

Article

Males of *Dalbulus maidis* attract females through volatile compounds with potential pheromone function: a tool for pest management

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Simple Summary

Insects use chemical compounds for communication, and sex pheromone is one of the most important signals used by males and females to find each other for mating purposes. The corn leafhopper, *Dalbulus maidis*, is an insect vector that transmits pathogens causing diseases in maize crops, but it was unknown whether it uses sex pheromones in their communication. In this study, we tested whether *D. maidis* produces volatile compounds that attract the opposite sex. We collected volatiles from live insects and evaluated their influence on the behavioral responses of conspecifics. We found that males produce odors that attract females. Interestingly, males avoided odors emitted by stressed females, which may suggest the release of an alarm pheromone. These findings highlight for the first time the role of pheromones in intraspecific *D. maidis* communication, and open new perspectives for the development of monitoring and management tools targeting this important pest.

Abstract

Insects use chemical compounds to communicate with conspecifics and other organisms. The corn leafhopper, *Dalbulus maidis* (Hemiptera: Cicadellidae) (DeLong & Wolcott), is an important pest in Brazilian maize crops due to its role as a vector of phytopathogens. Despite its economic importance, the chemical communication between sexes in this species remains to be elucidated. This research aimed to unveil whether *D. maidis* produces chemical compounds that influence the behavior of the opposite sex and may act as sex pheromones. To evaluate the influence of these volatiles, olfactometer bioassays were conducted as dynamic headspace volatile collections from live insects. Results showed that both male and female leafhoppers emit volatile compounds, however, with no sex-specific compounds detected. Females were attracted to male odors and male aeration extracts, suggesting males produce sex-specific volatiles. Interestingly, males avoided odors from non-acclimated females, which may indicate possible alarm pheromone release. Although the compounds were not identified, this is the first study to demonstrate intraspecific chemical communication in *D. maidis* mediated by volatiles, and the first such record in Membracoidea. These results contribute to understanding the pest's biology and support the development of monitoring and control strategies in maize crops.

Academic Editor: Firstname Last-name

Received: date

Revised: date

Accepted: date

Published: date

Citation: To be added by editorial staff during production.

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Keywords: pheromone; semiochemicals; chemical communication; olfactometry; corn leafhopper; pest management; Hemiptera; Cicadellidae

1. Introduction

Insects rely on chemical communication to interact with conspecifics (pheromones) or with organisms from other species (allelochemicals) [1,2]. Sex pheromones are chemical compounds released by sexually mature individuals that function to stimulate the opposite sex for mate location and copulation. These pheromones can also convey information about mate recognition, attraction, reproductive status, and the fitness of the emitter [3].

The corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott), is a phloem-feeding insect that primarily causes indirect damage to maize *Zea mays* L., its main host plant [4], due to its ability to efficiently transmit the pathogens associated with the corn stunt disease complex. These include corn stunt spiroplasma (CSS, *Spiroplasma kunkelii*), maize bushy stunt phytoplasma (MBSP, 'Candidatus Phytoplasma asteris'), as well as maize rayado fino virus (MRFV) and maize striate mosaic virus (MSMV) [4–6]. Currently, no curative management measures are available for these diseases [7,8].

The mating behavior of *D. maidis* has been previously described, including the use of vibrational and acoustic signals during courtship [9,10]. However, no studies have investigated whether this species emits long-range chemical signals, like sex pheromones. Considering that the acoustic signals produced by *D. maidis* are transmitted only over short distances when both sexes are on the same substrate [9]. Chemical communication is, nevertheless, known to play a role in host plant selection by *D. maidis* [11,12].

