cowpea is limited by both abiotic and biotic constraints. Insect pests are the major biotic limiting factor for cowpea production in Sub-Saharan Africa (Singh and Allen, 1980; Singh *et al.*, 1990). These insect pests include the legume pod borer, *Maruca vitrata* Fab. (Lepidoptera, Crambidae), one of the most devastating insect pests of cowpea, which can cause typical yield losses ranging from 20% to 80% (Singh *et al*., 1990). In Burkina Faso, *M. vitrata* is endemic in the southwestern region of the country (Ba *et al*., 2009; Baoua *et al*., 2011). Damage to cowpea, by *M. vitrata*,

is due to larvae that feed on the tender parts of the stem, peduncles, flower buds, flowers and pods (Singh and Jackai, 1988).

The economic importance of this pest species has been the main rationale behind the work that has been performed on its biology (Gblagada, 1982; Karel, 1985; Afun *et al*., 1991). The early instar larvae feed mainly on flowers (Karel, 1985) and a single larva can consume 4-6 flowers by time they reach the pupal stage (Gblagada, 1982). Up to 80% of cowpea flowers are infested with *M. vitrata* larvae in the field (Afun *et al*., 1991). However, the literature is devoid of information related to the feeding preferences of the larvae as it pertains to the age of the cowpea flower and the preferred flower components. Thus, this study aims to identify which age and which component of the cowpea flowers are preferred by *M. vitrata* larvae. Understanding these aforementioned parameters will be useful when engineering the Cry endotoxin (*Bt*) of *Bacillus thuringiensis* Berliner into cowpea (hereafter called *Bt*-cowpea). Thus, the scientists producing transgenic *Bt*-cowpea will be better informed as to which organs in the plant need the highest levels of *Bt* expression in order to maximize the impact on the *M. vitrata* populations. Where (or if) promoters exist, or can be discovered/developed, that can drive higher levels of expression in these tissues, this may provide for transgenic *Bt*-cowpeas that might be more effective in controlling *M. vitrata* populations.

Materials and methods

Study sites

Field. Field trials were conducted at the research station of the *Institut de l'Environemment et de Recherche Agricole (INERA)* in Farako-ba, Burkina Faso (latitude: 11°11'N, longitude: 04°18'W), during the 2011 rainy season. Burkina Faso has a unimodal rainfall pattern and a rainy season that lasts from June to October. A total rainfall of 831 mm was recorded in 2011 in the location of Farako-ba.

Laboratory. Laboratory bioassays were conducted in the Laboratory of Entomology of INERA, in Farako-ba, within temperature ranges of 25-32 °C and 60-80 % relative humidity.

Source of insects

The *M. vitrata* larvae used in the bioassays, in this study, were obtained from a mass rearing facility in the Laboratory of Entomology of INERA in Farako-ba. The insects were reared on a modified European corn borer diet obtained commercially from Bio-Serv Company, USA (Bio-Serv product No. F9478B-M without corncob grits) and were supplemented with cowpea seed flour (KVX-61-1 INERA variety).

Field experiments on M. vitrata feeding preferences

For this experiment, a 1-hectare plot of the KVx 404-8-1 (60 days) cowpea variety was planted in July 2011 with an intra-row spacing of 0.4 m and inter-row spacing of 0.8 m. Mineral fertilizers (100 kg/NPK 15-15-15) were applied to the entire plot before planting. The plot was kept free of any pesticide application.

At flowering time, observations were made daily, in each of the plots, up until the pod maturation stage. Flowers and pods were randomly picked in the plot. The sampling included two types of flowers, the green flower (non-opened and non-fertilized) and the yellow fecundated flowers. Sampling on pods included three types of pods accordingly to Dabiré *et al.* (2005): (1) the newly formed pods without seeds (ca. 3 days aged), (2) the pods in the filling stage (ca. 8 days aged) and (3) the mature pods (ca. 14 days aged). When available, each category of plant material (flower and pods) was randomly sampled within the field and brought back into the laboratory for dissection. The yellow opened flowers and the pods were sampled according to visible signs of presence of *M. vitrata* larvae (webbing or faeces or both). A total of 3000 non-opened green flowers, 3000 yellow opened-flowers and 700 pods were collected. The green flowers (non-opened and non-fertilized) were distributed into two batches before dissection: (1) flowers showing larval entrance holes, “perforated flowers” and

(2) flowers with no visible orifice “non perforated flowers”. The organs were then spread on a laboratory bench to avoid the transfer of larvae onto other flowers. The flowers were dissected individually under the magnifying glass and the following parameters where recorded: the number of larvae, the larval stage and the tissues of the flowers that were consumed. The numbers of green flowers, with more than one *M. vitrata* larvae, were also recorded.

