

Suitability of brachiaria grass as a trap crop for management of *Chilo partellus*

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Abstract

The cereal stemborer *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) is a major insect pest of sorghum (*Sorghum bicolor* L. Moench) and maize (*Zea mays* L.) in Africa. Trap cropping systems have been shown to be a valuable tool in management of this pest. To optimize trap cropping strategies, an understanding of host-plant preference for moth oviposition and host suitability for larval survival on potential trap plants is a prerequisite. Therefore, we assessed seven brachiaria accessions (Poaceae) for preference by *C. partellus* moths and subsequent larval performance. In two-choice tests with a local open-pollinated maize variety (cv. Nyamula), significantly higher numbers of eggs were deposited on brachiaria accessions Marandu, Piata, and Xaraes than on maize, whereas fewer eggs were recorded on plants of Mulato II, Mulato I, and Cayman. There was a significant and negative correlation between the trichome density on plant leaves and *C. partellus* oviposition preference for brachiaria. In addition to poor larval performance on brachiaria, there was no clear ranking in the accessions regarding larval orientation, settling, arrest, and food ingestion and assimilation. First instars did not consume leaf tissues of brachiaria plants but consumed those of maize, which also suffered more stem damage than brachiaria plants. No larvae survived on brachiaria plant tissue for longer than 5 days, whereas 79.2% of the larvae survived on maize. This study highlights the preferential oviposition of *C. partellus* on brachiaria plants over maize and the negative effects that these accessions have on subsequent larval survival and development. Our findings support the use of brachiaria as a trap crop for management of *C. partellus* through a push-pull technology.

Introduction

Plants exhibit extensive variation in their suitability as hosts for insect herbivores (Journet, 1980; Service & Lenski, 1982; Weis & Abrahamson, 1986) and evolved a diverse array of adaptations to reduce the degree of damage caused by herbivores. These adaptations include direct defense mechanisms, such as production of toxic secondary metabolites that kill or arrest development of herbivores and a number of structural defense systems (hairs, spines, and thorns) (Dicke & van Poecke, 2002; Gouinguéné & Turlings, 2002; Roda & Baldwin, 2003;

Hanley et al., 2007; Bukovinszky et al., 2008; Poelman et al., 2009). Variation in these adaptations can either be intraspecific (Degen et al., 2004; Broekgaarden et al., 2010) or interspecific (Ratnadass et al., 2012). Nevertheless, these adaptations depend on the direction of interaction in the trophic level, e.g., ‘bottom-up’ effects of plant traits on higher trophic levels (herbivores and their natural enemies) and ‘top-down’ effects of natural enemies on herbivores (Ratnadass et al., 2012).

Insects, on the other hand, recognize and respond to host cues to find plant species on which they can feed and reproduce (Bruce et al., 2005). Typically, host plant selection by insects is a multifaceted process involving visual and semiochemical stimuli (Atkins, 1980; Calatayud et al., 2008; Finch & Collier, 2012). Several theories explain the host selection process in herbivores, the most common

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being the optimal oviposition theory also known as the ‘mother knows best principle’ (Thompson, 1988; Scheirs et al., 2000; Johnson et al., 2006) and classically as the preference–performance hypothesis (Jaenike, 1978). This theory is based on the concept that juvenile life stages have little opportunity to change their developmental location and therefore it is the mother’s duty to find a suitable host for their survival and development (Mayhew, 1997). On the other hand, females may select hosts based on factors influencing her own survival rather than that of the juvenile offspring (Nanthagopal & Uthamasamy, 1989). For both scenarios, studies are usually done to encompass ‘preference traits’ that determine willingness to accept a host plant and ‘performance traits’ that encompass the ability of a juvenile to feed, grow, survive, and develop on the host plant.