Although several studies have demonstrated the use of acoustic signals among leafhoppers, for a long time there was no evidence of molecules functioning as sex pheromones in any species within the group (Hemiptera: Auchenorrhyncha: Cicadomorpha). This scenario began to change about a decade ago with the identification of an aggregation pheromone in *Callitettix versicolor* (Fabricius) [13], and, more recently, the first evidence of sex pheromones was reported for *Philaenus spumarius* (L.), although the chemical structure has not yet been identified [14]. Due to their high specificity and the remarkable sensitivity of insect olfactory systems, sex pheromones have been widely studied as tools for agricultural pest management [15,16]. Since it is a vector insect, there is no established economic threshold for *D. maidis*, and its management still relies primarily on the systematic use of chemical insecticides during the early stages of maize cultivation, which is the critical period for pathogen transmission [12, 17]. Therefore, alternative control strategies are urgently needed, including the potential use of sex pheromones for monitoring and management.

In this context, the objective of this study was to investigate whether *D. maidis* emit volatile compounds that can influence the behavioral response of conspecifics, with a particular focus on the sexual pheromone.

2. Materials and Methods

2.1. Corn leafhopper - *Dalbulus maidis*

Dalbulus maidis (DM) used in this study were obtained from a colony established in 2022 at Embrapa Cerrados (Planaltina, DF, Brazil), originally collected from adult individuals in experimental maize fields (15°36'16"S, 47°42'38"W). The colony was subsequently decontaminated following the recommended procedures [18] to eliminate potential carriers of pathogens (mollicutes and virus), ensuring a healthy colony.

The individuals used in the experiments were randomly selected from adult insects, without controlling for age, reproductive status or mating history.

2.2. Maize

Maize plants of the Synthetic Spodoptera (SS) genotype were used in the experiments, seeds were obtained from the germplasm bank of Embrapa Maize and Sorghum (Sete Lagoas, MG, Brazil). The seeds were sown in plastic pots (0.3 L) with a mixture of natural soil (Latosol) and organic substrate (Max Fertil, composition: pine bark, natural phosphate, carbonized rice husk, vermiculite, chemical fertilizer NPK) in a proportion of 1:1 w/w, without post-fertilization. Plants were kept in a greenhouse (Brasília, DF, Brazil) under natural conditions of temperature, humidity, and photoperiod (14L/10D; Brasília, DF, 15°46'46"S and 47°55'46"W) and manually irrigated with a watering can every two days. For experiments, plants were used at V3 stage (three expanded leaves, 10 to 13 days after germination).

2.3. Volatile Collection

Volatile organic compounds (VOCs) emitted by *D. maidis* were collected using dynamic headspace aeration systems across two experimental sets. In the first experimental set three treatments were established: DM that consisted of 100 unsexed adult leafhoppers, DM-Maize: 100 unsexed adults plus one maize plant at V4 growth stage, Maize: a maize plant at V4 stage. The objectives were as follows: DM to assess volatiles emitted exclusively by the leafhoppers; DM-Maize to evaluate whether volatiles are only emitted in the presence of a food resource; Maize to identify and exclude volatiles released by the plant itself. For each treatment 20 replicates were conducted.

In the second experimental set, two other treatments were conducted: volatiles were collected from 100 males or 100 females and another with one maize plant at V4 growth stage, these treatments were called: DM-Male (100 males), DM-Female (100 females). For each treatment 10 replicates were conducted.

All treatments were conditioned in glass chambers (2L volume; 14 cm x 24 cm) connected to a system supplied with charcoal-filtered air (4–20 mesh, Supelco, USA) at a constant flow rate of 1.0 L min⁻¹. Simultaneously, a vacuum pump maintained an outflow of 0.8 L min⁻¹, ensuring continuous air circulation through the chamber and directing volatiles into an adsorbent tube filled with HayeSep Q (polydivinylbenzene copolymer, 100 mg, 80–100 mesh, Supelco, PA, USA).

Volatiles trapped on adsorbent filters were eluted every 24 hours with 72-hour accumulations during weekends. All insects and plants were replaced weekly for new ones. For the DM treatment, which did not include maize plants, six replicates were conducted, and with volatiles collected for 24 hours, due to high mortality (individuals typically died after 24 hours without food).