Laboratory bioassays on the suitability of cowpea flower components for M. vitrata larval development

A continuous cowpea production, of the KVx 404-8-1 variety, was maintained under irrigation during the dry season (April to June 2011) in a 500 m² plot adjoining the laboratory. The healthy flowers were collected and dissected into six different components: (1) calyx, (2) corolla as a whole, and then (3) standard, (4) wing and (5) keel separately and then the (6) reproductive organs. The corolla included the standard, the wing and the keel. The reproductive organs of the flower included the stamen and the pistils. These components were used as food for bioassays with *M. vitrata* larvae. Neonate *M. vitrata* larvae were fed with each of the aforementioned cowpea flower components until they developed into pupae. For the aforementioned flower components, the food was renewed daily. Larvae, in groups of 20, were placed in a 250 cm^3 capacity plastic boxes covered with muslin cloth. An absorbent paper was placed at the bottom of each box to remove excess humidity contained in the flowers components. Four batches of 5 boxes were used for each flower component, each batch representing one replicate. The larvae were supplied daily with 1.5 g of one given flower component, which remained the same component, until they developed into pupae. Every 24-hrs the larvae were transferred with a camel brush to new boxes, of the same size, with the same quantity of the same flower component. Dead insects were discarded. When the

pupae formed, soft pliers were used to carefully remove them from their envelope, and then the pupae were placed in the boxes until adult emergence. When the adults emerged they were placed in mating cages, in male and female pairs, in a mass rearing room (25°C temperature and 80% relative humidity) until the females laid eggs.

The following parameters were measured to determine the impact of the larval diets: (1) the duration of larval development, (2) the duration of the pre-pupa and (3) pupa stages, (4) the size of pupae, (5) the weight of the pupae (weighed in batches of 50), (6) the adult emergence rate, (7) fecundity and (8) life-span of adults.

Statistical analysis of data

For each parameter, data were analyzed by an ANOVA using SAS software version 9.2 (PROC GLM, SAS Institute, 2001). When ANOVA F-values were significant, means were separated by the Student Newman-Keuls test at the 5% level.

Results

Natural infestation of M. vitrata larvae in the field

The perforated flowers infested, with at least one *M. vitrata* larvae, were significantly higher than the non-perforated flowers (Table 1a). However, the perforated flowers with at least two *M. vitrata* larvae were significantly lower than the non-perforated flowers (Table 1a).

We observed *M. vitrata* larvae on all stages of the pods. However, the pods in the filling stage contained significantly more *M. vitrata* larvae than did the pods without seeds or the mature pods (Table 1b).

Upwards of 50% of the flowers infested with first instar *M. vitrata* larvae had their reproductive organs damaged (Table 2). The first instar larvae damaged respectively 12% and

38% of the wings and the keels (Table 2). No damage, due to first instars larvae, could be observed on the standard the corolla and the calyx of the flowers (Table 2). For subsequent *M. vitrata* larval instars there was a significant increase in the damage to reproductive organs (Table 2).

Development of M. vitrata larvae feeding on different flower components

The *M. vitrata* larvae were able to develop to adulthood when feeding on each of the single cowpea flower components separately (Table 3). However, the larvae that fed on the reproductive organs of the flower had significantly shorter development times as compared to the larvae that fed on other flower components.

The component of the flower used as the diet, significantly influenced the size and the weight of the pupae (Table 4), with the reproductive organs being the best diet for the insects. The pupae that emerged from larvae, which were fed with the reproductive organs of the flower, were significantly greater in length, and were heavier, than the larvae that fed on others flower components. The calyx was the least suitable for insect development. However, there was no significant impact of the diet on the emergence of the adults (Table 4).

The females that emerged from the larvae, reared on the reproductive organs of the flowers, laid significantly more eggs than the females that emerged from larvae reared on others flower components (Table 5). However, the eggs of all the females had the same percentage of viability regardless of the medium the larvae were raised upon (Table 5). The life span of females emerging from the flower's reproductive organs and wings were significantly longer than the females that emerged from larvae raised on other floral parts. The larval diet did not significantly affect the life span of the males (Table 5).

Discussion

Our results demonstrate that *M. vitrata* larvae can develop on any single component of the cowpea flowers up to adulthood. Regardless of the medium, we noticed shorter total larval development duration, as compared to findings from Naveen *et al* (2009), when rearing *M. vitrata* larvae on cowpea whole flowers. Depending on the type of component the larva feed upon, the biology of the insect was affected. Several studies have reported the quality of the food, in terms of nutrients, as a parameter affecting insect development (Pollet *et al*., 1978; Binso, 1980). In our case, when the insects were reared on the reproductive organs of the flowers (stamen and pistils) the larval development time was shortened. Reduction of insect developmental time due to differences in feeding substrate have also been reported for the cowpea pod-sucking bug, *Clavigralla tomentosicollis* (Dabire *et al*., 2005). As a consequence, the pupae from larvae that developed on flower reproductive organs were heavier than pupae from larvae that developed on the other floral parts. Similar results were also reported with *M. vitrata* pupae (Onyango and Ochieng-Odero, 1993). This is in accordance with Jackai and Singh (1983) who reported that *M. vitrata* larvae feeding on more suitable substrates had higher weights as compared to larvae reared on less suitable substrates. However, the medium did not much influence the emergence of the adults, in contrast to what has been observed with *M. vitrata* larvae reared on artificial medium (Jackai and Raulston, 1988).