Some plants emit secondary metabolites that directly mask the specific chemical cues that another’s herbivores use to find their hosts, or harbor particularly effective natural enemies of one another’s herbivores (Finch & Collier, 2012). This is one of the key concepts that has enabled utilization of such plants as trap crops in management of crop pests (Shelton & Badenes-Perez, 2006). Trap cropping was a common method of pest management in several cropping systems prior to introduction of modern synthetic pesticides (Thurston, 1984; Hokkanen, 1991). In Africa, intercropping and trap cropping systems for management of the cereal stemborers *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Busseola fusca* (Fuller) is gaining wide adoption (Khan et al., 2000, 2016; Midega et al., 2011, 2015; Pickett et al., 2014). Vetiver grass [*Chrysopogon zizanioides* (L.) Roberty = *Vetiveria zizanioides* (L.) Nash], napier grass [*Pennisetum purpureum* (Schumacher)], and sudan grass (*Sorghum vulgare* Pers. var. *sudanense*) have also been shown to be effective trap crops in the management of stemborers (Khan et al., 2001; Haile & Hofsvang, 2002; Van den Berg, 2006a,b; Van den Berg & Van Hamburg, 2015).

Cereal stemborers are the most important pest constraints to sorghum and maize production in Africa, causing yield losses ranging from 10 to 88% (Kfir et al., 2002). Stemborer moths locate and oviposit on suitable hosts and their offspring feed inside the whorls of plants, damaging the leaves before entering the stem (Slabbert & Van den Berg, 2009). In east Africa, the estimated average yield loss from seasons due to stemborers was 13.5% which is equivalent to a quantity loss of 0.4 million tonnes, worth US\$ 80 million (De Groote et al., 2011). Due to the cryptic and nocturnal habits of the adult moths and the burrowing behavior of larvae into the host’s stem, effective control of the pest has proved difficult (Ampofo et al., 1986). Chemical control is one

of the strategies employed to control borers and reduce damage; however, it is largely uneconomical and impractical for resource-poor farmers in sub-Saharan Africa, besides posing environmental and health hazards if not used carefully or without proper safety measures (Van den Berg & Nur, 1998). A ‘stimulo-deterrent diversion’ or ‘push-pull’ strategy, based on a combination of a trap crop (pull component) with a repellent intercrop (push component) has allowed farmers to successfully suppress stemborer numbers on maize and sorghum in sub-Saharan Africa (Khan et al., 2000, 2001, 2012; Midega et al., 2015). The trap plant releases semiochemicals that attract stemborer moths while volatiles from the push crop further enhance the effectiveness of the trap-crop by repelling moths away from the main crop (Cook et al., 2007; Khan et al., 2010).

Members of the genus *Brachiaria* (Poaceae) are extensively grown as grass pasture crops in tropical Latin America and Africa (Keller-Grein et al., 1996; Cardona et al., 2004). There are over 100 species in this genus but only a few have been commercially exploited (Miles et al., 2004). In addition to use as a pasture crop, signal grass – *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf cv. Mulato II – has been adopted in combination with greenleaf desmodium in a climate smart push-pull strategy (Pickett et al., 2014; Khan et al., 2016). This combination of crops displayed beneficial effects in reducing infestations of stemborers as well as that of the parasitic weed, *Striga hermonthica* (Delile) Benth., resulting in a net increase in crop yield (Khan et al., 2014, 2016; Pickett et al., 2014; Midega et al., 2015).

Research has shown that *B. brizantha* is preferred to maize for egg laying by *C. partellus* moths (Midega et al., 2011). Additionally, the cultivar Mulato II supports minimal feeding and survival of *C. partellus* larvae (Midega et al., 2011). Moreover, this variety exhibits a sophisticated response to stemborer herbivory that involves volatile-mediated multi-trophic interactions with natural enemies (Bruce et al., 2010). Intra-specific genetic variation in volatile composition and volatile release rates does, however, exist in cereal crops, for example in rice (Rapusas et al., 1996), maize (Tamiru et al., 2012; Mutyambai et al., 2016), and wheat (Weaver et al., 2009). This variation in volatile blend influences host selection preference by insects within plant species. In view of this, our study aimed at determining the preference of adults and larvae of *C. partellus* for various brachiaria accessions and to identify those that could better suffice as trap crop for *C. partellus*. This information will contribute to the understanding and exploitation of brachiaria as a trap crop for *C. partellus* in an innovative push-pull system.

