

# Host plant selection behaviour of *Chilo partellus* and its implication for effectiveness of a trap crop

Charles A. O. Midega<sup>1\*</sup>, Zeyaur R. Khan<sup>1</sup>, John A. Pickett<sup>2</sup> & Sören Nylin<sup>3</sup>

<sup>1</sup>International Centre of Insect Physiology and Ecology (icipe), P.O. Box 30772, Nairobi, Kenya, <sup>2</sup>Biological Chemistry Division, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK, and <sup>3</sup>Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden

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## Abstract

Female lepidopterans can display a hierarchy of preference among potential host species, a trait thought to arise from the balance between attractants and deterrents to which the insects respond. Host plant ranking by moths and larvae of *Chilo partellus* Swinhoe (Lepidoptera: Crambidae), an important pest of cereals in Africa, was investigated, and whether eggs deposited on specific host plants yield larvae of particular host preferences. Trap plants are used in management of this pest. However, any 'disagreement' in host ranking between moths and larvae could potentially reduce effectiveness of trap crops as larvae emigrate to the main crop from the parent's preferred trap plant. We also investigated whether host plant preference is influenced by the diet upon which larvae fed as part of an integrated assessment of the relationship between host plant selection and learning in *C. partellus*. Five host plants (all Poaceae) were used: maize (*Zea mays* L.), sorghum (*Sorghum bicolor* Moench), Napier grass (*Pennisetum purpureum* Schumacher), and two varieties of signal grass [*Bracharia brizantha* (A. Rich.) Stapf], viz., local (henceforth signal grass) and improved ('Mulato'). In multiple choice tests, *C. partellus* female moths preferentially oviposited on Napier grass, followed by sorghum, maize, and signal grass, and least preferred 'Mulato'. Larvae however equally orientated and settled on leaf cuts of maize, sorghum, signal grass, and Napier grass, but least preferred 'Mulato'. Moreover, eggs from specific host plants did not yield larvae of particular host preferences. Furthermore, oviposition preference was not altered by the larval food. These results imply only a slight 'disagreement' in host ranking behaviour between moths and larvae, which is beneficial for trap cropping as larvae would not 'reject' the trap plant and appreciably disperse to the neighboring plants. Moreover, absence of larval learning behaviour indicates that regardless of the larval food *C. partellus* moths would still be attracted to the selected trap plant.

## Introduction

In Lepidoptera, host plant selection is generally made by the ovipositing female (Singer, 1984), and may be influenced by a number of evolutionary factors (see review by West & Cunningham, 2002). In the process of host selection among generalists, adult females often exhibit a hierarchy of preference among hosts (Nylin & Janz, 1993), but whether this is correlated with the performance of their offspring is controversial (Thompson, 1988). In cases where there exists a strong positive correlation between preference and larval performance, it is implied that the

females base their choice of host plants on the intrinsic properties of plants that can influence such performance differences (plant chemistry or morphology) (Nylin & Janz, 1996). In contrast, however, it has been shown that females prefer hosts upon which their immature stages do not appreciably survive, for example in the polyphagous spotted stem borer, *Chilo partellus* Swinhoe (Lepidoptera: Crambidae). This is a serious pest of cereal crops in Eastern and Southern Africa, whose larvae damage plants by feeding on the leaves and eventually boring into the stem thereby weakening the plant which then falls off. Larvae also feed on the growing tips of the plant which causes 'dead-heart' and eventual death of the plant (Kfir et al., 2002). The female *C. partellus* moth prefers Napier grass (*Pennisetum purpureum* Schumacher) to maize (*Zea mays*

\*Correspondence: Charles A. O. Midega, icipe, P.O. Box 30772-00100 Nairobi, Kenya. E-mail: cmidega@mbita.mimcom.net

L.) (both Poaceae) for oviposition, with subsequent poor survival of the larvae (van den Berg, 2006; Khan et al., 2006a). This observation has been exploited in the development of an effective 'push-pull' management approach for the pest where maize is intercropped with a repellent or push plant [such as *Desmodium* spp. (Fabaceae)], with the attractant or pull plant, Napier grass, planted as a perimeter crop around this intercrop (Cook et al., 2007; Hassanal et al., 2008; Khan et al., 2008).

