CHEMOECOLOGY

Caterpillar-induced plant volatiles attract conspecific and heterospecific adults for oviposition within a community of lepidopteran stemborers on maize plant

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Abstract

Olfactory cues may influence host plant preferences for oviposition of female moths within a community of stemborers that utilise the same resource. This study aimed to evaluate plant preferences for oviposition of gravid females of noctuid stemborers, *Busseola fusca* and *Sesamia calamistis*, and the crambid *Chilo partellus* for uninfested maize plants and plants infested by conspecific or heterospecific larvae. The involvement of volatile organic compounds (VOCs) emitted by uninfested and maize plants infested by conspecific or heterospecific larvae on moth orientation was studied in Y-tube olfactometer assays and in the field. All gravid female moths significantly preferred VOCs emitted by plants infested by conspecific or heterospecific larvae over those from uninfested plants, and female moths did not systematically prefer VOCs emitted by plants infested by conspecifics. Field trials confirmed these results. Chemical analysis by coupled gas chromatography/mass spectrometry showed that VOCs emitted by larvae-infested plants, regardless of the stemborer species, were compositionally richer than those released by uninfested plants but their emission intensity varied with species involved in the infestation. *Busseola fusca* larvae induced a compositionally richer VOCs profile than *S. calamistis* and *C. partellus* larvae. Eight candidate attractants were associated with larvae-infested plants. These results open new avenues to develop attractants specific to trap female stemborer moths in the field.

Keywords Lepidoptera stemborers · Maize plant · Volatiles · Olfaction · Interactions

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Introduction

Direct and indirect interactions between species maintain the structure and function of ecological communities (Wootton and Emmerson 2005). Often, these interactions occur through the same resource utilisation by phytophagous insects. Its outcome can be negative (e.g. competition), positive (e.g. facilitation) or neutral (Kaplan and Denno 2007; Speight et al. 2008). These interactions can be directly intraspecific or interspecific (Memmott et al. 2007) or indirectly through the mediation of the same host plant (Fisher et al. 2000; Kaplan and Denno 2007). The interactions among species can influence the oviposition preferences of gravid females utilising the same host plant in a community (Craig et al. 2000; Shiojiri et al. 2002). Thus, competition for or facilitation in the use of the same resource can influence the final choice by the female for oviposition. For example, prior feeding of larvae on a plant induces female oviposition on that plant in some cases (Anderson and Alborn 1999;

Craig et al. 2000; Facknath 2012; Groot et al. 2003; Viswanathan et al. 2005, 2015), while in other cases, this deters subsequent oviposition (De Moraes et al. 2001; Sato et al. 1999; Fatouros et al. 2012; Wise and Weinberg 2002). Constitutive and inductive plant volatile chemicals have been identified to play an important role in host plant selection by phytophagous insects for food or oviposition (Dicke and Van Loon 2000; Honda 1995). The infochemicals from infesting stages (eggs or larvae) from other conspecifics have been shown to influence gravid female oviposition choice, which serves to adjust population sizes to available resources with, in general, a preference for uninfested plants (Maclellan 1962; Rothschild and Schoonhoven 1977).

The lepidopteran species *Busseola fusca* (Fuller) (Noctuidae), *Sesamia calamistis* Hampson (Noctuidae) and *Chilo partellus* (Swinhoe) (Crambidae) are among the main pests of cereals in sub-Saharan Africa (Kfir et al. 2002). Because of the cryptic habit of their larval stages to feed in plant stems, these species are referred to as stemborers. In East and Southern Africa, where they co-exist, they occur as communities of single or mixed species infesting not only cereal crops in the fields (Krüger et al. 2008; Ong'amo et al. 2006a, b), but also wild graminaceous plants (Le Ru et al. 2006; Moolman et al. 2014). The composition of these stemborer communities varies with locality, altitude and season. For example, in Kenya, *B. fusca* is the dominant species in the highlands, while *C. partellus* dominates in the lowlands. *Sesamia calamistis* is present at all altitudes in low numbers. In the mid-altitudinal regions, the stemborers occur as a mixed community of the three species, but with variation in species dominance with respect to locality, season and year (Guofa et al. 2001; Ong'amo et al. 2006a, b). In parts of Southern Africa *C. partellus* occurs in mixed populations with *B. fusca* in both the highland (Bate and Van Rensburg 1992; Van Rensburg and Van den Berg 1992; Ebenebe et al. 1999) and lowland regions (Cugala and Omwega 2001; Krüger et al. 2008) but the dominance of a species might vary with environment. Under laboratory studies, both intra- and interspecific competitions were observed between the three species with stronger interspecific competition for food resource utilisation recorded between the two noctuids and the crambid than between the two noctuids (Ntiri et al. 2016). Additionally, ovipositing females prefer maize plant previously infested by larvae over uninfested plants suggesting a strong relation between larval feeding and female oviposition choice (Ntiri et al. 2018). These results indicated that maize plants infested by conspecifics or heterospecifics produce or elicit chemical signatures rendering the plants more attractive to female moths.

Olfaction plays a major role in insect–plant interactions and this has been extensively investigated (e.g. Giunti et al. 2016; Trematerra et al. 2007). Nevertheless, the impact of olfactory cues shaping the relationships among insects from the same guild competing for shared resources, mostly in hetero-specific interaction for oviposition site, is poorly explored. For instance, signals left by closely related species, as oviposition and host-marking pheromones, may be exploited by herbivores to detect competitor activity (Steidle et al. 2005; Ukeh et al. 2012). In this scenario, the prompt recognition of unsuitable or harmful habitats by host-seeking insects is critical for their survival and fitness. As such, semiochemicals emitted by infested plants could be exploited by host-seeking insects to avoid competition. On the other hand, for some insect species such cues rather elicit responses which indicate attractiveness (e.g. Agrawal and Sherriffs 2001; Horgan 2012).

Here, we focused on the olfactory responses of the gravid females of *B. fusca, S. calamistis* and *C. partellus* to maize plant odours infested by conspecific and heterospecific larvae, and to uninfested plants. First, we evaluated the attractiveness of each species to uninfested and maize plants infested by either *B. fusca, S. calamistis* or *C. partellus* larvae. Second, we also compared the preference of odours emitted between plants infested by either *B. fusca, S. calamistis* or *C. partellus* larvae. Third, we linked these results to the levels of volatile organic compounds (VOCs) from uninfested and larvae-infested maize plants captured by both dynamic headspace and Solid Phase MicroExtraction (SPME) techniques and analysed through gas chromatography/mass spectrometry (GC/MS).

