Effect of learning on the oviposition preference of field-collected and laboratory-reared *Chilo partellus* (Lepidoptera: Crambidae) populations

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Abstract

Recent studies show that Vetiver grass, (*Vetiveria zizanioides* (L.) Nash), may have potential as a dead-end trap crop in an overall habitat management strategy for the spotted stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae). Vetiver grass is highly preferred for oviposition, in spite of the fact that larval survival is extremely low on this grass. The oviposition behaviour of female *Chilo partellus* moths was investigated by determining the amount and size of egg batches allocated to maize and Vetiver plants and studying the effect of rearing conditions and oviposition experience on host plant selection. Two-choice preference tests were used to examine the effect of experience of maize (a suitable host plant) and Vetiver plants on the oviposition choice of *C. partellus*. For both field-collected and laboratory-reared moths, no significant differences were found in the preference distributions between the experienced groups. It is concluded that females do not learn, i.e. that they do not change their preference for Vetiver grass after having experienced oviposition on either maize or this grass, which supports the idea that trap cropping could have potential as a control method for *C. partellus*. Differences observed between field-collected and laboratory-reared moths in the amount and size of egg batches laid on maize and Vetiver grass indicate that data obtained from experiments with laboratory-reared insects should be treated with caution.

Keywords: *Chilo partellus*, oviposition, Vetiver grass, trap crop, learning, Africa

Introduction

The stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae), is an economically important pest of maize (*Zea mays* L.) (Poaceae), and other cereal crops in eastern and southern Africa (Overholt, 1998; Kfir *et al.*, 2002). The species

is indigenous to Asia and invaded Africa sometime before 1930 (Tams, 1932). Like most cereal stem borers, *C. partellus* is polyphagous; and it has a wide variety of host plants, both cultivated and wild (Ingram, 1958; Seshu Reddy, 1983; Harris, 1990; Khan *et al.*, 1997; Polaszek & Khan, 1998; Van den Berg *et al.*, 2001; Rebe *et al.*, 2004).

In recent years, there has been an increased interest in the application of trap cropping in pest management (Hokkanen, 1991; Shelton & Badenes-Perez, 2006). In East Africa, trap cropping with a number of wild host plants,

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including Napier grass, (*Pennisetum purpureum* Schumach.), is applied in the management of *Chilo partellus* (Khan *et al.*, 2001, 2006).

Results from laboratory and greenhouse studies show that Vetiver grass, (*Vetiveria zizanioides* (L.) Nash) (Poaceae), is highly preferred for oviposition by *C. partellus*, but that larval survival is extremely low on this grass (Van den Berg *et al.*, 2003). Vetiver grass has, therefore, been indicated as a potential dead-end trap plant in an overall habitat management strategy for *C. partellus* (Van den Berg *et al.*, 2003; Van den Berg, 2006a). The term dead-end trap crop is used to describe plants, like Vetiver grass, that are highly attractive to insects but on which their offspring cannot survive (Shelton & Badenes-Perez, 2006).

For the development of a sound application of trap cropping as a pest management strategy, it is important to understand the factors influencing the oviposition behaviour of *C. partellus*. In spite of its economic importance, the host selection behaviour of the herbivorous insect is still poorly understood.

It has been demonstrated in a number of insect species that egg-laying females may gain experience when they oviposit on a specific substrate for the first time (Papaj & Lewis, 1993). This experience can influence subsequent choices of oviposition substrates, a phenomenon called learning (Papaj & Prokopy, 1989; Schoonhoven *et al.*, 1998). In Lepidoptera, learning in host selection for oviposition has been clearly demonstrated in experiments on several butterflies, with ovipositing females preferring host plants of which they have experience (Papaj & Prokopy, 1989). However, only relatively recently the existence of learning has been studied in adult moths (e.g. Firempong & Zalucki, 1991; Cunningham *et al.*, 1998). Experimental evidence has shown that learning occurs in the host selection and oviposition behaviour of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) (Cunningham *et al.*, 1998). In a recent study, it was shown for the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), that an oviposition experience on a non-host plant can alter the oviposition behaviour of this moth to accept the non-host plant for oviposition (Zhang & Liu, 2006).

The objective of this study was to investigate the factors influencing the oviposition behaviour of *C. partellus* female moths. The role of oviposition experience and rearing history was investigated. Knowledge of these two factors influencing the oviposition behaviour of *C. partellus* could be essential in the application and design of pest management strategies to control this pest through trap cropping.

Materials and methods

Two identical experiments were conducted, one using field-collected moths and one using laboratory-reared moths. All experiments were conducted in the summer of 2005/2006 at the North-West University in Potchefstroom, South Africa.