Experience of host plants can modify insect feeding (Wiklund, 1973; Karowe, 1989) and oviposition preferences (Prokopy et al., 1986; Jaenike, 1988; Vet et al., 1995; Bjorksten & Hoffmann, 1998; Cunningham et al., 1998; Zhang et al., 2007). One of the most controversial theories seeking to explain host plant selection among phytophagous insect adults is the 'Hopkins' host plant selection principle'. According to this principle, a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted (Hopkins, 1917; Barron, 2001). It postulates that an insect would show preference for the host species upon which its immature stages developed, implying that larval experience can influence adult host preference (Craighead, 1921; Huettel & Bush, 1972).

Although it is the adult insects that primarily select host plants, studies have shown that in some species neonate larvae emerging from the eggs exhibit a strong tendency to disperse and move out to other plants even when there is an adequate food supply on the plants chosen by their mothers (Saxena & Rembold, 1984). These larvae may use both visual and chemical cues in orientation (Knight & Light, 2001; Singh & Mullick, 2002; Castrejon et al., 2006). In addition, contact chemical and tactile cues may affect the larval behaviour once insects have arrived on the plants (Eigenbrode et al., 1991; Harris et al., 1999). If the insects do not prefer the plant surface, they may show non-acceptance behaviour and move away from that surface (Stoner, 1990; Eigenbrode et al., 1991).

We investigated host plant ranking by both *C. partellus* adults and offspring, and whether eggs deposited on specific host plants yield larvae of particular host preferences. This is important as it could influence the effectiveness of a trap crop with regards to larvae emigrating to the main crop from the parent's preferred host (trap plant) in case of a 'disagreement'. Similarly, moths that invade the target crop originate from the wild (Khan et al., 1997), but a number of the colonizers also come from the crop residues in both the surrounding fields and within the very fields. It is hypothesized that if larval experience determines host plant preference by moths then *C. partellus* moths originating from crop residues (maize or sorghum, *Sorghum bicolor* L.) inside the fields would less likely be attracted to

the trap crop, planted either within-field or as a perimeter crop. This would thus render the trap cropping ineffective, as these moths would lead to population build-up within the target crop. Therefore, we sought also to establish whether host plant preference is influenced by the diet upon which larvae fed as part of an integrated assessment of the relationship between host plant selection and learning, and how it might affect trap cropping as a management approach for *C. partellus* in smallholder cereal farming systems in Eastern and Southern Africa.

## Materials and methods

### Plants and insects

Napier grass, variety Bana, a hybrid of *P. purpureum* and *P. americanum* commonly used in western Kenya as fodder, was taken from a stock of plants supplied by the Kenya Agricultural Research Institute as described by Khan et al. (2006a). Maize (Hybrid 505), sorghum (Gadam Hamam), and two varieties of signal grass, *Brachiaria brizantha* (A. Rich.) Stapf, viz. local (henceforth called signal grass) and improved (var. Mulato) (henceforth called 'Mulato'), were also included. Signal grass was raised from wild plants collected from the International Centre of Insect Physiology and Ecology (*icipe*), Thomas Odhiambo Campus (ITOC) fields, Mbita Point (0°25'S, 34°12'E; approximately 1 200 m a.s.l.) in western Kenya, whereas 'Mulato' was obtained from the International Centre for Tropical Agriculture (CIAT), Colombia. Signal grass and Napier grass were grown from root splits in 5-l plastic pots, whereas maize, sorghum, and 'Mulato' seeds were sown in similar pots filled with soil, with no fertilizer added, in a screen house (natural light conditions, approximately L12:D12 h) at ITOC. The maize and sorghum varieties used are susceptible to *C. partellus* attack (Khan et al., 2006b,c). Plants were 3–4 weeks old at the time of experiments. Original populations of *C. partellus* moths were reared from larvae collected from the wild, principally sorghum fields because *C. partellus* is often found more on sorghum fields, and reared on an artificial diet, as described by Onyango & Ochieng-Odero (1994), for one generation.