Methods and materials

Plants and insects

Maize plants of hybrid H513 (Simlaw, Kenya Seed Company, Nairobi, Kenya) were grown in plastic pots (12 cm in height × 13 cm in diameter) in a greenhouse at the Duduville campus of the International Centre of Insect Physiology and Ecology, (*icipe*) Nairobi, Kenya. Mean temperatures were approximately 31/17 °C (day/night) with a L12:D12 photoperiod. Plants were used in experiments when they were between 4 and 6 weeks old, i.e. about 60–75 cm.

Because wild insects are more responsive to plant odours compared to laboratory-reared insects, as shown for *B. fusca* (Calatayud et al. 2008), only field-collected insects of *B. fusca* (Bf), *S. calamistis* (Sc) and *C. partellus* (Cp) were used in the Y-tube experiments. For each species, fourth to fifth instar larvae were collected from maize fields. They were then reared until pupation on the artificial diet of Onyango and Ochieng'-Odero (1994) for *B. fusca* and *S. calamistis* and on the artificial diet of Ochieng et al. (1985) for *C. partellus*. Pupae were sexed according to the method described by Underwood (1994) and males and females were kept separately in plastic containers (21 × 15 × 8 cm) until

adult emergence. A cotton pad moistened with water was placed inside the container to maintain relative humidity at >80%. The insects were kept in a rearing room at a temperature of 25 ± 0.05 °C, RH of $58.5 \pm 0.4\%$ and a photoperiod of L12:D12.

Emerged adult males and females of each species were put together in a mating cage ($40 \times 40 \times 63$ cm), at the onset of the scotophase. The mating status was checked at hourly intervals until end of the scotophase. Pairs of moths that were mating were collected in plastic jars (8 cm high×5 cm in diameter). The gravid females were used in experiments on the following night. After each experiment, all females used were dissected to check for the presence of spermatophores in the *bursa copulatrix*, which in Lepidoptera indicates successful mating (Lum 1979). Only females bearing spermatophores were considered in the results. For plant infestations, larvae of *B. fusca, C. partellus* and *S. calamistis* were obtained from colonies reared at the Animal Rearing and Containment Unit (ARCU) at *icipe*, Nairobi, Kenya. All colonies were rejuvenated twice a year with field-collected larvae.

Plant infestations

For each stemborer species, single maize plants were manually infested by putting them in the whorl with 12 (for Y-tube experiments) or 5 (for field experiments) third and fourth instar larvae, the larval stages which can co-occur with adult moths in the field (Le Ru B. & Calatayud P.-A., Pers. Observ.). These larval stage and infestation level were chosen to ensure a high degree of feeding damage within 24 h before start of the experiments. Because of the long duration of the field experiments, the number of larvae used for infestation had to be lower to ensure survival of the maize plants.

Olfactometer bioassays

This experiment was carried out in a Y-tube olfactometer (Ngi-Song et al. 1996), which has been shown to be more useful for demonstrating differences in attration to odours in moths than wind tunnel (Calatayud et al. 2014). Similarly to Petit et al. (2018), it had the following dimensions: length of stem (18 cm); length of each arm (34 cm); diameter (4 cm). Observations were performed 0–4 h after onset of the scotophase for females corresponding to the period of oviposition for the species under study (Calatayud et al. 2007). The pot and soil of each potted plant (1 plant per pot) were wrapped with aluminium foil to prevent the introduction of volatiles from the plastic pot and soil into the Y-tube. Each plant was introduced into a Perspex chamber measuring $30 \times 30 \times 120$ cm large enough to contain the whole potted plant. The closed ends of each chamber were connected with Teflon tubing to either of the two arms of

the Y-tube. Clean air was drawn into the system over the sample through the arms of the olfactometer. The airflow was set at 15 cm s^{-1} per arm and measured by flow meters connected between the chambers and the activated charcoal. For 30 min before each test, air was left flowing through the olfactometer setup to reach equilibrium in the two chambers and the Y-tube. The Y-tube experiments were carried out at 25 ± 2 °C and 50–60% RH. To avoid visual cues, all the experiments were carried out in a dark room illuminated with red fluorescent tubes (20 W). For each stemborer species, gravid females were released individually into the base of the Y-tube placed horizontally on the table and allowed to choose either of the two arms. The duration of a single evaluation was a maximum of 10 min. For each species, the following choice combinations were done: uninfested maize vs empty chamber; uninfested maize *vs* maize infested by either *B. fusca, S. calamistis* larvae or by *C. partellus* larvae. To assess interactions among insects, the following choice combinations were offered to each species: maize infested by *B. fusca* larvae *vs* maize infested by *S. calamistis* larvae; maize infested by *B. fusca* larvae maize *vs* maize infested by *C. partellus* larvae; maize infested by *S. calamistis* larvae maize *vs* maize infested by *C. partellus* larvae. For each test, a choice was recorded when the insect passed 5 cm from the intersection into one arm and remained motionless there for more than 20 s. Those that made no choice were also recorded. After every five insects, odour source connections to the chambers were reversed to minimise any location bias and the chambers were cleaned thoroughly with normal water. In each case, the number of gravid females ranging from 20 to 37 were tested ($n = 20$–37). For each conditioning procedure, the percentage of insects that made a distinct choice was calculated.

Field trials

Field trials were carried out to check if caterpillar-induced volatiles attract con- and hetero-specific wild moths for oviposition under field conditions in Makutano (S 0°43.616, E 37°16.373) where *C. partellus* and *S. calamistis* are the most abundant species and in Murang'a (S 0°55.387, E 37°09.004), where *B. fusca* and *S. calamistis* co-infest maize fields, (Ntiri 2015). The Murang'a and Makutano areas in central region of Kenya are intensively maize cultivated regions situated at 1500 and 1150 m asl, respectively. Annual mean rainfall is 1195 mm and 981 mm, mean annual temperatures 20 °C and 21.2 °C, respectively, whereas mean annual relative humidity ranges from 50 to 72%, respectively. Six farmer fields (3 in Murang'a and 3 in Makutano) were selected for the experiment, and in each field, maize plants were grown in pots (12 cm in height x 13 cm in diameter) inside a cage ($2 \times 2 \times 2$ m) covered with a net to avoid

natural infestations. The plants used in the experiments were between 4 and 6 weeks old, i.e. about 60–75 cm high.