Field collection of C. partellus

Sorghum stems were collected during the winter months from a monocrop block of sorghum (approx. 1 ha), consisting of different sorghum varieties planted for research purposes. The stems were brought under a metal framework that was covered with a net. During the spring, *C. partellus* moths

emerged late afternoon from pupae inside the stalks, and individuals were caught in small tubes in the early evening. This was done every night during the time that the experiments were running. A flashlight was used to locate the moths in the dark on the net. Females that were caught were assumed to have mated, as it was found in a study by Päts (1990) that 97% of *C. partellus* females mated shortly after they emerged during the last five hours of the scotophase on the night of eclosion. For this study, moths were caught at 7 pm in the evening, which implies that moths present at this time should have emerged and mated the previous night.

Laboratory-reared C. partellus

Laboratory colonies of *C. partellus* had been reared for 30 years (about 360 generations) before being used for this study and had been maintained on an artificial diet, according to protocol described by Kfir (1992) at the Agricultural Research Council – Plant Protection Research Institute (ARC-PPRI) in Pretoria.

Production of potted maize and Vetiver grass

Maize plants (cv. Pan 6804) were grown outside in 2-l pots during summer (October–February). Plants were thinned to one plant per pot and used in the experiments when they were about 4 weeks old (with 5–9 leaves). Maize plants of this age are expected to attract maximum oviposition (Singh & Sandhu, 1978). The potted Vetiver grass patches, raised from stem cuttings, were 3–6 months old and full-grown when used in the experiments. Dead Vetiver grass leaves were removed before using plants in the experiments.

No-choice experiment

A no-choice experiment was conducted to provide moths with an oviposition experience. Experienced moths were defined as females that had laid at least one egg batch on maize or Vetiver grass in the no-choice experiment. Naïve moths were defined as moths without an oviposition experience. Moths tested in the no-choice experiment were mated and 1 day old.

The experiment was conducted in muslin cloth cages measuring $0.50 \times 0.55 \times 0.75$ m. Cages were placed in a greenhouse under natural light conditions, in which the temperature varied between 18–26°C. Pots containing maize or Vetiver grass plants were placed singly in the centre of each cage. Individual females were released into the centre of each cage and moths were allowed to oviposit overnight. The plants were removed from the cages and their leaves were carefully inspected for egg batches. The numbers of egg batches were recorded only in the experiment with the laboratory-reared moths. Moths that had laid eggs (and thus had an oviposition experience) were caught and put in small tubes for use in the subsequent two-choice experiment.

No-choice experiments with maize and Vetiver plants were always done on the same day to avoid day-specific effects. In each of the three no-choice experiments, approximately 50 female moths were evaluated and the cages containing the pots were completely randomized. Moths that did not oviposit in the no-choice experiment were excluded from the rest of the experiment.

Table 1. Average number of egg batches ($\pm$SE) and total number of eggs ($\pm$SE) laid on maize and Vetiver grass in the no-choice experiment by naïve laboratory-reared *C. partellus* female moths.

	Maize ($n = 14$ moths)	Vetiver grass ($n = 17$ moths)	t-value	Significance (p-value)
Number of egg batches	1.3 (0.1)	3.5 (0.6)	-3.709	0.002
Number of eggs/batch	39.6 (6.7)	38.2 (4.1)	0.188	0.852
Total number of eggs/plant	47.6 (6.6)	132.8 (23.3)	-3.512	0.002

Table 2. Average number of egg batches ($\pm$SE) laid on maize (M) and Vetiver grass (VG) by (a) field-collected and (b) laboratory-reared *C. partellus* female moths in the two-choice experiment.

(a)

Experience tests	# replications	Egg batches laid on M	Egg batches laid on VG
Naïve	$n = 12$	1.0 (0.4)	2.9 (0.7)
Experienced on M	$n = 13$	1.3 (0.6)	2.1 (0.4)
Experienced on VG	$n = 14$	0.0 (0.0)	0.4 (0.3)

(b)

Experience tests	# replications	Egg batches laid on M	Egg batches laid on VG
Naïve	$n = 16$	0.4 (0.3)	3.6 (0.9)
Experienced on M	$n = 13$	0.8 (0.3)	4.2 (0.9)
Experienced on VG	$n = 13$	0.8 (0.3)	5.0 (1.1)

Two-choice experiment

A two-choice experiment was conducted to determine the oviposition preference of moths when presented with a choice between maize and Vetiver grass. For each insect population three different tests were performed: (i) with naïve female; (ii) with experienced female on maize; and (iii) with experienced female on Vetiver grass.