### Host plant ranking behaviour of the parents

Oviposition tests were conducted with *C. partellus* moths that had been reared on artificial diet for one generation to determine the host ranking. Methodologies adapted from Khan et al. (2006a, 2007) were employed in these studies. Multiple-choice tests were carried out in cylindrical oviposition cages (1 m high × 1 m diameter), and covered by fine wire mesh netting. Five potted plants representing each plant species, 3–4 weeks old, were placed in each cage.

A 10-cm-diameter wad of cotton wool moistened with water was introduced into the cage for the moths to feed on. The five pots placed in a radius around the middle of the cage, with the leaves intermingled to allow the moths to choose any leaf from any plant for oviposition, regardless of the positioning of the plant stem (Khan et al., 2006a). Twenty replications were conducted with five mated female and five male *C. partellus* moths introduced into each oviposition cage and allowed to oviposit overnight. The plants were then removed and the egg batches and eggs in each batch on each plant were counted.

#### Offspring choice tests

**Larval orientation and settlement.** Two sets of studies were conducted to determine orientation and settlement of *C. partellus* larvae on leaf cuts of different plant species. First, leaf cuts (10 × 4 cm) from the five plant species were put equidistantly in a 15-cm-diameter Petri dish and 10 neonate larvae (all from eggs oviposited on each of the plant species) were released from the centre of the Petri dish. This arrangement was kept in a dark room and observed after 1 h to establish orientation and after 24 h for settlement. The larvae on each leaf cut were counted during each observation. This was replicated 20 times for each larval group. In this experiment, we tested the possibility that eggs could be conditioned by the plant or be genetically determined to give rise to larvae with a particular preference (Nylin & Janz, 1996). Secondly, neonate larvae from egg batches oviposited on paper by moths from the rearing unit of *icipé* (not previously exposed to the plants) were given a choice of the host plants and observations made as above.

**Larval feeding preference.** This was conducted in no-choice and multiple-choice situations. First, a piece of leaf (ca. 5 × 5 cm) from each of the plants was placed in a Petri dish as above. Ten neonate larvae were then introduced into the dish and the arrangement was kept in the dark for 24 h. Because there were no differences in host plant preference behaviour between larvae originating from different host plants and those originating from the insectary, we used larvae from the rearing facility. The leaf area consumed by the larvae was then measured. This was replicated 20 times. For the multiple-choice tests, similar leaf cuts of all the test plants were placed equidistantly in a Petri dish and 20 neonate larvae were released in the middle of the Petri dish. This was conducted in 20 replications. Traces of larval feeding were observed and area (%) of the leaf cut eaten after 24 h was calculated. The leaf cuts with the largest and smallest area eaten represented the most and least preferred plants for larval feeding, respectively.

**Larval experience studies.** To establish whether the larval experience hypothesis, that adults will prefer host plants from which their larvae had been reared, was true, we set up a multiple choice oviposition test as above. First, *C. partellus* eggs, oviposited on paper, were obtained from the laboratory colony as above and allowed to hatch, and soon thereafter the neonate larvae were provided with soft tissues from a particular host plant, either maize or sorghum. They were then reared on the same host plant until pupation. Two sets of emerged adults (from maize and sorghum) were used in multiple choice oviposition preference tests as above with 20 replications for each set.

Data were averaged for each test and subjected to one-way analysis of variance (ANOVA) using the generalized linear model procedure in SAS (SAS Institute, 2002) and means separated using Tukey's studentized range test. Mean proportion of larval orientation and settlement were arcsine transformed before analysis. Non-transformed means are presented in tables.