The average lifespan of the males were not affected by the rearing medium whereas for females they lived longer on the flower reproductive organs and flower wings. However, regardless of the type of rearing medium both male and female lifespans were longer than what has previously been observed by Naveen *et al* (2009) and Huang and Peng (2001), but shorter than the findings of Chi *et al* (2005). These differences are likely due to the rearing medium and environmental conditions (e.g., temperature). As regards to fecundity, females from the larvae that developed on flower reproductive organs laid more eggs than females from larvae that developed on the other floral parts. The quality of the diet on female

fecundity has previously been reported in the cowpea pod-sucking bug *C. tomentosicollis* system (Dabire-Binso *et al*., 2010).

Our laboratory finding indicates that the reproductive organs of the flowers are much better for *M. vitrata* development: shorter development time for larvae, heavier weigh for pupae, as well as increased longevity for females and higher fecundity. Our field data corroborates our laboratory findings. When dissecting the flowers that had visible signs of *M. vitrata* damage, it was observed that the larvae fed preferentially on the reproductive organs. Similar observations were reported by Taylor (1978). It is not known why *M. larvae* have this preference, however, the reproductive parts of the flowers may contain nutrients, water levels, or plant secondary compounds, or a combination thereof, that are beneficial to the *M. vitrata* larvae.

However, feeding preference of *M. vitrata* larvae in the field may also be related to a camouflage defence strategy of the *M. vitrata* larvae. The larvae are thought to use several strategies to defend themselves against predators. This microhabitat feeding preference has been reported as an insect anti-predation strategy (Wellbornet and Robinson, 1987; Pierce, 1988; Lima and Dill, 1990). Thus, *M. vitrata* larvae may use the corolla as a shelter in an attempt to reduce predation. Within the flower, the pistils and stamen may offer a better shelter, to avoid predation, than the other parts of the flower. In fact when feeding on this inner flower component, the *M. vitrata* larvae are thereby covered by a series of three protective envelopes: the keel, the wing and the standard. The larvae are thus relatively shielded, securely embedded inside the flower.

In the field, we also noticed that the *M. vitrata* larvae consumed green non-open cowpea flowers either perforated or non-perforated. Oviposition behaviour studies indicated that *M. vitrata* females deposited eggs on flower buds, vegetative buds, flowers and sometimes on leaf axils (Taylor, 1967, 1978). Thus, the presence of larvae within flowers;

with no visible entry orifice indicate that the female may directly deposit eggs within the flower or flower buds. First instars larvae were observed within cowpea flowers with sometimes more than one larva per flower. Since first instars larvae are not highly mobile, they do not typically move from the flower where oviposition has occurred to new flowers. The presence of more than one larvae within a flower indicated that the females might have deposited more than one egg in a flower bud or more than one female deposited an egg on that flower. This is in accordance with previous studies, which indicated that eggs are deposited singly or in batches of 2-6 (Taylor, 1967, 1978). The young larvae were most often associated with young flowers as well as on young pods in keeping with previous observations (Singh and Jackai, 1988; Atachi and Gnanvossou, 1989).

Conclusion

Our findings indicate that *M. vitrata* larvae feed on all type of flowers regardless of their age and on all the components of the cowpea flower with a preference for the reproductive organs of the flowers. Thus, for *Bt*-engineered cowpea discovery and development of promoters, which would optimize expression of *Bt* across all of these flower issues, without having negative impacts on production, would be highly desirable.

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Table 1a: *Maruca vitrata* larval infestation (Mean ± SE) in green non-open cowpea flowers

Type of flower	Percentage of flowers infested with at least one larvae	Percentage of flowers with more than one larvae
Perforated flowers	91.59±1.92 A	16.79±1.35 B
Non perforated flowers	48.98±1.93 B	35.03±1.96 A
	(F = 243.49; P<0.0001)	(F = 58.07; P<0.0001)

Means followed by the same letters within columns were not significantly different by the Student Newman-Keuls test at the 5% level.

Table 1b: *Maruca vitrata* larval infestation ((Mean ± SE) in cowpea pods

Type of pods	Percentage of pods infested with at least one larvae
Young pods without seeds	26.29 ± 1.1 B
Pods in filling stage	50.71 ± 2.4 A
Mature pods	23.00 ± 1.82 B
	(F=55; P<0.0001)

Means followed by the same letters within columns are not significantly different by the Student Newman-Keuls test at the 5% level.