Materials and methods

Study site

This study was carried out at *icipi* Thomas Odhiambo Campus (ITOC), Mbita Point (0°25'S, 34°12'E, 1 200 m above sea level), a field station on the shores of Lake Victoria in western Kenya. The area receives an average annual precipitation of 900 mm. Temperature in the screen house ranged between 25 and 30 °C and relative humidity was 65%. Mean temperatures inside the laboratory were 25.5 °C by day and 23.5 °C at night, with 70 ± 5% r.h. and natural light conditions of approximately L12:D12. The area is considered a 'hot-spot' for cereal stemborers with the vegetation type mainly comprising of savannah grassland with mixed combretum and acacia trees to the north and papyrus along the shores of the lake.

Study plants and insects

Planting material of the brachiaria accessions used in the study were sourced from the International Center for Tropical Agriculture (CIAT), Columbia. These accessions were *B. brizantha* cv. Mulato II, *B. brizantha* cv. Marandu, *Brachiaria decumbens* Stapf cv. Basilisk, *B. brizantha* cv. Piata, *B. brizantha* cv. Mulato I, *B. brizantha* cv. Cayman, and *B. brizantha* cv. Xaraes. Mulato II is a commercial hybrid which has previously been incorporated into a push-pull strategy as a trap crop mainly due to its attractiveness to the cereal stemborer moths and its benefits as a fodder crop (Midega et al., 2011; Khan et al., 2014). An open-pollinated landrace maize variety Nyamula, a farmer-preferred but stemborer-susceptible maize variety (Midega et al., 2015; Tamiru et al., 2015), was included as a control. All plants were grown in pots. The brachiaria varieties were grown from root splits whereas maize was grown from seeds. Plants were 3–4 weeks old when they were used in the experiments and all experiments commenced in the morning.

To build up a sufficient insect culture for the study, original populations of *C. partellus* larvae were collected from sorghum fields and reared on an artificial diet to obtain moths, as described by Onyango & Ochieng'-Odero (1994). Rearing was done at ITOC under laboratory conditions of 24 ± 3 °C, 70 ± 5% r.h., and L12:D12 photoperiod. The insects used in the experiments were of the second generation of the founder colony and infestations were done early in the morning.

Adult selection of host plants

Two-choice oviposition test. Oviposition tests with *C. partellus* moths were conducted following a procedure adapted from Khan et al. (2007) and Midega et al. (2011). Two-choice tests were carried out in oviposition cages

(80 × 40 × 40 cm) covered with fine wire mesh netting. Two potted 3- to 4-week-old plants representing each brachiaria variety and maize, were placed in opposite corners of each cage. A 10-cm-diameter wad of cotton wool was moistened with water and introduced into the cage for the moths to feed on. Five gravid naïve moths were introduced in the cage and allowed to oviposit for 48 h under natural light conditions of L12:D12. Afterwards, the plants were removed and the eggs were counted under a light microscope at 6.5× magnification. 'Preference' in this context was taken as significant differential oviposition on a plant when the moth was given a choice between two plants of different species.

Trichome assessment. The possible effect of leaf architecture on oviposition was evaluated by determining the trichome density on leaves and correlating that with egg numbers per plant variety. The last five fully emerged leaves representing five replicates from each test plant were obtained and the numbers of trichomes were determined on a 0.5 × 0.5 cm area on the adaxial surface of each leaf using a binocular light microscope. Samples were taken from the intermediate position between the leaf margin and the midrib on the leaf lamina and halfway between the proximal end and base of the leaf.

Larval performance

Larval orientation and settlement. Host-plant preference of *C. partellus* larvae for different brachiaria varieties was assessed in a two-choice test following a modification of procedure described by Khan et al. (2007). Experiments were conducted inside 15-cm-diameter Petri dishes lined with moist filter paper discs. Four 3-cm-long leaf cuts of brachiaria variety and maize were laid alternately and radially, two for each plant, with their adaxial sides facing up. At the center of each Petri dish, 10 first instars of *C. partellus* were introduced. The Petri dishes were then placed in a dark room. The larvae on/underneath each leaf cutting were counted after 1 and 24 h to determine orientation and settling preference respectively. This experiment was replicated 10×.

Arrest and dispersal of first instars. This experiment was conducted in a dark room. The leaf cuts were placed individually, with their adaxial side facing upwards, in the center of a 9-cm Petri dish lined with moist filter paper. A moist cotton wad was placed at either end of a 6-cm-long leaf cutting of each of the plants. Ten first instars of *C. partellus* were then introduced on top of each leaf cutting. The larvae remaining on the leaf tissue were counted after 1 and 24 h of release. The experiment was replicated 10×.