For each species, five potted maize plants were each infested with 5 of 3rd instar larvae and individually protected with a small cage (90 cm in height × 33 cm in diameter) equipped with a one-way drawstring mesh cloth bag to limit the larval escape to the plant on which the larvae have been deposited, 24 h prior to their exposure to the field to guarantee sufficient feeding damage. Each field consisted of treatments replicated five times (i.e. for each species 5 potted plants plus 5 uninfested plants as control). The treatments were distributed along a straight line in each field in a random pattern. Then, each mesh cloth bag over each plant was removed and after one week, egg laying from wild moths as well as the remaining larvae (for infested plant) was checked on each potted plant and the number of egg batches as well as the numbers of eggs per batch were recorded. Thereafter, oviposited eggs collected were transferred in the laboratory for hatching to confirm species identity. In parallel, three pheromone traps (Pherobank BV, Wageningen), one for each of the three species (*B. fusca*, *S. calamistis* and *C. partellus*) were also placed in nearby fields at a height of 1.5 m from the ground to monitor the male moth flight activity period of each stemborer species in the trial fields. The experiment was conducted from April to July 2017 corresponding the long rainy season (i.e. maize cultivation). During that period, a total of 16 replicates have been conducted at Makutano and 13 replicates at Murang'a.

Collection of VOCs

Dynamic headspace

VOCs emitted from un-infested maize plants and plants infested with 5 and 12 larvae were collected by using a dynamic headspace sampling system as described by Fombong et al. (2016). Two blanks (odours collected from empty oven bags) were collected to verify the absence of background. The soil in the pot was covered with aluminium foil to avoid odour emitting from the soil. The plant was covered with oven bags (520 × 580 mm) and equipped with a valve by which charcoal-purified air entered the system at 0.5 L/min. Volatiles were collected from the plants by passing the outlet air through a Super-Q filter (50 mg adsorbent) at a rate of 2 L/min. Before use, the Super-Q filter was cleaned using hexane, dried and placed in aluminium foil to avoid any contamination. After each collection, the volatiles were eluted from the traps with 150 μL of hexane and concentrated to 40 μL under a stream of nitrogen to enable detection of compounds that are present in very trace amounts when carrying out GC-MS analysis. To the 40 μL concentrated, 10 μL of the internal standard (heptadecane) concentrated at 4 ng μL^{-1} was added and immediately injected into a gas

chromatograph (GC) for analysis or stored at − 80 °C before analyses. VOCs were collected for 12 h (from 6:00 p.m. to 6:00 a.m.). Five plant headspace replicates were carried out in each case.

Solid phase microextraction (SPME)

VOCs emitted from uninfested and infested maize plants with 12 larvae were collected by placing a solid phase microextraction (SPME) fiber in a 20 × 20 × 120 cm glass chamber with these plants. The open end of the cylinder was capped using aluminium foil. The cylinder cap was fortified using Parafilm to make it airtight. The SPME septum-piercing needle was driven through a self-sealing, gas-tight septum (sandwiched between the foil cap) into the plant headspace. Before use, SPME fibers (DVB/CARBOXEN/PDMS 50/301 m, Supelco) were cleaned by heating in a gas chromatograph injector at 250 °C for 20 min. About 195 μg of heptadecane was injected into the cylinder as internal standards and left to equilibrate for 10 min. Extraction of VOCs was carried out for a period of two hours per sample, and then the fibre was retracted from the headspace and immediately introduced into a gas chromatograph (GC) injector port for analysis or stored at − 80 °C before analyses. Four plant headspace replicates were carried out for each case.

Analyses of VOCs

After volatile collection, the eluates were analysed using coupled gas chromatography-mass spectrometry (GC–MS) on an Agilent Technologies 7890B GC linked to a 5977 MS, equipped with a non-polar HP-5 MS ultra-inert column (30 m × 0.25 mm i.d., 0.25 μm) (J&W, Folsom, CA, USA). The temperature program was 5 min at 35 °C, then 10°C/min to 280 °C. A 1-μl aliquot of each volatile extract was analysed in the splitless mode using helium as a carrier gas at a flow rate of 1.2 ml/min. Spectra were recorded at 70 eV in the electron impact (EI) ionization mode. Similar to Leppik and Frérot (2014), compounds were identified by comparison of mass spectral data with library data: (Adams terpenoid/natural product library 1995), (National Institutes of Standards and Technology 2008) and Chem-Station data system (G1701EA, version E.02.00). Furthermore, structure assignments of a fraction of each compound were confirmed based on co-injection with commercially authentic standards. These compounds included: Anisole (purity ≥ 98%), β-Bisabolene (purity > 85%), Butyl butanoate (purity 98%), (E)-Caryophyllene (purity ≥ 80%), α-Cedrene (purity ≥ 95%), (E)-β-Farnesene (purity ≥ 90%), (Z)-3-Hexenyl acetate (purity ≥ 98%), (E)-3-Hexenyl acetate (purity ≥ 98%), Indole (purity ≥ 99%), Linalool (purity 96%), (R)-(+) Limonene (purity ≥ 95%), Methyl salicylate (purity ≥ 99%), Myrcene (purity 98%), n-Nonanal (purity

95%), (*S*)-(−) α-Pinene (purity 99%), Sabinene (purity 99%), γ-Terpinene (purity 97%), Thymol (purity 99%) and α-Zingiberene (purity ≥ 99%). All the standards compounds were purchased from Sigma-Aldrich Chemical Company except α-Zingiberene which was purchased from Santa Cruz Biotechnology.

The VOC peak area information was extracted from the raw GC/MS data and transformed into nanograms (ng) using internal standard peak area. The relative amount of each compound was calculated by dividing the overall weight of the compound (ng) by the sum of the detected compounds from the same analysis and expressed as percentages and calculated as the mean ± standard error.