## Results

#### Host plant ranking by *Chilo partellus* moths

There were significant differences in the number of egg batches and eggs oviposited by *C. partellus* female moths on the test plants ( $F_{4,45} = 16.5$  and  $34.4$ , respectively; both  $P < 0.0001$ ) (Table 1). Average number of eggs per batch was however significantly lower in 'Mulato' than in the other plants ( $F_{4,45} = 10.1$ ,  $P < 0.0001$ ). In order of preference, Napier grass was the most preferred by the moths for oviposition, sorghum, maize, and signal grass were equally preferred, whereas 'Mulato' was the least preferred (Table 1).

#### Offspring choice tests

**Larval orientation and settlement.** Mean percentage orientation rates of larvae from the insectary colony (those oviposited on paper) were similar between maize,

**Table 1** Mean ( $\pm$  SE) number of egg batches, eggs, and eggs per batch oviposited by insectary-reared *Chilo partellus* moths on host plants under multiple-choice tests

Plant	No. egg batches	No. eggs	No. eggs/batch
Maize	3.7 $\pm$ 0.5b	91.1 $\pm$ 8.1b	27.3 $\pm$ 3.3a
Sorghum	3.8 $\pm$ 0.4b	96.2 $\pm$ 6.0b	27.5 $\pm$ 3.1a
Napier grass	5.7 $\pm$ 0.5a	158.6 $\pm$ 11.7a	29.0 $\pm$ 2.5a
Signal grass	3.4 $\pm$ 0.5b	86.7 $\pm$ 12.4b	25.7 $\pm$ 2.4a
Mulato	0.8 $\pm$ 0.2c	10.2 $\pm$ 3.5c	7.9 $\pm$ 2.5b
$F_{4,45}$	16.5 ( $P < 0.0001$ )	34.4 ( $P < 0.0001$ )	10.1 ( $P < 0.0001$ )

Within a column, the means marked by different letters are significantly different by Tukey's studentized range test ( $P < 0.05$ ).

**Table 2** Mean ( $\pm$  SE) percentage orientation and settling of first instars of insectary-reared *Chilo partellus* on leaf cuts of test plants after 1 and 24 h, respectively

Plant	% orientation	% settling
Maize	21.0 $\pm$ 2.0a	20.5 $\pm$ 2.0a
Sorghum	23.5 $\pm$ 1.8a	20.0 $\pm$ 1.8a
Napier grass	18.5 $\pm$ 2.2a	18.0 $\pm$ 2.0a
Signal grass	22.5 $\pm$ 1.4a	19.0 $\pm$ 1.8a
Mulato	10.0 $\pm$ 1.8b	8.0 $\pm$ 1.4b
F <sub>4,95</sub>	8.4 (P<0.0001)	8.3 (P<0.0001)

Within a column, the means marked by different letters are significantly different by Tukey's studentized range test (P<0.05).

sorghum, signal grass, and Napier grass, but were significantly lower on leaf cuts of 'Mulato' (F<sub>4,45</sub> = 8.4, P<0.0001). Settlement rates followed the same trend, suggesting that these larvae ranked maize, sorghum, signal grass, and Napier grass the same, with 'Mulato' being the least preferred (Table 2). Moreover, orientation and settlement rates of larvae originating from eggs oviposited on different test plants largely followed the same trend, with generally similar ranking of the four plants and least preferring 'Mulato', regardless of the host plant upon which the larvae emerged (Table 3A-E). These results therefore suggest that eggs deposited on specific host plants do not yield larvae of particular host preference behaviour.

**Larval feeding choice.** In no-choice tests, larvae fed significantly larger portions of maize, sorghum, and signal grass leaf cuts than of Napier grass and 'Mulato' leaf cuts (F<sub>4,45</sub> = 25.5, P<0.0001) (Figure 1A). Similarly, the larvae consumed significantly larger portions of maize and sorghum leaf cuts than of signal grass, Napier grass, and 'Mulato' leaf cuts under multiple choice tests (F<sub>4,45</sub> = 7.5, P<0.0001) (Figure 1B).