The experiment was conducted under similar conditions as the no-choice experiment and using the same type of cages. Two pots were placed in diagonally opposite corners inside each cage. One pot contained a maize plant while the other contained a Vetiver grass plant. Each two-choice experiment was replicated 12–15 times. Females were allowed to oviposit within a 3-day period before they were removed. After the test, plants were removed from the cages and the number of egg batches was counted on each plant. Egg batches were removed and eggs were counted using a light microscope after a few days when they turned brown and could easily be distinguished from each other. For each replication, pots were shifted to avoid positional bias by the moths. Cages containing differently experienced moths were completely randomized.

Statistical analyses

A replicated goodness-of-fit *G*-test was used to compare the numbers of egg batches deposited on each pair of plants in each of the three experience tests with the null hypothesis of no preference. A *G*-test of an R × C table of independence was used to compare the overall relative proportions of egg batches laid on maize and Vetiver grass between the different experience tests. Data from the no-choice test on mean number of egg batches and mean number of eggs per plant were analyzed by means of *t*-tests. *T*-tests were also used to compare total number of egg batches and eggs between field-collected and laboratory-reared moths.

Results

The females were very unwilling to oviposit on the plants. Therefore, the number of nights that moths were exposed to plants in the two-choice experiment was increased from one to three during the experiment to give females more time for oviposition. However, this did not result in an increase in the number of females that actually laid eggs nor had this a significant effect on the total number of egg batches laid by moths during the two-choice experiment ($t = -0.7059$, $P = 0.48$).

No-choice experiment

Unfortunately, the number of egg batches and eggs per plant laid by field-collected moths in the no-choice experiment were not recorded.

The laboratory-reared females laid on average significantly more egg batches on Vetiver grass than on maize (table 1). The size of the egg batches did not differ significantly between maize and Vetiver grass. Therefore, the average number of eggs was significantly higher on Vetiver grass than on maize plants (table 1).

Oviposition preference of field-collected and laboratory-reared *C. partellus* populations in the two-choice experiment

Naïve field-collected females laid significantly more egg batches on Vetiver grass than on maize plants ($G_P = 11.8$, $P < 0.001$; table 2a) (G_P measures the difference between treatments when all replicates are pooled). Variation between replicates was large but not significant. Field-collected females with an oviposition experience on maize preferred to lay eggs on Vetiver grass in the choice experiment but the difference was not significant and there was significant variation between replicates ($G_H = 29.3$, $P < 0.01$) (G_H measures heterogeneity between replicates). Field-collected females with an oviposition experience on

Table 3. Average number of egg batches (±SE) and total number of eggs (±SE) laid by field-collected and laboratory-reared *C. partellus* females on both maize and Vetiver plants in the two-choice experiment.

	Field collected moths ($n=39$)	Laboratory-reared moths ($n=42$)	*t*-value	Significance (*p*-value)
Number of egg batches	5.3 (0.3)	7.9 (0.3)	6.980	0.000
Number of eggs/batch	25.4 (1.6)	21.7 (1.0)	2.042	0.042
Number of eggs/plant	88.8 (7.3)	171.7 (6.2)	8.695	0.000

Vetiver grass laid very few egg batches and only on Vetiver grass ($G_P = 6.9$, $P < 0.01$).

Naïve laboratory-reared females laid significantly more egg batches on Vetiver grass than on maize plants ($G_P = 47.7$, $P < 0.001$; table 2b). Laboratory-reared females, which were experienced on maize or Vetiver grass, also showed a significant preference for Vetiver grass ($G_P = 33.2$, $P < 0.001$ and $G_P = 45.1$, $P < 0.001$, respectively). Variation between replicates was not significant for laboratory-reared females in each of the three experience tests.

Overall, there was no significant difference in choice distribution for maize or Vetiver grass plants between field-collected females with different oviposition experiences ($G = 5.517$, df = 2, $P = 0.063$). In the experiment with the laboratory-reared moths, an oviposition experience with maize or Vetiver grass did not induce a significant preference shift either ($G = 1.107$, df = 2, $P = 0.575$).

In the two-choice experiment, egg batches laid by field-collected moths (on both type of plants) were on average significantly larger compared to egg batches laid by laboratory-reared moths ($P < 0.05$; table 3). The average number of egg batches laid by laboratory-reared moths was, however, significantly higher than for field-collected moths and, therefore, the total number of eggs laid by laboratory-reared moths was also significantly higher compared to field-collected moths (table 3). On maize plants, field-collected and laboratory-reared moths laid approximately the same number of egg batches and eggs. Significantly more egg batches ($t = 3.876$, $P = 0.000$) and more eggs per plant ($t = -3.227$, $P = 0.002$) were laid on Vetiver grass by laboratory-reared moths than by field-collected moths.