2.4. Chemical analysis

All volatile samples were analyzed using an Agilent 7890A gas chromatograph equipped with a flame ionization detector (GC-FID) and a non-polar DB-5MS column (30 m x 0.25 mm ID, 0.25 µm film thickness, Supelco, USA). The oven temperature was initially set at 40 °C for 2 minutes, then ramped at 5 °C min⁻¹ until reaching 180 °C, held for 0.1 minute, followed by an increase of 10 °C min⁻¹ to 250 °C, where it was held for 20 minutes. The injector was set to 250 °C and the FID to 270 °C. Each sample (2 µL) was injected in splitless mode, with helium as carrier gas. Chromatographic data acquisition was performed using the GC ChemStation software (Agilent, version 2.4). For qualitative analyses selected volatile samples was analyzed using an Agilent 5975 mass selective

detector (GC-MSS) coupled to a quadrupole mass analyzer, equipped with the same non-polar DB-5MS capillary column (30 m × 0.25 mm ID, 0.25 µm film thickness; J&W Scientific, Folsom, CA, USA). Injections were performed in splitless mode with 2 µL of sample, and helium was used as the carrier gas. Ionization was conducted by electron impact (EI) at 70 eV, with the ion source temperature set at 230 °C. The oven program followed the same temperature profile as the GC-FID analyses: 40 °C for 2 minutes, ramped at 5 °C min⁻¹ to 180 °C, followed by 10 °C min⁻¹ to 250 °C, with a final hold of 20 minutes. Data acquisition and analysis were conducted using the MassHunter Qualitative software (version 10.1, Agilent, CA, USA). Compound identification was performed by comparing the mass spectra to those in the NIST library (2020) and to published spectra, along with retention index calculations based on the DB-5MS column. Tentative identifications were confirmed by co-injection with authentic standards, either commercially sourced or synthesized in-house.

2.5. Chemicals

Authentic chemical standards of decane (99%), tetradecane (99%), pentadecane and hexadecane (99%), octanal (≥ 98.0% (GC)), nonanal (98%), decanal (98%), dodecanal (97%), camphene (95%), α-pinene (98%), β-pinene (99%), 3-carene (≥ 90%), limonene (97%), methyl salicylate (99%), 6-methyl-5-hepten-2-one (99%), β-caryophyllene (98%), geranylacetone (97%), cyclosativene (99%) were purchased from Sigma-Aldrich (Steinheim, Germany). Linalool was purchased from TCI America (Portland, USA). (*E*)-4,8-Dimethylnona-1,3,7-triene (DMNT) (95%) were synthesized from geraniol [19]. The solvent hexane (97%) was purchased from Sigma-Aldrich (Steinheim, Germany) and redistilled before use.

2.6. Olfactometer Bioassays

To assess whether *D. maidis* is attracted to the opposite sex through chemical, olfactometer bioassays were conducted using a Y-shaped dual-choice olfactometer (19 cm × 19 cm; choice arms: 7 cm × 1.7 cm; main arm: 5 cm × 1.7 cm). Female and male responses, separately, were tested by contrasting the odor of live 20 males or 20 females versus clean air, followed by testing male responses against the odor of live 20 females or 20 males versus clean air.

Odor sources were generated by placing 20 individuals of each treatment inside a 40 mL glass container (5 cm × 6 cm) without food. Initially, 20 females were placed into the containers, and bioassays were immediately started in the afternoon (n = 30). One insect was released in the release area of the olfactometer, and its behavior was monitored for 10 minutes. Due to the high mobility of the odor sources insects in the glass container, bioassays were repeated with acclimated individuals. Acclimation was achieved by keeping the insects that were used as odor source inside the container for two hours, and the insects whose response was evaluated inside the olfactometer system, during this time only clean air was circulating inside of the olfactometer. After this time odor sources were connected to the olfactometer, and the insect present a response behavior clearer to the odors being tested.