**Larval experience studies.** *Chilo partellus* moths originating from larvae reared on maize oviposited significantly more egg batches on Napier grass than on the other test plants (F<sub>4,45</sub> = 22.5, P<0.0001) (Table 4). These moths oviposited significantly more eggs on Napier grass, sorghum, and signal grass than on maize and 'Mulato' (F<sub>4,45</sub> = 14.5, P<0.0001). In order of preference, Napier grass was the most preferred by the moths for oviposition, sorghum, maize, and signal grass were equally preferred, whereas 'Mulato' was the least preferred (Table 4).

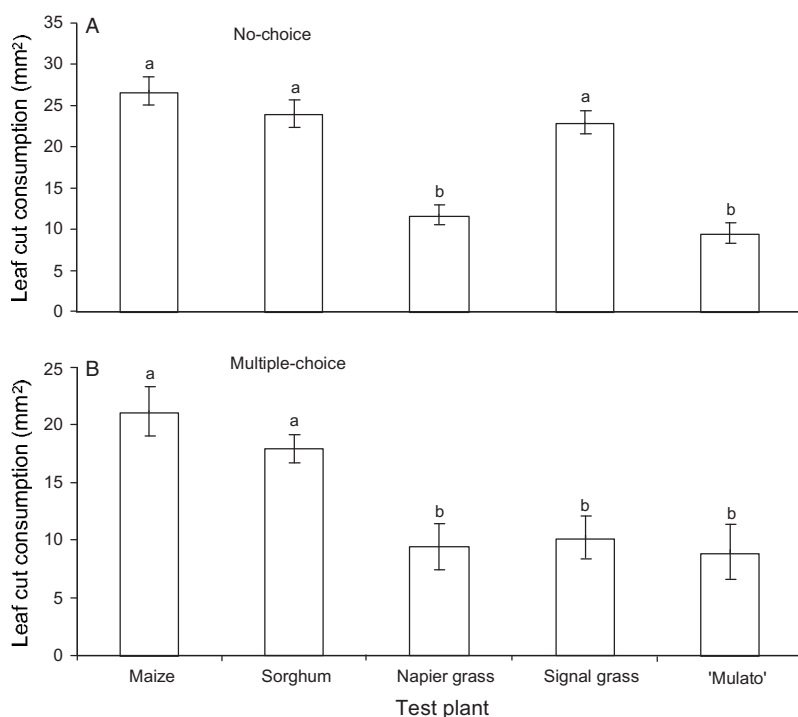
The moths originating from sorghum followed a similar trend, with Napier grass and 'Mulato' being the most and least preferred, respectively (Table 5). These moths oviposited significantly more egg batches on Napier grass than on the other test plants (F<sub>4,45</sub> = 25.6, P<0.0001). The

**Table 3** Mean ( $\pm$  SE) percentage of *Chilo partellus* larval orientation and settling on leaf cuts of test plants after 1 and 24 h, respectively