Leaf and stem feeding, and food assimilation. This study was conducted to assess feeding of *C. partellus* larvae on leaves and stem cuttings of experimental plants. Pieces of the second-youngest leaf (2.5×2.5 cm) of 3-week-old plants were placed in a 6-cm-diameter Petri dish lined with wet filter paper to limit desiccation. Each piece of leaf was placed in a different Petri dish. Five newly hatched and unfed larvae were placed on each leaf cutting. The Petri dishes were covered and sealed with Parafilm to prevent larvae from escaping and kept in a dark room. The leaf area (mm^2) consumed by the larvae was measured after 24 h using a graph paper (Mohamed et al., 2007). The surface area removed or damaged after feeding indicates feeding levels of the larvae on the leaf tissue. This experiment was replicated $10 \times$.

To determine the degree of stem feeding by *C. partellus* larvae, 4-cm-long stem segments of each of the 3-week-old potted plants were obtained. Each segment was weighed (S1) and then placed in a glass vial (4.1×1 cm). A third instar, previously starved for 3 h under high humidity conditions, was also weighed (W1) on a Mettler PM460 microbalance (Mettler Instrument, Greifensee, Switzerland) and put on the piece of stem inside the vial. The vials were then covered with cotton wool plugs and kept in a dark room for 24 h. Non-consumed parts of the stem segments were weighed again (S2) after discarding the larvae and excreta. To determine weight loss due to evaporation, 10 stem segments (4 cm long) of each treatment were weighed (CE1), kept in similar vials alongside the experimental ones, and weighed again after 24 h (CE2). The difference between the initial and the final weight (S1–S2) of the stem tissue after adjustment for weight loss due to evaporation represents the degree of feeding on the plant by the larvae (Khan & Saxena, 1985). Each treatment was replicated $10 \times$. To determine the amount of food assimilated, each larva was weighed again (W2). To determine larval weight loss due to metabolism, 10 larvae were weighed (C1), kept alongside the experiment in similar vials without stem pieces and weighed again after 24 h (C2). The amount of food metabolized by each larva was determined using the equation from Khan & Saxena (1985). The following equation was used to calculate food accumulation:

$$\text{Food assimilation} = W1 \times (C1 - C2)/C1 + W2 - W1$$

where W1 is the initial weight of larva, W2 the final weight of larva, C1 the initial weight of control larva, and C2 the final weight of control larva.

Larval development and survival on stem tissue under laboratory conditions. To evaluate development and

survival of *C. partellus* larvae on the test plants, a study was carried out in a laboratory setting. This was done in a room with lower temperatures during the day due to shading (mean of 26.5°C), but similar to outside temperatures at night (mean of 23.5°C). Relative humidity was maintained at 65%. Five sections of stems of 3-week-old potted plants grown in a screen house were placed in screw-top glass jars (20 cm high, 8 cm wide). Each of these sections measured between 0.5 and 1.5 cm diameter at the base, was ca. 15 cm long, and consisted of stem, leaf, and sheath regions for the larvae to feed on (Khan et al., 2007). Newly hatched larvae (25) were introduced into each jar using a fine camel-hair paint brush. Two replicates were established for each of the plants. The lids of the jars were tightly closed, and paper towels were used to tighten the seal and prevent the larvae from escaping (Khan et al., 2007). The larvae were then allowed to feed for 5 days, the least number of days taken between instars. Afterwards, the plants were removed and carefully dissected to recover and determine the number of live larvae per plant.

Data analysis

All analyses were performed by R v.3.3.1 software (R Core Team, 2016). Unpaired two-sample Student's *t*-test was used to analyze differences between maize and each of *Brachiaria* spp. with regard to the number of eggs deposited, and larval orientation and settling on the various varieties. ANOVA was done to determine whether the density of trichomes differed among the *Brachiaria* accessions. Prior to analysis, data on oviposition, larval orientation, and settlement were $\log(x+1)$ transformed to satisfy assumptions of *t*-tests as indicated by normality tests.