Statistical analyses

All analyses were carried out in R version 3.4.1 (R Core Team 2017). The number of responding gravid female obtained from the dual choice olfactometer assays were recorded as the number of gravid females that responded to the different treatments and expressed as per cent response $[(n/N) \times 100]$; N corresponds to the total number of responding gravid females, while n is the number of gravid females corresponding to a given treatment. The proportions of the females that did a choice from the dual choice olfactometer assays were analysed by Chi square goodness of fit performed at 5% significance level. From the field trials, the proportions of males captured between pheromone lures were compared using the Tukey Kramer's test. The total number of egg batches oviposited by wild moths

recovered on uninfested potted plants was compared to the total number of egg batches recovered on infested plants using the Fisher's exact test. For chemicals, before statistical comparisons of VOCs between plants status, all data were checked for normality and homogeneity of variance using Shapiro–Wilk and Bartlett tests, respectively. A non-parametric Kruskal–Wallis test was initially used to show differences of VOCs emitted between uninfested and infested plants as well as between infested plants, and Dunn's test (a non-parametric post-hoc test for unpaired data) to discriminate the means. Principal Component Analysis (PCA) was then performed on relative amount values of each VOCs using the R package, Factoextra. This allowed us to assess how the proportions of the VOCs were distributed between uninfested and infested plants, as well as between stemborer species among infested plants. Mann–Whitney *U* Test was used to show the significant differences of VOCs emitted by the density of 5 and 12 larvae feeding upon the plant.

Results

Olfactometer bioassays

In the Y-tube olfactometer, 78–95% of the females made a choice in the dual-choice biossays (Figs. 1, 2, 3). Regardless of the species, all females oriented significantly towards maize plant volatiles as compared to blanks (Fig. 1), and they had a significant preference for plants infested by the same or another species over
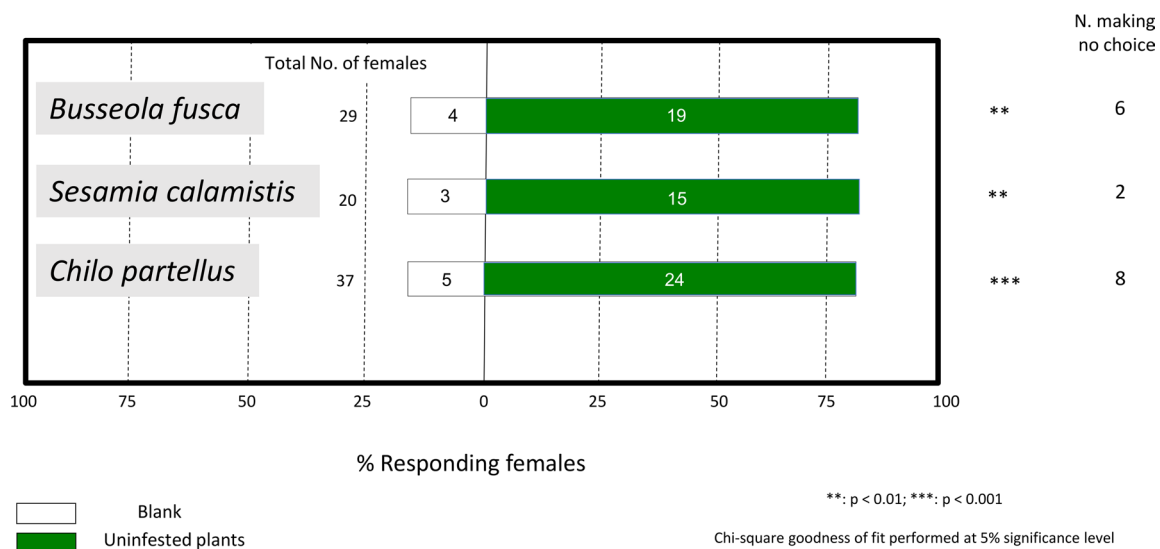

Fig. 1 Response of *Busseola fusca, Sesamia calamistis* and *Chilo partellus* females to uninfested maize plant and blank (dual choice situation) in a Y-tube olfactometer. On each bar, the number of females choosing the odours was given as well as the number of females making no choice (*n* ranging from 20 to 37). The number of females making a choice was set to 100% to calculate the percentage of responding females. *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$ according to Chi square goodness of fit performed at 5% significance level
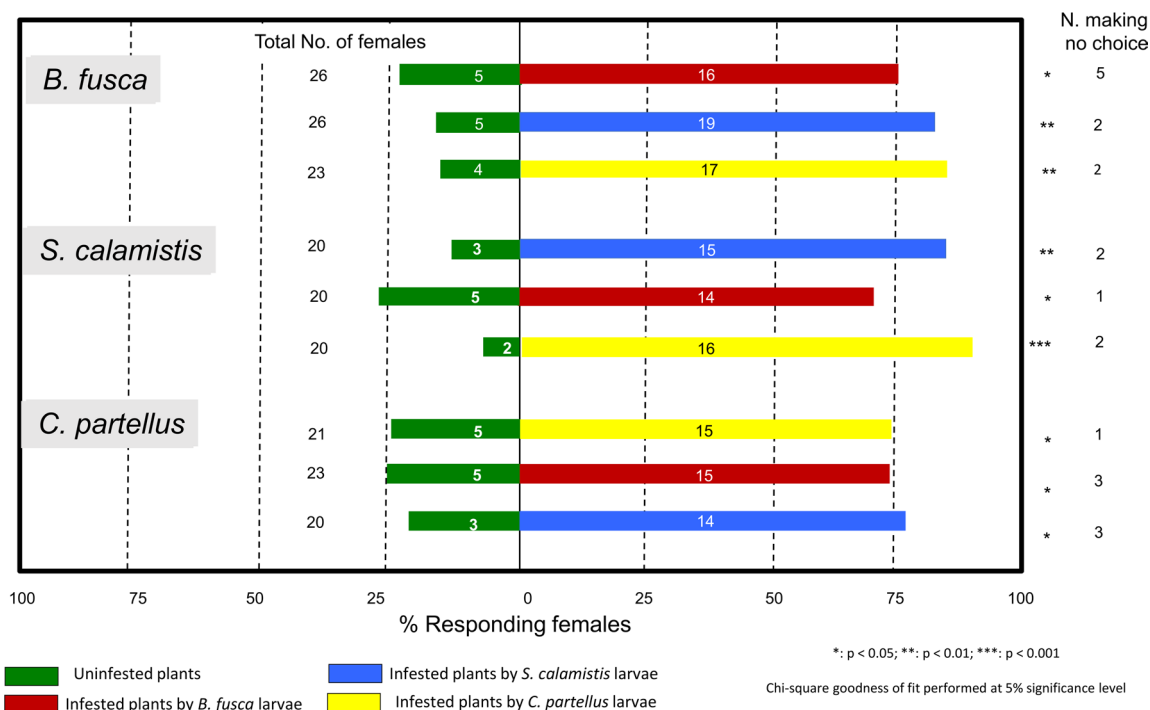
Fig. 2 Response of *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* females to uninfested maize plant and infested plants (dual choice situation) in a Y-tube olfactometer. On each bar, the number of females choosing the odours was given as well as the number of females making no choice (*n* ranging from 20 to 26). The number of females making a choice was set to 100% to calculate the percentage of responding females. *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$ according to Chi square goodness of fit performed at 5% significance level