Plant	% orientation	% settling
<i>A. Larvae arising from eggs deposited on Napier grass</i>		
Maize	19.5 $\pm$ 1.1a	19.5 $\pm$ 2.0a
Sorghum	20.0 $\pm$ 1.4a	18.0 $\pm$ 1.9ab
Napier grass	16.5 $\pm$ 1.7a	15.0 $\pm$ 1.7ab
Signal grass	15.0 $\pm$ 1.8ab	17.0 $\pm$ 1.8ab
Mulato	10.0 $\pm$ 1.7b	12.0 $\pm$ 1.5b
F <sub>4,95</sub>	6.8 (P<0.05)	2.9 (P<0.05)
<i>B. Larvae arising from eggs deposited on sorghum</i>		
Maize	18.5 $\pm$ 2.0a	18.5 $\pm$ 1.9a
Sorghum	18.5 $\pm$ 1.9a	17.0 $\pm$ 1.9a
Napier grass	16.5 $\pm$ 2.2ab	15.5 $\pm$ 2.1a
Signal grass	16.5 $\pm$ 2.1ab	14.5 $\pm$ 2.1a
Mulato	10.0 $\pm$ 2.0b	5.5 $\pm$ 1.7b
F <sub>4,95</sub>	2.9 (P<0.05)	6.7 (P<0.05)
<i>C. Larvae arising from eggs deposited on maize</i>		
Maize	22.0 $\pm$ 1.9a	20.0 $\pm$ 1.4a
Sorghum	20.5 $\pm$ 1.7a	20.0 $\pm$ 1.4a
Napier grass	17.0 $\pm$ 1.6a	19.0 $\pm$ 1.6a
Signal grass	19.5 $\pm$ 1.7a	19.5 $\pm$ 1.5a
Mulato	12.5 $\pm$ 1.6b	12.5 $\pm$ 1.6b
F <sub>4,95</sub>	3.7 (P<0.05)	3.6 (P<0.05)
<i>D. Larvae arising from eggs deposited on signal grass</i>		
Maize	22.0 $\pm$ 1.9a	20.0 $\pm$ 1.4a
Sorghum	20.5 $\pm$ 1.7a	20.0 $\pm$ 1.4a
Napier grass	17.0 $\pm$ 1.6ab	19.0 $\pm$ 1.6a
Signal grass	19.5 $\pm$ 1.7a	19.5 $\pm$ 1.5a
Mulato	12.5 $\pm$ 1.5b	12.5 $\pm$ 1.5b
F <sub>4,95</sub>	4.8 (P<0.05)	4.4 (P<0.05)
<i>E. Larvae arising from eggs deposited on 'Mulato'</i>		
Maize	18.0 $\pm$ 1.7a	16.5 $\pm$ 1.7a
Sorghum	19.5 $\pm$ 1.8a	19.0 $\pm$ 2.3a
Napier grass	18.0 $\pm$ 1.8a	16.5 $\pm$ 1.7a
Signal grass	19.5 $\pm$ 1.7a	17.0 $\pm$ 1.8a
Mulato	12.5 $\pm$ 1.4b	13.5 $\pm$ 1.5b
F <sub>4,95</sub>	2.8 (P<0.05)	2.6 (P<0.05)

For each study (larval group), the means marked by different letters within a column are significantly different by Tukey's studentized range test (P<0.05).

mean number of eggs oviposited was significantly higher on Napier grass and sorghum than on the other test plants (F<sub>4,45</sub> = 14.3, P<0.0001). However, the mean number of eggs oviposited per batch did not differ significantly between the test plants in either experiment (Tables 4 and 5). However, in both cases generally smaller egg batches were laid on 'Mulato'. Thus, the ranking of host plants was in all aspects similar between the experiments, showing that oviposition preference was not altered by the larval food.



**Figure 1** Mean ( $\pm$  SE) portion of leaf cuts ( $\text{mm}^2$ ) consumed by *Chilo partellus* larvae under (A) no-choice and (B) multiple-choice conditions. Within a panel, bars bearing different letters are significantly different (Tukey's studentized range test:  $P < 0.05$ ).

**Table 4** Mean ( $\pm$  SE) number of egg batches, eggs, and eggs per batch laid by maize stock-reared *Chilo partellus* moths on host plants in multiple-choice tests

Plant	No. egg batches	No. eggs	No. eggs/batch
Maize	3.5 $\pm$ 0.4b	93.2 $\pm$ 7.2b	27.9 $\pm$ 2.2a
Sorghum	3.6 $\pm$ 0.3b	98.9 $\pm$ 7.0ab	29.2 $\pm$ 3.1a
Napier grass	5.3 $\pm$ 0.4a	139.8 $\pm$ 9.0a	27.2 $\pm$ 1.5a
Signal grass	3.9 $\pm$ 0.3b	99.1 $\pm$ 20.3ab	28.0 $\pm$ 6.3a
Mulato	0.9 $\pm$ 0.2c	22.0 $\pm$ 5.5c	17.6 $\pm$ 4.0a
$F_{4,45}$	22.5 ( $P < 0.0001$ )	14.5 ( $P < 0.0001$ )	1.5 ( $P = 0.205$ )

Within a column, the means marked by different letters are significantly different by Tukey's studentized range test ( $P < 0.05$ ).