A special correlation (Polyserial) analysis was computed using the 'polycor' package for trichome density and preference for oviposition, which was separated into two categories and allocated dummy values of 1 (preferred) and 0 (non-preferred). Similarly, data on arrest and dispersal, leaf feeding, food ingestion and assimilation of stem tissue, and larval survival were subjected to one-way ANOVA using the generalized linear model to test for any differences among the test plants. Before analysis, the data on arrest, dispersal, and leaf feeding were $\log(x+1)$ transformed. Student–Newman–Keuls (SNK) test was used to separate the means ($\alpha = 0.05$). Means of non-transformed data are presented in figures and tables.

Results

Adult selection of host

Two-choice oviposition test. The number of eggs laid on maize and each of *brachiaria* grasses differed significantly

except for Basilisk (Figure 1). Compared to maize, more eggs were deposited on Marandu, Piata, and Xaraes, whereas fewer eggs were recorded on Mulato I, Mulato II, and Cayman.

Trichome assessment. Trichome numbers per 0.25 m² of leaf area differed among treatment plants ($F_{7,32} = 14.98$, $P < 0.001$; Table 1). Means separation following ANOVA indicated that trichome densities were similar among Mulato I, Cayman, and Mulato II, but lower on Xaraes, Marandu, and Piata. The latter three varieties of brachiaria recorded significantly higher number of eggs than those deposited on maize (Figure 1). Polyserial correlation displayed a strong and negative correlation between trichome density and *C. partellus* preference of brachiaria for oviposition ($r = -0.86$, $P < 0.05$).

Larval performance

Larval orientation and settlement. First instars did not show any significant preference in orientation when offered a choice between leaf cuttings of maize and brachiaria after 1 h of release. After 24 h of release, higher numbers of larvae had settled on maize than on any of the brachiaria plants, the differences being significant for all the tests (Table 2).

Larval arrest and dispersal. The mean numbers of *C. partellus* larvae arrested on leaf cuts after 1 h of release were similar ($F_{7,72} = 1.9$, $P = 0.08$; Table 3) in all two-choice combinations. Leaf cuttings of maize did, however, record the highest number of larvae compared to all brachiaria grasses. The number of larvae remaining on leaf cuts after 24 h of release was higher for maize than for any of the brachiaria plants tested ($F_{7,72} = 2.8$, $P = 0.01$; Table 3).

Larval leaf and stem feeding, and food assimilation. Leaf consumption differed among the test plants ($F_{7,72} = 347.9$, $P < 0.001$) – first-instar *C. partellus*

Table 1 Mean (\pm SEM) trichome number on a 0.25 mm² adaxial surface of leaves of 3- to 4-months-old brachiaria accessions and maize plants, and preference for oviposition by *Chilo partellus* moths in a two-choice tests between a brachiaria accession vs. maize

Test plant	No. trichomes	Preference for oviposition compared to maize
Mulato I	66.2 \pm 3.2a	No
Cayman	65.6 \pm 2.3a	No
Mulato II	59.2 \pm 2.9a	No
Basilisk	50.8 \pm 1.5b	No
Maize	21.6 \pm 2.5c	–
Xaraes	11.6 \pm 3.7d	Yes
Marandu	7.2 \pm 1.6d	Yes
Piata	6.8 \pm 3.1d	Yes

Means followed by the same letter are not significantly different (SNK test: $P > 0.05$).

consumed larger areas of maize leaves than of any of the brachiaria accessions (Table 4). Also stem consumption differed among the test plants ($F_{7,72} = 175.6$, $P < 0.001$). Remarkably, the third instars consumed some material from the stem segments of brachiaria plants although significantly heavier larvae were recovered from maize than from brachiaria (Table 4). Xaraes ranked second to maize in terms of larval mass recovered and significantly higher than the other brachiaria accessions. Similarly, the amount of food assimilated by larvae fed on the stem segments differed among the test plants ($F_{7,72} = 26.8$, $P < 0.001$) – it was significantly higher in maize than in the other test plants (Table 4).

Larval survival and development under laboratory conditions. By the 5th day of experiment, no live larva was recovered on any of the brachiaria accessions whereas 79.2% survived on maize (Table 5). This implies that

Figure 1 Mean (\pm SEM) number of eggs laid by *Chilo partellus* on maize and various brachiaria accessions in two-choice tests. Means within a plant pair capped with different letters are significantly different (Student's t-test: $P < 0.05$).