uninfested plants (Fig. 2). By contrast, female orientation under interspecific dual choices depended on the species (Fig. 3). *Busseola fusca* did not discriminate the odours from plants infested by noctuids (comparison *B. fusca vs S. calamistis* infested plants: $\chi^2 = 1.384$, $df = 1$, $P > 0.05$) but preferred odours of plants infested by their conspecifics over plants infested by *C. partellus* (comparisons *C. partellus vs B. fusca* infested plants: $\chi^2 = 5.143$, $df = 1$, $P = 0.023$). *Sesamia calamistis* oriented preferably towards plants infested by their conspecifics in a choice involving only noctuids (comparisons *B. fusca vs S. calamistis* infested plants: $\chi^2 = 6.368$, $df = 1$, $P = 0.011$) but it preferred plants infested by *B. fusca* over plants infested by *C. partellus* (comparisons *C. partellus vs B. fusca* infested plants: $\chi^2 = 9.80$, $df = 1$, $P = 0.001$).

Chilo partellus did not discriminate between plants infested by *B. fusca* and plants infested by their conspecifics (comparisons *B. fusca* vs *C. partellus* infested plants: $\chi^2 = 0.615$, $df = 1$, $P > 0.05$) but it preferred conspecifics over *S. calamistis* (comparisons *S. calamistis vs C. partellus* infested plants: $\chi^2 = 4.545$, $df = 1$, $P = 0.033$) and plants infested by *S. calamistis* over *B. fusca* (comparisons *B. fusca vs S. calamistis* infested plants: $\chi^2 = 7.347$, $df = 1$, $P = 0.006$).

Field trials

In each field, ~ 2 to 3 larvae of each stemborer species remained per infested potted plant. The number of male moths captured inside pheromone traps differed significantly between species and site (Table 1). *Busseola fusca* was absent in Makutano while *C. partellus* was absent in Murang'a. Therefore, no eggs of *B. fusca* were found on potted maize plants in Makutano, and no eggs of *C. partellus* in Murang'a. In Makutano, although few *C. partellus* males were trapped as compared to *S. calamistis*, both *S. calamistis* and *C. partellus* eggs were laid on potted plants. In Murang'a, significantly higher numbers of *B. fusca* males were trapped than *S. calamistis* males and eggs of both species were found on potted plants. In total, 21 and 19 egg batches of wild moths were collected in Makutano and in Murang'a, respectively. For each locality, significantly more egg batches were collected on infested than uninfested plants (Table 1).

Identification of VOCs on uninfested and infested plants

From mass spectral data comparisons between GC/MS compounds with library data and from co-injection procedure
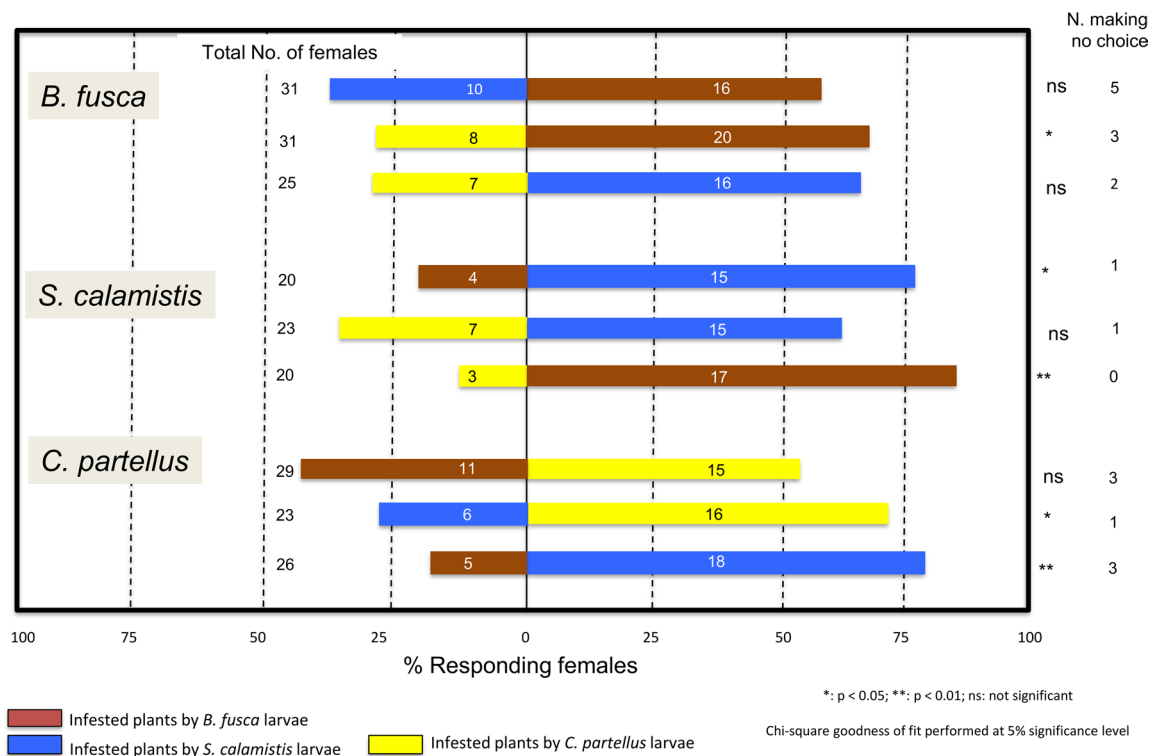
Fig. 3 Response of gravid female *Busseola fusca, Sesamia calamistis* and *Chilo partellus* to maize plants infested by different species (dual choice situation) in a Y-tube olfactometer. On each bar, the number of females choosing the odours was given as well as the number of females making no choice (*n* ranging from 20 to 31). The number of females making a choice was set to 100% to calculate the percentage of responding females. *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$ according to Chi square goodness of fit performed at 5% significance level