Then, females were tested with male aeration extract (obtained from previous volatile collections of DM-Male over 24 hours) against n-hexane, since only females were attracted to the odor of live males in the previous experiment. For male aeration extract bioassays, 5 µL of DM-Male samples (equivalent to the aeration of 20 individuals) were applied to a paper filter (0.5 cm × 0.5 cm) and compared to 5 µL of n-hexane. The paper filters were placed at glass containers (20 ml; 3 cm × 3 cm) and connected to the system. After three bioassays (10 min each), the filter papers containing the 5 µL of the sample volatile or hexane were replaced by new ones.

Thirty different individuals of the tested sex were used to evaluate their choice in response to the odor treatments. The parameters measured were first choice (the first arm entered for more than 30 seconds) and residence time (total time spent in each arm). Individuals that made no choice within this period were classified as non-responsive and excluded until 30 valid bioassays with a choice were obtained. To avoid contamination with chemical cues, the olfactometer was cleaned after every five bioassays, and odor source positions were alternated to prevent side bias. A maximum of 10 bioassays were conducted per day to minimize the influence of environmental factors such as temperature, humidity, atmospheric pressure, and insect condition. All bioassays were performed between 14:00 and 17:00h.

2.7. Statistical Analyses

Olfactometers bioassays data were analyzed using a chi-square test for first choice and paired t-tests for residence time with 95% level of confidence, all tests were conducted on R platform [20].

3. Results

3.1. Bioassays

When exposed to the odor of males not acclimated, *D. maidis* females did not show preference to male odor compared to air in terms of first choice ($\chi^2 = 3.33$, $p = 0.067$), but they spent significantly more time in the arm containing male odor (t-test = 25.299, $p = 0.017$) (Figure 1A and B). Using odor of males acclimated, females corroborate the previous results, with non-acclimated males, and showed a clear preference for male odor, both in first choice ($\chi^2 = 10.8$, $p = 0.001$) and in-residence time (t-test = 33.104, $p = 0.002$) (Figure 1A and B). Females also showed a preference to male aeration extract compared to hexane ($\chi^2 = 8.533$, $p = 0.003$; t-test = 3.023, $p = 0.005$). Finally, females did not show a significant preference to female odor compared to air ($\chi^2 = 0.142$, $p = 0.705$; t-test = -1.145, $p = 0.261$).

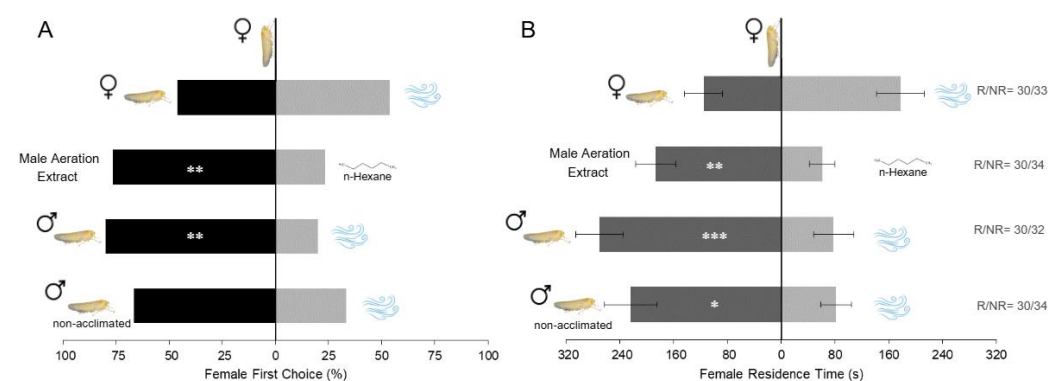
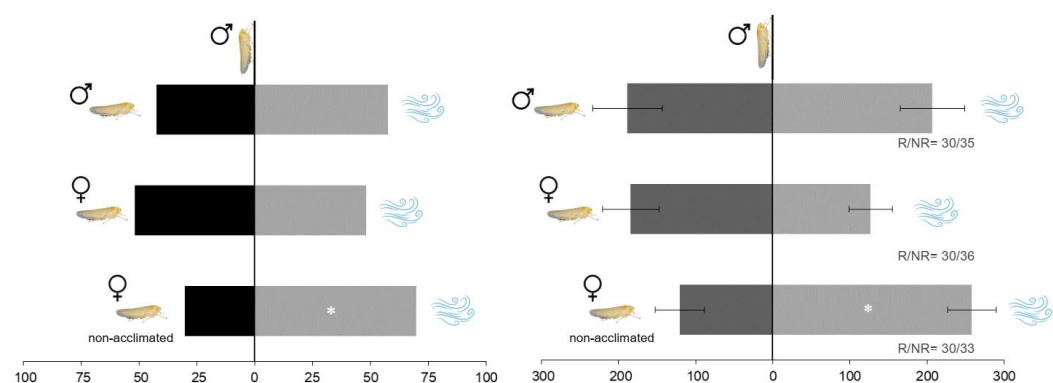