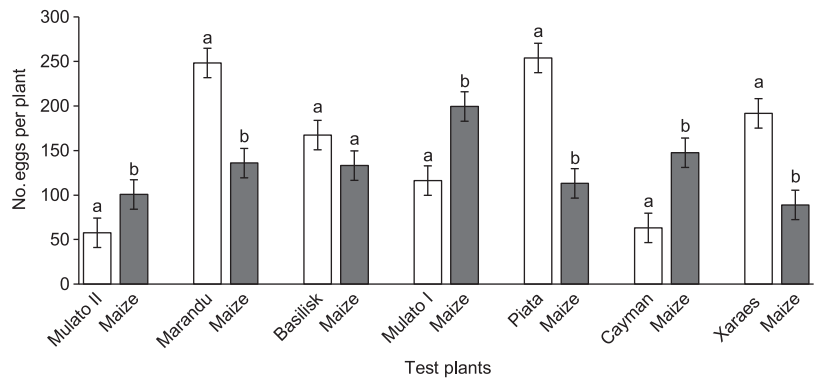


Table 2 Mean (\pm SEM) number of *Chilo partellus* larvae after 1 (orientation) and 24 h (settlement) on leaf cuts of various brachiaria accessions and maize plants

Test plant combination	Orientation			Settlement		
	1 h	t	P	24 h	t	P
Mulato II vs. maize	1.7 \pm 0.5 vs. 3.7 \pm 0.8	-2.09	0.05	0.7 \pm 0.2 vs. 4.4 \pm 0.8	-4.59	<0.001
Marandu vs. maize	2.5 \pm 0.3 vs. 2.1 \pm 0.6	0.58	0.56	0.5 \pm 0.3 vs. 4.8 \pm 0.7	-4.65	<0.001
Basilisk vs. maize	2.6 \pm 0.7 vs. 3.5 \pm 0.7	-0.9	0.37	0.5 \pm 0.3 vs. 4.8 \pm 1.0	-4.0	0.002
Piata vs. maize	2.3 \pm 0.7 vs. 4.2 \pm 0.6	2.09	0.05	0.5 \pm 0.3 vs. 5.7 \pm 0.7	7.3	<0.001
Mulato I vs. maize	2.2 \pm 0.6 vs. 3.7 \pm 0.6	-2.1	0.05	0.7 \pm 0.2 vs. 4.4 \pm 0.6	-4.5	<0.001
Cayman vs. maize	2.2 \pm 0.4 vs. 3.9 \pm 0.7	-2.1	0.06	0.3 \pm 0.2 vs. 5.7 \pm 0.8	-6.2	<0.001
Xaraes vs. maize	2.5 \pm 0.5 vs. 4.0 \pm 0.7	1.7	0.39	1.2 \pm 0.3 vs. 5.2 \pm 0.5	6.7	<0.001

Table 3 Mean (\pm SEM) number of *Chilo partellus* larvae arrested on leaf cuts of various brachiaria accessions and maize plants after 1 and 24 h

Test plant	1 h	24 h
Mulato II	3.7 \pm 0.7a	2.0 \pm 0.5a
Marandu	2.6 \pm 0.7a	2.4 \pm 0.5a
Basilisk	3.3 \pm 0.6a	2.3 \pm 0.6a
Piata	2.4 \pm 0.5a	1.9 \pm 0.6a
Mulato I	2.7 \pm 0.7a	2.0 \pm 0.4a
Cayman	2.0 \pm 0.5a	1.8 \pm 0.5a
Xaraes	2.9 \pm 0.6a	2.6 \pm 0.5a
Maize	5.0 \pm 0.4a	5.9 \pm 0.9b

Means within a column followed by the same letter are not significantly different (SNK test: $P>0.05$).

larvae did not survive beyond the first instar on brachiaria plant tissue.

Discussion

There is a wide range of grass species in Africa that support insect species including the maize stemborers (Le Ru et al., 2006; Moolman et al., 2014). Because attractive wild host plants may act as a sink for crop pests, they could be exploited as trap crops (Shelton & Nault, 2004). Host plant recognition by lepidopterous species is a complex process. Location and subsequent selection of suitable hosts for oviposition by adults and for feeding by larvae is strongly influenced by chemical, physical, and visual characteristics of the host plants (Van den Berg, 2006b; Calatayud et al., 2008, 2014; Dicke et al., 2009; Bruce et al., 2010; Hare, 2011; Bruce, 2015; Mutyambai et al., 2016; Pickett & Khan, 2016).