Table 2: Flowers components (Means ± SE) damaged by *Maruca vitrata* larvae

Floral parts	Percentage of flowers damaged by first instar larvae	Percentage of flowers damaged by older instar larvae
Calyx	0	1.6 ± 0.19 E
Corolla	0	28.37 ± 1.52 D
Standard	0	28.37 ± 1.52 D
Wings	11.58 ±0.42 C	46.5 ± 1.09 C
Keels	37.03 ± 0.55 B	65.4 ± 1.33 B
Reproductive organs	51.38 ± 0.6 A	76.1 ± 1.24 A
	(F = 1260.39; P<0.0001)	(F = 486.62; P<0.0001)

Means followed by the same letters within columns are not significantly different by the Student Newman-Keuls test at the 5% level.

Table 3: *Maruca vitrata* larval development time (Means ± SE) on different medium

Floral parts	Developmental time (days)			
	Larval stage	Pre-pupal stage	Pupal stage	Total post embryonic duration
Calyx	8.60 ± 0.03 B	2.00 ± 0.00 A	7.18 ± 0.02 A	17.78 ± 0.04 A
Corolla	8.24 ± 0.04 C	1.58 ± 0.03 D	7.18 ± 0.02 A	17.00 ± 0.06 B
Standard	8.66 ± 0.02 B	2.00 ± 0.00 A	7.00 ± 0.00 C	17.66 ± 0.02 A
Wings	8.77 ± 0.03 A	1.89 ± 0.01 B	7.11 ± 0.02 B	17.77 ± 0.03 A
Keels	7.98 ± 0.04 D	1.73 ± 0.02 C	7.25 ± 0.02 A	16.96 ± 0.07 B
Reproductive organs	6.82 ± 0.03 E	1.11 ± 0.02 E	7.23 ± 0.02 A	15.17 ± 0.06 C
	(F = 443.10; P<0.0001)	(F = 356.12; P<0.0001)	(F = 22.42; P<0.0001)	(F= 314.44; P<0.0001)

Means followed by the same letters within columns are not significantly different by the Student Newman-Keuls test at the 5% level.

Table 4: Size and weight of *Maruca vitrata* pupae (Means ± SE), and emergence rate of adults (Means ± SE), depending on the medium the larvae developed upon

Floral parts	Pupa size (mm)	50 pupa weight (mg)	Emergence rate (%)
Calyx	9.04 ± 0.05 E	15.33 ± 0.21 C	92.47 ± 0.55 A
Corolla	11.34 ± 0.08 B	22.0 ± 0.51 B	94.48 ± 1.85 A
Standard	10.56 ± 0.07 D	21.00 ±0.44 B	93.28 ± 2.50 A
Wings	10.96 ± 0.08 C	21.67 ± 0.33 B	92.84 ± 1.18 A
Keels	11.20 ± 0.07 B	22.33 ± 0.61 B	96.15 ± 0.55 A
Reproductive organs	11.86 ± 0.08 A	25.83 ± 0.16 A	95.93 ± 0.74 A
	(F = 180.49; P<0.0001)	(F = 67.62; P<0.0001)	(F = 1.22; P=0.34)

Means followed by the same letters within columns are not significantly different by the Student Newman-Keuls test at the 5% level.

Table 5. Fecundity of *Maruca vitrata* females, fertility of eggs, and longevity of *M. vitrata* adults reared (Means ± SE), at the larval stage, on different parts of the cowpea flowers

Floral parts	Total eggs laid	% Eggs hatching	Total life spans (days)	
			Male	Female
Calyx	421.88 ± 12.31 C	82.00 ± 0.97 A	14.50 ± 0.40 A	16.50 ± 0.23 B
Corolla	650.64 ± 17.75 B	81.00 ± 2.01 A	13.28 ± 0.40 A	16.68 ± 0.24 B
Standard	605.16 ± 18.42 B	80.91 ± 1.36 A	13.20 ± 0.42 A	16.92 ± 0.24 B
Wings	634.60 ± 18.66 B	83.01 ± 1.61 A	15.08 ± 0.42 A	18.12 ± 0.25 A
Keels	655.92 ± 22.38 B	81.61 ± 1.17 A	12.94 ± 0.41 A	16.72 ± 0.27 B
Reproductive organs	734.42 ± 23.03 A	82.32 ± 0.25 A	13.28 ± 0.47 A	17.42 ± 0.27 AB
	(F = 30.09; P<0.0001)	(F = 0.36; P = 0.87)	(F = 0.06; P = 0.99)	(F = 5.73; P<0.0001)

Means followed by the same letters within columns are not significantly different by the Student Newman-Keuls test at the 5% level.