Discussion

Vetiver grass is highly preferred for oviposition by *C. partellus*, despite the fact that this plant is a poor host for its offspring. Host plant volatiles are often an important search cue for host-seeking herbivorous females. Host plants of *C. partellus* produce green leaf volatiles, which are used in host location (Khan *et al.*, 2000). It has recently been suggested that the 'differential attraction/oviposition' between cultivated and wild hosts may be associated with differences in production of green leaf volatiles between cultivated and wild hosts (Birkett *et al.*, 2006). Future studies should focus on the volatile profiles of Vetiver grass and maize to provide insight into the differential oviposition between maize and Vetiver grass. Limited information is available on Vetiver grass volatiles, e.g. it has been reported that they contain many terpenoids (Huang *et al.*, 2004).

Plant morphology is also an important factor in host plant selection and recognition (Ampofo, 1985; Khan *et al.*, 2006; Van den Berg, 2006b). For moths in general, plant surface texture is crucial in the evaluation of potential oviposition sites (Ramaswamy, 1988). Unlike other moth species, *C. partellus* prefers smooth surfaces for oviposition (Ampofo, 1985; Kumar & Saxena, 1985). The smooth surface of Vetiver leaves may be a factor that can explain the high preference of moths for Vetiver grass. Mabuda (2001) determined the number of trichomes cm^{-2} for Vetiver leaves, which was 20 and 90 for the adaxial and abaxial sides, respectively, while for maize leaves it was 120 trichomes cm^{-2} and 600 trichomes cm^{-2} on the adaxial and abaxial sides, respectively. It has been suggested that *C. partellus* selects oviposition sites for egg survival rather than for a suitable host for the larvae as larvae are able to disperse (Roome *et al.*, 1977). Further studies are required to determine whether chances for egg survival are higher on Vetiver grass than on maize.

A second hypothesis to explain the strong preference of *C. partellus* for Vetiver grass is the possible existence of an old association between this insect and Vetiver grass as they both originated in Asia. Vetiver grass seldom flowers outside tropical areas, but produces flowering stems in its area of origin, in which *Chilo* sp. are able to survive once they enter these stems, although at very low levels (Van den Berg, 2006a). Since it is known that the preference-performance relationship can vary under different ecological conditions and is influenced by geographic variation in host use (Thompson, 1988), the behaviour of *C. partellus* in this study may be explained by this effect of geography on the growth of the host plant.

Further studies are required to investigate whether natural enemies of *C. partellus* are attracted to Vetiver grass in order to test the 'enemy-free space hypothesis', which suggests that host preference is influenced by the occurrence of natural enemies on the host plant (Thompson, 1988).

In this study, the ovipositional response of *C. partellus* moths to maize and Vetiver plants was determined. Even with an oviposition experience on maize and in the presence of this suitable host plant, females still preferred to lay their eggs on Vetiver grass. This finding may have important implications for the efficacy of Vetiver grass as a trap crop. Currently, field studies are being conducted in Malawi, where the Vetiver grass technology is already widely applied for soil and water conservation by small-scale farmers (Carr, 2000), to investigate the effectiveness of Vetiver grass as a trap plant for *C. partellus*. Such studies are required to point out whether female moths show the same attractiveness to Vetiver in the field as observed in this laboratory study. Absence of learning in *C. partellus* moths would mean that the most abundant host in the field (e.g. the major crop) does not necessarily have to become the most preferred crop, as in the case of *H. armigera*, where learning is hypothesized to result in higher oviposition percentages on host species that are locally most abundant (Cunningham

et al., 1999; Jallow *et al.*, 2004). The absence of learning in *C. partellus*, thus, gives opportunities to control this pest through trap cropping.

Results from a simulation study by Potting *et al.* (2005) indicate that diversification strategies like trap cropping have the potential to control insect species, such as moths, because they are generally highly mobile insects having the ability of directed flights and good sensory abilities that enable orientated movements. Plants with a strong behaviour-altering effect (like Vetiver grass), which are employed in an optimal spatial arrangement, can result in good control effects for these type of herbivores (Potting *et al.*, 2005).

Conclusion

The results of this study show that the preference of *C. partellus* females for Vetiver grass does not change after having experienced oviposition on either maize or on this grass. The absence of learning in *C. partellus* means that trap cropping could have potential as a control method for this insect pest. Further long-term studies are required to evaluate the effect of Vetiver grass as a trap plant for *C. partellus* under field conditions. The observed differences between field-collected and laboratory-reared moths indicate the need to test field-collected specimens in laboratory studies.

Acknowledgements

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