**Table 5** Mean ( $\pm$  SE) number of egg batches, eggs, and eggs per batch laid by sorghum stock-reared *Chilo partellus* moths on host plants in multiple-choice tests

Plant	No. egg batches	No. eggs	No. eggs/batch
Maize	3.5 $\pm$ 0.4b	92.3 $\pm$ 11.0b	26.7 $\pm$ 2.2a
Sorghum	4.2 $\pm$ 0.4b	116.1 $\pm$ 16.4ab	27.9 $\pm$ 3.3a
Napier grass	5.7 $\pm$ 0.3a	166.4 $\pm$ 13.1a	30.0 $\pm$ 3.0a
Signal grass	3.5 $\pm$ 0.3b	87.0 $\pm$ 16.3b	23.4 $\pm$ 2.6a
Mulato	1.2 $\pm$ 0.3c	28.4 $\pm$ 6.6c	18.6 $\pm$ 3.5a
$F_{4,45}$	25.6 ( $P < 0.0001$ )	14.3 ( $P < 0.0001$ )	2.3 ( $P = 0.075$ )

Within a column, the means marked by different letters are significantly different by Tukey's studentized range test ( $P < 0.05$ ).

## Discussion

Ovipositing female Lepidoptera can show a graded discrimination among potential host species, termed a hierarchy of preference (e.g., Nylin & Janz, 1993). This relative preference for different hosts is thought to arise from the balance between attractants and deterrents to which the insect responds (Renwick & Chew, 1994). Plants with lower acceptance may have fewer positive or more negative stimuli. Irrespective of the order of plant ranking for oviposition, *C. partellus* gravid females accepted all plants tested, confirming that cues from cereal stemborer host plants within the Poaceae family are often general (Khan et al., 2000; Birkett et al., 2006; Chamberlain et al., 2006). In these studies, Napier grass was clearly preferred by the moths for oviposition, which corroborates earlier reports (van den Berg, 2006; Khan et al., 2006a, 2007). Sorghum, maize, and signal grass were ranked the same, although in a two-choice test, signal grass is preferred to maize for oviposition by *C. partellus* moths (CAO Midega, unpubl.). 'Mulato' was clearly the least preferred. The low preference extended even to smaller egg batches being laid on 'Mulato'. Lepidoptera batch size regulation in response to plant species in host choice studies was also reported by Bergstrom et al. (2006).

Previous studies have shown that the preferential selection of Napier grass over maize and sorghum is not based on the plant's suitability for larval survival and

development (van den Berg, 2006; Khan et al., 2006a). Indeed larval survival is poorer on Napier grass (Khan et al., 2006a), signal grass, and 'Mulato' (CAO Midega, unpubl.) than on maize and sorghum. Napier grass produces significantly more (amount and number) physiologically active compounds than maize and sorghum within the first 2 h of the scotophase (Birkett et al., 2006; Chamberlain et al., 2006), when the moths seek host plants for oviposition (Päts, 1991). It is this convergence of period of increased production and release of attractive volatile cues and the moths' active period that explains the higher attractiveness of Napier grass relative to the cultivated host plants. Moreover, we recently observed another unique phenomenon in signal grass where emission of the green leaf volatiles, particularly (Z)-3-hexenyl acetate, significantly reduces once the plant is oviposited on by *C. partellus* moths, resulting in reduced further attack by the herbivore (Bruce et al., 2010).