with commercially authentic standards, a total of 42 compounds were tentatively identified and found to be emitted from both uninfested and infested maize plants consisting of sesquiterpenes, monoterpenoids, green leaf volatiles, cyclic hydrocarbons and alkaloids. A total of 34 compounds were identified using the dynamic collection system, whereas 24 compounds were identified with the SPME collection system (Fig. 4) (Supplementary Tables S1 and S2). 22 VOCs were produced by all maize plants tested, whereas 20 VOCs were only emitted by infested plants irrespective of the stemborer species involved (Fig. 4).

The mean ratios of some VOCs varied significantly between uninfested and infested plants irrespective of the stemborer species. Both collection systems yielded higher amounts of α-pinene, n-nonanal, 7-epi-sesquithujene and butyl butanoate from uninfested than infested plants (Supplementary Tables S1, S2 & Fig. 5), while greater amounts of (E)-2-hexenal, 4,8-Dimethyl-1,3-(Z),7-nonatriene, (E)-caryophyllene were emitted by infested plants irrespective of the stemborer species (Supplementary Tables S1 & S2).

However, there were differences in the compounds between insect species infesting the plant (Fig. 5). With both collection systems, *B. fusca* larvae induced the compositionally richest VOCs profile, followed by both *S. calamistis* and *C. partellus*

larvae. (E)- β-Farnesene, linalool, myrcene and β-bisabolene were characteristics to VOCs emitted by plants infested by *B. fusca* only, whereas α-zingiberene, sesquisabinene, indole and α-cis-bergamotene were characteristics of VOCs emitted by plants infested by *C. partellus* or *S. calamistis* (Supplementary Tables S1, S2 & Fig. 5).

VOCs with increasing larval density

Irrespective of the stemborer species most of the VOCs detected from plants infested with 5 larvae were also detected in plants infested with 12 larvae (Supplementary Table S3). Among the 34 VOCs identified using the dynamic collection system, all were found with both larval densities and 9 varied significantly with larval density (Supplementary Table S3). Among them, linalool, indole, α-cedrene, sesquisabinene, (E)-β-farnesene and α-zingiberene increased while α-pinene, n-nonanal and 7-epi-sesquithujene decreased with the larval density, irrespective of the stem borer species.

Table 1 Catches of egg batches laid by females and catches of males in traps baited with different pheromone lures of stem borers from the natural population in two localities of Kenya (Makutano and Murang'a)

Wild moth species involved in egg laying	Makutano				Murang'a			
	Control plants	Plants infested by Busseola fusca	Plants infested by Sesamia calamistis	Plants infested by Chilo partellus	Control plants	Plants infested by Busseola fusca	Plants infested by Sesamia calamistis	Plants infested by Chilo partellus
Total number of egg batches recorded on each maize plant								
Busseola fusca	0	0	0	0	3	1	2	3
Sesamia calamistis	2	1	3	2	2	3	2	3
Chilo partellus	2	4	4	3	0	0	0	0
	Uninfested plants	Infested plants			Uninfested plants	Infested plants		
Total number of egg batches	4 a	17 b			5 a	14 b		

Moths flight monitoring

	Makutano			Murang'a		
Pheromone lures	Lure of *Busseola fusca*	Lure of *Sesamia calamistis*	Lure of *Chilo partellus*	Lure of *Busseola fusca*	Lure of *Sesamia calamistis*	Lure of *Chilo partellus*
Total males captured	0 a	68 b	5 a	593 a	87 b	0 c

For each locality, the number of males captured followed by different letters were significantly different at the 5% level according to Tukey–Kramer test (proportion comparisons) and the total number of egg batches from uninfested and infested plants followed by different letters were significantly different at the 5% level according to Fisher's exact test. Catches of egg batches laid by females ($N=16$ in Makutano and 13 in Murang'a), male captures in both localities ($N=22$)
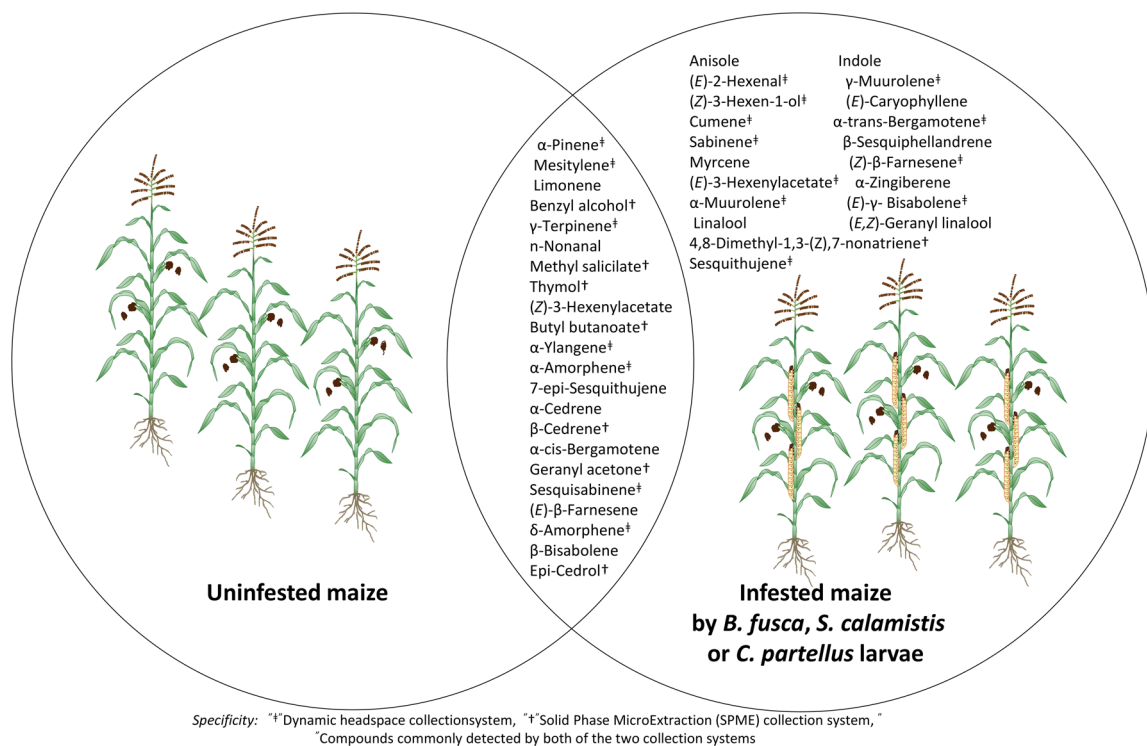
Uninfested maize