Our results indicate that female *C. partellus* moths, under two-choice test conditions, discriminated between maize and the brachiaria varieties tested. Marandu, Piata, and Xaraes were more preferred to maize. Preference for

Table 4 Mean (\pm SEM) feeding and food assimilation parameters by *Chilo partellus* for 5 days on leaves and stems of various brachiaria varieties and maize

Test plant	Leaf area (cm ²) consumed by five first instars	Stem weight (mg) consumed by a third instar	Stem weight (mg) assimilated by a third instar
Mulato II	0 \pm 0a	5.80 \pm 4.28a	0.14 \pm 0.1a
Marandu	0 \pm 0a	17.49 \pm 8.9a	2.23 \pm 0.8a
Basilisk	0 \pm 0a	10.87 \pm 2.0a	1.42 \pm 0.6a
Piata	0 \pm 0a	11.51 \pm 4.3a	0.98 \pm 0.5a
Mulato I	0 \pm 0a	14.02 \pm 6.7a	0.98 \pm 0.5a
Cayman	0 \pm 0a	7.75 \pm 2.9a	2.24 \pm 1.1a
Xaraes	0 \pm 0a	52.90 \pm 8.9b	1.56 \pm 0.6a
Maize	8.4 \pm 1.3b	293.87 \pm 14.5c	15.44 \pm 1.8b

Means within a column followed by the same letter are not significantly different (SNK test: $P>0.05$).

Table 5 Survival of *Chilo partellus* larvae (mean number recovered \pm SEM) on brachiaria varieties and maize after 5 days under laboratory conditions

Test plant	No. larvae recovered per plant
Mulato II	0 \pm 0a
Marandu	0 \pm 0a
Basilisk	0 \pm 0a
Piata	0 \pm 0a
Mulato I	0 \pm 0a
Cayman	0 \pm 0a
Xaraes	0 \pm 0a
Maize	19.8 \pm 1.7b

Means followed by different letters are significantly different (SNK test: $P<0.001$).

maize to Mulato I and Mulato II is in agreement with previous studies where Mulato I ranked lower than maize in multiple preference tests (Khan et al., 2007; Midega et al., 2011). Nevertheless, Mulato II is currently being

exploited as a trap crop for management of stemborers in maize and sorghum in a push-pull habitat management system in which its efficiency can be enhanced especially when combined with an intercropped push crop of *Desmodium* spp. (Khan et al., 2001, 2016). According to Cook et al. (2007) and Khan et al. (2010), effectiveness of a trap crop is further enhanced by volatiles released from the push crop, which repels insects away from the main crop. Furthermore, Mulato II is a highly nutritious and drought-resistant fodder crop which is gaining rapid adoption in Africa (Maass et al., 2015). Notably, the three brachiaria varieties Marandu, Piata, and Xaraes which are significantly preferred to maize for oviposition have higher densities of trichomes than maize. Correlation analysis revealed a strong and negative relationship between trichome density and preference for oviposition, suggesting that trichomes on the leaf surface may have, in part, influenced oviposition preference of the insect. Influence of leaf texture on oviposition by stemborer females has been observed on maize (Van den Berg, 2006a; Rebe et al., 2007; Calatayud et al., 2008) and on napier grass (Van den Berg, 2006a). According to Myers (1991), the presence of trichomes provides structural or chemical resistance, or both as for glandular trichomes, which can repel the attacking insects or arrest their movement. Studies with *B. fusca* shows that oviposition is adversely affected by rough and pubescent surfaces, making it difficult for moths to sweep and insert their ovipositors (Calatayud et al., 2006).