Figure 1. (a) - First choice of *Dalbulus maidis* females in dual-choice olfactometer bioassays between different odors sources: 20 males, 20 females, clean air, male aeration extract and n-hexane (n = 30). **(b)** - Mean residence time of females during the bioassays. * Indicates $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ for chi-square tests (A) and t-tests (B). Error bars represent standard error of the mean. R/NR indicates the number of responsive/non-responsive insects.

Males exhibited avoidance behavior toward female odor when females were not acclimated for two-hour period (Figure 2A and B). They showed a significant preference for the arm releasing clean air over the odor of 20 females, both in first choice ($\chi^2 = 4.8$, $p = 0.024$) and residence time (t-test = 22.838, $p = 0.03$). By other hand, when females were acclimated, males showed no attraction either to female odor or to clean air, displaying

no significant preference ($\chi^2 = 0.133$, $p = 0.718$ for first choice; t-test = 0.972, $p = 0.338$ for residence time). When exposed to male's odor, males did not show preference among the sides ($\chi^2 = 0.615$, $p = 0.432$; t-test = -0.267, $p = 0.791$).



What is the reason for the presence of these compounds in the odor extracts of individual females and males? These compounds are generally common in plants

Figure 2. (a) - First choice of *Dalbulus maidis* males in dual-choice olfactometer bioassays between different odor sources: 20 males, 20 females and clean air (n = 30). (b) – Mean residence time of males during the bioassays. * Indicates $p < 0.05$ for chi-square tests (A) and t-tests (B). Error bars represent standard error of the mean. R/NR indicates the number of responsive/non-responsive insects.

3.2. Volatiles

A total of 30 volatile compounds were identified from headspace collections containing either male or female *D. maidis* individuals that were similar for both sexes (Figure 3). The chemical profile of volatiles obtained when only the insects were used for volatile collection, did not show qualitative difference between both sexes. The main compounds identified were monoterpenes like, α (2) and β (4) pinenes, limonene and linalool (14) sesquiterpenes like β -caryophyllene, aldehydes (Figure 3). The chemical analysis of volatile samples conducted with both sexes did not show differences compared when the insects had their volatiles collected separated by sex. When maize plants were used as food sources for the insects during the volatile collections, we did not detect different compounds that could be attributed to the insects. The new peaks observed in the chromatographic profile in the presence of both insects and maize plants were associated with plant-derived compounds, such as DMNT (16) and cyclosativene (26) (Figure 3).