α-Pinene‡
Mesitylene‡
Limonene
Benzyl alcohol†
γ-Terpinene‡
n-Nonanal
Methyl salicilate†
Thymol†
(Z)-3-Hexenylacetate
Butyl butanoate†
α-Ylangene‡
α-Amorphene‡
7-epi-Sesquithujene
α-Cedrene
β-Cedrene†
α-cis-Bergamotene
Geranyl acetone†
Sesquisabinene‡
(E)-β-Farnesene
δ-Amorphene‡
β-Bisabolene
Epi-Cedrol†

Anisole   Indole
(E)-2-Hexenal‡   γ-Muurolene‡
(Z)-3-Hexen-1-ol‡   (E)-Caryophyllene
Cumene‡   α-trans-Bergamotene‡
Sabinene‡   β-Sesquiphellandrene
Myrcene   (Z)-β-Farnesene‡
(E)-3-Hexenylacetate‡   α-Zingiberene
α-Muurolene‡   (E)-γ- Bisabolene‡
 Linalool   (E,Z)-Geranyl linalool
4,8-Dimethyl-1,3-(Z),7-nonatriene†
Sesquithujene‡

Infested maize
by *B. fusca*, *S. calamistis*
or *C. partellus* larvae

Specificity: ‡Dynamic headspace collectionsystem, †Solid Phase MicroExtraction (SPME) collection system, Compounds commonly detected by both of the two collection systems

Fig. 4 VOCs detected in uninfested maize plant and maize plant infested by *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* larvae. None was detected exclusively in uninfested plants; 22 VOCs were shared by the both uninfested and infested plants and 20 VOCs were only detected in infested plants. 18 compounds were exclusively detected by dynamic system "‡", 8 exclusively by SPME system "†" and 16 compounds were common to both two collection systems

Discussion

In the Y-tube olfactometer bioassays gravid females of the three stemborer species oriented preferably towards odours emitted by plants infested by both con- and hetero-specific larvae over odours emitted by uninfested plants. Field trials confirmed these results. These findings, though contrasting with the fundamental concept of competition, have been shown for several other lepidopteran phytophagous insects (e.g. Anderson and Albron 1999; Shiojiri et al. 2002; Poelman et al. 2008; Facknath 2012; Viswanathan et al. 2015). Enhancements of oviposition by *C. partellus* on maize plants infested with conspecific larvae have already been reported by Kumar (1986). In addition, under interspecific choices, although the results are not conclusive enough to warrant a general interpretation, our Y-tube experiments showed that the female moths did not orient systematically preferably towards the plant infested by conspecific larvae. Our findings suggest an adaptive behaviour that may help ovipositing stemborer females to identify plants suitable for survival of their offsprings.

Herbivore feeding often modifies the volatile profiles emitted by plants (Honda 1995; Dicke and Van Loon 2000; El-Sayed et al. 2016). The common volatiles identified in the present study were previously reported by Birkett et al.

(2006), Khan et al. (2000) and Konstantopoulou et al. (2004) from uninfested maize plant and by Carroll et al. (2006), Gouinguené et al. (2001) and Peñaflor et al. (2011) from infested plants. However, in the present study, the volatile profile partly depended on the collection method. In the dynamic system more VOCs were collected than in the SPME system. Similarly, Elmore et al. (1997) reported that the dynamic headspace method extracted a greater number of volatile compounds from the same samples than did SPME. This can be explained by several factors in SPME collection system such as the need to be in the linear range of detection and the competition effects on the fiber between volatiles which can cause biases in the quantitative and qualitative determination of compounds (Jelen et al. 1998; Roberts et al. 2000).