After host selection and oviposition by an adult moth, plant suitability for larval feeding and development is the next step in the host colonization process. For phytophagous lepidopterous insects, the larva, which is the damaging stage, typically has minimum mobility. Results from two-choice tests clearly indicated that more *C. partellus* larvae settled on leaf cuts of maize than on brachiaria within the first 1 h and the effect was stronger after 24 h. A similar trend was observed regarding larval arrest in a no-choice test after 1 and 24 h. The results conform to those of Khan et al. (2007) and Mohamed et al. (2007) which assert *C. partellus* larvae prefer maize leaf cuts over those of wild grasses for settling and arrest. Other workers (Berger, 1992; Päts, 1992) have also reported dispersal behavior caused by lepidopterous larvae on non-preferred hosts. The results of the current study suggest that larval non-preference for brachiaria may be due to the presence of plant chemicals and/or physical characters and/or poor nutrient quality, which stimulated the larvae of *C. partellus* to disperse away from the test plant.

First-instar *C. partellus* did not consume leaf parts of any plants except maize. Third instars, however, ingested some tissue from stems of all test plants with significantly

more feeding by the larvae on stems of maize, followed by Xaraes. Larvae that fed on maize assimilated significantly higher amounts of food than those feeding on brachiaria. There was no clear difference in the amount of food ingested and assimilated by larvae feeding on brachiaria. First instars of *C. partellus* introduced to stem, leaf, and sheath tissue of brachiaria were all dead by the 5th day of the laboratory experiment. Contrary to this, there was 79% survival on maize sections. Other studies conducted with plant parts of napier grass indicated similar detrimental effects to *C. partellus* larvae, and the pattern was observed when entire plants were used (Van den Berg, 2006a; Khan et al., 2007). This could validate the use of plant parts in *C. partellus* larval performance studies testing the potential of trap plants. Our observations on larval performance are corroborated by the 'optimal bad motherhood' principle (Mayhew, 1997). In this case, adults sometimes spend more time, consequently laying eggs on the host plant that enhances their own long-term fitness, even if the consequence of this behavior is a reduction in offspring survival.

In other studies, Van den Berg & Van der Westhuizen (1997) and Khan et al. (2007) observed high levels of oviposition on sorghum varieties that were not suitable for larval development due to high levels of larval antibiosis. Moreover, Van den Berg (2006a) observed that napier grass varieties were preferred to sorghum for oviposition but supported minimal larval survival. As is the case in behavior of the adults, the larval mortality on the host may also be alluded to various morphological, biochemical, and molecular mechanisms that the host counters or that otherwise offset the effects of herbivore attack (Howe & Jander, 2008; Verhage et al., 2010; Hare, 2011). In his studies with *C. partellus*, Van den Berg (2006a) observed that migrating larvae were arrested by trichomes of napier grass and that upward migration to the whorl was severely hampered. Khan et al. (2000) ascribed the high mortality of stemborer larvae on Napier grass to sticky sap that is produced by the grass in response to penetration by first and second instars. This may have been the case in the current study, more surprising is the fact that even brachiaria varieties that have lower trichome densities nonetheless did not support feeding and survival of larvae. This suggests that there are also other important factors than just trichomes that affect larval survival. The current study highlights discrepancies between adult preference for oviposition and larval survival. Some brachiaria varieties were more preferred to maize for oviposition but subsequently did not support juvenile survival. Mortality of the stemborer larvae observed on brachiaria was very high and could be of value, under field conditions, in reduction in pest populations without acting as a 'nursery' crop on

which stemborers could multiply and invade the main crop (Midega et al., 2015). We propose that this is a prerequisite for trap crops in a 'dead end' trap cropping system (Shelton & Nault, 2004).

This study indicated that all brachiaria accessions tested attracted stemborer oviposition but supported minimal larval survival. These results support the use of brachiaria as a 'dead end' trap crop for management of stemborers through a push-pull technology. Of value will be Marandu, Piata, Xaraes, and Basilisk varieties, all which were preferred to maize for oviposition. The differential preference of moths for brachiaria varieties for oviposition and variation in trichome density presents an aspect of genetic variation which could be further exploited in brachiaria and another grass species. A highly interesting study of Magara et al. (2015) indicated that *B. brizantha* exposed to *C. partellus* oviposition signaled the maize open pollinated varieties Nyamula and Jowi and the landrace Cuba 91 causing these plants to release volatile signals that attract the braconid parasitoid *Cotesia sesamiae* Cameron. This, coupled with the observations from our study, necessitates further investigation and exploitation of genetic diversity in brachiaria for induction of defense mechanisms against stemborers in cereals through plant-plant signaling.

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