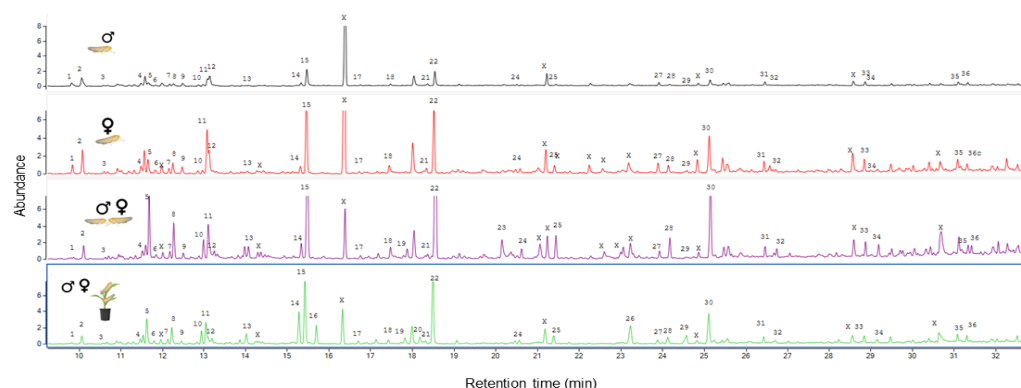


Figure 3. Chromatograms of headspace collections from males, females, both sexes, and both sexes with maize plants analyzed by gas chromatography coupled with mass spectrometry (GC-MS). X indicates phthalate group contaminants. 1 – β -thujone, 2 – α -pinene, 3 – camphene, 4 – β -pinene, 5 – 6-methyl-5-hepten-2-one, 6 – 2-pentylfuran, 7 – decane, 8 – octanal, 9 – 3-carene, 10 – p-cymene,

11 – 2-ethyl-1-hexanol, 12 – limonene, 13 – γ -terpinene, 14 – linalool, 15 – nonanal, 16 – DMNT: (*E*)-4,8-dimethyl-1,3,7-nonatriene, 17 – 2-ethylhexyl acetate, 18 – NI-1, 19 – terpinen-4-ol, 20 – methyl salicylate, 21 – dodecane, 22 – decanal, 23 – 4-phenyl-2-butanol, 24 – NI-2, 25 – NI-3, 26 – cyclosativene, 27 – tetradecane, 28 – dodecanal, 29 – (*E*)- β -caryophyllene, 30 – geranylacetone, 31 – pentadecane, 32 – tridecanal, 33 – hexadecane, 34 – tetradecanal, 35 – heptadecane, 36 – pentadecanal. NI = non-identified.

4. Discussion

The bioassays results showed that female corn leafhopper *D. maidis*, are attracted to volatiles released by males. Males are not attracted to these volatiles, suggesting that these compounds could play a role as sex-pheromone in this species. The chemical analysis of volatile samples containing the volatiles emitted by *D. maidis* did not identify male-specific compounds that could explain this attraction. It is possible that the male specific compounds are produced in very tiny amounts, below the detection limits of the equipment used. Nevertheless, the observed females to odor of live males and to male aeration extract support the hypothesize that males produce volatiles working as a sex pheromone.

Male of leafhoppers mate multiple times throughout their life [9]. Therefore, it is reasonable to expect that mated individuals may continue producing and emitting sex pheromones. The results obtained in this study appear to support this hypothesis, as part of the insects used were mated, and males were still able to attract females in olfactometer bioassays, even though females' mate only once in their lives [9]. Further research should be conducted using virgin males and females to assess whether virgin individuals exhibit stronger behavioral responses in bioassays and whether they produce higher levels of sex pheromones.

Mating communication in leafhoppers (Auchenorrhyncha) has been characterized primarily by acoustic and vibrational signals [21–23]. However, multiple studies have demonstrated the use of chemical cues in these insects for host-plant location, including in *D. maidis* [11–12; 24,25]. Only recently has evidence emerged for the presence of sex pheromones within this suborder. In 2022, the first indication of a sex pheromone was reported for *P. spumarius* (Hemiptera: Auchenorrhyncha: Aphrophoridae), where males were attracted to female odors in Y-tube olfactometer assays [14]. Similarly, *Lycorma deli-catula* (White) (Fulgoridae) males were shown to be attracted to female body extracts in Y-tube bioassays [26].

The mating behavior of *D. maidis* has been previously studied, including sexual behavior and the role of vibrational and acoustic signals [9,10]. Notably, male behaviors such as wing fanning, which the authors believed might be associated with the release of medium-range chemical signals [9], although this was not experimentally tested. Now, the present study is the first to demonstrate intraspecific chemical communication in this species, showing that females are attracted to male odor even in the absence of visual or acoustic cues. To the best of our knowledge, **this is the first study to demonstrate the potential use of sex pheromones within the superfamily Membracoidea**, and notably, in this case, it is the females rather than the males that are attracted. It also represents the first characterization of the volatile compounds emitted by *D. maidis* and within the family Cicadellidae.