Both methods showed a higher number of volatiles emitted by infested maize plants than uninfested ones irrespective of the stemborer species involved, a phenomenon already reported by several studies (e.g. Dicke and Van Loon 2000; Ngi-Song et al. 2000; Pare and Tumlinson 1999). Some of these caterpillar-induced volatiles, which can either be produced de novo by the plant, as an indirect defence, as well as directly excreted by the larvae inside the plants, have also been reported in other studies (e.g. De Moraes et al. 2001; Kessler and Baldwin 2001; Pinto-Zevallos et al. 2016).
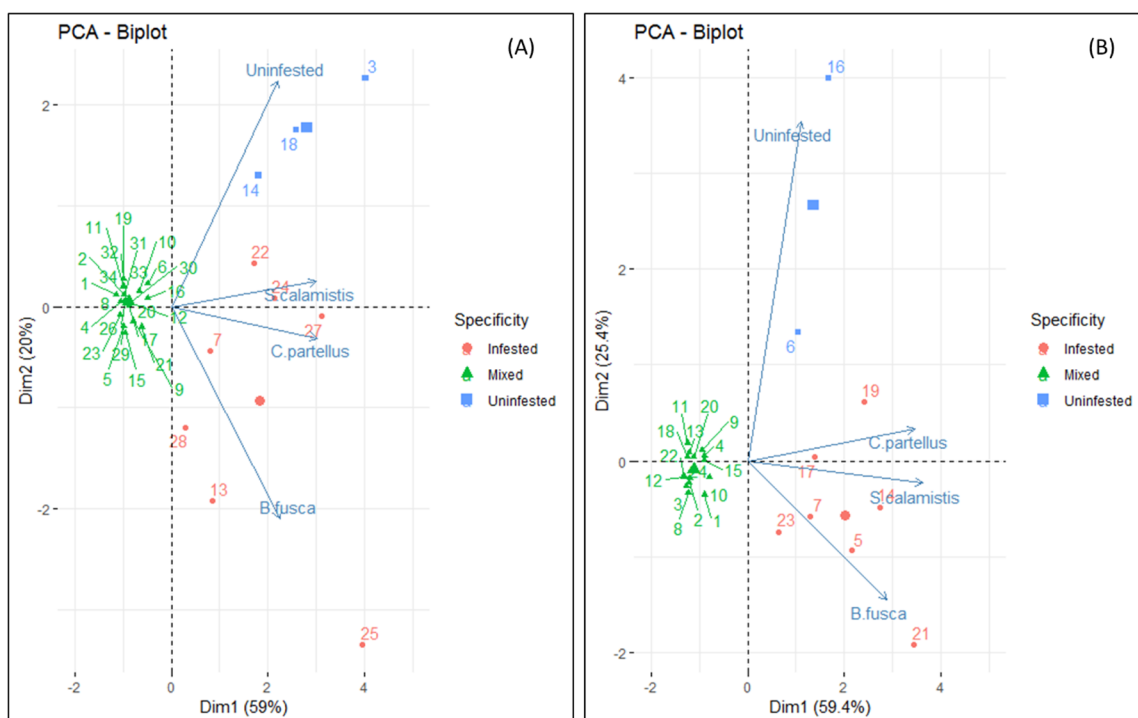
Fig. 5 Principal Component Analysis (PCA) of volatile profiles from differentially infested maize plant. PCA score plots, highlighting cluster of volatiles attributable to different infestation status (ellipses = 95% of confidence) and PCA loading plot, showing variable correlations with the first and second principal component were together bi-plotted with Factoextra R Package. Biplot (A) from Dynamic headspace collection system [1. (*E*)-2-Hexenal, 2. (*Z*)-3-Hexen-1-ol, 3. α-Pinene, 4. Cumene, 5. Sabinene, 6. Mesitylene, 7. Myrcene, 8. (*Z*)-3-Hexenyl acetate, 9. (*E*)-3-Hexenyl acetate, 10. Limonene, 11. γ-Terpinene, 12. α-Muurolene, 13. Linalool, 14. n-Nonanal, 15. Indole, 16. α-Ylangene, 17. Sesquithujene, 18. 7-epi-Sesquithujene, 19. α-Cedrene, 20. γ-Muurolene, 21. (*E*)-Caryophyllene, 22. α–cis-Bergamotene, 23. α–trans-Bergamotene, 24. Sesquis-abinene, 25. (*E*)-β-Farnesene, (*Z*)-β-Farnesene, 27. α-Zingiberene, 28. β-Bisabolene, 29. (*E*)-γ-Bisabolene, 30. (*E,Z*)- Geranyl_linalool, 31. δ-Amorphene, 32. α-Amorphene, 33. β-Sesquiphellandrene, 34. δ-Amorphene] and biplot (B) from Solid-Phase MicroExtraction (SPME) collection system [1. Anisole, 2. (*Z*)-3-Hexenyl acetate, 3. Limonene, 4. 4,8-Dimethyl-1,3-(*Z*),7-nonatriene, 5. Linalool, 6. n-Nonanal, 7. Myrcene, 8. Benzyl alcohol, 9. 7-epi-Sesquithujene, 10. α-Cedrene, 11. Methyl salicylate, 12. (*E*)-Caryophyllene, 13. β-sesquiphellandrene, 14. Indole, 15. Thymol, 16. Butyl butanoate, 17. α-Zingiberene, 18. β-Cedrene, 19. α-cis-Bergamotene, 20. Geranyl acetone, 21. (*E*)-β-Farnesene, 22. epi-Cedrol, 23. β-Bisabolene, 24. Geranyl Linalool]

Our results indicate that all the odour sources of infested plants were innately attractive to the female of the species tested. Giunti et al. (2018), Kumar (1986) and Poelman et al. (2008) also demonstrated that infested plants attracted and increased fitness of other conspecific species.

However, there were quantitative variations in the VOCs emitted by maize plants irrespective of the stemborer species involved in the infestation. The two collection systems revealed that the VOC profiles emitted by plants infested by *B. fusca* were very distinct and compositionally richer in VOC profile to those emitted by plants infested by both *S. calamistis* and *C. partellus*. Two elicitors in the oral excretion of larvae, volicitin and *β*-glucosidase, have been identified as being responsible for the induction of specific volatiles from plants they attack, which are different from intact or mechanically damaged plants (Dicke and Van Loon 2000; Gouinguené et al. 2001; Mattiacci et al. 1994). Thus, the type of elicitors specific to the different stemborer larval species may be responsible for these variations in HIPVs by the different stemborer species. This has been adequately established in other herbivore species (Dicke 2000; Geervliet et al. 1997; Takabayashi et al. 1994).

In addition, the intensity of caterpillar-induced VOCs depended on the larval density thus, as shown by Skoczek et al. (2017), on the extent of plant feeding damage or the amount of plant tissue consumed. Similarly, Gouinguené et al. (2003) found a correlation between the intensity of the HIPV emission and the number of *Spodoptera littoralis* (Boisduval 1833) (Lepidoptera, Noctuidae) larvae feeding on a plant and with the amount of damage inflicted. In the present study, the VOCs which decreased with larval density were those characteristic of uninfested plants while the VOCs which increased with larval density were those characteristic of infested plants. However, all VOCs characteristic of infested plants were found in both larval densities.

In conclusion, our results indicate that VOCs influence interactions between members of the same guild and thus might play an attractiveness role in the coexistence among maize stemborers. Eight candidate attractants were associated with larvae-infested plants that attracted conspecific and heterospecific females. These results open new avenues to develop attractants specific to trap female stemborer moths in the field.

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