*Chilo partellus* larvae originating from the laboratory culture (ex-sorghum) equally orientated and settled on leaf cuts of maize, sorghum, signal grass, and Napier grass, and preferred least those of 'Mulato'. Those originating from the various test plants showed a similar ranking of hosts, with no preference for the plants on which they emerged. This suggests that plants did not condition the eggs to yield larvae of altered host preferences, and that eggs deposited on specific host plants were not genetically determined to give rise to larvae with a particular preference. Therefore, although adult females of *C. partellus* clearly preferred Napier grass to the other host plants, the larvae equally ranked the host plants except 'Mulato'. This slight 'disagreement' in host ranking between parents and offspring is likely to be beneficial for trap cropping as the larvae emerging from the egg batches on the trap plant may not appreciably disperse to the neighbouring target plants (maize or sorghum). Castrejon et al. (2006) found that larvae of a generalist insect, *Estigmene acrea* (Drury), used host plant chemical cues to orientate to its hosts, preferring cues from soybean (*Glycine max* L. Merr.) over those of maize and tomato (*Solanum lycopersicum* L.). There is thus need to evaluate whether *C. partellus* larvae use chemical cues to locate hosts, and if so, identify what type of chemicals are influencing their orientation and locomotory behaviour, including the location of the receptors responsible for detecting the plant chemicals. Nonetheless, the test plants in the current study are all Poaceae and would be expected to release similar volatile chemicals, with little variation in ratios of the constituent compounds (Khan et al., 2000).

Maize, sorghum, and signal grass were the most preferred hosts for larval feeding, followed by Napier grass and lastly 'Mulato' under no-choice tests, but larvae

preferentially fed on maize and sorghum over the wild hosts in multiple-choice tests. These results indicate that although Napier grass and signal grass are ranked equally with maize and sorghum by the larvae for orientation and settlement, they are less preferred for feeding when oviposited on by females or once found by larvae. The preferred plants have softer tissues and allow significantly higher *C. partellus* larval survival rates than the wild hosts (Khan et al., 2006a; van den Berg, 2006; CAO Midega, unpubl.).

Host plant selection was not influenced by the type of host plant on which the larvae were reared. The moths emerging from maize and those emerging from sorghum oviposited significantly more egg batches and eggs on Napier grass than on the other test plants, indicating that preference was not altered by the larval food. These results support those of Rojas & Wyatt (1999) who found that responses of the female cabbage moth, *Mamestra brassicae* (L.), to host plants were not affected by the plant species used for feeding the larvae. Similarly, in *Ostrinia nubilalis* (Hübner) and *Helicoverpa zea* (Boddie) no evidence of altered oviposition preference as a consequence of larval food has been found (Thompson & Parker, 1928; Palmiter, 1966). Similar results have also been reported for the diamondback moth, *Plutella xylostella* L. (Liu & Liu, 2006), *Heliconius erato* (L.) (Kerpel & Moreira, 1999), as well as in many other insects (Hérard et al., 1988; van Emden et al., 1996; Barron & Corbet, 1999). Janz et al. (2009) discuss theoretical reasons for why Hopkins' host selection principle is expected to be only rarely applicable. Moreover, Glas et al. (2007) concluded that *C. partellus* females do not learn, i.e., that they do not change their preference for Vetiver grass, *Vetiveria zizanioides* (L.) Nash, after having experienced oviposition on either maize or this grass. This, together with results of the current study support the idea that trap cropping has potential as a control method for *C. partellus*.

In conclusion, we observed only slight disagreements and some similarities between *C. partellus* moths and larvae in host ranking. Moths preferentially oviposited on Napier grass, whereas maize, sorghum, and signal grass were ranked the same. Larvae did not have any clear ranking behaviour, but equally orientated and settled on maize, sorghum, Napier grass, and signal grass, although maize and sorghum were ranked highest for feeding. 'Mulato' ranked lowest by both moths and larvae. Host plant preference in adults was not influenced by larval food and host plant did not yield larvae of particular host preference. These results imply that the particular form of 'disagreement' in host ranking behaviour between parents and offspring seen in this study is beneficial for trap cropping as larvae would not 'reject' the trap plant and disperse to the

neighbouring plants, except for the normal ballooning activity of stemborer larvae (Berger, 1989). Moreover, absence of larval learning behaviour indicates that regardless of the larval food *C. partellus* moths would still be attracted to a selected trap plant.

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