The results obtained with non-acclimatized females could suggest the existence of an alarm pheromone. This is supported by the observation that males preferred clean air over the odor of stressed female conspecifics, indicating avoidance of environments that may signal potential threats [27]. Leafhoppers may use chemical cues to mediate various behaviors as it is common to observe aggregations of individuals on the same maize plant, similar to aphids, which rely on multiple chemical signals [28]. Likewise, aggregated

treehoppers also release alarm pheromones, but only when their body wall is pierced, such as during a predator attack [29].

This study demonstrates that chemical communication plays a role in the reproductive behavior of *D. maidis*, alongside acoustic signaling. Given that insects must locate mates over long distances, it is reasonable to propose that many members of Auchenorrhyncha may also rely on chemical signals. These findings highlight the need for further investigation into chemical communication in this group.

Sexual pheromones are currently employed in various control strategies [30], including mass trapping with pheromone-baited traps, as is the case for *Tuta absoluta* (Meyrick) [31] mating disruption, which involves the release of synthetic pheromones in the field to reduce mate location and copulation rates [32], population monitoring [33–35] and attract-and-kill techniques [36]. Even in the absence of identified sex pheromones, chemical-based control strategies have been developed for other leafhopper species. For instance, a push-pull system using plant volatile compounds has been proposed for the tea green leafhopper *Empoasca flavescens* (Cicadellidae) [37,38]. Another system with *Lycorma deli-catula* (White) showed effective trap attraction using pheromone lures based on body extracts, to capture males and females during the oviposition period [39].

In this way, these findings are a step toward advancing knowledge of the chemical communication of *D. maidis*, to understand their biology and ecology. Furthermore, it is also a possibility to develop new strategies to monitor or control this pest using chemical signals or extracts from living insects, specifically to capture females.

Author Contributions: Conceptualization, M.S.S. and M.C.B.M.; methodology, M.S.S., M.B., R.A.L., C.M.O, M.R.F. M.C.B.M.; validation, M.C.B.M.; formal analysis, M.S.S and M.C.B.M.; investigation, M.S.S. and M.C.B.M.; resources, M.B., R.A.L., C.M.O., M.C.B.M., M.R.F.; data curation, M.S.S., M.C.B.M.; writing—original draft preparation, M.S.S.; writing—review and editing, M.B., R.A.L., C.M.O, M.R.F. M.C.B.M.; supervision, M.R.F. and M.C.B.M.; project administration, M.C.M.B.; funding acquisition, M.B., R.A.L., C.M.O., M.C.B.M., M.R.F. All authors have read and agreed to the published version of the manuscript.

Funding: This work received financial support from the Coordination for the Improvement of Higher Education Personnel (CAPES) through a grant to MSS (process nr. 88887.939463/2024-00), the Brazilian Corporation of Agricultural Research (EMBRAPA, project N°. 20.18.04.004.00.00 and 20.19.00.182.00.00) and Research Support Foundation of the Federal District (FAP-DF) with grant from 2021 to 2023 to MSS (project N°. 00193.00001056/2021-68), CNPQ project N°. 405307/2023-3.

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Acknowledgments: The authors would like to thank the National Council for Scientific and Technological Development (CNPq), the Coordination for the Improvement of Higher Education Personnel (CAPES), the Research Support Foundation of the Federal District (FAP-DF), and the Brazilian Agricultural Research Corporation (Embrapa) for financial and institutional support. We also thank Michely F.S. Aquino, Erika A.G. Jesus, Marisa L. Britto e Gabriel R.S. Macedo for helping with the insect colony.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study, in the collection, analyses, or interpretation of the data, in the writing of the manuscript, or in the decision to publish the results.

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